



Multi-scale path-level analysis of jaguar habitat use in the Pantanal ecosystem

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ABSTRACT

Jaguars (*Panthera onca*), like other apex predators, are highly susceptible to habitat loss and fragmentation given their low demographic potential and large habitat area requirements. Across their range, the Pantanal is considered critical for the jaguar's long-term conservation. Here we provide the first multi-scale path selection function model for jaguars, and the first empirically-based movement model covering the entire Pantanal ecosystem. Out of eight investigated variables, six were related to jaguar habitat use in the Pantanal: terrain roughness, human population density, grassland, percentage of tree cover, flooded habitats and shrubland. The results of scale optimization revealed that jaguars responded primarily to landscape variables at broad scales (32 km) of habitat availability, with only one variable (grassland) influencing jaguar path selection at a finer scale (4 km). Jaguar habitat use was positively associated with flooded habitats and densely forested areas and negatively associated with grassland, terrain roughness, and human population density, with the latter having the strongest negative effect on jaguar movement. The prediction map suggested that only 9.3% of the total suitable jaguar habitat in Pantanal is protected by Conservation Units. Among the most suitable areas, the largest continuous habitats were located in the northwestern portions of the Pantanal, which corresponds to the interfluvial areas between Corixo Grande and Cuiaba rivers. Our results suggested that the implementation of already proposed North Pantanal Conservation Unit Mosaic in this area would be highly valuable for jaguar conservation. This study provides a foundation for future research to delineate and prioritize core areas and corridors for jaguars in the region.

1. Introduction

The unparalleled conversion of wilderness by human development over the past century has contributed to a massive global decline of wildlife populations (Koh and Gardner, 2010; Pimm and Raven, 2000;

WWF, 2018). Large apex carnivore species are particularly susceptible to habitat loss given that they naturally occur in low population densities, often require extensive home ranges, which necessitates protection of large swathes of suitable habitat to maintain viable populations (Sunkist and Sunkist, 1989). To develop effective management and

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conservation efforts for large carnivores it is essential to understand how species interact with landscape features (Mateo Sánchez et al., 2014) and to investigate the scale-dependence of these interactions (Elliot et al., 2014; Zeller et al., 2017).

Jaguars are the largest cat species in the Western Hemisphere and the third largest cat species in the world (Seymour, 1989). Historically, they occurred from the southwestern United States to central Argentina (Sanderson et al., 2002). However, recent studies have estimated at least a 48% reduction of jaguar's geographical range over the past century as a result of habitat loss and fragmentation, coupled with direct persecution and extirpation by humans (Quigley et al., 2017; De la Torre et al., 2018). Almost all populations outside the Amazonian forest are likely declining and many are highly vulnerable to local extirpation (Zanin et al., 2015; Roques et al., 2016; De la Torre et al., 2018). Although the species is classified by the IUCN Red List as Near Threatened (Quigley et al., 2017), recent estimates have suggested that 25 out of the 33 populations occurring outside the Amazonian forest should be categorized as Critically Endangered, and eight as Endangered (De La Torre et al., 2018).

One of the largest populations of jaguars throughout its range inhabits the Pantanal ecosystem, which is widely recognized for its pristine wilderness and diverse wildlife (Sanderson et al., 2002; Soisalo and Cavalcanti, 2006). Despite its significant value in sustaining wildlife populations, only a small part of Brazilian Pantanal is protected (~5%) and about 95% is privately owned, mainly by cattle ranchers (Seidl et al., 2001). As a consequence, jaguar attacks on cattle are common, and retaliatory hunting of jaguars is considered to be the main direct threat to the species in this region (Azevedo and Murray, 2007; Cavalcanti et al., 2010; Marchini et al., 2019; Marchini and Macdonald, 2018). Moreover, during the last few decades, the Pantanal has experienced increasing rates of anthropogenic land use change (Cavalcanti et al., 2012; Guerra et al., 2020). It is estimated that about 60% of the native Pantanal plateau vegetation and about 20% of native floodplain vegetation has been already lost (Roque et al., 2016; SOS-Pantanal et al., 2015). Along with the land cover change, recent studies have predicted a progressive increase in the frequency of extreme climate conditions (e.g. extended droughts and floods) triggered by warming sea surface temperatures (Thielen et al., 2020). In fact, the consequences of anthropic pressure and severe droughts are already garnering worldwide attention through the worst fire events in decades (INPE, 2020).

Several local studies suggested that forest patches and areas of close proximity to water bodies represent important components of jaguar habitat in this region (Schaller and Crawshaw, 1980; Gese et al., 2018; Morato et al., 2018a). Forest cover is widely thought to be important for jaguars, allowing them to use their camouflage to stalk and ambush prey more easily (Crawshaw and Quigley, 1991; Schaller and Crawshaw, 1980). On a regional scale, though, little is known about jaguar behavior and resource selection. The only regional study on jaguars' habitat use was conducted by the Brazilian National Action Plan for Jaguar Conservation and was limited to the Brazilian portion of the Pantanal (Desbiez et al., 2013). That study estimated that jaguars occupied approximately 42% of the biome (Ferraz et al., 2013). Furthermore, the authors predicted a potential division of the population into northern and southern populations due to high deforestation rates in the southern region. To improve future conservation actions and to prevent the fragmentation of the jaguars' population, large-scale studies are necessary. Long-term sustainability of the Pantanal jaguar population depends on identification, and then protection, of habitats that are crucial for the species movement and resource use across the entire region to support demographic dynamics and gene flow between sub-populations (Cushman, 2006).

