Predator-Prey movement interactions: jaguars and peccaries in the spotlight

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Abstract

Understanding how the landscape influences the distribution and behavior of predators and prey gives us insights into the spatial dynamics of their interactions and the factors that shape their populations across space and time. This study analyzed interactions between jaguars (*Panthera onca*) and white-lipped peccaries (*Tayassu pecari*) at different forest and grassland distances and under varying predator or prey densities. To investigate the influence of these variables on interactions, we considered analytical contexts "The Dynamic Interaction Index, which represents attraction or avoidance behavior. We also calculated the proximity between predator and prey over time by assessing the distance among their locations. By analyzing GPS-movement data from three jaguars and five peccaries over 44 days, we observed that close distances (within 700 m) were uncommon, and distances within a range of 3 to 5 km were more prevalent. Most interactions occurred at greater distances from grasslands. In addition, our results show an increased frequency of jaguar-peccary interactions under low, white-lipped peccary densities. These insights enhance our understanding of the Pantanal's predator-prey dynamics, highlighting spatial-temporal movement patterns. Considering this, we can better inform conservation strategies by identifying zones that facilitate these interactions. Emphasizing habitat structures and prey density's roles contributes to preserving the ecosystem's delicate predator-prey balance. In conclusion, our findings show for the first time a more detailed analysis of the interaction of these two species that are currently threatened, and conserving them and their natural habitats is vital for maintaining the Pantanal's ecological balance.

Keywords: carnivores, ungulates, forest edge, dynamics, Pantanal, habitat structure, conservation, spatial-temporal dynamics, *Tayassu pecari*, *Panthera onca*

Introduction

Predator-prey interactions, a cornerstone of ecological systems, greatly influence ecosystem population dynamics (Schmitz, 2005; Creel & Christianson, 2008). The landscape structure is crucial in facilitating these interactions, providing opportunities for successful hunting for large carnivores and predator avoidance strategies for the prey (Schmitz et al., 2017; Smith et al., 2019; Suraci et al., 2022). The spatial distribution of prey availability to predators is related to landscape characteristics, such as predator density and habitat selection (Creel et al., 2005). By understanding how landscape structure influences the distribution and behavior of predators and prey, we can gain insights into the spatial dynamics of their interactions and the factors that shape their population dynamics. This information is essential when designing more efficient conservation programs (Creel & Christianson, 2008).

Large tropical carnivores facing habitat reduction or alteration exhibit diverse prey preferences depending on their surroundings (Fernández-Sepúlveda & Martín, 2022; Middleton et al., 2021). Consequently, they employ various hunting strategies, including stalking and capture, which are influenced by both prey type and landscape structures that facilitate them (Gaynor et al., 2019; Smith et al., 2019). Furthermore, these interactions are influenced by various factors that are challenging to measure, such as scent, vision, and traces, which both predator and prey employ as part of their survival strategies (Gaynor et al., 2019; Smith & Ruxton, 2020). Furthermore, these scent marks can be influenced by the density of animals and how they move in the environment (Potts et al., 2013) as they deposit these marks (Potts et al., 2014). Moreover, animals often exhibit movement patterns aimed at tracking their resources (Abrahms et al., 2021), moving toward increasing the probability of finding them (Kanda et al., 2019; Antunes et al., 2016).

Investigating behavioral interactions poses challenges due to the hierarchical nature of predation sequences, which are difficult to document due to species-specific behavioral variations (Suraci et al., 2022). In studies of predator-prey interactions in large vertebrates of tropical regions, researchers primarily rely on temporal activity patterns recorded by camera traps and, in some cases, their home ranges overlap (Caravaggi et al., 2018; Foster et al., 2013; Schmitz et al., 2017; Suraci et al., 2022). However, obtaining movement data exhibiting spatial and temporal overlap is a major challenge due to the costs and logistics of tracking large mammals.

The Pantanal, an eco-region known for its abundant biodiversity and rich vertebrate fauna, has been a focal point for concomitant studies on the movement of carnivores, such as the jaguar (e.g., Morato et al., 2018; Kanda et al., 2019; Thompson et al. 2021), and ungulates, such as the white-lipped peccary (e.g. Keuroghlian et al., 2004; Oshima, 2019), from which valuable information on their interactions can be extracted. The jaguar, a carnivore, has a diet that varies based on the opportunities in its environment (e.g., marine turtles in Costa Rica; Carillo et al., 2009; Middleton et al., 2021). In the southern Pantanal, the three most frequent prey items registered for jaguars were cattle, caiman, and white-lipped peccary (Cavalcanti & Gese, 2010; Perilli et al., 2016), Weighing between 30 and 40 kg, white-lipped peccary is considered one of the most common jaguar's bigger natural prey.

