



Habitat use, ranching, and human-wildlife conflict within a fragmented landscape in the Pantanal, Brazil



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ABSTRACT

Deforestation, ecosystem homogenization, and diversity loss are frequent problems in tropical livestock systems, which can foster substantial human-wildlife conflict when wild carnivores with declining prey bases turn to cattle depredation. The objective of this paper was to examine spatial and temporal variation in the presence, composition, and diversity of wild fauna, including predators and their prey base, in a well-established tropical livestock system. The study was conducted on a ~140,000 ha ranch in the Cerrado-Pantanal transition zone in Brazil, where large areas of improved pasture are bounded by blocks of intact montane forests and seasonally flooded lowland habitat. The study sampled wildlife with camera traps distributed across the land use gradient and rancher depredation observations were also obtained. Depredation accounted for the loss of 0.9% of the total herd in the sampling year, and the number of depredation events was greater closer to intact forest and distant from centralized ranch structures and mechanized operations. Mammal diversity was greatest adjacent to intact forest and supported a complete representation of the native trophic structure, including large predators such as jaguar (*Panthera onca*), puma (*Puma concolor*), and maned wolf (*Chrysocyon brachyurus*) and a diverse and abundant prey base. Sites progressively distant from intact forest and with more intensive conversion and development supported smaller subsets of the diversity and composition, and no apex predators. Livestock management practices to reduce the economic impact of depredation on calves requires faithful adherence, while opportunities exist for landscape management that will enhance diversity and facilitate movement of large mammals between intact forests.

1. Introduction

Large-scale deforestation and conversion of tropical lands, including conversion to pasture for livestock production, has simplified and homogenized ecosystems to the point they often cannot support complex functions and diversity (Lamb et al., 2005; Murgueitio et al., 2010). Few forest specialists can maintain viable populations in tropical livestock systems (Esquivel et al., 2008). The impacts of livestock on wildlife may be direct, e.g. interference competition, or indirect with changes in vegetation structure that influences the availability of food, cover, and nesting sites (Schielz and Rubenstein, 2016). Some wild predators are associated with large undisturbed sites (Noss et al., 1996; Gittleman et al., 2001; Athreya et al., 2013), because overhunting, habitat loss, and fragmentation can disrupt trophic interactions by reducing wild prey species (Crawshaw, 2003). For example, jaguars

(*Panthera onca*), which require 3000–7000 km² of intact habitat to maintain viable populations (Zanin et al., 2015), are emblematic of these impacts. As many as 75% of Brazil's jaguar populations may not be viable in the long-term due to increasing habitat loss and fragmentation (Harris et al., 2005; Sollmann et al., 2008; Zeilhofer et al., 2014).

Tropical livestock systems are subject to substantial human-wildlife conflict because of the distinct vulnerability of domestic herbivores to depredation (Frank and Woodroffe, 2001). Consequently, depredation of large predators on livestock is one of the more frequently studied human-wildlife conflicts in Brazil (Marchini and Crawshaw, 2015). When humans and carnivores compete for resources and habitat is lost and/or fragmented, wild carnivores specializing in wild ungulates may begin to prey upon domesticated species, which may result in predator extermination without regard to their ecosystem role or conservation status (Linnell et al., 1999; Ogada et al., 2003; Polisar et al., 2003;

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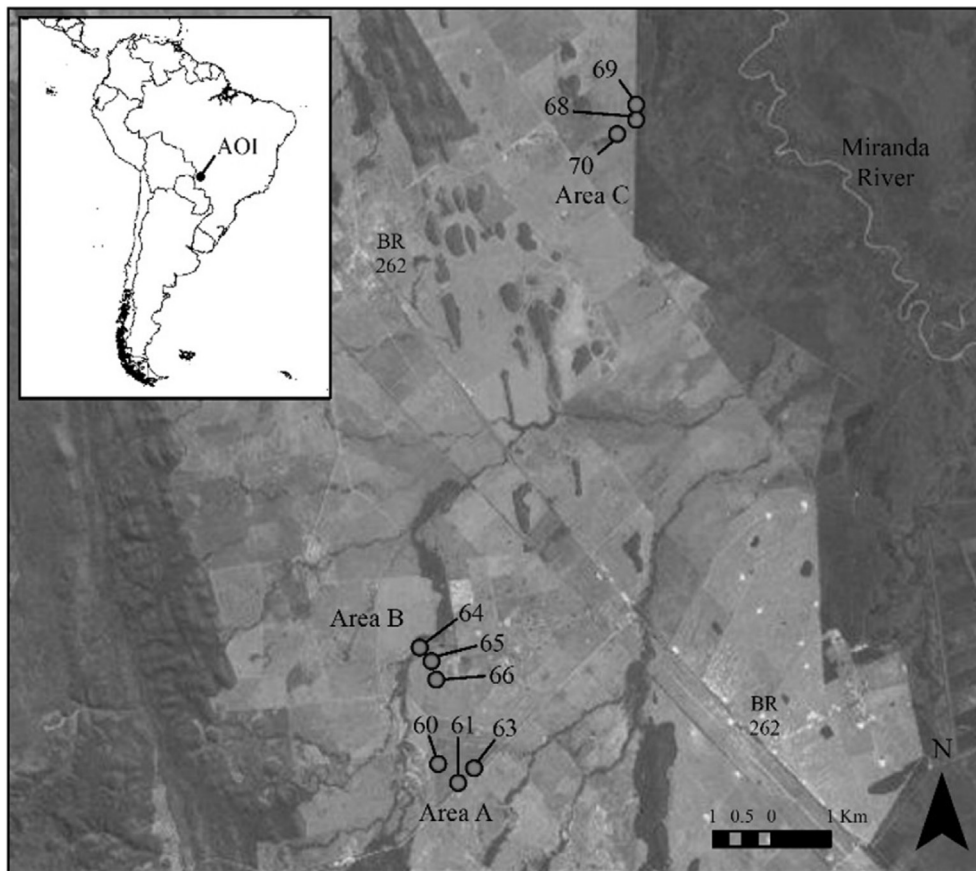


Fig. 1. Map of study Areas A, B, and C and their corresponding camera locations. Area of interest (AOI) in southwestern Brazil shown on inset map.