Resource selection models are useful for predicting species distributions and understanding species-habitat interactions (Guisan and Zimmermann, 2000). Path Selection Functions (PathSF; Cushman and Lewis, 2010) employ a 'used' versus 'available' design, comparing the used resources along the path versus the available ones around it (Zeller

et al., 2012). The PathSF takes into account the entire movement path to assess the landscape variable selected or avoided by the species (Zeller et al., 2016), and therefore, has several advantages as analytical method, including avoiding pseudo-replication and autocorrelation of the locations (Cushman, 2010), and ability to test a wide range of scale dependent effects (Elliot et al., 2014; Zeller et al., 2016). Selection of resources by organisms is scale dependent (McGarigal et al., 2016). Selection of habitat and its elements may depend not only on site-specific characteristics, but also on the characteristics of the landscape surrounding a site providing the environmental context that influences animal behavioral choices (Holland et al., 2004; Cushman et al., 2016; Zeller et al., 2016). For our purposes, we considered the criteria described by McGarigal et al. (2016), in which 'scale' (also known as 'neighborhood') is "the area within which environmental variation influences habitat selection". In that context, we used a single-level (the 2nd hierarchical level – Johnson, 1980) multi-scale approach (sensu McGarigal et al., 2016).

The aim of this study was to construct a multi-scale habitat path selection model for jaguars across the entire Pantanal ecosystem and to assess the effectiveness of protected areas in conserving jaguar habitats in this region. Jaguars have a high movement capacity and are able to travel great distances per day (Morato et al., 2016; McBride and Thompson, 2018). Following this, we hypothesized that the species would respond to landscape variables primarily at broader scales. This broad-scale pattern of path selection has previously been shown in other highly mobile large carnivore species, such as bears (Cushman and Lewis, 2010), lions (Elliot et al., 2014), tigers (Krishnamurthy et al., 2016) and pumas (Zeller et al., 2016). Furthermore, we expected that jaguar movement would be positively correlated to forest cover, while avoiding areas of relative higher human pressure, as demonstrated locally in different ecosystems of the jaguar range (Colchero et al., 2011; Cullen et al., 2013; Rodríguez-Soto et al., 2013; Morato et al., 2018a).

2. Material and methods

2.1. Study area

The Pantanal ecosystem is the largest freshwater wetland in the world, extending through parts of Paraguay, Brazil and Bolivia, and covering an area of approximately 193,000 km² between 16°–20° S and 55°–58° W at an altitude of 80–170 m (Alho et al., 1988) (Fig. 1). The annual mean temperature is 25 °C, but winter temperatures occasionally drop to near 0 °C (Alho et al., 1988). During the rainy season (December–March), the area receives more than half of the 1200 mm annual mean precipitation; as a result, large lowland areas are flooded during that time. During the dry season (June to October), water is limited to the permanent water bodies (Crawshaw and Quigley, 1991).

The Pantanal is considered an ecotone, consisting of Brazilian savanna in the east, Paraguayan Gran Chaco in the west and Amazon forest in the north (Prance and Schaller, 1982). Most of the Pantanal ecosystem is periodically inundated characterized by savannas and forested islands spreading over the floodplain (Nunes da Cunha and Junk, 2009). The lowland floodplains are dominated by grasslands and open woodlands, interspersed with closed riparian forests growing along the rivers and streams. The Pantanal's plateaus never flood; therefore their vegetation is adapted to six months of severe drought and comprises mesic and xeric species of the Chaco flora and Brazilian savanna (Prance and Schaller, 1982). This high diversity of vegetation communities, associated with the continuous nutrient input provided by flood pulses, supports abundant animal populations and a high species richness (Alho, 2011). Among medium and large-sized mammals commonly found in the savannas are maned wolf (*Chrysocyon brachyurus*), giant anteater (*Myrmecophaga tridactyla*), marsh deer (*Blastocerus dichotomus*) and capybara (*Hydrochoerus hydrochaeris*), as well as species typically found in forested habitats, like white-lipped peccary (*Tayassu pecari*), collared peccary (*Peccari tajacu*), and tapir (*Tapirus terrestris*).

