Achilles heel of a powerful invader: restrictions on distribution and disappearance of feral pigs from a protected area in Northern Pantanal, Western Brazil

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ABSTRACT

This paper focuses a rare case of natural disappearance of feral pigs (*Sus scrofa*) in an extensive area without using traditional methods of eradication programs. The study was conducted both in the Private Reserve of Natural Heritage (PRNH) Sesc Pantanal and in an adjacent traditional private cattle ranch. In 1998 feral pigs were abundant and widely distributed in the PRNH. However, the feral pigs were gradually disappeared from the area and currently the absence of pigs in the PRNH contrasts with the adjacent cattle ranch where the species is abundant. To understand the current distribution of the species in the region we partitioned the effects of variation of feral pig’s presence considering the habitat structure (local), landscape composition and the occurrence of potential predators. Additionally, we modeled the distributions of the species in Northern Pantanal, projecting into the past using the classes of vegetation cover before the PRNH implementation (year 1988). Our results show areas with more suitability for feral pigs in region where the landscape is dominated by pastures and permeated by patches of Seasonal Dry Forest. The species tends to avoid predominantly forested areas. Additionally, we recorded that the environmental suitability decreases exponentially as the distance from water bodies increases. The disappearance of feral pigs into PRNH area seems to be associated with changes in the landscape and vegetation structure after the removal of the cattle. In the Brazilian Pantanal, the feral pigs occurrence seems strongly conditioned to environmental changes associated to livestock activity.
INTRODUCTION

The different morphotypes of *Sus scrofa* Linnaeus - wild boar (javali), domestic (different breeds) and wild pigs (feral) - are the most widespread exotic ungulates in the world, with populations in demographic and spatial expansion in almost all Eurasian countries (Fonseca & Correia, 2008) and in most of the regions where they were introduced (Australia, South and North America). The species have achieved success in the conquest and occupation of foreign lands for centuries. Pig management and domestication probably began sometime between the 10th to 8th millennium BP in western Eurasia, and from then domesticated pigs were dispersed widely around the globe by humans (Larson et al. 2007). Currently, pigs are considered one of the world's worst invasive alien species (Lowe et al. 2000) and are present on all continents except Antarctica, and many oceanic islands (Barrios-Garcia & Ballari 2012; Long 2003). *Sus scrofa* have several biological traits and strong invasive abilities that allow them to occupy different habitat types throughout their exotic distribution range, thus making the eradication of this species (feral pigs) very difficult and expensive (Mccann and Garcelon 2008; Morrison et al. 2007; Parkes et al. 2010). When compared to other ungulate species, wild boar show several attributes that are typical of r-strategists (Geisser and Reyer 2005). They have the highest reproductive rate among ungulates, and their local density can double in one year (Massei et al. 1997). Additionally, the species has high ecological plasticity, a very opportunistic feeding behavior and a generalist approach to landscape use (Gabor and Hellgren 2000; Geisser and Reyer 2005).

In the Brazilian Pantanal (one of the largest continuous wetlands on the planet, covering approximately 140,000 km²), *S. scrofa* introduction is believed to have occurred in the second half of the eighteenth century through traditional breeding of domestic pigs (Alho and Lacher 1991). As reported in other areas of the world, pigs escaped from the ranches and became feral in a few generations through free reproduction in the wild (Barrios-Garcia and Ballari 2012; Bieber and Ruf 2005; D’Eath and Turner 2009; Dexter 1998; Nogueira et al. 2009). In 2000, the population of feral pigs was estimated at 10,000 individuals distributed throughout Pantanal (Mourão et al. 2002). In the Pantanal, the feral form is known as porco-monteiro. The species occurs primarily in open areas in seasonally flooded plains and near permanent lakes (Alho et al. 2011; Desbiez and Keuroghlian 2009; Desbiez et al. 2009; Keuroghlian et al. 2009; Oliveira-Santos 2013). The species is strongly dependent on water bodies due to heat stress, which has been observed in other hot regions with periods of severe drought throughout the year (Baber and Coblentz 1986;
Choquenot and Ruscoe 2003; Dexter 1998, 1999; Mayer and Brisbin 2009). Although water is an environmental resource whose importance is obvious to most animal species, identifying important environmental parameters bounding species distributions is a complex task because animals respond to the environment at a range of spatial scales (Turner et al. 1997). Ungulates like feral pigs make foraging decisions both within and across a variety of spatial scales, making it difficult to relate species to specific habitats across their entire range (Turner et al. 1997). Therefore, the description of the species-habitat relationships is an important first-step towards understanding the linked ecological processes, that can direct conservation decision-making, since the agents that determine population viability may include factors related to habitat or elements that transcend spatial scales, such as dynamically linked variables or unlinked elements (Hutchinson 1978; Peterson et al. 2011).

We present a rare case of natural disappearance of feral pigs in an extensive area without using traditional methods of control (eradication) programs. The drastic reduction in population of feral pigs occurred in a 14-year period (1998-2012) due to the transformation of cattle ranches into a Protected Area (PA). In PA there is no estimate of density or frequency of occurrence in previous periods, but the occurrence was common, as regularly observed by the reserve staff and by researchers (Cordeiro and Oliveira, pers. obs.) during in a mammal survey in the region. In this context, feral pigs gradually “disappeared” from the PRNH. Park rangers report that visual records of feral pigs were extremely rare in recent past, with no records for years (RPPN Park rangers, pers. comm; Cordeiro and Oliveira, pers. obs). However, the current absence of pigs in PA area contrasts with the adjacent cattle ranch where the species is abundant. To understand the current distribution of feral hogs in the region we partitioned the effects of variation of feral pig’s presence considering the habitat structure (local), landscape composition and the occurrence of potential predators (jaguar and puma). Additionally, we modeled the distributions of feral pigs in Northern Pantanal, projecting into the past using the classes of vegetation cover before the PA implementation (year 1988). Our goal includes (i) identifying the spatial distribution patterns of feral pigs and (ii) inferring about the effect of landscape change, due to the implantation of a Protected Area (PA), in the occurrence of the species.
METHODS

Study area

The study was conducted in the municipality of Barão de Melgaço, state of Mato Grosso (MT), in the northeastern Brazilian Pantanal. The climate in the region is savanna type, "Aw," according to the Köppen's classification system (Hasenack et al. 2010; Hofmann et al. 2010). Rainfall is concentrated in the austral summer and severe drought prevails in the rest of the year (Nimer 1979). The region presents a flooding period from December through April, due to the accumulation of local rainfall and flooding of the headwaters of the Upper Paraguay River Basin (Gonçalves et al. 2011). The herbaceous and woody vegetation in the region are influenced by the flooding regime adding variability to the landscape, characterized by a plain with low relief variability.