Graham et al., 2005; Cavalcanti et al., 2010; Amador-Alcalá et al., 2013). Although livestock depredation represents economic losses for ranchers, most studies have found predation rates by large carnivores, such as jaguars, to be relatively low in comparison to losses related to low productivity, neonatal mortality, and mortality due to disease (Hoogesteijn et al., 2002; Hoogesteijn and Hoogesteijn, 2008; Azevedo and Murray, 2007; Loveridge et al., 2010).

Despite the potential for habitat loss and fragmentation, declines in wild populations, and increased human-wildlife conflict, grazing lands can have promising conservation value due to their potential to preserve wildlife habitat and open space on private lands and connectivity between fragmented ecosystems (FAO, 2009; du Toit et al., 2010; Schieltz and Rubenstein, 2016). In the Brazilian Pantanal, where 95% of the land is privately owned and beef cattle production has occurred for ~300 years, jaguar densities are high in relation to other regions of Brazil because land management practices are influenced by a seasonal flooding regime that has preserved native vegetation and high prey abundance (Swartz, 2000; Soisalo and Cavalcanti, 2006; Silveira et al., 2014). Both Boulhosa and Azevedo (2014) and Cavalcanti et al. (2010) have reported that ranchers in the Pantanal perceive that jaguar populations are increasing. The correlation of these impressions with increased deforestation, human populations, and improved pastures (Seidl et al., 2001; Alho et al., 2011), suggests that the push of people into forested habitat is increasing human-jaguar interactions (Boulhosa and Azevedo, 2014). However, only a minority (28.6%) of ranchers in the Pantanal region of Brazil suggest a preference to living without jaguars in the environment (Boulhosa and Azevedo, 2014).

Ecotourism is booming in the Pantanal and provides an alternative economy in a region dominated by ranching (Alho and Sabino, 2011). Although some of the unregulated tourist trade in the region has contributed to environmental degradation (e.g. overfishing, wildlife harassment, and improper waste management), wildlife watching and

ecotourism are based upon conservation and making positive sustainable contributions to the natural and cultural environments that benefit the host communities (Tapper, 2006; Alho and Sabino, 2011). Unfortunately, baiting by tourist operators to guarantee jaguar sightings has contributed to acclimation to people (Boulhosa and Azevedo, 2014). The combination of habitat and prey loss, association of humans with food, and an increase in the tourist population have potentially contributed to jaguar attacks on humans and one death in the Pantanal (Neto et al., 2011).

The objective of this project was to examine spatial and temporal variation in the presence, composition, and diversity of wild fauna, including predators and their prey base, in a well-established tropical livestock system. The study was conducted in the Cerrado-Pantanal transition zone in Brazil, where habitat conversion for improved pasture has resulted in a landscape of large areas with intensive habitat loss bounded directly by vast blocks of intact montane forests in the Cerrado and seasonally flooded lowland habitat in the Pantanal. This land use and landscape pattern introduces potential for conflict between ranching activities and local wildlife and concomitant opportunities for ecotourism and conservation. The study sampled wildlife with camera traps distributed across the land use gradient and obtained rancher depredation observations. The results interpreted in the context of habitat use patterns of wild fauna, especially predators and their prey base, human-wildlife conflict due to depredation on cattle, and sustainable husbandry and land management practices in tropical livestock systems for simultaneous livestock production and wildlife conservation.

2. Methods

2.1. Study area

The Pantanal biome, located in the states of Mato Grosso and Mato Grosso do Sul, Brazil, is the world's largest freshwater wetland and internationally recognized for its biodiversity, unique environmental characteristics, and fragile ecosystem (Alho et al., 2011; Souza et al., 2012; Santos et al., 2016). The region has a climate classification of Aw, i.e. tropical wet with extended winter dry season or savanna climate, according to the Köppen classification system, with daily mean values of 23.80 °C for temperature and 70.26% for humidity, and mean yearly precipitation of 1197 mm (Alvares et al., 2014).

Sampling was conducted at Fazenda Bodoquena, a large cattle ranch of ~140,000 ha straddling the Cerrado-Pantanal transition zone in Mato Grosso do Sul state, Brazil. The main economic activities on the property are divided into calving, rearing, and fattening beef cattle. The average herd in the sampling year (2012/2013) was 36,583 animals. During the study, 14,511 cows, with 9678 births, and 8208 weaned calves (77.65% fertility rate) were recorded, and calf mortality was 15.19%.

Sampling was divided between the Guaicurus (Areas A and B) and Três Pedras (Area C) sections of the ranch (Fig. 1). The Guaicurus section has a total area of 10,974.25 ha with 58.06% converted pasture, 37.61% natural reserves, 0.47% exploitable areas, and 3.86% unprofitable areas (i.e. roads, hills and buildings). The Três Pedras section's total area is 7552.35 ha, consisting of 61.55% converted pasture, 29.98% natural reserves, 4.64% exploitable area, and 3.83% unprofitable areas. The Guaicurus section included two selected pastures, the first, referred to as Area A, is 86 ha at ~140 masl and is dominated by Koronivia grass (*Brachiaria humidicola*) with limited tree cover. Area A is also adjacent to the developed areas of the ranch, i.e. access roads, airstrip, residences, and production facilities. A mean 133 total head/day were grazed in Area A during the study period. The second pasture in the Guaicurus section, Area B, is 104.6 ha at ~133 masl and is dominated by Koronivia grass and is located adjacent to a variable width, 30–100 m wide, treed riparian zone and includes a ~3.8 ha pond. A mean 86 total head/day were grazed in Area B during the study period. The third pasture, Area C, in the Três Pedras section, is 65.1 ha at ~101 masl and supports improved pastures dominated by both signal grass (*Brachiaria brizantha*) and Koronivia grass, but with denser vegetation. Area C is situated adjacent to the edge of the extensive intact bottomland riparian wetland reserves along the Miranda River that have not been converted to improved pasture due to seasonal flooding. A mean 27 total head/day were grazed in Area C during the study period. The distances between the centroids of each study area were Area A to B = 1.9 km, Area A to C = 11.5 km, and Area B to C = 9.9 km.