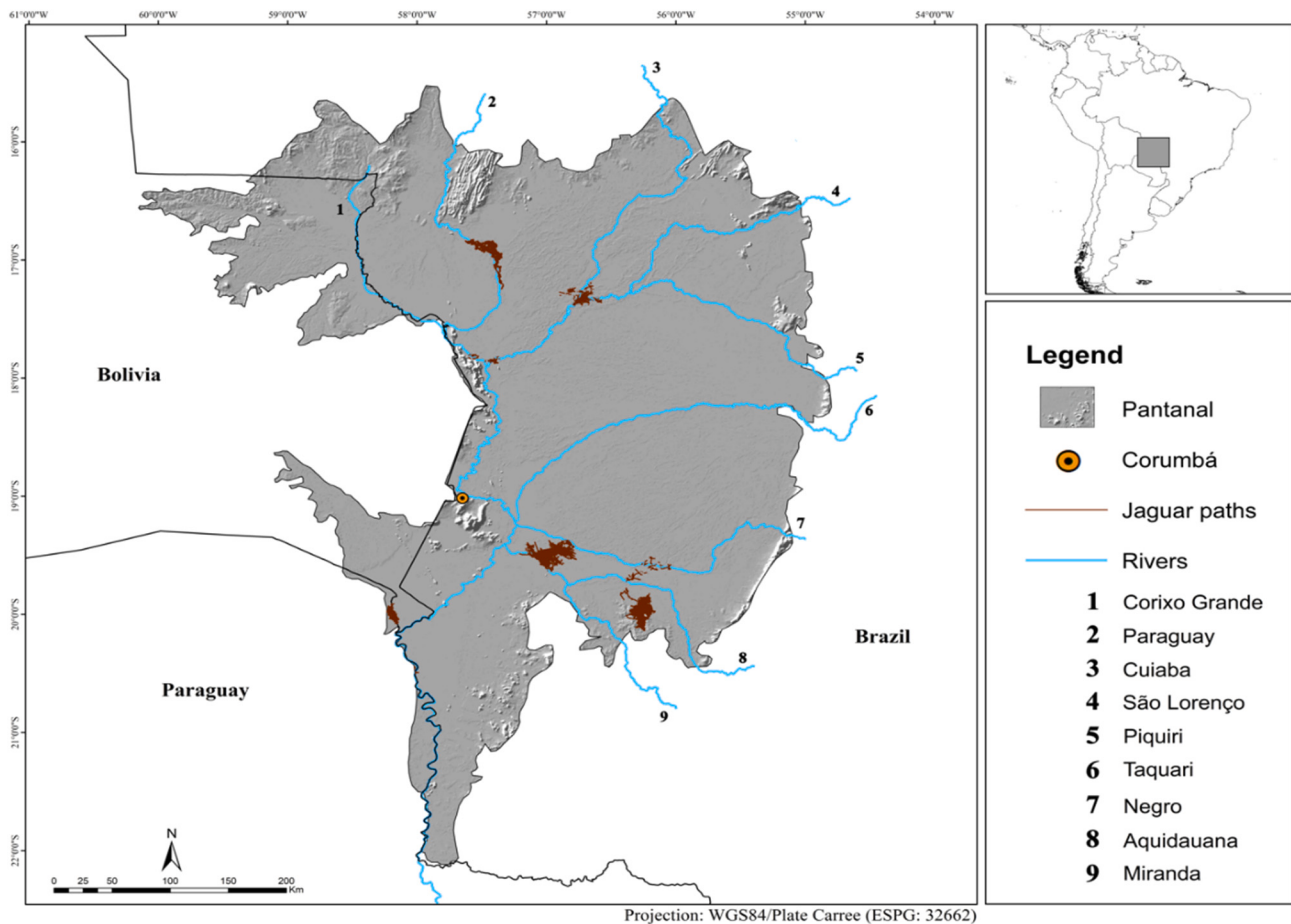


Fig. 1. Pantanal ecosystem with the main city Corumbá, the jaguar paths, and the major rivers (numbered from 1 to 9).

2.2. Jaguar movement paths

The jaguar movement dataset used in this study is the result of an extensive effort of more than 50 researchers (see Morato et al., 2018b). The dataset consisted of 56 GPS-collared jaguars (31 females and 25 males), representing 71,134 locations distributed over the portions of the Pantanal in Brazil and Paraguay. Jaguars were monitored from 2005 to 2016, and the frequency of location varied, with an average interval between subsequent locations of 1.62 h.

PathSF uses the information between subsequent locations by linking individual locations into paths; thus, it is important to maintain intervals as short as possible to avoid introducing uncertainty in the estimations of the used habitat features (Zeller et al., 2016). Therefore, to construct the paths of each animal, we connected subsequent locations recorded with a maximum time interval of 4 h, with 55% of these locations being within temporal distance lower or equal 1 h (Fig. A1). After temporal selection of the locations, one individual was excluded for lacking subsequent locations within the chosen threshold, which resulted in an average of 1293.35 ± 1947.87 locations (mean $\pm$ SD) per individual (Table A1) and a total of 4635 paths across all jaguars. Paths length ranged from 0 to 129,558.6 m, averaging $4240.4 \pm 10,495.4$ m (mean $\pm$ SD).

Movement patterns tend to change through the year in temporally variable habitats, such as Pantanal. This variation in long-term movement data might cause non-stationarity (Cushman et al., 2005; Wasserman et al., 2012). To reduce the effects of non-stationarity, we split the paths into short periods of time - monthly intervals - that are more likely to be stationary (Cushman et al., 2005). Finally, we split the jaguar paths, using 70% of them to calibrate the model and 30% to validate it. We transformed the jaguar point locations into movement paths, using

the packages *sp* and *maptools* (Bivand and Lewin-Koh, 2018; Bivand and Pebesma, 2013; Pebesma and Bivand, 2005) in R version 3.1.3 (R Core Team, 2016). All the tasks related to preparation of paths were performed in R software (R Core Team, 2016).

2.3. Landscape variables

To assess jaguar habitat selection we chose a set of environmental, topographical and anthropogenic variables that have been shown in previous studies to influence jaguar habitat use (Morato et al., 2018a; Paviolo et al., 2016; Petracca et al., 2018; Rabinowitz and Zeller, 2010; Rodríguez-Soto et al., 2011) (Table 1). The environmental variables included percentage tree cover (Hansen et al., 2013), and three independent land cover types: grassland, shrubland, and flooded habitats (ESA, 2017), which were converted to separate binary layers. Flooded habitats are composed of natural and semi-natural herbaceous-shrubby vegetation influenced by flooding (ESA, 2017). The Pantanal ecosystem is distinctive due to its terrain topography and the fluctuation of the

Table 1
Data used to derive variables tested in the jaguar movement model.

Data	Resolution (m)	Source
Percentage tree cover	30	Global Forest Change (Hansen et al., 2013)
Land cover	300	Climate Change Initiative Land Cover (ESA, 2017)
Elevation	30	USGS (Danielson and Gesch, 2011)
Human population density	1000	Human Footprint Index (Venter et al., 2016)

flood pulse, affecting both flora and fauna (Alho, 2011). The topographic variables were derived from the Global Multi-resolution Terrain Elevation dataset (Danielson and Gesch, 2011), and included topographical roughness and Compound Topographic Index (CTI). These were calculated using the ArcGIS toolbox for surface gradient and geomorphometric modeling (Evans et al., 2014). Roughness represents how rugged the landscape surface is, while CTI measures hydrological flow accumulation (Beven and Kirby, 1979). A high CTI is associated with large drainage depressions, whereas mountaintops and ridgelines are characterized by lower CTI values (Sørensen et al., 2006). Jaguars tend to avoid areas disturbed by human activity (Colchero et al., 2011; Paviolo et al., 2016). To investigate this effect, we used layers of human population density from the Global Human Footprint Index (Venter et al., 2016). We resampled all raster layers to 500 m resolution as a reasonable trade-off between representation of the environmental features, the vast extent of the study area and the temporal interval between subsequent jaguars' locations used to derive the movement paths. Furthermore, all layers were re-projected to Plate Carrée projection (EPSG: 32662).

2.4. Multi-scale path selection function

To test which resources are used or avoided by jaguars and derive the jaguar movement model, we applied a path selection function to the set of paths previously selected for model calibration. To determine the 'used' resources, we extracted the average value/proportion of each covariate across the length of each path (e.g., Cushman and Lewis, 2010; Cushman et al., 2010). The 'available' resources were determined by fitting a Gaussian kernel around each movement path (Zeller et al., 2017). To identify the optimal scale of selection we varied the kernel width across seven scales: 0.5 km, 1 km, 2 km, 4 km, 8 km, 16 km and 32 km. These scales were selected based on jaguar movement capability (more than 15 km/day – Morato et al., 2016; McBride and Thompson, 2018) and on other large cat studies (Elliot et al., 2014; Krishnamurthy et al., 2016; Zeller et al., 2016; Macdonald et al., 2018).