During the wet season, white-lipped peccaries form large herds of approximately 100-200 individuals, capitalizing on fruit abundance and communal care for their offspring (Fragoso, 1998). In contrast, during the dry season, when fruits are scarce, herds adjust their range utilization (Keuroghlian et al., 2004), relying on native grasses and aquatic vegetation found near lakes (Keuroghlian & Eaton, 2008; Keuroghlian et al., 2009; Desbiez et al., 2009). These open habitats increase visibility and may bring the herds closer to forest edges, offering escape opportunities from jaguars. The white-lipped peccary is categorized as "Vulnerable" and is considered an endangered species by the IUCN due to extensive deforestation, hunting, and severe habitat fragmentation (Keuroghlian et al., 2013).

Interactions between jaguars and white-lipped peccaries in the Pantanal involve predation by the jaguar as well as defensive mobbing and attacks on individual jaguars by peccary herds (Rampim et al., 2020). However, fine spatial-temporal resolution data on where and when those interactions occur are still scarce. The main objective of this study was to determine if the landscape structure influences the spatial distribution and timing of these interactions. To accomplish this, we assessed the direction and speed of movement through the Dynamic Interaction Index (DII) while also examining the distance between species over time using contact analysis, computing the distance separating the two entities. As the first study in this movement ecology context, our questions are exploratory: How are the interaction patterns between the jaguar and the white-lipped peccary presented? At what distance are the movements of these interactions recorded (predator-prey), and in what period of the day do they occur? Finally, we are interested in understanding the spatial context of the DII between predator and prey. This study fulfilled the objective of shedding light on the dynamics of jaguar-peccary interactions in the Pantanal and providing insights for conservation strategies to preserve this delicate balance.

Methods

Jaguar and White-lipped peccary movement dataset

Jaguar movement data come from three individuals monitored between August 17th and September 30th, 2015 (GPS database, Morato et al., 2018). White-lipped peccary movement data comes from five individuals' GPS tracked in the same period and at sites in the Jaguar dataset (Oshima 2019). Both databases come from Pantanal's areas; Fazenda Barranco Alto, an eco-lodge situated on the shores of the Rio Negro (A, Figure 1), and Caiman Ecological Refuge, an area destined for mixed exploration, which includes ecotourism and extensive livestock farming (B, Figure1). The data was collected during the dry season in the Pantanal.

Species interaction analysis

We analyzed all the locations in which both predator-prey moved in synchronization through shared home range sections to determine the nature of their movement in relation to each other. As a result, we had a dataset of 525 pairs (predator and prey) locations (Table 1). Subsequently, we employed the Dynamic Interaction Index (DII), proposed by Long and Nelson (2013), which classifies attraction between individuals when the direction of the step and speed is positive and above a threshold of 0.4. Conversely, avoidance is identified when the direction and speed are negative and below -0.4. Random movement, exhibited by both species, is considered when the direction and speed are not synchronized (values between 0.4 and -0.4).

Considering the DII's limitation regarding the absence of predator-prey distance evaluation, we supplemented our analysis by computing the distance separating the two entities. These analytical procedures were executed using the wildlifeDI package (Long et al., 2022) within the R program (R Core Team, 2022). No previous study has determined the distance at which a jaguar can spot a white-lipped peccary (and vice versa). Since this distance can vary depending on the surrounding environment, we have decided to use a maximum distance of 5000 meters. Previous studies have demonstrated that jaguars interact with their environment at this scale (e.g., Alvarenga et al., 2021; Alegre et al., 2023).

Model and environmental variables

We used generalized linear mixed models to determine the landscape structure in which interactions occur. We coded the interactions (e.g., the interaction of Sossego and Canela was coded as "sc") as random variables. We utilized the glmmTMB package in R (Brooks et al., 2017) to carry out the model. This package is well-suited for handling generalized mixed models with various extensions, including zero inflation. To assess the performance and validity of the models, we conducted diagnostic tests, including the KS, Dispersion, and Outlier tests, using the DHARMa package in R (Hartig, 2022). These tests provided essential insights into the accuracy and reliability of our models.