2.2. Data collection

To collect data about the diversity of wild fauna within the sampling areas we used nine Bushnell Trophy Cam 8 mpxl trail cameras with LED IR flash to photograph passing animals and record the date and time of each photo. Three cameras were deployed in each study area. Distances between adjacent cameras in each area ranged from 380 to 450 m in Area A, 300–320 m in Area B, and 250–380 m in Area C. The entire sampling period lasted from November 20, 2012 through November 19, 2013. However, for most cameras the number of camera days did not consistently cover this entire period due to temporary camera dysfunction or because of localized flooding during the wet season (Table 1). The interval between shots was set to 2 s. The picture trigger speed for these trail cameras was 1 s, detection and flash range were 15 m and detection angle was 45°, i.e. detection area of 88 m². The cameras were fixed to opportunistically selected trees and wooden poles with open fields of view or adjacent to animal trails at the edge of

the tree line within each study area at an average height of 55 cm. The cameras were inspected every twenty-eight days, and photos were transferred from the memory card to an external hard drive.

Fazenda Bodoquena regularly keeps records of all losses of cattle due to any cause. We specifically obtained data for the ranch as a whole, and the sampled sections specifically, for losses with evidence of potential depredation during the study period. The ranch used methods consistent with previous studies to identify incidences of depredation by jaguar and puma (*Puma concolor*), and differentiate such instances from scavenging (e.g. Rosas-Rosas et al., 2010). These data were used to make qualitative comparisons with the wildlife monitoring data.

2.3. Data analysis

In order to insure capture independence and remove repeated captures of the same individuals from a capture event, all but one capture in a series of photos taken of the same species within 1 h at the same camera location were removed from the data set (following Bowkett et al., 2007 and Rovero and Marshall, 2009). The preserved capture from the capture event included the largest quantity of individuals if more than one individual was present at the event. Once the repeated captures were removed from the data set 838 captures remained.

The first method for assessing species richness, naïve species richness, is a simple count of the number of species observed at each camera location or sampling area. Naïve species richness assumes that the detection probabilities for each species are equal, and if present the species are assumed to be detected. This method also does not take into account differences in sampling effort, i.e. variation in the number of camera trap days at each location. This estimator tends to be negatively biased for species richness (Williams et al., 2002). We calculated naïve species richness for each area and camera location and for all species taken together, and also separated by avifauna and mammals. Species richness was calculated for all events over the entire sampling period at each camera location, (i.e. all camera days between November 20, 2012 through November 19, 2013), and for 8 separate sampling sub-periods that were commonly sampled in blocks of consecutive days without breaks across 5 of the 9 camera locations (Area A camera locations 61 and 63, Area B 64, and Area C 69 and 70) (consecutive camera days from sub-periods 1 to 8, respectively: 24, 11, 27, 25, 22, 48, 19, and 26 days). Because the 8 sampling periods varied in number of days sampled, species richness was converted to a rate, i.e. the number of species captured per day. In the 4 remaining camera locations only a subset of the common sampling sub-periods was covered, and due to missing data were not used for repeated measures ANOVA (description following). We also calculated species accumulation curves with 100 random replications using the MS Excel macro AccuCurve 1.0 (Drozd and Novotny, 2010) to assess whether the number of camera trap days was sufficient to identify all the species found in each sampling area.

Following Rovero et al. (2014), species richness that accounts for imperfect detection was calculated using a Bayesian model by Dorazio et al. (2006), which requires repeated temporal replications to resolve the ambiguity between species absence and non-detection when species are unobserved at sample locations. The input data consisted of presence and absence of each species detected in each sampling area for all camera trap days combined for the three cameras placed in each area. The model was specified in BUGS language and fitted to data using WinBUGS and the package 'R2WinBUGS' in R software (Sturtz et al., 2005; R Development Core Team, 2013). Simulations were executed with five Markov chains; 55,000 iterations for each chain, discarding 5000 iterations at the beginning (burn-in) and setting the thinning rate to 50. This returned 4000 samples from the posterior distributions.

We calculated the relative abundance index (RAI) as the number of capture events divided by the number of camera trap days and multiplied by 100 (i.e. events per 100 days of camera trapping) (O'Brien et al., 2003). This was repeated for each area and camera location and

Table 1
RAI values and naïve species richness for all species taken together and separated by mammal and avian species.

Area/camera	Camera days	Total RAI	Mammal RAI	Avian RAI	Naïve species richness	Naïve mammal richness	Naïve avian richness
Area A	631	30.9	11.4	19.5	19	10	9
60	52	73.1	3.8	69.2	5	2	3
61	285	39.3	20.0	19.3	16	7	9
63	294	15.3	4.4	10.9	12	6	6
Area B	607	19.1	14.3	4.8	25	14	11
64	365	18.9	17.0	1.9	18	12	6
65	176	18.8	13.1	5.7	13	8	5
66	66	21.2	3.0	18.2	5	1	4
Area C	948	55.6	43.7	11.5	35	19	16
68	274	30.7	20.8	9.9	24	13	11
69	337	62.0	51.3	10.4	22	15	6
70	337	69.4	54.6	13.9	22	16	5