For multi-scale optimization we used a two-step framework (McGarigal et al., 2016). First, to identify the most relevant scale for each variable, we constructed univariate mixed-effect conditional logistic models at each scale using the *coxme* package (Therneau, 2018) in R. The conditional logistic regression compares each utilized path with its corresponding available area in the seven kernel buffers (Hegel et al., 2010). We chose mixed-effect conditional logistic regression to account for differences between individuals by incorporating jaguar ID as a random effect (e.g., Elliot et al., 2014). Then, we used model selection based on Akaike Information Criterion corrected for small sample size (AICc) to identify the best supported scale for each variable (Zuur et al., 2009).

After univariate scaling, we checked for multicollinearity across the variables at their best scales. We first calculated Pearson's correlation index (Dormann et al., 2013), excluding highly correlated variables ($|r| > 0.7$) and retaining the ones with lower AICc. Pearson's correlation only detects pairwise correlations, therefore we also used Variance Inflation Factor (VIF) retaining variables with $VIF < 3$ (Zuur et al., 2009). Specifically, we applied a forward selection approach, which removes one variable at a time, recalculating the VIF values until all values were < 3 .

In the second step, all remaining variables at their best scales, were then incorporated in a multiple mixed-effect conditional logistic regression model. We used the dredge function (*MuMIn* package – Barton, 2018) to generate a set of candidate models with all combinations of the terms from the full model. These models were ranked by their $\Delta AICc$ value and Akaike's model weight (w_i). We used only the best model - lowest AIC - to produce the final prediction layer representing jaguar path selection probability across the Pantanal. We evaluated the importance of each variable for the final model by calculating change in probability of jaguar path selection as variable values increase from the

10th to 90th percentile, holding other variables at their medians. Finally, to assess the effectiveness of Conservation Units we calculated currently protected percentage of the summed predicted habitat suitability across the Pantanal.

2.5. Model validation

Habitat suitability models are rarely validated, especially using independent data (Zeller et al., 2012). To maintain independence and avoid bias in the validation (Manel et al., 1999), we used the 30% of the movement paths held out of the initial model building to validate our final path selection model. To evaluate the prediction layer we used the Boyce index - a technique based on presence-only data, assessing how much the model differed from random expectations (Boyce et al., 2002). The method divides the prediction layer into bins (classes) based on intervals of predicted values, and measures the frequency of predicted and expected values for each class (Boyce et al., 2002). The Boyce index varies between -1 and 1 , with negative values indicating counter predictions, values close to zero a random model, and values near 1 a highly accurate prediction (Hirzel et al., 2006).

3. Results

We analyzed eight variables at seven spatial scales. Univariate scale optimization selected seven variables (CTI, elevation, roughness, shrubland, flooded habitats, tree cover, and human population density) at the broadest scale of 32 km, while only one variable (grassland) had the strongest response at a finer scale of 4 km (Table A2). We removed elevation from the analysis due to the high positive pairwise correlation with CTI, while none had a high VIF. After running the "dredge" function, CTI was excluded from the best model, resulting in six final variables (roughness, human population density, grassland, tree cover, flooded habitats and shrubland; Table 2).

All variables retained in the final model were significantly ($p < 0.001$) associated with the jaguar's movement. Percentage of tree cover, flooded habitats and shrublands were positively associated with jaguar's movement and habitat use, while grassland, roughness and human population were negatively related to movement path selection. The variables effect size, calculated as change in path selection probability with change of variables from 10th to 90th percentile of their values represented in the dataset, showed that human population density, roughness, and grassland had the strongest negative effect on jaguar path selection (Table 3, Fig. A2). The validation of the final prediction layer using the Boyce Index with an independent hold-out data shown that the model was highly predictive ($f = 0.82$).

The largest continuous areas of highly suitable habitat for jaguar movement were located in the northwestern portions of the Pantanal, in the swampy areas of the interfluvial Corixo Grande and Cuiaba rivers. The areas exposed to relatively higher anthropogenic pressure, such as the plateau region in the northeastern parts of the Pantanal, and

Table 2

AICc top models selected by the dredge function for jaguars in the Pantanal ecosystem.

Models	AICc	$\Delta AICc$	Weight (w_i)
Flooded.hab + Grassland + Hum.Pop + Roughness + Shrubland + Tree Cover	24,394.4	0	0.659
CTI + Flooded.hab + Grassland + Hum.Pop + Roughness + Shrubland + Tree Cover	24,396.1	1.65	0.288
Flooded.hab + Grassland + Hum.Pop + Roughness + Tree Cover	24,400.2	5.81	0.036
CTI + Flooded.hab + Grassland + Hum.Pop + Roughness + Tree Cover	24,402.0	7.61	0.015
CTI + Flooded.hab + Grassland + Hum.Pop + Roughness + Shrubland	24,407.6	13.15	0.001

Table 3

The final path selection model and the variable effect sizes, defined as change in probability of path selection (P [10%–90%]) with change of focal variable from the 10th to the 90th percentile of values in the dataset.

Variables	Scale (km)	β coefficient	SE	Pr(> z)	Change in P (90%–10%)
Human population	32	−1.983	0.114	<0.0e+00 ***	−0.283
Roughness	32	−0.206	0.015	<0.0e+00 ***	−0.241
Flooded habitats	32	0.946	0.092	<0.0e+00 ***	0.224
Grassland	4	−15.754	0.731	<0.0e+00 ***	−0.193
Tree cover (%)	32	0.006	0.001	<3.8e−05 ***	0.075
Shrubland	32	0.287	0.010	<4.1e−03 ***	0.034

*** signifies $p < 0.001$.

Corumbá in central-western parts of the study area, were predicted to be of low habitat quality for jaguars (Fig. 2).