We categorized the dependent variable of our model based on the DII results. The observations of the interaction between both species, such as attraction and avoidance, were assigned a value of 1. This means that any value greater than 0.4 and less than -0.4 would fall into this classification. Random data was assigned a value of 0. The independent environmental variables were obtained from the Mapbioma platform for the year 2015. They were obtained at a resolution of 30 m (Projeto Mapbioma - 2015; https://brasil.mapbiomas.org/).

We used forest and grassland as environmental variables and analyzed them in LSMetrics software (Niebuhr et al., 2020) to calculate the distance. We used the boundaries between distinct land cover patches on the land cover map as reference distances (0 m). Negative values indicate distances within a specific land cover patch (for example, within forests), while positive values indicate distances outside. We used these two environmental variables because they are crucial in the habitat selection of both species (Alvarenga et al., 2021; Alegre et al., 2023; Oshima, 2019).

We also use the predator and prey density within our model's independent variables. To estimate the density for jaguars and white-lipped peccaries separately, we performed a kernel density estimation for each GPS-data species of this study with a 1000-m radius and pixel resolution of 30 meters, with QGIS 3.10.7-A Coruña (QGIS Development Team, 2020). We also included individuals monitored with GPS who were not selected for the interaction analysis for the kernel density estimates (Table A in Supplementary material indicates the selected individuals).

Results

We investigated movement predator-prey interactions between three jaguars (namely Esperança, Nusa, and Sossego) and five peccaries (Marcello, Roberta, Canela, Nanda, and Trina) with different home ranges (Figure 1). Over 44 days, we observed six interactions in which attractions and avoidances were recorded (Table 1).

We recorded 118 dynamic interactions index (attraction and avoidance behavior) (Figure 2 and Table 1). Nusa and Roberta had the highest DII proportion, at 35.1%, followed by Esperança and Marcello (24,1%). The lower DII proportion was of Sossego and Trina, with 14.6 % (Table 1). The distance between predator-prey exhibited considerable variability, with few instances occurring within distances less than 700 meters between them (Figure A and Appendix A in Supplementary Material). Distances within a range of 1 to 3 kilometers were more prevalent.

Interactions within this range of less than 700 meters mainly involved Sossego-Nanda, totaling five locations and one avoidance interaction (Table 2). Interactions within this range of less than 700 meters mainly involved Sossego-Nanda, totaling five locations and one avoidance interaction

(Table 2). Meanwhile, Nusa-Marcello had nine locations within this range, resulting in one avoidance and two attraction interactions. It's worth noting that the interactions occurring within a distance of 700 meters were mostly during the twilight and night periods (see Appendix A, Supplementary Material).

The dynamics of interaction index in the landscape

Our DII model analysis revealed two significant variables: distance from grassland areas and white-lipped peccary density (Table 3). The results indicate that the probability of interaction increased with greater distance from the grassland areas and lower density of peccaries (Figure 3). On the other hand, the effect of distance from the forest was not significant (Table 3). Although jaguar density was not statistically significant, a trend suggested that higher densities correlate with greater interaction (Figure 3). Our interaction dynamics model passed all diagnostic tests for accuracy and reliability (Figure B Supplementary Material).

When analyzing the distribution of distances between predators and prey, shorter distances occurred at the edge of the grassland areas (Figure 4—the first set of plots). However, no pattern was observed between the density of white-lipped peccary and the minimum distance at which they came in contact with predators (Figure 4—the second set of plots).

Discussion

Studies on the interaction between a Neotropical predator and one of its prey pose a significant challenge as they depend arbitrarily on the behavior of each participating individual (Suraci et al., 2022). From a large-scale GPS dataset, our study recorded 44 days of overlap between predator and prey in both time and space. Furthermore, as far as we are concerned, this is the first study to explore these species interaction dynamics in the Neotropics. Moreover, we explored how landscape structure could influence these interactions.

Our results are the starting point for understanding the complexity of interactions between large predators and their prey and help identify the fundamental landscape structure that influences these interactions. In six interactions involving three jaguars and five peccaries, we observed that grassland distances and prey density played pivotal roles in determining the interaction dynamics at two regions of the Pantanal. Conversely, the distances of interactions were predominantly recorded at shorter distances along the edges of grasslands, particularly during crepuscular and night periods. Also, a study exploring moonlight influence suggests that Jaguars typically remain close to forest surroundings and tend to venture deeper into grasslands only under medium to high levels of moonlight illumination (dos Santos et al., 2022).