The data were collected in the Private Reserve of Natural Heritage (PRNH) SESC Pantanal, the largest private Protected Area (PA) in Brazil (with 1076 km²) and in a traditional private cattle ranch (approximately 800 km²). The two areas are adjacent and separated by the São Lourenço River (Fig.1). The PA was established in 1998, after a long period of extensive livestock. Therefore, as other ranches in the region, PRNH contains exotic pastures cultivated in former areas of savanna or in forested areas cleared for pasture and artificial ponds for cattle (Cordeiro 2004). However, after the removal of cattle in 1999, continuous monitoring of the landscape showed the gradual expansion of native forests in areas previously used by cattle (e.g. scrublands, pastures and earthmounds savannas) (Nunes da Cunha and Junk 2004; Oliveira et al. 2013). Furthermore, with the removal of cattle and control of fire by PA staff, the open areas have undergone a succession process with a large increase in herbaceous/scrub vegetation density and biomass (Oliveira et al. 2013).

Occurrence Data

Camera traps Reconyx PC90 High Output (Reconyx ®, Inc., Holmen, WI, USA) were used to record feral pigs in the PA and in the cattle ranch (2010 and 2012). The cameras were programmed to operate in their standard module of motion sensitivity and pictures per trigger (3 pictures, 1 second interval, no quiet period). No bait was used. The installation of camera trap sites was chosen...
randomly by direction and distance to be traveled (maximum of two kilometers) from roads (rivers, roads and trails) and considering the minimum distance of 600 m between sites. In the total, 180 sampling units were established (118 in the PA and 62 in the cattle ranch). The sampling effort per station varied from 15 to 28 days, totaling 3,862 trap days (2,559 in the reserve and 1,503 in the cattle ranch) and 92,688 hours. Data were collected in both dry and rainy seasons. Additionally, we monitored 20 artificial ponds and 19 natural licks throughout 90 consecutive days, and we recorded all type of feral pigs’ signs along the sampling campaigns. The camera trap survey in the PA, which resulted in a large record of the regional fauna (manuscr. in prep.), gives us support (Hofmann, et al. 2015), confirming the absence or rarity of the species in the region.

**Feral pigs relationships with landscape and habitat structure**

We used two complementary methods, Variation Partitioning and Species Distribution Models (SDMs) was used to quantify the importance of environmental variables and to understand the reasons that led to the disappearance of this species in the PRNH. Variation Partitioning approach allowed us to compare the relative contribution of the variables (conditional or partial effect) and their independent effect (marginal effect) explained by factors in scales that are hardly addressed by methods such as SDMs (e.g. predation or structural components of vegetation measured at the local scale). On the other hand, SDMs approach allowed us to generate current (2010) and past (1988) potential distribution range using environmental factors associated with the areas currently occupied.

**Landscape Characterization**

We generated two land cover maps, for 1988 and 2010, based on satellite images classification (LANDSAT 5 TM, 27-Jul-1988 and 12-Oct-2010, with a spatial resolution of 30 meters). The geoprocessing tasks were performed in Idrisi Taiga software (Clark Labs©). Ten land cover classes were identified (Table 1; Fig. 1A and 1B). Two types of landscape descriptors were used: (i) the proportions of each land cover class; and (ii) the average distance to rivers or others water sources. The values were calculated by extracting the proportion of each class of cover or the average distances in the area formed by the buffers with a 500-m radius centered in each sampling unit.
**Variation Partitioning Analysis**

We created an Index of Use (IU), for each species (S. scrofa, Puma concolor, puma, and Panthera onca, jaguar) at each site, considering the ratio between the time the species was recorded and the number of days the camera trap was active. After testing different time intervals (15, 30 minutes and 1 hour) as a criterion for the independence of the records, we recognized that the longer periods resulted in an inflated index. We then considered consecutive shots of the same species at a maximum interval of 15 minutes as independent records. Likewise, at each sampling unit we evaluated the vegetation structure in five plots of 100 m², the first centered on the camera trap and the others at a 50 meters distance in the four cardinal directions. We measured 11 attributes in each square (more details of the variables and methods used are provided in Table 2). The average values of the five plots were used to characterize habitat structure in the sampling unit.

We evaluated the size of the gradient through Detrended Canonical Correspondence Analysis (DCCA; ter Braak 1986; ter Braak & Smilauer 2002), considering the feral pigs IU as a response variable in each sample unit and the predators IU, and habitat structure and landscape classes of cover (only data of 2010 land cover map) as environmental variables. Based on the length of the gradients we opted for RDA (Redundancy analysis), a linear method (ter Braak 1986; ter Braak & Smilauer 2002). We used the variation partitioning approach described by Cushman & McGarigal (2002). Principal Component Analysis (PCA) was used to reduce the habitat structure and landscape data sets to seven and five uncorrelated components, respectively. The latent root criterion was considered to define the number of PCA axes to be used in the analysis (Cushman & McGarigal 2002). We then submit the whole data set to forward selection (ter Braak & Smilauer 2002) to find a minimal set of variables that explain the species data about as well as the full set, and dropped all variables that were not significant at p= 0.05 to reduce collinearity among explanatory variables (Cushman & McGarigal 2002; ter Braak 1986; ter Braak & Smilauer 2002). Noisy temporary predictive variables as burned areas were deleted from the analysis. The PCA analyses were performed using Statistica 6.1 (StatSoft ©). RDA's analyses were performed in CANOCO for Windows 4.5 (ter Braak & Smilauer 2002).

**Species Distribution Models**

We used maximum entropy niche modelling approach, as implemented in the MAXENT version 3.3.3k to describe environmental suitability, potential feral hog distributions and estimate the past
distribution considering the environmental conditions. The method considers the requirement of the species based on the presence and on the set of environmental variables (Phillips et al. 2006), providing environmental variable response curves indicating how each variable affects the predicted distribution (Phillips and Dudík 2008). We ran Maxent under the ‘auto-features’ mode and the default settings, with 10-fold replicates generated by bootstrap (Phillips and Dudík 2008). The logistic output was used (habitat suitability on a scale of 0-1), with higher values in the Environmental Suitability Map (ESM) representing more favorable conditions for the presence of the species (Elith et al., 2006; Phillips & Dudík, 2008). For binary potential distribution maps (suitable/unsuitable), we applied the Minimum Training Presence (MTP) as a threshold value for model, because it is the most conservative threshold, identifying the maximum possible predicted area, while still maintaining a zero-omission rate for both training and test data. We ran Maxent under the ‘auto-features’ mode and the default settings, with 10-fold replicates generated by bootstrap (Phillips and Dudík 2008). The logistic output was used (habitat suitability on a scale of 0-1), with higher values in the Environmental Suitability Map (ESM) representing more favorable conditions for the presence of the species (Elith et al., 2006; Phillips & Dudík, 2008). For binary potential distribution maps (suitable/unsuitable), we applied the Minimum Training Presence (MTP) as a threshold value for model, because it is the most conservative threshold, identifying the maximum possible predicted area, while still maintaining a zero-omission rate for both training and test data.