Few Conservation Units (CU's) in the Pantanal coincided with predicted high-quality areas, the equivalent to only 9.3% of the total jaguar habitat suitability (defined as the sum predicted probability) (Fig. 2). In the southern part of the study area, most of the highly suitable jaguar's habitat is protected by Parque Estadual do Pantanal do Rio Negro and Reserva Particular do Patrimônio Natural Fazenda Rio Negro (Fig. 2 – a, b). In the north, the main CU's with highly suitable areas are Parque Estadual do Guirá, Parque Nacional do Pantanal Matogrossense, Estação Ecológica de Taiaí and Parque Estadual Encontro das Águas (Fig. 2 – c, d, e, f). Notably, only a small proportion of the large extent of suitable habitat in the northern part of the study area is protected, and nearly none is protected in the central parts of the Pantanal (Fig. 2).

4. Discussion

Our study is the first to produce multi-scale path selection movement models for jaguars anywhere in their range, based on an extensive data set of over 4000 paths from 55 individuals. Through well-distributed data, we focused on predicting synoptic, landscape-wide path suitability, instead of moment-to-moment movement of jaguars. We found that jaguar path selection is strongly associated with increased forest cover and that jaguars avoid areas of non-forest, particularly those under human modification. Based on independent validation, our models showed high predictive power using an independent validation dataset ($f = 0.82$). The predictions highlight the most important areas for jaguar conservation and future land management in the Pantanal, while stressing that only 9.3% of the aggregate jaguar habitat suitability in the Pantanal is currently protected.

We found that jaguar path selection was strongly depended on the scales at which environmental context was considered, which is consistent with past multi-scale movement modeling studies (e.g., Cushman et al., 2010; Elliot et al., 2014; Krishnamurthy et al., 2016; Zeller et al., 2017). As hypothesized, our analysis showed a strong and consistent pattern of jaguars selecting resources at broad scales of available habitat. Similar patterns were found by other authors studying large felids (Elliot et al., 2014; Krishnamurthy et al., 2016; Khosravi et al., 2019; Macdonald et al., 2019; Zeller et al., 2017). Jaguars are a highly mobile species, capable of moving more than 15 km per day (Morato et al., 2016; McBride and Thompson, 2018, 2019). In addition, their large home ranges (Morato et al., 2016; McBride and Thompson, 2018, 2019) and prey requirements (Rueda et al., 2013) likely drive selection of resources at broad spatial scales. Grassland was the only variable avoided at a relatively fine scale of available habitat (4 km). This might be related to the predominance of short vegetation classes, such as grasslands and pastures, covering Pantanal (Miranda et al.,

2018), and the elevated exposure and risk to human conflict in these areas that may drive fine scale avoidance of these areas by jaguars. Furthermore, as an opportunistic species, jaguars may avoid open areas as they do not provide camouflage, which plays an important role in a successful attack (Gese et al., 2018; Schaller and Crawshaw, 1980).

Our jaguar movement model indicated various degrees of avoidance of three variables (human population density, roughness, and grassland). The strongest negative effect in our model was associated with areas of high human density, and with relatively rough topography (corresponding in the Pantanal to upland and ridge locations). Jaguar avoidance of areas of high human population density was previously reported in other parts of the jaguar range (Colchero et al., 2011; McBride and Thompson, 2019; Paviolo et al., 2016). Human populated areas, such as the region around Corumbá in central-west Pantanal, tend to have higher levels of anthropogenic disturbance such as poaching and wood extraction. These activities increase the possibility that the thriving current jaguar population in this area is negatively impacted, both directly and through a depleting prey base (Galetti et al., 2016; Michalski et al., 2006). The negative relationship with roughness indicates that jaguars tend to choose areas located in the flat floodplains surrounding the main rivers, and avoiding uplands and ridges (which are rougher topographically).

This tendency for flat floodplains is also supported by the strong positive correlation with flooded habitats, and by previous studies, such as the other only large-scale jaguar study in the Pantanal (Ferraz et al., 2013), and other seasonally flooded regions in the Atlantic forest (Cullen et al., 2013) and in the Amazon (Palomares et al., 2017; Ramalho and Magnusson, 2008). Junk et al. (1989) hypothesized that, in seasonally flooded habitats, predator-prey interaction is concentrated in the aquatic/terrestrial transition zones (ATTZ); although this is not tested in this study, it is a likely association that could explicate our findings. The positive correlation between jaguar path selection with both vegetated variables (tree cover and shrubland), suggests that jaguars respond to forest density and select more dense vegetation for their movement paths, which is consistent with literature in Pantanal (Gese et al., 2018; Kanda et al., 2019), as well as other Brazilian biomes (e.g. Morato et al., 2018a).

Our predicted jaguar habitat use layer partially corroborates expert knowledge and expectations for jaguar habitat in the Pantanal ecosystem. However, the prediction surface also indicated additional potential areas of high suitability for the species, not predicted in other studies. Specifically, our model predicted high suitability in the interfluvial between the Corixo Grande - Paraguay rivers, which is an area where jaguars are frequently reported, despite high rates of habitat degradation by conversion to livestock pastures (Ferraz et al., 2013). Furthermore, the predicted layer indicated high suitability in central-eastern Pantanal, between the Piquiri - Taquari rivers, along the western-central border of the Taquari river, and in areas associated with the valley of the Negro river. From these, only the latter area was previously reported as important for jaguars by Ferraz et al. (2013). Contrary to findings of Ferraz et al. (2013), our model indicated that the southeastern parts of the Pantanal, around Miranda and Aquidauana rivers, are not highly suitable for jaguar movement. Although this region has been reported to support high jaguar population densities in the past (6.6–11.7 jaguars/100 km² - Soisalo and Cavalcanti, 2006), recent deforestation for charcoal production and high rates of pasture conversion (Cavalcanti et al., 2012) might have influenced our predictions.