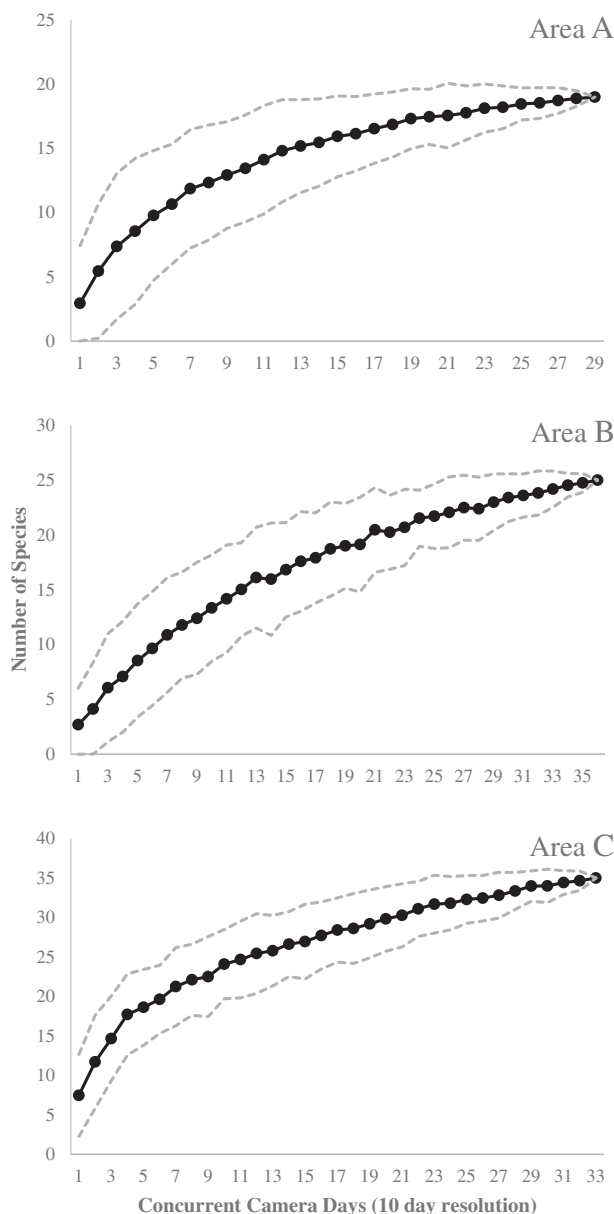


Fig. 2. Species accumulation curves over concurrent camera days for three pooled camera locations at each of Areas A, B, and C.

for all species taken together, and also separated by avifauna and mammals. RAI was calculated for all events over the entire sampling period at each camera location, and for the same 8 separate sampling

sub-periods described previously that were commonly sampled across 5 of the 9 camera locations.

Indicator species analysis was performed with PC-Ord v. 5.10 (McCune and Mefford, 2006). Input data consisted of RAI values of all observed species at each of the 9 camera locations. Data were grouped by sampling area, i.e. Area A, B, or C. Significant indicator species were determined by a Monte Carlo test of significance ($\alpha = 0.05$) of observed maximum indicator values for each species, based on 4999 permutations. Indicator analysis combines data on abundance in particular groups and faithfulness of occurrence in those groups. Indicator species may be associated with treatments, levels of disturbance, habitat types, or environmental variables that differ between groups (McCune and Grace, 2002).

Repeated measures ANOVA was conducted for transformed (e.g. log, square root, or other power transformations) RAI and the number of species captured per day for all species pooled, and for mammal and avian species separately. Repeated measures ANOVA models were run with area (Areas A, B, and C) and camera location nested within area included as among subject effects. The repeat variable was the previously described 8 common photo collection sub-periods at 5 of the 9 camera locations (i.e. 40 observations total), and the interaction of photo collection sub-period and area were included as within subject effects. The Greenhouse-Geisser correction was used when the assumption of sphericity was violated. Tukey's Wholly Significant Difference (WSD) post-hoc test was conducted for pairwise comparisons when significant F-tests were encountered.

Cluster analysis was performed with PC-Ord v. 5.10 (McCune and Mefford, 2006), using RAI values of all observed species at each camera location and the relative Euclidean distance measure and Ward's linkage method. Species that were detected at less than two cameras were removed from the dataset. The cluster analysis was conducted for camera locations, and avian and mammal species were also analyzed separately.

3. Results

During the study period (2012/2013 sampling year) Fazenda Bodoquena recorded 321 cattle losses to depredation by jaguar and puma, but the specific feline predators could not be discerned. Twenty-seven (27) reported deaths were in Guaicurus section, where they preyed upon 18 heifers and 9 calves. Forty-three (43) deaths occurred in the Três Pedras section (3 cows, 1 heifer, and 39 calves). No depredation events were recorded in the three pastures monitored by camera trap during this study.

Patterns of naïve species richness follow a consistent pattern, with total, mammal, and avian richness greatest in Area C and least in Area A (Table 1). Of the camera locations in Areas A and B, only camera location 64, adjacent to a forested riparian buffer, had a comparable mammal richness to any of the camera locations in Area C. Species accumulation curves suggest that the number of concurrent camera

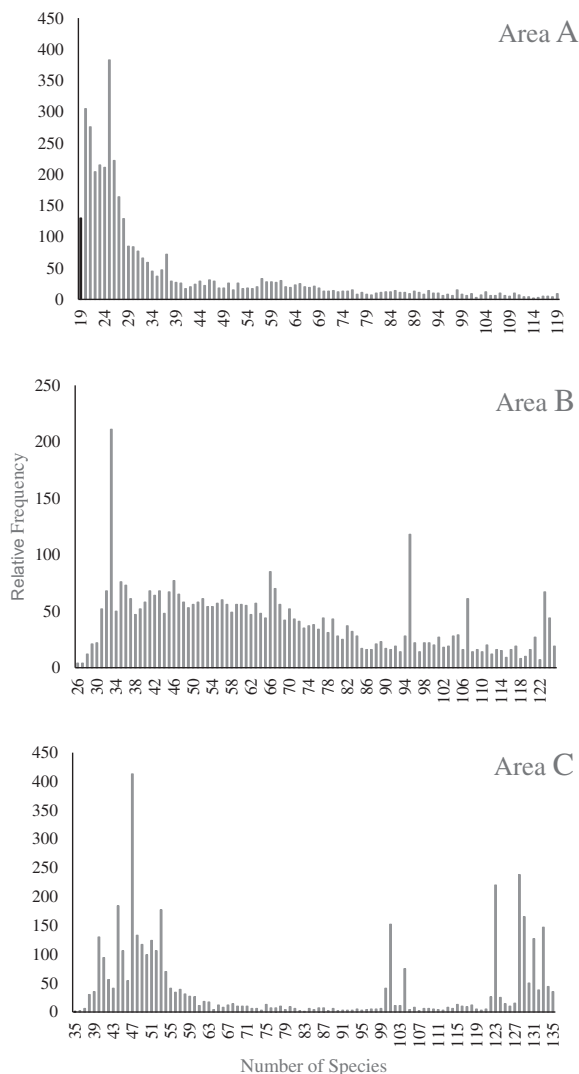


Fig. 3. Posterior distributions of species richness for Areas A, B, and C (following Dorazio et al., 2006). Values of naïve species richness shown with black bars where present on graphs, Area A = 19 and Area C = 35. The naïve species richness of Area B (25) had a frequency of zero and is not shown on the graph.