The interaction between predators and prey in natural ecosystems critically depends on track perception (Creel & Christianson, 2008; Gaynor et al., 2019). The jaguar, as a predator, exhibits remarkable perceptual capacity, supported by evidence of interactions with the landscape on a large scale (Alegre et al., 2023; Alvarenga et al., 2021). In contrast, peccaries, as prey, form herds that allow them to alert each other and perceive large predators (Nogueira et al., 2017; Rampim et al., 2020), and the landscape composition highly influences their movements in Brazil (e.g., Jorge et al., 2021; Costa et al., 2023; Neto et al., 2024). In the context of our study, various interaction dynamics between both species have been identified, mainly at greater distances. Contacts at distances less than 700 meters were scarce and showed few events (four) with a notable DII of avoidance and attraction. Because DIIs primarily reflect attraction and avoidance movement between species (Long and Nelson 2013), this observation suggests that the interaction between predator and prey could not be limited to physical proximity but also involves tracking traces left by the prey at considerable distances. This finding underscores the complexity of ecological interactions and highlights the need to consider multiple factors to understand predator-prey dynamics fully.

As the recorded distances in the grasslands, our research also recorded that the close distances of approach between predator and prey occurred during crepuscular and nocturnal periods. The jaguar is a predator characterized by its acute nocturnal vision (Botts et al., 2020) and can approach aggressive prey such as peccaries in this vulnerable period. Our model recorded a higher probability of interactions in areas of low white-lipped peccary density, and this is due to their aggressive group behavior, in which jaguars have been harassed (Rampim et al., 2020).

Furthermore, our findings identified that the distance from grassland areas plays a significant role in the interaction dynamics between jaguars and peccaries. Our records indicate this interaction is more evident at greater distances from the grassland. However, the closest encounters between both species usually occur at the edges of these grasslands. Predators such as the jaguar prefer these transition zones between forest and grassland (dos Santos et al. 2022, Alegre et al., in preparation), which may be related to vital activities such as prey hunting, as corroborated in our study. This behavior pattern underscores the influence of landscape structure on the ecology of predator-prey interactions in these ecosystems.

Finally, it is crucial to highlight that our records reveal variability in the dynamics and encounters between predator and prey during each interaction, suggesting the influence of additional factors in this interaction. Among these factors, mention should be made of the physiological state of the species involved and their age and individual experience (Gaynor et al., 2019; Suraci et al., 2022). These aspects can modulate the proximity of encounters and the movement dynamics during such interactions. In our data, we observed that at distances less than 700 meters, some high DII simultaneously show avoidance and attraction movement patterns. These patterns at shorter distances could indicate behaviors related to hunting attempts by the jaguar, although such activity has not been directly observed.

It is essential to recognize our study's limitations, such as the low number of spatially and temporally overlapping individuals between the two data sets used. Additionally, the selected white-lipped peccaries belonged to the same herd, despite individuals exhibiting fusion-diffusion behavior with the group, which could have influenced the variability of the observed interactions. Furthermore, the possible presence of other unmonitored jaguars and peccaries in the evaluated landscapes was not investigated and incorporated. These limitations underscore the need for future research to address these aspects and provide a more comprehensive picture of these species' ecology in the Pantanal.

Our study has identified several promising areas for future research on the interaction between jaguars and peccaries. For example, it would be beneficial to conduct long-term studies examining how changes in resource distribution and anthropogenic pressure can influence the dynamics of these species over time. Furthermore, integrating advanced techniques such as biologging tags capable of recording physiological data and behaviors alongside GPS data would provide a more complete interpretation.

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Table 1: Interactions placed in both areas, the number of locations in time and within the predator and prey's home range space, and the number and percentage of interactions (Dynamic Interaction Index (DII) - attraction and avoidance) within those locations.

Area	Interactions (jaguar - peccary)	Date	# Locations per Individual pair	# DII
A	Sossego-Canela	22/Ago/2015 to 25/Sept/2015	89	21 (23.6%)
A	Sossego-Nanda	22/Ago/2015 to 25/Sept/2015	103	21 (20.4%)
A	Sossego-Trina	22/Ago/2015 to 25/Sept/2015	103	15 (14.6%)
B	Esperanza-Marcello	17/Ago/2015 to 30/Sept/2015	108	26 (24.1%)
B	Nusa-Marcello	17/Ago/2015 to 25/Sept/2015	65	15 (23.1%)
B	Nusa-Roberta	18/Ago/2015 to 25/Sept/2015	57	20 (35.1%)

Table 2: The distance between predator and prey in less than 700 meters and the resulting DII (all complete data in the dataset are available within the supplementary material S1). In red, avoidance, and in blue, attraction.