Overall, we found that only 9.3% of the total habitat suitability in Pantanal is formally protected. Protected areas are particularly important for jaguars in many parts of their range as they maintain essential remnants of natural ecosystems among highly disturbed landscapes (McBride and Thompson, 2019; Paviolo et al., 2016). However, there are relatively few Conservation Units in the Pantanal, many of them poorly funded, which compromises their effectiveness to protect wildlife (ICMBio and WWF-Brasil, 2011). In recent years, researchers have proposed the creation of a mosaic of protected areas connecting the four

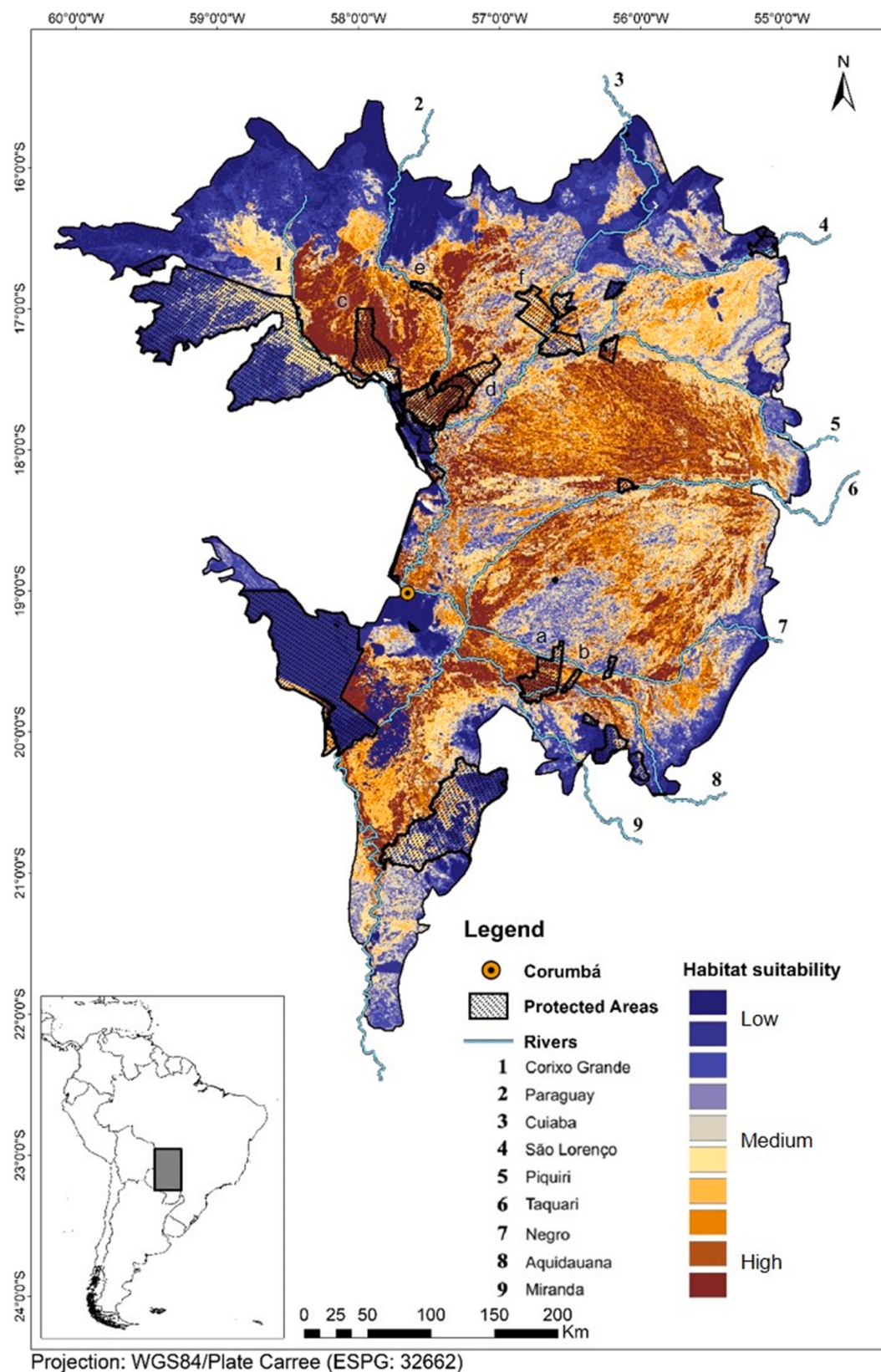


Fig. 2. Jaguars' habitat use/suitability in Pantanal. a) Parque Estadual do Pantanal do Rio Negro; b) Reserva Particular do Patrimônio Natural Fazenda Rio Negro; c) Parque Estadual do Guirá; d) Parque Nacional do Pantanal Matogrossense; e) Estação Ecológica de Taiamã; f) Parque Estadual Encontro das Águas.

northern CU's (Fig. 2 – c, d, e, f) (ICMBio, 2018). This proposed connection almost entirely overlaps with areas predicted as highly suitable for jaguars by our model, which suggests that implementation of the proposed protected area network would be highly valuable for jaguar conservation.

Our independent model validation showed a high reliability of our predictions, which suggests that the path selection approach has the capacity to retain the landscape information available from animal movements across a range of scales (Cushman, 2010; Zeller et al., 2017). It is important, though, to stress some limitations of our model. The Pantanal ecosystem is a highly dynamic area with marked flooded and unflooded seasons (Alho and Sabino, 2012). The goal of this work was to develop a general model of jaguar movement across the entire ecosystem. However, we believe that future work should focus on developing seasonal models to look at temporal change in jaguar behavior.