The model was developed using 69 occurrence points (sampling units with S. scrofa presence) (Table S1) and ten (10) environmental variables (landscape descriptors). The program was configured to use 80% of occurrence data (56 points) for training and 20% (13 points) for test. The final models for feral pigs were based on the mean of the 10 replicated models. For the projection of the model to the past, to before the PA implementation, we used a 1988 land cover map (Fig. 1A). The Area Under Curve (AUC) of the Receiver Operating Characteristics (ROC) analysis was used as a measure of model performance (Fielding and Bell 1997; Manel et al. 2001; Peterson et al. 2007; Phillips et al. 2006). For comparative purposes, the resulting ESM images (2010 model and 1988 past projection), with continuous values from 0 to 1, were reclassified into five environmental suitability zones, (1) an Unsuitable Zone (USZ; value pixel suitability < Minimum Training Presence, MTP), (2) a Low Suitability Zone (LSZ, value pixel suitability between MTP value and 0.25), (3) an Intermediate Suitability Zone (ISZ, value pixel suitability between 0.25 and 0.50), (4) a High Suitability Zone (HSZ, value pixel suitability 0.50 and 0.75), and (5) a Very High Suitability Zone (VHSZ, value pixel suitability > 0.75).

Additionally, in order to quantify the spatial similarity between the model (2010) and its projection to the past (1988), we used Fuzzy index for continuous ESM, and Kappa index for binary maps (suitable/unsuitable). Both indices were implemented in Map Comparison Kit software, version 3.2.3 (Visser & Nijs 2006) and express the pixel similarity for a value between 0 (fully distinct) and 1 (fully identical).
RESULTS

Variation partitioning

Abrupt changes in the landscape mosaic (DCCA; longest gradient shorter than 3.0) may affect the distribution of feral pigs. Landscape features and habitat structure explained 27.9% of the variation in feral pigs use in the study region (RDA model, $P = 0.001$) (Fig. 2). However, only one variable which describes habitat structure (first PCA axis related to sky view factor, basal tree area and canopy height) and three axes related to landscape features (Pasture, Scrubland and Seasonally Flood Forests cover; first, second and third axis, respectively) were included in the RDA model, based on the forward selection criterion ($P \leq 0.05$). Feral pigs do not seem to be conditioned on the use of the region by predators; this variable were not selected in the model. The first tier of the decomposition separated only habitat structure and landscape. The second tier decomposed feral pigs use variation, partitioning the landscape-level conditional effects by quantifying the unique explanatory power provided by each landscape variable: Pasture 19.7%, Scrubland 1.8% and Seasonally Flood Forests 1.7% (Fig 2).

Species Distribution Models

The model showed a very good overall performance, presenting high AUC values for both training (AUC = 0.932; SD = 0.010) and test data (AUC = 0.893; SD = 0.025), indicating that the modeled distribution performed better than the random one; high AUC denotes good observation/prediction fit of the test points in the spatial distribution model (Lobo et al. 2008). The most important environmental variable explaining the occurrence of feral pigs was Pasture (PAS), followed by scrubland (SCR) and Seasonal Dry Forest (SDF) (Fig. 3). The gain decreased most when the distance to water (WAT) was omitted, evidencing that this variable contains most of the information missing in the others (Fig. 3).

Feral pigs “prefer” (more suitability) landscapes dominated by Pastures (Fig. 4A), permeated by patches of Seasonal Dry Forest (Fig. 4C), with small portions of Scrubland areas (Fig. 4B), and areas with proximity to water sources (Fig. 4D). The species tends to avoid predominantly forested areas (SCH, RIP and SFF), and Termite Savannas (TSV).
The model indicates that the most suitable zones for feral pigs in 2010 are those located on large cattle ranches in the east, northeast and northwest of the protected area (Fig. 5A). Within the PA area, Low Suitability Zone (LSZ) predominate except in small isolated patches of intermediate and high suitability zones. On the other hand, the 1988 Environmental Suitability Map shows a different scenario (Fig. 5C); the current PA area was filled with intermediate and high suitability zones contrasting with 2010. Figures 5B and 5D shows [represents] the potential distribution binary map (suitable/unsuitable) based on the MTP cutoff criteria (MTP = 0.09).

Between 1988 and 2010, there was a reduction of 84.1% in the suitable areas (suitability >MTP) within the PA area (Table 3), contrasting with the reduction of area occupied by these categories in the cattle ranch, which was less than 10%. The spatial and temporal similarities are shown in Table 3. Thereby, taking into account different criteria (Fuzzy for continuous values of suitability, and Kappa for binary maps- suitable/unsuitable), the PA area had the highest rate of change when compared to the cattle ranch and other areas of the study region.

**DISCUSSION**

**Disappearance of feral pigs**

The absence of feral pigs records for many years in PA was intriguing, considering that we have been studying ungulates in the region since 1999 and we have many records of the species. *S. scrofa* is recognized for having large fluctuations of density and population size in native and exotic areas of occurrence (Mayer & Brisbin 2009). Birth and mortality rates of young and adults are directly affected by the availability of food and environmental variations (Baber & Coblentz 1986; Bieber & Ruf 2005; Geisser & Reyer 2005; Jedrzejewska et al. 1997; Massei et al. 1997; Melis et al. 2006; Keuling et al 2013). However, due to their high reproductive potential, wild pigs are resilient, quickly recovering from such dramatic population reductions (Mayer & Brisbin 2009). Sampling bias were discarded because both areas are part of a relatively similar ecological system in northern Pantanal, suggesting that the differences are not due to a drastic reduction in the ability to detect the species generating pseudo-absences (Engler et al. 2004; Morrison et al. 2007). Nevertheless, despite a large additional sampling effort being put in areas potentially attractive for feral pigs we did not obtain any record of this species. In 2004, even with a much lower sampling effort feral pigs were recorded by camera traps in natural licks in this region.
Additionally, throughout the sampling campaign we traversed hundreds of kilometers across the area and we did not find any evidence or signs of feral pigs, such as wallowing sites, feces or tracks. We then assume that the lack of records in the PRNH Sesc Pantanal area is a real absence of feral pigs and not a pseudo-absence generated by the detection or sampling effort. Since we got only two records of feral pigs in the PRNH - both near the northeastern PA boundary, close to the limits of cattle ranch - and 261 records in the cattle ranch area between June and September 2012, we performed an intensive sampling campaign in areas potentially attractive for feral pigs in the PA monitoring 20 artificial ponds and 19 natural licks throughout 90 consecutive days. However, this sampling did not result in a single record of feral hog.