Area	Interactions	Distances (m)	DII
A	Sossego-Nanda	610.5	-0.005
A	Sossego-Nanda	514.7	-0.105
A	Sossego-Nanda	570.9	**-0.640**
A	Sossego-Nanda	594.2	-0.090
A	Sossego-Nanda	502.7	-0.002
B	Nusa-Marcello	190.7	0.054
B	Nusa-Marcello	329.9	0.324
B	Nusa-Marcello	554.2	-0.246
B	Nusa-Marcello	541.7	**-0.499**
B	Nusa-Marcello	546.7	**0.476**
B	Nusa-Marcello	544.6	-0.364
B	Nusa-Marcello	633.9	**0.839**
B	Nusa-Roberta	456.8	0.269
B	Nusa-Roberta	370.1	-0.143

Table 3: Summary of mixed-effects generalized linear models relating to the dynamic interaction between jaguar and white-lipped peccary movement versus environmental variables. Predator-prey interaction as random effects. Coefficient estimates and confidence intervals (CI). Variables whose CI did not intersect zero were considered significant.

DII ~ Forest_dist + Grassland_dist + Jaguar_density+Peccary_density + (1|int)

Variables	**Estimate**	**CI (2.5%)**	**CI (97.5%)**
Forest_distance	-0.020	-0.169	0.130
Grassland_distance	0.245	0.081	0.409
Jaguar_density	0.076	-0.081	0.233
Peccary_density	-0.244	-0.419	-0.068