5. Conclusion

Our analyses demonstrated strong relationships between jaguar path selection and habitat features at multiple spatial scales, with jaguars strongly selecting dense forest areas and strongly avoiding areas with high human impact and high topographical complexity. Jaguar resource selection models have supported conservation decisions from north (Ramirez-Reyes et al., 2016) to south (Jorge et al., 2013) across their range. The Pantanal ecosystem, although, one of the last jaguar strongholds remained largely unstudied until recently. Our study comes to complement the findings of the Brazilian portion of Pantanal from the National Action Plan for Jaguar Conservation (Desbiez et al., 2013), and the implications area worrisome. Our model indicates low suitability in regions acknowledged to have thriving jaguar populations, such as the interfluvial between Miranda and Aquidauana rivers and the Corumbá surroundings. This suggests that current jaguar populations in these areas may be out of equilibrium with recent habitat loss and may decline in the future in the absence of strong measures to mitigate these negative effects (e.g., Kaszta et al., 2019). In recent decades, the Pantanal has experienced rapid farming expansion, which has increased under recent policy changes, which is coupled with increasing deforestation (Souza et al., 2020). Unfortunately, future projections indicate this pattern is likely to continue (Miranda et al., 2018). The current fires in Pantanal, for instance, are the largest in the entire historical series (22 years), having doubled in 2020 compared to the last year (INPE, 2020) – most of it in the areas we predicted as highly suitable for jaguars in the interfluvial between Corixo Grande - Paraguay rivers, northern Pantanal. In addition to these fires, the small portion (9.3%) of total habitat suitability formally protected is also of concern. We advocate not only for the implementation of new CU's, such as the northern mosaic, but also for

more investment in already established CU's. Last, but not least, the next step could be to extend this analysis into population connectivity modeling (e.g., Cushman et al., 2016, 2018). Identifying and preserving core areas for jaguar movement, as well as linkages between them, allowing for dispersal and gene flow to maintain a healthy jaguar population in Pantanal should be the focus of a comprehensive jaguar conservation strategy in the region.

CRedit authorship contribution statement

Guilherme C. Alvarenga: Conceptualization, Software, Validation, Formal analysis, Writing- Original draft. **Luca Chiaverini:** Conceptualization, Software, Validation, Formal analysis, Writing - Review & Editing, Supervision. **Samuel A. Cushman:** Methodology, Writing - Review & Editing, Supervision. **Egil Drøge:** Writing - Review & Editing, Supervision. **David W. Macdonald:** Resources, Writing - Review & Editing, Supervision, Funding acquisition. **Daniel Luis Zanella Kantek:** Investigation, Writing- Reviewing and Editing. **Ronaldo Gonçalves Morato:** Investigation, Writing - Review & Editing. **Jeffrey J. Thompson:** Investigation, Writing - Review & Editing. **Ricardo B. L. M. Oscar:** Software, Formal analysis, Writing - Review & Editing. **Leandro Abade:** Writing - Review & Editing. **Fernando Cesar Cascelli de Azevedo:** Investigation, Writing - Review & Editing. **Emiliano E. Ramalho:** Resources, Writing - Review & Editing, Supervision, Funding acquisition. **Zaneta Kaszta:** Conceptualization, Methodology, Software, Validation, Formal analysis, Writing - Review & Editing, Supervision, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Table A1

Dataset used to construct the habitat suitability model for jaguar (*Panthera onca*) in the Pantanal ecosystem.

Jaguar ID	Number locations	Sex	Sampled years
12	2677	F	2014/2015
13	5040	M	2014/2015
14	191	M	2012
15	1323	M	2013/2014
18	2311	M	2014/2015
19	730	F	2011
22	4707	M	2014/2015
23	572	M	2014
25	3219	F	2012/2015

(continued on next page)

Table A1 (continued)

Jaguar ID	Number locations	Sex	Sampled years
27	310	F	2010/2011/2013
28	124	F	2010
29	21	F	2011
30	206	F	2011/2012
31	43	F	2013/2014
32	119	F	2012/2013
33	72	F	2013/2014
41	4952	F	2014/2015
51	601	M	2010
52	615	F	2014
53	189	M	2010/2013
54	93	M	2010
55	48	M	2011
56	44	M	2011
57	6	M	2011
59	157	M	2011/2012/2013
60	425	M	2012/2013
61	58	M	2013
68	999	M	2011
69	3459	F	2013/2014
74	1137	F	2005/2006
75	1534	F	2005/2007
79	2300	F	2015
81	10,981	M	2013/2014/2015
84	4859	F	2013/2014
86	1389	F	2013/2014
87	413	F	2012
88	1220	F	2013/2014
91	6	M	2008/2012
92	10	F	2012
101	99	M	2015/2016
102	103	F	2016
103	0	F	2014
104	32	M	2015
105	1837	F	2008/2009
106	200	M	2009
107	239	M	2008
108	434	M	2008
109	131	F	2008
110	107	M	2010
111	1494	F	2008/2009
112	174	F	2008
113	616	F	2008/2009
114	1509	F	2008/2009
115	839	F	2008/2009
116	3340	M	2015/2016
117	2820	F	2015/2016

Table A2

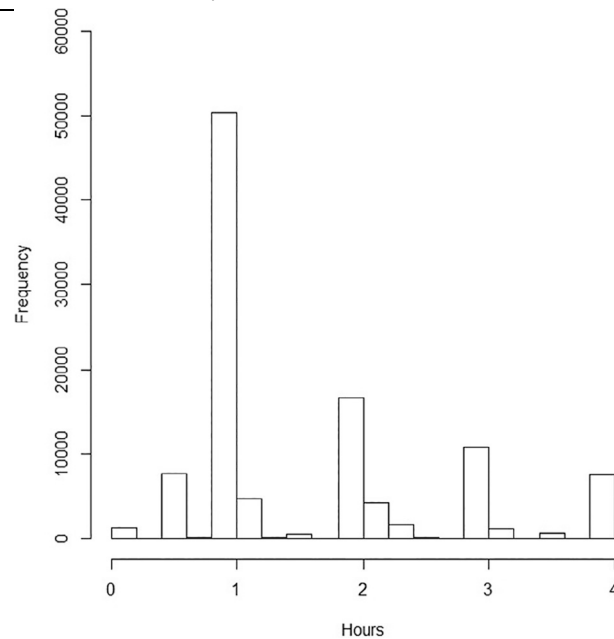
Univariate ranking of the landscape variables used to model the jaguar (*Panthera onca*) habitat suitability in the Pantanal.