**Suitable habitats and limiting factors**

Pastures were the most important land cover class related to the landscape feature, and they explain the distribution of feral pigs in the study region (RDA and SDM). This herbaceous class is maintained by grazing pressure (e.g. native grasses intensively grazed by cattle, exotic pastures, grasslands with very small earthmounds and bare soil areas). The intensive use of grasslands and pastures had already been described in southern Pantanal and in other regions (Barrett 1982; Baubet et al. 2004; Choquenot & Ruscoe 2003; Desbiez et al. 2009; Dexter 1998, 1999; Graves 1984; Oliveira-Santos 2013), and plants like grass, herbs and forbs usually represent a considerable part of the feral pigs and wild boar diets (Baber & Coblentz 1986; Cuevas et al. 2013a; Cuevas et al. 2013b; Giménez-Anaya et al. 2008; Hellgren 1993; Taylor & Hellgren 1997). Furthermore, the SDM approach showed that habitats with greater suitability for feral pigs are those predominantly herbaceous (around 80% coverage), interspersed with patches of seasonally dry forest (optimum between 35 and 40% coverage) and not too far from water bodies (around one kilometer). Feral pigs are known for their generalist habitat use (Ilse & Hellgren 1995; Mayer & Brisbin 2009) and by the preference for patchy habitats (Acevedo et al. 2006; Gabor et al. 2001; Oliveira-Santos 2013). The forest patches associated with a predominantly herbaceous matrix are very important because the dense vegetation is used as shelter from potentially lethal heat and as resting sites (Choquenot & Ruscoe 2003; Dexter 1998; Graves 1984; Huynh et al. 2005a; Huynh et al. 2005b).

*S. scrofa* has a low tolerance to high temperature in nature due to the lack of sweat glands or other efficient physiological cooling mechanisms (Baber & Coblentz 1986; Choquenot & Ruscoe 2003;
Collin et al. 2001; Huynh et al. 2005b), and low ability to concentrate urine (Gabor et al. 1997; Zervanos and Naveh 1988), being dependent on shaded habitats and reservoirs of water to avoid dehydration and promote thermoregulation (Baber & Coblentz 1986; Cuevas et al. 2013b; Dexter 1998; Ilse & Hellgren 1995). Data available for southern Pantanal shows that the species has a high fidelity, returning to resting sites where they stay during the hottest hours of the day (Oliveira-Santos 2013). We observed that away from forest patches feral pigs use small aggregations of trees (e.g. Licania parvifolia, Couepia uiti and Calophyllum brasiliense) and isolated small mounds with woody vegetation as thermal shelters.

The environmental suitability for feral pigs decreases exponentially as the distance from water bodies increases, as has already been observed for populations inhabiting arid and semiarid regions (Baber & Coblentz 1986; Cuevas et al. 2013b; Ilse & Hellgren 1995; Mayer & Brisbin 2009). In arid regions of Australia, the species cannot persist in areas more than 10 km away from water sources, suggesting that the margin of their range is associated to inland river systems. Such areas vary temporally, acting as sources, pseudosinks and sinks (Choquenot & Ruscoe 2003). However, areas closer than 500m to water bodies were not identified as highly suitable, particularly those close to rivers, reflecting the absence of feral pig records near the riverbanks within the study area. This may be due to the structure of the river banks, which have sharp slopes in long stretches. The low activity of feral pigs in riparian forests was already observed in southern Pantanal (Keuroghlian et al. 2009). Habitats with close links with natural water bodies such as lakes and natural riparian forests were those with high records of jaguar in our study region. Jaguars have a close association with water in the Pantanal (Crawshaw & Quigley 1991) and predation therefore could be an explanation for the lack of records of feral pigs in these habitats. These relationships could not be explored through the analysis, since the predator variable was excluded through the selection process. In any case, the existence of dozens of artificial ponds in the midst of extensive areas of pastures in cattle ranch region probably reduces the need of feral pigs to access riparian forests where predation risk is higher, or even these areas can act as sinks. Likewise, the species showed negative relationships with structural features of the vegetation associated with forest habitats, such as tree density, and areas with closed canopy. The low biomass of grasses and herbs due to high shading caused by increasing canopy cover may be an additional explanation for the low utilization of riparian and the seasonally flood forests.
Changes in the landscape features and loss of suitability areas for feral pigs

In Brazilian Pantanal, the occurrence of feral pigs seems to be closely associated with the environmental changes resulting from the land use by traditional livestock. The management system employed in the PA must have been the main factor that led to drastic reduction of suitable habitats and disappearance of feral pigs in this area. Important changes have been recorded over the last 40 years in plant communities and in the landscape of the Brazilian Pantanal by several authors (Junk et al. 2006; Nunes da Cunha et al. 2007; Pott et al. 2011; Scremin-Dias et al. 2011). As from the seventies, the successions of wet years and large floods favored the colonization of tree and shrub species on the grasslands and pastures (Nunes da Cunha & Junk 2004; Nunes da Cunha et al. 2007; Pott et al. 2011). Within this scenario, Vochysia divergens (Vochysiaceae) is the species whose expansion in the study region is most evident, although other species such as L. parvifolia, Combretum lanceolatum, C. uiti, Byrsonima orbignyana and Ipomoea fistulosa also have advanced over old open areas (Nunes da Cunha & Junk 2004; Oliveira et al. 2013; Pott et al. 2011). Since then, deforestation and ‘controlled’ fires have been the main forms of clearing land used by ranchers to increase cattle stocking rates (Harris et al. 2005; Junk et al. 2006; Seidl et al. 2001; Wilcox 1992). After the creation of the PA in 1999, thousands of cattle were removed from the area and a well-equipped fire brigade was established to control fires throughout the dry season (Brandão et al. 2008). With the absence large fires and grazing, the grasslands and other vegetation classes in the PA contrasted sharply with adjacent areas. (Oliveira et al. 2013). However, the environmental changes resulting from the traditional livestock are not restricted to the landscape scale, as they also affect the vegetation structure. Experiments of exclusion of cattle in the Pantanal showed that the absence of grazing pressure leads to strong growth of woody species (Nunes da Cunha & Junk 2004). In the central area of the PA there was a huge increase in the biomass of grasses. The grasses reach about 1.5 meters high and the access to many areas is difficult or almost impossible on foot or on horseback. In regions where grasses predominated a few years ago, in the floodplain of the Cuiabá River (western boundary of PA), shrubs dominate the landscape. In other words, nowadays the grasslands in the PA differ greatly from those occupied by feral pigs in the cattle ranch.
Implications for conservation and management

Feral pigs are strongly associated with livestock. Over 80% (118,000 km$^2$) of Pantanal lands are cattle ranches and only 2.5% is formally protected in national and state parks and in private protected areas (Harris et al. 2005; Seidl et al. 1999). Historically, many authors argue that traditional livestock plays an important role in the maintenance of the parkland physiognomy of the Pantanal and low density cattle ranching is considered an ecologically sound and sustainable management method (Alho et al. 1988; Junk et al. 2006; Pott & Pott 2004). Therefore, it is impossible to make an efficient plan for the conservation of the Pantanal without the inclusion of ranchers and their properties (Harris et al. 2005). Nevertheless, over the past 30 years the traditional livestock practices have been replaced by more intensive ones and ranchers have planted exotic pastures in forest areas cleared in order to increase cattle stocking rates (Alho et al. 1988; Oliveira et al. 2013; Seidl et al. 2001). In the long run, however, these actions may be reversed against the ranchers. The reduction of natural areas and increase of environmental degradation due to the intensification of livestock in the region has certainly favored the growth of feral hog populations and this should result in large economic losses by damaged crops and husbandry (Barrios-Garcia & Ballari 2012; Bieber & Ruf 2005; Gabor et al. 2001). Feral pigs are known in the Pantanal and in other regions to cause damage to large areas of grassland by foraging activity (Desbiez et al. 2009; Mayer & Brisbin 2009; Sicuro & Oliveira 2002). In the study area, large extensions of native and exotic pastures were completely wiped out (Fig. 6), with virtually no fodder for cattle or native grazers. Additionally, the high predation of eggs and native animals certainly are just some of the direct consequences of the increased density of feral pigs in these pasture areas (Barrios-Garcia & Ballari 2012).