days for three cameras in each study area were not sufficient to fully characterize the species diversity (Fig. 2). The accumulation curve for Area A appears to most closely approach, but not fully reach, asymptote. The results suggest that the naïve species richness may be an underestimate of true species richness in all of the study areas.

The Bayesian model for estimating total species richness showed that the species richness with the highest frequency in the posterior distribution of each area was greater than the observed naïve species richness (Fig. 3). In Area A, the probability for the naïve species richness value of 19 was substantially less than the highest probability value of 25 species and median of 27 species. For Area B, the probability for the naïve species richness value of 25 was zero, and the highest probability value was 33 species and median was 61 species. In Area C, the probability for the naïve species richness value of 35 was again nearly zero, and the highest probability value was 47 species and median was 55 species.

Total and mammal RAI values were greater in Area C than Areas A and B (Table 1). Avian RAI was greatest in Area A, largely driven by the great frequency of species such as buff-necked ibis (*Theristicus caudatus*) and southern crested caracara (*Caracara plancus*), both of which were significant indicator species for Area A ($\alpha = 0.05$), as well as abundant southern lapwing (*Vanellus chilensis*) and red-legged seriema (*Cariama*

Table 2
RAI values for avian and reptile species detected across the three sampling areas.

Common name	Scientific name	Area A	Area B	Area C
Aves				
Black Vulture	<i>Coragyps atratus</i>	2.1		
Southern Lapwing	<i>Vanellus chilensis</i>	35.0		
Whistling Heron	<i>Syrigma sibilatrix</i>	1.4		
Buff-necked Ibis ^a	<i>Theristicus caudatus</i>	15.5	0.6	
Guira Cuckoo	<i>Guira guira</i>	0.7	3.0	
Turkey Vulture	<i>Cathartes aura</i>	0.4	0.6	
Cattle Egret	<i>Bubulcus ibis</i>	4.5	5.9	0.4
Red-legged Seriema	<i>Cariama cristata</i>	9.0	2.4	4.5
Southern Crested Caracara ^a	<i>Caracara plancus</i>	11.3	3.6	0.7
Chaco Chachalaca ^a	<i>Ortalis canicollis</i>		0.3	9.8
Common Piping Guan	<i>Pipile pipile</i>		0.5	0.7
Rufescent Tiger-heron	<i>Tigrisoma lineatum</i>		0.3	0.4
Great Rhea	<i>Rhea americana</i>		0.5	
Bare-faced Curassow	<i>Crax fasciolata</i>			0.3
Chopi Blackbird	<i>Gnorimopsar chopi</i>			0.3
Gray-fronted Dove ^a	<i>Leptotila rufaxilla</i>			7.5
Gray-necked Wood-rail	<i>Aramides cajaneus</i>			0.7
Great Black-hawk	<i>Urubitinga urubitinga</i>			0.3
Great Egret	<i>Ardea alba</i>			0.7
Snowy Egret	<i>Egretta thula</i>			0.4
Wood Stork	<i>Mycteria americana</i>			1.5
Reptiles				
Red-footed Tortoise	<i>Gerochelone carbonaria</i>			0.3
Tegu Lizard	<i>Tupinambis merianae</i>			0.6

^a Significant indicator species.

Table 3
RAI values for mammals detected across the three sampling areas.

Common name	Scientific name	Area A	Area B	Area C
Mammals				
Capybara	<i>Hydrochoerus hydrochoeris</i>	0.4	2.5	1.0
Collared Anteater	<i>Tamandua tetradactyla</i>	1.0	0.8	0.6
Collared Peccari	<i>Pecari tajacu</i>	1.0	1.7	3.0
Crab-eating Fox	<i>Cerdocyon thous</i>	0.3	3.1	5.5
Giant Anteater	<i>Myrmecophaga tridactyla</i>	14.9	9.5	5.4
Gray Brocket Deer ^a	<i>Mazama gouazoubira</i>	1.0	0.6	10.0
Nine-banded Armadillo	<i>Dasypus novemcinctus</i>	1.4	0.5	0.6
Ocelot ^a	<i>Leopardus pardalis</i>	0.3	0.3	6.9
Six-banded Armadillo	<i>Euphractus sexcinctus</i>	3.0	4.3	0.3
Tapir ^a	<i>Tapirus terrestris</i>	1.1	1.1	16.3
Brazilian Rabbit	<i>Sylvilagus brasiliensis</i>		1.1	13.9
Coati	<i>Nasua nasua</i>		0.3	5.3
Crab-eating Raccoon ^a	<i>Procyon cancrivorus</i>		0.3	3.6
White-lipped Peccary	<i>Tayassu pecari</i>		4.9	15.8
Tayra	<i>Eira barbara</i>		0.3	
Agouti ^a	<i>Dasyprocta azarae</i>			10.2
Jaguar ^a	<i>Panthera onca</i>			6.0
Maned Wolf	<i>Chrysocyon brachyurus</i>			0.4
Marsh Deer	<i>Blastocercus dichotomus</i>			1.0
Puma	<i>Puma concolor</i>			1.8

^a Significant indicator species.

cristata) (Table 2). The composition of mammals is clearly nested (Table 3), with Area B supporting a subset of species found in Area C (excepting a lone mesopredator tayra (*Eira barbara*) found in Area B) and Area A supporting a subset of species found in Area B. Three of the five species found only in Area C are large apex predators, i.e. jaguar, puma, and maned wolf (*Chrysocyon brachyurus*). Significant indicator species ($\alpha = 0.05$) for Area C included chaco chachalaca (*Ortalis canicollis*) and gray-fronted dove (*Leptotila rufaxilla*), and from the mammals agouti (*Dasyprocta azarae*), ungulates gray brocket deer (*Mazama gouazoubira*) and tapir (*Tapirus terrestris*), mesopredators crab-eating raccoon (*Cerdocyon thous*) and ocelot (*Leopardus pardalis*), and jaguar (Tables 2 & 3). No species were significant indicators of Area B.