Variables	Scale (km)	AICc	ΔAIC
Elevation	32	23,254.5	0
	16	25,412.3	2157.7
	8	27,279.6	4025.0
	4	27,630.7	4376.2
	2	27,658.3	4403.8
	1	27,664.9	4410.4
	0.5	27,665.5	4410.9
CTI	32	27,360.6	0
	8	27,552.9	192.3
	16	27,554.9	194.3
	4	27,622.7	262.1
	2	27,654.4	293.8
	1	27,661.8	301.2
	0.5	27,664.8	304.2
Roughness	32	25,380.2	0
	16	27,230.0	1849.8
	8	27,266.1	1885.9
	4	27,354.1	1973.9
	2	27,498.9	2118.7
	1	27,647.7	2267.5
	0.5	27,661.9	2281.7

(continued on next page)

Table A2 (continued)

Variables	Scale (km)	AICc	ΔAIC
Flooded habitat	32	23,418.5	0
	16	24,288.0	869.6
	8	25,922.7	2504.2
	4	26,830.5	3412
	2	27,313.7	3895.3
	1	27,638.8	4220.4
	0.5	27,654.8	4236.4
	4	26,045.2	0
Grassland	16	26,109.0	63.8
	2	26,523.6	478.4
	1	27,073.0	1027.8
	0.5	27,604.3	1559.2
	8	–	–
	32	–	–
	32	24,890.1	0
	16	25,533.1	643.0
Shrubland	8	26,482.7	1592.6
	4	26,681.4	1791.3
	2	27,087.1	2197.0
	1	27,660.7	2770.6
	0.5	27,661.7	2771.6
	32	27,114.7	0
	16	27,216.5	101.8
	8	27,346.8	232.2
Tree cover (%)	4	27,507.2	392.5
	2	27,634.5	519.9
	0.5	27,658.4	543.8
	1	27,660.2	545.6
	32	22,734.4	0
	16	23,152.6	418.2
	8	23,496.1	761.8
	2	27,655.4	4921.0
Human Pop.	1	27,663.0	4928.7
	0.5	27,665.1	4930.7
	4	–	–

Fig. A1. Histogram of temporal distances among consecutive locations from the monitored jaguars (*Panthera onca*) in the Pantanal.

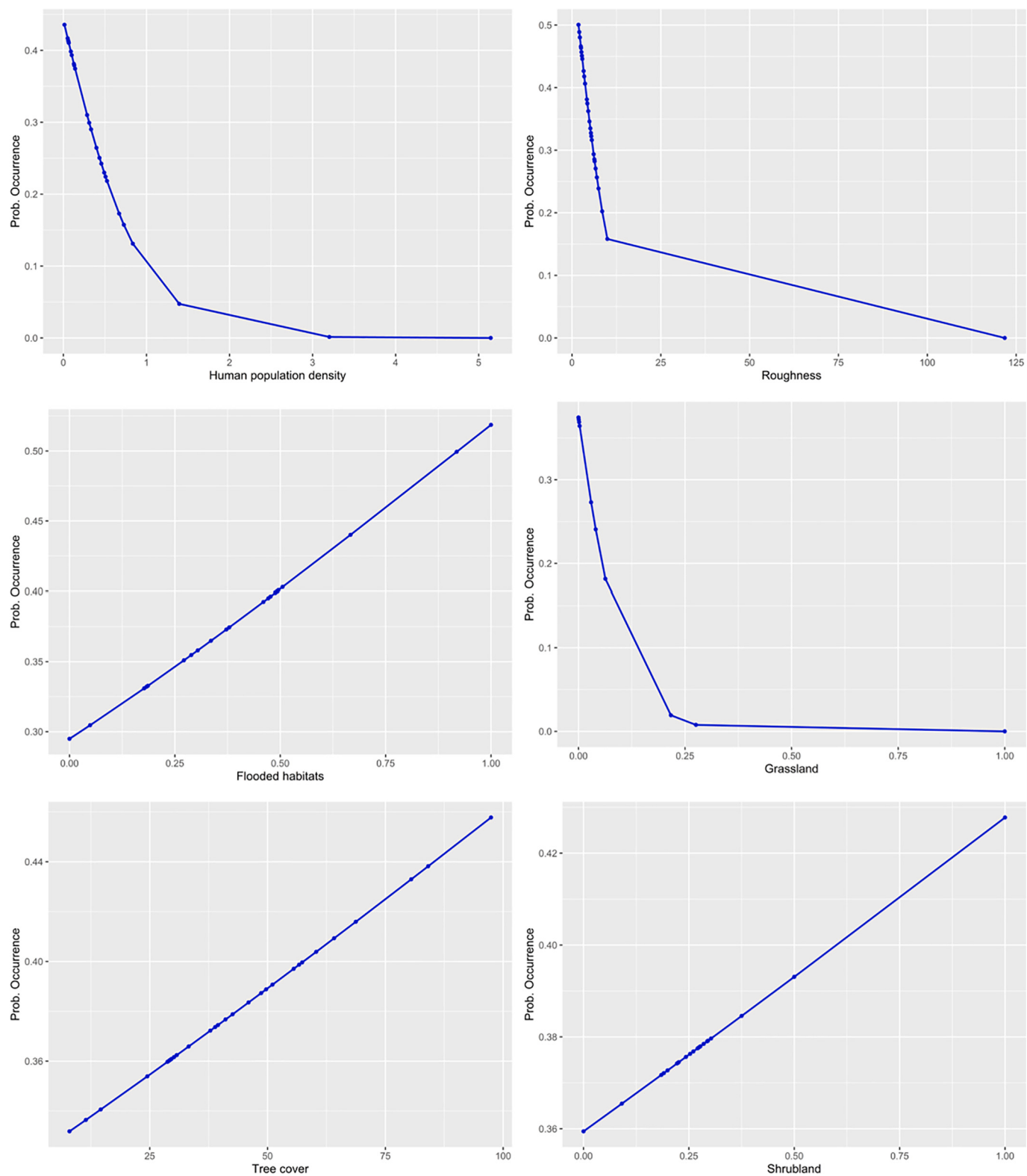


Fig. A2. Effect-size analysis for the final variables used to model the jaguar (*Panthera onca*) habitat/use suitability in the Pantanal.

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