The disappearance of feral pigs in the PA area after the implementation of the management plan shows the vulnerability of the species and opens new possibilities for an eradication program in the region. The decline of feral pigs in this area appears to be intimately associated with the drastic reduction and fragmentation of pasture areas, a natural consequence of the fast succession of the vegetation after the cattle exclusion. Therefore, the loss and fragmentation of habitats by human actions, which are pointed as major factors that lead to the extinction of species in global scale (Banks-Leite et al. 2012; Cushman 2006; Dobrovolski et al. 2013; Fahrig 2002) seem to have helped expel a powerful invader from the PA. The increased density and height of grasses due to
the suspension of grazing cattle may also have a negative effect on feral pigs. Questions are open if the species disappearance is related to the reduction of habitat quality, low detection of predators, reduction of foraging efficiency or synergistic effect of various factors. In any case, changes in the land use regime, particularly in grasslands, can increase the chances of feral pigs management. Furthermore, a key factor to reduce feral pigs in areas with hot and dry season climate or semi-arid regions is to restrict their access to water sources (Baber & Coblenz 1986; Choquenot & Ruscoe 2003; Dexter 1998; Mayer & Brisbin 2009). Although it is virtually impossible to restrict the feral hog access to all water sources in a wetland like the Pantanal, increasing hunting in these places (especially those near to pastures and grasslands in dry seasons) as a major factor in limiting the size of the populations, targeting especially females and piglets, can be a way to keep the population in sub-optimal areas in order to facilitate management. The reduction in birth and survival rates by hunting focused on females and piglets can have a direct impact on local populations (Bieber & Ruf 2005). *S. scrofa* is a highly cooperative and cognitive species. Under high hunting pressure survivors avoid techniques and sites targeted by hunters (Morrison et al. 2007) using their spatial memory to habitat selection, considering factors such as predation risk, thermal comfort and forage quality (Oliveira-Santos 2013). Permanent hunting pressure near artificial ponds in pasture areas forces feral pigs to seek alternative sources of water, increases energy expenditure and reduces time spent in thermoregulation, hence forcing the use of less suitable habitats such as riparian forests increasing the risk of predation. Synergic interaction between several factors may be more important in limiting the population growth of the species in remote areas like Pantanal than simply directing efforts to a single method of population control.

**CONCLUSION**

The disappearance of feral pigs after the conversion of old cattle ranches into a protected area was associated with changes in the landscape and vegetation structure after the removal of the cattle and the implementation of the management plan for the area. In the Brazilian Pantanal the feral pigs occurrence seems conditioned to environmental changes associated to livestock activity, particularly related to the proportion of pastures available, although the availability of forest patches and water sources are also important. They are rare in continuous and riparian forests. Occurrences of potential predators are not significant. However, predation cannot be completely ruled out as an important factor in conditioning the distribution of this species in Pantanal, but
more data should be raised about this factor, in this region with varied mosaic and still rich fauna. Under current conditions the chances of recolonization of the protected area are low, particularly by the absence of suitable habitats. For the same reason it is hard to believe in a "resurgence" of feral pigs via “Lazarus effect” as refered as "Lazarus pig" (Morrison et al. 2007), the last animal in the region. Thus, our results suggest a point of weakness in the exotic distribution of S. scrofa, directly related to the ressurgence of grazed areas. The distribution of the species in the Brazilian Pantanal is the result of the effect of human activity on the structure and spatial arrangements of plant formations in the region.

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REFERENCES

Acevedo P, Escudero MA, Munoz R, Gortazar C. 2006. Factors affecting wild boar abundance across an environmental gradient in Spain. Acta Theriologica 51: 327-336 DOI:10.1007/BF03192685.

Alho CJR, Lacher TE. 1991. Mammalian conservation in the Pantanal of Brazil. In: Mares MA and Schmidly DJ, eds. Latin American mammalogy, history, biology, and conservation. Norman: University of Oklahoma Press, 280-294.

Alho CJR, Lacher TE and Goncalves HC. 1988. Environmental Degradation in the Pantanal Ecosystem - in Brazil, the Worlds Largest Wetland Is Being Threated by Human Activities. Bioscience 38: 164-171.

Alho CJR, Mamede S, Bitencourt K, Benites M. 2011. Introduced species in the Pantanal: implications for conservation. Brazilian Journal of Biology 71: 321-325.
Baber DW, Coblentz BE, 1986. Density, Home Range, Habitat Use, and Reproduction in Feral Pigs on Santa-Catalina Island. *Journal of Mammalogy* 67: 512-525.

Banks-Leite C, Ewers RM, Metzger JP. 2012. Unraveling the drivers of community dissimilarity and species extinction in fragmented landscapes. *Ecology* 93(12) 2560-2569.

Barrett RH. 1982. Habitat preferences of feral hogs, deer, and cattle on a Sierra Foothill Range. *Journal of Range Management* 35: 342-346.

Barrios-Garcia MN, Ballari S. 2012. Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biological Invasions* 14: 2283-2300.

Baubet E, Bonenfant C, Brandt S. 2004. Diet of the wild boar in the French Alps. *Galemys* 16 101-113.

Bieber C, Ruf T. 2005. Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology* 42: 1203-1213.

Brandão LG, Antas PTZ, Oliveira LFB, Pádua MTJ, Pereira NC, Valutky WW. 2008. Plano de Manejo da Reserva Particular de Patrimônio Natural do SESC Pantanal. SESC, Departamento Nacional Rio de Janeiro, Rio de Janeiro, 119 p.

Choquenot D, Ruscoe WA. 2003. Landscape complementation and food limitation of large herbivores: habitat-related constraints on the foraging efficiency of wild pigs. *Journal of Animal Ecology* 72: 14-26.

Coelho IP. 2006. Relações entre barreiros e a fauna de vertebrados no nordeste do Pantanal, Brasil. Master Thesis, Universidade Federal do Rio Grande do Sul, Brazil. Available at http://hdl.handle.net/10183/7747

Collin A, van Milgen J, Dubois S, Noblet J. 2001. Effect of high temperature and feeding level on energy utilization in piglets. *Journal of Animal Science* 79: 1849-1857.