Study area was the only variable with a significant effect in the repeated measures ANOVA models for RAI and the number of species

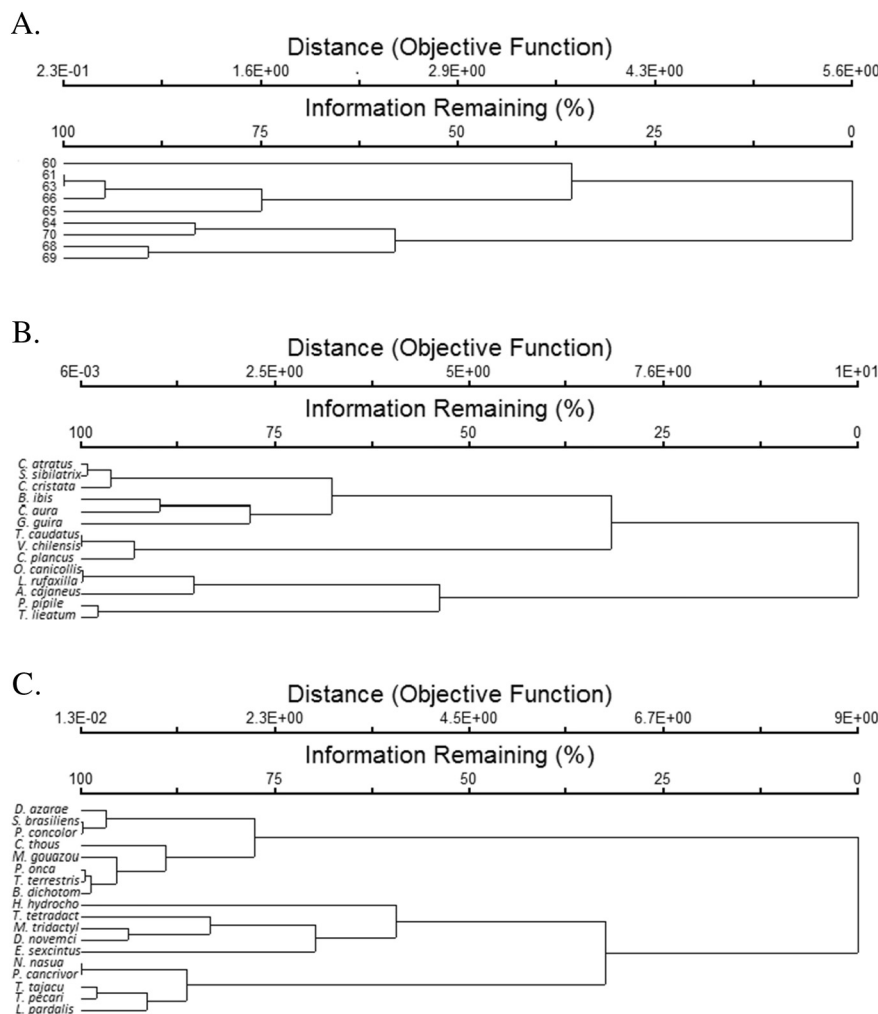


Fig. 4. Cluster analysis using the relative Euclidean distance measure and Ward's linkage method for a. all camera locations, b. avifauna, and c. mammals (some species' scientific names abbreviated).

captured per day for all species pooled, and for mammals and avifauna separately ($\alpha = 0.05$, adj. R^2 range 0.26–0.39). For both RAI and the number of species captured per day for all species pooled and mammals, Area C had significantly greater values than both Area A and B with Tukey's WSD test ($\alpha = 0.05$), but differences between Areas A and B were not significant. For avifauna the pattern was somewhat different; RAI values were significantly greater in both Areas A and C than Area B, and the number of species captured per day was only significantly greater in Area A than Area B with Tukey's WSD test.

The cluster analysis of camera locations resulted in two distinct clades (Fig. 4), one included 5 out of 6 camera locations found in Areas A and B, and the other clade included all 3 camera locations from Area C and one camera location, 64, from Area B. Camera location 64 captured more mammal species than the other cameras in Areas A and B (Table 1), a number equivalent to camera locations in Area C. A number of avian and small mammal species captured at camera location 64 were only shared with locations in Area C, i.e. chaco chachalaca, common piping guan (*Pipile pipile*), coati (*Nasua nasua*), white-lipped peccary (*Tayassu pecari*), and crab-eating raccoon (Tables 2 & 3).

The cluster analysis of avifauna also resulted in two distinct clades with a geographic divide mirroring that of the camera locations cluster analysis (Fig. 4). The first clade included species that were unique to camera locations in Areas A and B, or whose presence was far more frequent in Areas A and B than in Area C. There are two subclades that constituted this first major clade, a subclade that included the species with the greatest RAI in any area, southern lapwing, and two indicator species of Area A, buff-necked ibis and southern crested caracara. The second subclade included the other Area A and B dominant species. The

second major clade was composed only of species unique to Area C and camera location 64 in Area B.