Cordeiro JLP. 2004. Estrutura e heterogeneidade da paisagem de uma unidade de conservação no nordeste do Pantanal (RPPN SESC Pantanal), Mato Grosso, Brasil: efeitos sobre a
distribuição e densidade de antas (Tapirus terrestris) e de cervos-do-pantanal (Blastocerus dichotomus). D Thesis, Universidade Federal do Rio Grande do Sul, Brasil. Available at http://hdl.handle.net/10183/5155

Crawshaw PG, Quigley HB. 1991. Jaguar Spacing, Activity and Habitat Use in a Seasonally Flooded Environment in Brazil. Journal of Zoology 223: 357-370.

Cuevas MF, Ojeda RA, Dacar MA, Jaksic FM. 2013a. Seasonal variation in feeding habits and diet selection by wild boars in a semi-arid environment of Argentina. Acta Theriologica 58: 63-72.

Cuevas MF, Ojeda RA, Jaksic FM. 2013b. Multi-scale patterns of habitat use by wild boar in the Monte Desert of Argentina. Basic and Applied Ecology 14: 320-328.

Cushman SA. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological conservation 128: 231-240.

Cushman SA, McGarigal K. 2002. Hierarchical, multi-scale decomposition of species-environment relationships. Landscape Ecology 17: 637-646.

D’Eath RB, Turner SP. 2009. The Natural Behaviour of the Pig. In: Marchant-Forde JN, ed. The Welfare of Pigs. Springer, 13-45.

Desbiez ALJ, Keuroghlian A. 2009. Can bite force be used as a basis for niche separation between native peccaries and introduced feral pigs in the Brazilian Pantanal? Mammalia 73: 369-372.

Desbiez ALJ, Santos SA, Keuroghlian A, Bodmer RE. 2009. Niche Partitioning among White-Lipped Peccaries (Tayassu Pecari), Collared Peccaries (Pecari Tajacu), and Feral Pigs (Sus Scrofa). Journal of Mammalogy 90: 119-128.

Dexter N. 1998. The influence of pasture distribution and temperature on habitat selection by feral pigs in a semi-arid environment. Wildlife Research 25: 547-559.

Dexter N. 1999. The influence of pasture distribution, temperature and sex on home-range size of feral pigs in a semi-arid environment. Wildlife Research 26: 755-762.
Dobrovolski R, Loyola RD, Guilhaumon F, Gouveia SF, Diniz-Filho JAF. 2013. Global agricultural expansion and carnivore conservation biogeography. *Biological Conservation* 165: 162-170.

Elith JH, Graham CP, Anderson RP, Dudík M, Ferrier S, Guisan A, Hjelmans RJ, Huerdtmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JMM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE. 2006. Novel methods improve prediction of species’ distributions from occurrence data. *Ecography* 29: 129–151.

Engler R, Guisan A and Rechsteiner L (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology* 41: 263-274.

Fahrig L. 2002. Effect of Habitat Fragmentation on the Extinction Threshold: A Synthesis. *Ecological applications* 12: 346-353.

Fielding AH, Bell JF. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38-49.

Fonseca C, Correia F. 2008. *O Javali. Coleção Património Natural Transmontano*. Mirandela: João Azevedo Editor (1.ª Edição), 168 p.

Gabor TM, Hellgren EC. 2000. Variation in peccary populations: landscape composition or competition by an invader? *Ecology* 81: 2509-2524.

Gabor TM, Hellgren EC, Silvy NJ. 1997. Renal morphology of sympatric suiforms: Implications for competition. *Journal of Mammalogy* 78: 1089-1095.

Gabor TM, Hellgren EC, Silvy NJ. 2001. Multi-scale habitat partitioning in sympatric suiforms. *Journal of Wildlife Management* 65: 99-110.

Geisser H, Reyer HU. 2005. The influence of food and temperature on population density of wild boar Sus scrofa in the Thurgau (Switzerland). *Journal of Zoology* 267: 89-96.
Giménez-Anaya A, Herrero J, Rosell C, Couto S, García-Serrano A. 2008. Food habits of wild boars (Sus scrofa) in a Mediterranean coastal wetland. *Wetlands* 28: 197-203.

Gonçalves HC, Mercante MA, Santos ET. 2011. Hydrological cycle. *Brazilian Journal of Biology* 71: 241-253.

Graves HB. 1984. Behavior and Ecology of Wild and Feral Swine (Sus Scrofa). *Journal of Animal Science* 58: 482-492.

Harris MB, Tomas W, Mourao G, Da Silva CJ, Guimaraes E, Sonoda F, Fachim E. 2005. Safeguarding the Pantanal wetlands: Threats and conservation initiatives. *Conservation Biology* 19: 714-720.

Hasenack H, Cordeiro JLP, Hofmann GS. 2010. Macroclima, o clima regional, e Mesoclima, o clima local. O clima na Reserva do Patrimônio Natural SESC Pantanal (Conhecendo o Pantanal 5). Rio de Janeiro: SESC/Departamento Nacional, 62-85.

Hellgren EC. 1993. Biology of feral hogs (Sus scrofa) in Texas. In: Hanselka CW., Cadenhead JE, Eds. *Feral swine: a compendium for resource managers*. Kerrville: Texas Agricultural Extension Service, 50-58.

Hofmann GS, Oliveira LFB, Hasenack H. 2010. Microclima e a estrutura de formações vegetais. O clima na Reserva Particular do Patrimônio Natural SESC Pantanal (Conhecendo o Pantanal 5). Rio de Janeiro: SESC/Departamento Nacional, 12-59.

Hofmann GS, Bastazini VAG, Cordeiro JLP, Oliveira, LFB 2015. Implications of climatic seasonality on activity patterns and resource use by sympatric peccaries in northern Pantanal. *International Journal of Biometeorology*, 9:1-13. Hutchinson GE. 1978. *An Introduction to Population Ecology*. New Haven: Yale University Press, 271 p.

Huynh TT, Aarnink JA, Verstegen WA, Gerrits JJ, Heetkamp MJ, Kemp B. 2005a. Evaporative heat loss from pigs at different temperature and relative humidity. *Journal of Animal Science* 83: 340-340.
Huynh TTT, Aarnink AJA, Verstegen MWA, Gerrits WJJ, Heetkamp MJW, Kemp B, Canh TT. 2005b. Effects of increasing temperatures on physiological changes in pigs at different relative humidities. *Journal of Animal Science* 83: 1385-1396.

Ilse LM, Hellgren EC. 1995. Resource Partitioning in Sympatric Populations of Collared Peccaries and Feral Hogs in Southern Texas. *Journal of Mammalogy* 76: 784-799.

Jedrzejewska B, Jedrzejewski W, Bunевич AN, Milkowski L, Krasinski ZA. 1997. Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. *Acta Theriologica* 42: 399-451.

Junk WJ, da Cunha CN, Wantzen KM, Petermann P, Strussmann C, Marques MI, Adis J. 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. *Aquatic Sciences* 68: 278-309.

Keuling O, Baubet E, Duscher A, Ebert C, Fischer C, Monaco A, Podgórski T, Prevot C, Ronnenberg K, Sodeikat G, Stier N, Thurfjell H. 2013. Mortality rates of wild boar Sus scrofa L. in central Europe. *European Journal of Wildlife Research* 59(6): 805–814 DOI: 10.1007/s10344-013-0733-8.

Keuroghlian A, Eaton DP, Desbiez ALJ. 2009. Habitat use by Peccaries and Feral Pigs of the Southern Pantanal, Mato Grosso do Sul, Brazil. *Suiform Soundings* 8: 9-17.

Larson G, Albarella U, Dobney K, Rowley-Conwy P. 2007. Current views on Sus phylogeography and pig domestication as seen through modern mtDNA studies. In: Albarella U, Dobney K, Ervynck A, Rowley-Conwy P, Eds. *Pigs and humans: 10,000 years of interaction*. Oxford: University Press, 30-41.

Lobo JM, Jiménez-Valverde A, Real R. 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global ecology and Biogeography* 17: 145-151.

Long JL, 2003. *Introduced mammals of the world: their history, distribution and influence*. Collingwood: Csiro Publishing, 589 p.
Lowe S, Browne M, Boudjelas S, De Poorter M. 2000. *100 of the World’s Worst Invasive Alien Species A selection from the Global Invasive Species Database*. Auckland: Invasive Species Specialist Group (ISSG, SSC-IUCN), 12p.

Manel S, Williams HC, Ormerod SJ. 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38: 921-931.

Massei G, Genov PV, Staines BW, Gorman ML. 1997. Mortality of wild boar, *Sus scrofa*, in a Mediterranean area in relation to sex and age. *Journal of Zoology* 242: 394-400.

Mayer J, Brisbin IL. 2009. *Wild Pigs: Biology, Damage Control Techniques and Management*. Aiken: Savannah River National Laboratory, 408p.

Mccann BE, Garcelon DK. 2008. Eradication of feral pigs from Pinnacles National Monument. *Journal of Wildlife Management* 72: 1287-1295.

Melis C, Szafranska PA, Jedrzejewska B, Barton K. 2006. Biogeographical variation in the population density of wild boar (*Sus scrofa*) in western Eurasia. *Journal of Biogeography* 33: 803-811.

Morrison SA, Macdonald N, Walker K, Lozier L, Shaw MR. 2007. Facing the dilemma at eradication's end: uncertainty of absence and the Lazarus effect. *Frontiers in Ecology and the Environment* 5: 271-276.

Mourão GDM, Coutinho ME, Mauro RDA, Tomás WM, Magnusson W. 2002. Levantamentos aéreos de espécies introduzidas no Pantanal: porcos ferais (porco monteiro), gado bovino e búfalos. Embrapa Pantanal. *Boletim de Pesquisa e Desenvolvimento* 28: 1-22.

Nimer E. 1979. *Climatologia do Brasil*. Rio de Janeiro, Brasil: IBGE, 422 p.

Nogueira SLG, Nogueira SSC, Fragoso JMV. 2009. Ecological impacts of feral pigs in the Hawaiian Islands. *Biodiversity and Conservation* 18: 3677-3683.

Nunes da Cunha C, Junk WJ. 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 WJ, Leitão-Filho HF. 2007. Woody vegetation in the Pantanal of Mato Grosso, Brazil: a preliminary typology. *Amazoniana* 19: 159-184.

Oliveira-Santos LGR. 2013. Ecology of feral hogs (*Sus scrofa*) in the Pantanal wetland: temporal overlap and spatial interference with native pigs, movement and spatial memory. D Thesis, Universidade Federal do Rio de Janeiro, Brazil.

Oliveira LFB, Cordeiro JLP, Hasenack H. 2013. Padrões e tendências regionais em uma paisagem antropizada no norte do Pantanal: uma perspectiva espaço-temporal. In: Peres CA, Barlow J, Gardner TA, Vieira ICG, Eds.) *Conservação da biodiversidade em paisagens florestais antropizadas do Brasil*. Curitiba: Editora da Universidade Federal do Paraná, 231-262.

Parkes JP, Ramsey DSL, Macdonald N, Walker K, McKnight S, Cohen BS, Morrison SA. 2010. Rapid eradication of feral pigs (*Sus scrofa*) from Santa Cruz Island, California. *Biological Conservation* 143: 634-641.

Peterson AT, Papes M, Eaton M. 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and MAXENT. *Ecography* 30: 550–560.

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB. 2011. *Ecological Niches and Geographic Distributions*. Princeton: Princeton University Press, 328 p.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259.

Phillips SJ, Dudík M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31: 161-175.

Pott A, Oliveira AKM, Damasceno GA, Silva JSV. 2011. Plant diversity of the Pantanal wetland. *Brazilian Journal of Biology* 71: 265-273.

Pott A, Pott VJ. 2004. Features and conservation of the Brazilian Pantanal wetland. *Wetlands Ecology and Management* 12: 547-552.
Scremin-Dias E, Lorenz-Lemke AP, Oliveira AKM. 2011. The floristic heterogeneity of the Pantanal and the occurrence of species with different adaptive strategies to water stress. Brazilian Journal of Biology 71: 275-282.

Seidl A, Davila AMR, Silva RAMS. 1999. Estimated financial impact of Trypanosoma vivax on the Brazilian pantanal and Bolivian lowlands. Memorias Do Instituto Oswaldo Cruz 94: 269-272.

Seidl AF, de Silva JDV, Moraes AS. 2001. Cattle ranching and deforestation in the Brazilian Pantanal. Ecological Economics 36: 413-425.

Sicuro FL, Oliveira LFB. 2002. Coexistence of peccaries and feral hogs in the Brazilian pantanal wetland: An ecomorphological view. Journal of Mammalogy 83: 207-217.

Taylor RB, Hellgren EC. 1997. Diet of feral hogs in the western South Texas Plains. The Southwestern Naturalist 42: 33-39.

ter Braak C, Smilauer P. 2002. CANOCO reference manual and user’s guide to Canoco for Windows: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca.

ter Braak CJF. 1986. Canonical Correspondence Analysis: A New Eigenvector Technique for Multivariate Direct. Ecology 67: 1167-1179.

Turner MG, Pearson SM, Romme WH, Wallace LL. 1997. The Influence of Landscape Scale on the Management of Desert Bighorn Sheep. In: Bissonette JA, Ed. Wildlife and Landscape Ecology: Effect of Pattern and Scale. New York:Springer-Verlag, 349-367.

Visser H, Nijs T. 2006. The Map Comparison Kit. Environmental Modelling & Software 21: 346–358.

Wilcox R. 1992. Cattle and Environment in the Pantanal of Mato-Grosso, Brazil, 1870-1970. Agricultural History 66: 232-256.