The cluster analysis of mammals also demonstrated a geographical structure consistent with the previously described analyses (Fig. 4), however, because no mammal species were unique to Areas A or B and only a few were more frequent in Areas A or B, the geographical signature was somewhat weaker. The first major clade included species unique or more frequent in Area C and camera location 64, and included the two large predatory felines, puma and jaguar, as well as the mesopredator, the crab-eating fox (*Cerdocyon thous*), and a number of large, tapir and marsh deer (*Blastocerus dichotomus*), and small herbivores. The second major clade was composed of two subclades, the first dominated by species more frequently found in Areas A and B, both anteater (*Myrmecophaga tridactyla* and *Tamandua tetradactyla*) and both armadillo species (*Dasybus novemcinctus* and *Euphractus sexcinctus*). The second subclade composed of species unique or more frequent in Area C and camera location 64, and included a number of omnivores, i.e. both peccary species (*Pecari tajacu* and *Tayassu pecari*), and the ocelot.

4. Discussion

4.1. Wild predator and prey habitat use

The trophic structure of fauna across the converted and fragmented landscape of the Cerrado-Pantanal transition zone strongly aligns with the previously established patterns in similar ranching dominated landscapes (e.g. Schieltz and Rubenstein, 2016; Zimbres et al., 2017). Areas adjacent to large blocks of intact forest support a robust

complement of characteristic species native to the region, including rare large consumers such as marsh deer, and large predators such as jaguars, pumas, and maned wolves. In comparison, the most extensive and intensively converted and developed areas of the ranch are depauperate in mammal species that also have generally low relative abundance, and support a divergent avifauna community. The substantially reduced diversity, especially large predators, suggests the core pasture areas are largely non-functioning contiguous blocks within the landscape that may create barriers to movement among functional intact habitat (Zeilhofer et al., 2014). However, the converted pastures are not completely devoid of conservation value, IUCN red-list vulnerable species giant anteater and tapir were observed using both Area A and B.

Species respond variably to anthropogenic land uses, with some actively accessing the modified matrix and others demonstrating strong avoidance behaviors of degraded open-habitat, which can have effects across a broad range of ecosystem functions involving these species (Parry et al., 2007; Zimbres et al., 2017). Species such as nine-banded armadillo and tapir exhibit substantial tolerance to open matrix habitat despite being forest dependent, and open-habitat specialists, such as the crab-eating fox present in all areas of this study, are expanding their ranges with land conversion (Michalski et al., 2006; Zimbres et al., 2017). Large mammals, such as jaguars, are intimately associated with riparian vegetation and waterways, limiting their use of areas with a high percentage of open grassland and a minimum amount of permanent watercourses (Quigley and Crawshaw, 1992; Paula et al., 2015). In this study, jaguars and pumas were only captured on cameras adjacent to intact forest, and none were captured in open pasture.

Hernández-SaintMartín et al. (2015) reported that jaguars and pumas in northern Mexico shared diets composed mainly of white-tailed deer and collared peccary, the latter being the most commonly reported jaguar prey (see citations in Hernández-SaintMartín et al., 2015). They also found, in contrast to other studies (e.g. Novack et al., 2005; Foster et al., 2010), that in this fragmented habitat jaguars and pumas remained specialists in their use of wild artiodactyls (Hernández-SaintMartín et al., 2015). Jaguars in northern Mexico did advantageously consume a number of medium and small species that are resilient or common to fragmented habitats, such as coati and rabbit (Thornton et al., 2011), but there was no evidence of cattle in the diet of jaguars or pumas (Hernández-SaintMartín et al., 2015). At Fazenda Bodoquena, jaguars, pumas, and their prey were present in the same environment, areas adjacent to riparian forests. Artiodactyls were only abundant, and some species were limited to, areas adjacent to intact forest or substantial riparian buffers, and the same was also true for some of the potential small and medium prey, e.g. Brazilian rabbit (*Sylvilagus brasiliensis*), coati, and agouti.

4.2. Human-wildlife conflict and management

The cattle losses to large felines at Fazenda Bodoquena over the sampling period represent a small percentage (0.9) of the total herd size in that year. In the Pantanal, predation by big cats was reported as the largest source of loss in the Santa Tereza Ranch, and the impact variably ranged from 0.02 to 2.83% of total herd size over 5 years (Tortato et al., 2015). On other ranches in the Pantanal the rate of depredation has been somewhat lower, with a maximum of 1.2% in other studies (Dalponte, 2002; Azevedo and Murray, 2007; Cavalcanti, 2008).

Despite the fact that no large predators were captured by the 6 camera traps deployed in 2 separate pastures in the interior of the Guaicurus section of the ranch, 18 heifers and 9 calves were killed by felines in Guaicurus. Similar to the Três Pedras section, substantial blocks of forest abut converted pastures in the Guaicurus section along the edge of the Cerrado upland. Unfortunately, our cameras were not placed along the Guaicurus pasture/forest boundary. Jaguars and puma activity near the edges of these intact forest blocks likely put them in occasional close contact with cattle, as they would in the Três Pedras

section where the felines were captured and cattle losses were greater, especially among calves. Most attacks by predators occur in pastures surrounded by forest fragments and distant from the homes of officials and employees (Amador-Alcalá et al., 2013), which is a spatial pattern found with other studies and large predators (Polisar et al., 2003; Woodroffe et al., 2004; Michalski et al., 2006; Gula, 2008). However, pumas are more inclined to venture away from forested areas and use pastures and croplands than jaguars (Silveira, 2004; Polisar et al., 2003; Cullen et al., 2005).

Proper herd management and providing permanent drinking water sources away from forests may reduce such risks (Michalski et al., 2006). Calves are more likely to be attacked than adults (Rosas-Rosas et al., 2008; Soto-Shoender and Giuliano, 2011; Polisar et al., 2003; Tortato et al., 2015). Boulhosa and Azevedo (2014) reported that predation by large cats was one of the most frequently reported causes of cattle mortality before weaning in the Pantanal. Michalski et al. (2006) also found that depredation peaks correlated with peaks in calving in the fragmented Amazon forest region of Mato Grosso, Brazil. Cows can be moved to safer locations near centralized developed production areas before they give birth and calves can be penned or grazed in safer pastures until they are able to defend themselves from attack, ~1 year of age (Azevedo and Murray, 2007; Michalski et al., 2006; Amit et al., 2013). These measures, according to Azevedo and Murray (2007), can reduce the probability of jaguar attacks by 60%.