Zervanos SM, Naveh S. 1988. Renal Structural Flexibility in Response to Environmental Water-Stress in Feral Hogs. Journal of Experimental Zoology 247: 285-288.
**Table 1:** Description of land cover classes of the study area.

| Land Cover Class       | Acronyms | Description                                                                                                                                 |
|------------------------|----------|---------------------------------------------------------------------------------------------------------------------------------------------|
| Scrubland              | SCR      | Open areas dominated by Byrsonima orbygniana, Hibiscus furcellatus and Combretum lanceolatum                                                |
| Seasonally Flood Forest| SFF      | Monospecific forests dominated by *Vochysia divergens* “cambarazais” or by *Licania parvifolia* “corixos”                                      |
| Termite Savanna        | TSV      | Fields with Curatella americana and rounded earthmounds covered by woody vegetation “murundus”                                            |
| Seasonal Dry Forest    | SDF      | Forests with a predominance of deciduous trees such as Anadenanthera colubrina, Cedrela fissilis, Enterolobium contortisiliquum and Cordia glabrata |
| Scheelea Forest        | SCH      | Semideciduous forests where the understory is dominated by “Acuri” palm tree (*Scheelea phalerata*)                                          |
| Bamboo Forest          | BAM      | Forest physiognomy with an emergent tree stratum and sparse understory dominated by "taboca" (*Guadua sp.*)                                    |
| Riparian Forest        | RIP      | Unflooded forests that occur mainly on the banks of the São Lourenço River                                                                   |
| Pasture                | PAS      | Herbaceous vegetation associated with intensive livestock, e.g. native and exotic grasses, and bare soil areas                               |
| Water                  | WAT      | Water bodies such as rivers and lakes                                                                                                      |
| Burned areas           | BRN      | Burned areas by the ranchers in order to clear land and increase the cattle stocking rates                                                |
Table 2: Description of environmental variables and their units used as habitat structure metrics.

| Variable (unit)           | Description                                                                                                                                                                                                                                                                 |
|---------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Sky view factor (%)       | Proportion of the sky hemisphere obscured by vegetation photographed at the center of each plot (Frazer et al., 1999).                                                                                                                                                    |
| Canopy height (m)         | Canopy height estimated using a clinometers.                                                                                                                                                                                                                                                                                           |
| Dicots density (ind/ha⁻²) | Number of individual flowering plants per unit area.                                                                                                                                                                                                                                                                                  |
| Basal area (m²/ha⁻²)      | Area occupied by the cross-section of tree trunks and stems (CBH ≥ 5 cm) at breast height.                                                                                                                                                                                                                                             |
| Dicots fruits (%)         | Estimated by record of fruit in plots 5 (absence of fruit = 0%; registration in 1 plot = 20%, to record in 5 plots = 100%).                                                                                                                                                                                                               |
| Palm fruits (%)           | Estimated by record of palm fruit in plots 5 (absence of fruit = 0%; registration in 1 plot = 20%, to record in 5 plots = 100%).                                                                                                                                                                                                         |
| Palm density (ind/ha⁻²)   | Number of individual palm trees per unit area.                                                                                                                                                                                                                                                                                         |
| Horizontal obstruction at | Average proportion of the profile board when viewed from across a distance of 5 m in the four cardinal directions (Hays et al., 1981).                                                                                                                                  |
| ground level (%)          |                                                                                                                                                                                                                                                                                                                                      |
| Horizontal obstruction at | Average proportion of the profile board when viewed from across a distance of 5 m in the four cardinal directions (Hays et al., 1981).                                                                                                                                  |
| a height of 50 cm (%)     |                                                                                                                                                                                                                                                                                                                                      |
| Horizontal obstruction at | Average proportion of the profile board when viewed from across a distance of 5 m in the four cardinal directions (Hays et al., 1981).                                                                                                                                  |
| a height of 1 m (%)       |                                                                                                                                                                                                                                                                                                                                      |
| Horizontal obstruction at | Average proportion of the profile board when viewed from across a distance of 5 m in the four cardinal directions (Hays et al., 1981).                                                                                                                                  |
| a height of 1.5 m (%)     |                                                                                                                                                                                                                                                                                                                                      |
Table 3: The spatial and temporal similarities of suitable areas (> MTP*) for *Sus scrofa* in the study area.

| Site             | Area with value pixel suitability >MTP | 1988       | 2010       | Change rate | Fuzzy** | Kappa |
|------------------|---------------------------------------|------------|------------|-------------|---------|-------|
| All Study Area   | 539,122.4 ha                          | 332,871.8 ha | -38.3%     | 0.33        | 0.24    |
| Protected Area   | 51,074.28 ha                          | 8,123.67 ha | -84.1%     | 0.21        | 0.09    |
| Cattle Ranch Area| 78,714.5 ha                           | 73,677.2 ha | -6.4%      | 0.41        | 0.26    |

*Minimum Training Presence; ** for continuous map
Figure 1: Study area location in Brazilian Pantanal, *Mato Grosso* (MT) and *Mato Grosso do Sul* (MS) states. Land cover maps generated by Landsat image classification, A) 1988 and B) 2010. Seasonally Flood Forest (SFF); Riparian Forest (RIP); Scheelea Forest (SCH); Seasonally Dry Forest (SDF); Bamboo Forest (BAM); Scrubland (SCR); Termite Savanna (TSV); Pasture (PAS); Burned areas (BRN), Water (WAT).
Figure 2: Venn diagram showing the first- and second-tier decompositions of feral hog RDA model (P = 0.001) in the study region. The first-tier of the decomposition separates habitat structure and landscape contribution. The second-tier partitioned the landscape-level effect by quantifying the unique explanatory power provided by each landscape variable: Pasture (PAS) Scrubland (SCR) and Seasonally Flooded Forests (SFF).
Figure 3: Jackknife test results of individual environmental variable importance in the development of the MAXENT model relative to all environmental variables (dark grey bar) for each predictor variable alone (black bars), and the drop in training gain when the variable is removed from the full model (gray bars). Pasture (PAS); Scrubland (SCR); Seasonally Dry Forest (SDF); (WAT) Distance to Water; Scheelea Forest (SCH); Seasonally Flood Forest (SFF); Termite Savanna (TSV); Riparian Forest (RIP); Bamboo Forest (BAM); Burned areas (BRN).
Figure 4: Response-curves of the variables in the *Sus scrofa* distribution model. (A) Pasture (PAS); (B) Scrubland (SCR); (C) Seasonally Dry Forest (SDF); (D) Distance to Water (WAT). These curves show how each environmental variable affects the MAXENT prediction when all environmental variables are used to build the model.
Figure 5: MAXENT Environmental Suitability Maps for *Sus scrofa* in Northern Pantanal. A) 2010 model, B) 2010 potential distribution binary map (suitable/unsuitable) based on the MTP cutoff criteria (MTP = 0.09); C) model project to 1988 environmental conditions and D) 1988 potential distribution binary map. Unsuitability Zone (UNZ), Low Suitability Zone (LSZ), Intermediate Suitability Zone (ISZ), High Suitability Zone (HSZ), and Very High Suitability Zone (VHSZ) identified.
Figure 6: Ground rooting by feral pigs in northern Pantanal showing their activity in pasture areas. Photo credit: Luiz Flamarion Barbosa de Oliveira.