Fazenda Bodoquena, as well as most other operations located in the Pantanal, uses a management schedule to reduce losses to predators, limiting the production of calved cows and other younger categories in distant and overgrown pastures adjacent to intact forests, and concentrating cows and their calves closest to developed areas and extensively converted pastures. The effect of this management strategy is illustrated by the low calf mortality numbers in the Guaicurus section during the sampling year. The loss of calves was an order of magnitude greater in the Três Pedras section, i.e. close to intact forest, than in the Guaicurus section where most substantial and intensive ranch operations are located. This is despite the fact that the stocking rate in Guaicurus section was 300 to 500% greater than in the Três Pedras section. These results also indicate that loss to depredation could be further reduced at Fazenda Bodoquena by a stricter adherence to the management schedule, and complete exclusion of calves from riskier pastures until such time they can adequately defend themselves. A much more fundamental shift in management in the region was suggested by Tortato et al. (2015), involving a switch from breeding operations to fattening operations where adult cattle are kept in the herd for a longer period, which will likely decrease depredation due to adult cattle's defensive abilities.

Similar to other tropical ranching regions in the Americas, jaguars and pumas were the most frequent predators of domestic ungulates. However, in southeastern Mexico, black vultures were also blamed for the deaths of 5 calves (Amador-Alcalá et al., 2013), and reports of vultures preying on sick and injured calves are not an anomaly (Lowney, 1999; Avery and Cummings, 2004). The greater abundance of carnivorous birds found in Area A of Fazenda Bodoquena may be due to the concentrated presence of calves. Vultures are commonly present in greater numbers during calving periods, where they consume placental remains, initiate attacks on newborn calves in search of meconium, and remove other soft tissues, e.g. calf eyes and tongue (Avery and Cummings, 2004).

Inherent characteristics of the Pantanal make it difficult to prevent predator access to cattle (Marchini and Crawshaw, 2015). The threats to cows and calves in the Pantanal are numerous, including species not detectable by camera trap, such as snakes. Boulhosa and Azevedo (2014) suggested that conservation actions by ranchers should not focus on prevention of loss to predators. Instead, ranchers should focus on improved animal husbandry practices, e.g. stocking rate, age of cows at first birth, and inter-calving period, that will increase productivity, cattle quality, and beef prices to offset losses due to predation.

4.3. Wildlife conservation in tropical livestock systems

Preservation of greater concentrations of natural prey may reduce possible attacks of wild animals on cattle. If there is reduction of natural prey, cattle are more likely to become substitute prey due to their susceptibility to depredation (Quigley and Crawshaw, 1992; Patterson et al., 2004; Azevedo and Murray, 2007; Hoogesteijn and Hoogesteijn, 2011). Increased livestock depredation by jaguars, according Hoogesteijn and Hoogesteijn (2011), is a strong sign that natural prey biomass is overexploited.

There are a number of private reserves (RPPNs) in the Pantanal that provide large tracts of intact and well preserved habitat that play an important conservation role in the ecosystem (Sollmann et al., 2008). However, conservation efforts have focused narrowly on remaining fragments of unspoiled forest, while ignoring the potential contribution to conservation of agricultural landscapes (Murgueitio et al., 2010). Some have begun to recognize that sustainable agricultural land uses can be incorporated as a tool for conservation in tropical regions (Daily et al., 2003; Fischer et al., 2005; Harvey et al., 2008; Perfecto and Vandermeer, 2010; Murgueitio et al., 2010). The alternative to traditional improved pasture management dominated by a few native and non-native grasses are silvopastoral systems (SPS) that combine grasses and leguminous herbs with shrubs and trees for not only animal nutrition, but additional complementary uses (Murgueitio et al., 2010). SPS create more complex habitats and support greater biodiversity than pastures (McAdam et al., 2007), and increase connectivity between forest fragments while concomitantly providing marketable wood products and food for humans, cattle, and wild animals (Rice and Greenberg, 2004; Murgueitio et al., 2010). Evidence suggests that SPS increase stocking rates and milk production (Murgueitio et al., 2010), while also increasing the abundance and diversity of birds, plants, and animals, and sightings of rare species (Calle et al., 2009).

Jaguars, as mobile and wide-ranging predators, occupy home ranges up to several hundred square kilometers (Astete et al., 2008), and prefer natural habitat in riparian zones (Crawshaw and Quigley, 1991; Lees and Peres, 2008; Silveira et al., 2014). Because of this habitat affinity, and Brazilian legislation requiring protected buffers along streams, stream buffers provide great potential as corridors for jaguars and other forest interior specialists (Silveira et al., 2014). However, riparian corridor width and quality influence their conservation value, and the minimum legal requirements may be insufficient to maintain diversity in some species assemblages (De Fraga et al., 2011). Zimbres et al. (2017) found that riparian corridors needed to be at least 100 m wide to retain the same average species richness of forest specialists as riparian areas that were not affected by fragmentation, and jaguar occurrence was related to wider corridors. Supplementing narrow and degraded buffers with SPS type land management may improve existing corridors and increase diversity and connectivity within areas where habitat was converted for improved pasture.

Because some of the jaguar's preferred sympatric prey are vulnerable to or threatened with future local extinction, e.g. tapir, giant anteater, marsh deer, and white-lipped peccary (IUCN, 2013), conservation for the jaguar will likely produce positive outcomes for many ecologically important species (Zanin et al., 2015). Due to top-down regulation of ecosystems, the continued presence or local extinction of large predators, including felids, can influence populations of wild herbivores and smaller predators, diversity, and ecosystem dynamics (Gittleman et al., 2001; Miller and Rabinowitz, 2002). Jaguar, puma, and the other large and charismatic megafauna are also particularly important species for ecotourism. Maintenance of intact forest blocks, improved habitat in economically productive pastures, and functional corridors among forest fragments will promote the success of conservation and ecotourism target species, benefiting the ecosystem and local economies.

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