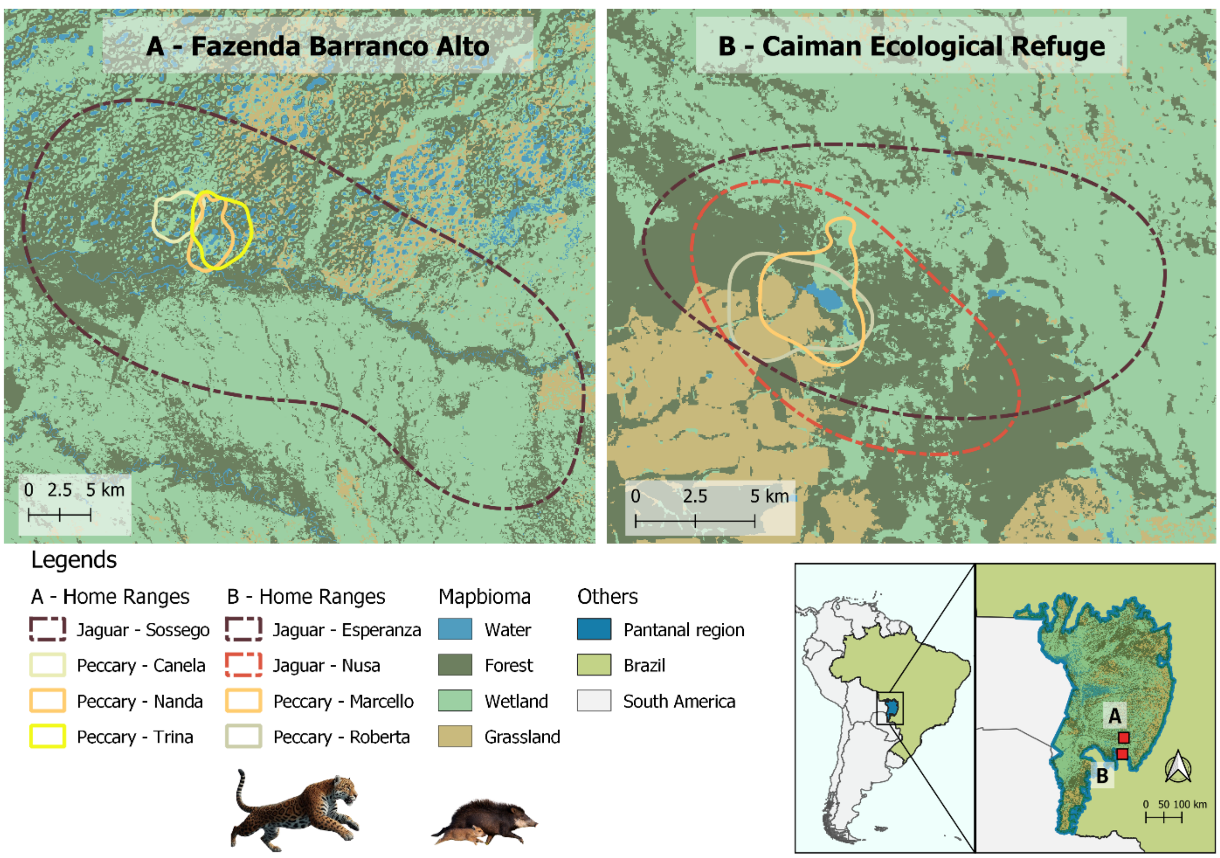

Figure 1: Study areas where the interactions took place. A, Fazenda Barranco Alto, cattle ranch with the interaction of one jaguar and three peccaries. B Caiman Ecological Refuge ecotourism farm with two jaguars and two peccaries. Both regions part of the Brazilian Pantanal

Figure 2: Predator-prey dynamic interaction index. A - Fazenda Barranco Alto, where the interactions of Sossego-Canela (sc), Sossego-Nanda (sn), and Sossego-Trina (st) were monitored. B - Caiman Ecological Refuge, where the interactions of Esperança-Marcello (em), Nusa-Marcelo (nm), and Nusa-Roberta(nr) were monitored.

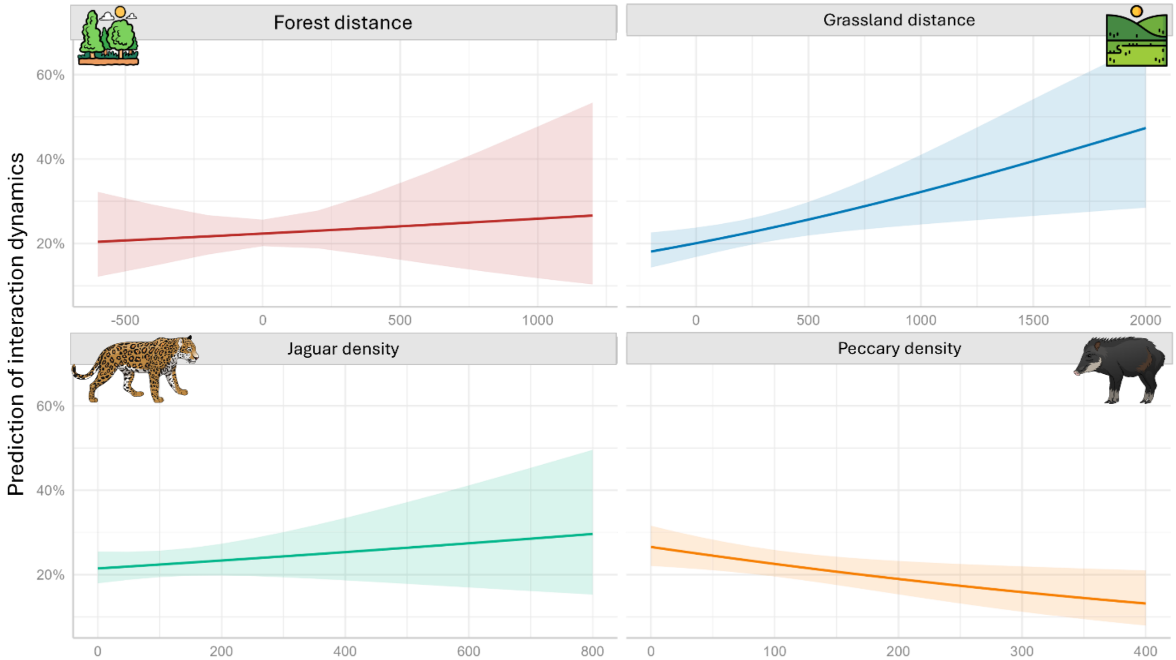

Figure 3: Prediction of the four variables explored using generalized mixed effect models to test the predator-prey movement interaction. Distance from the forest and jaguar density were non-significant variables within the model, while distance from grassland and white-lipped peccary density.

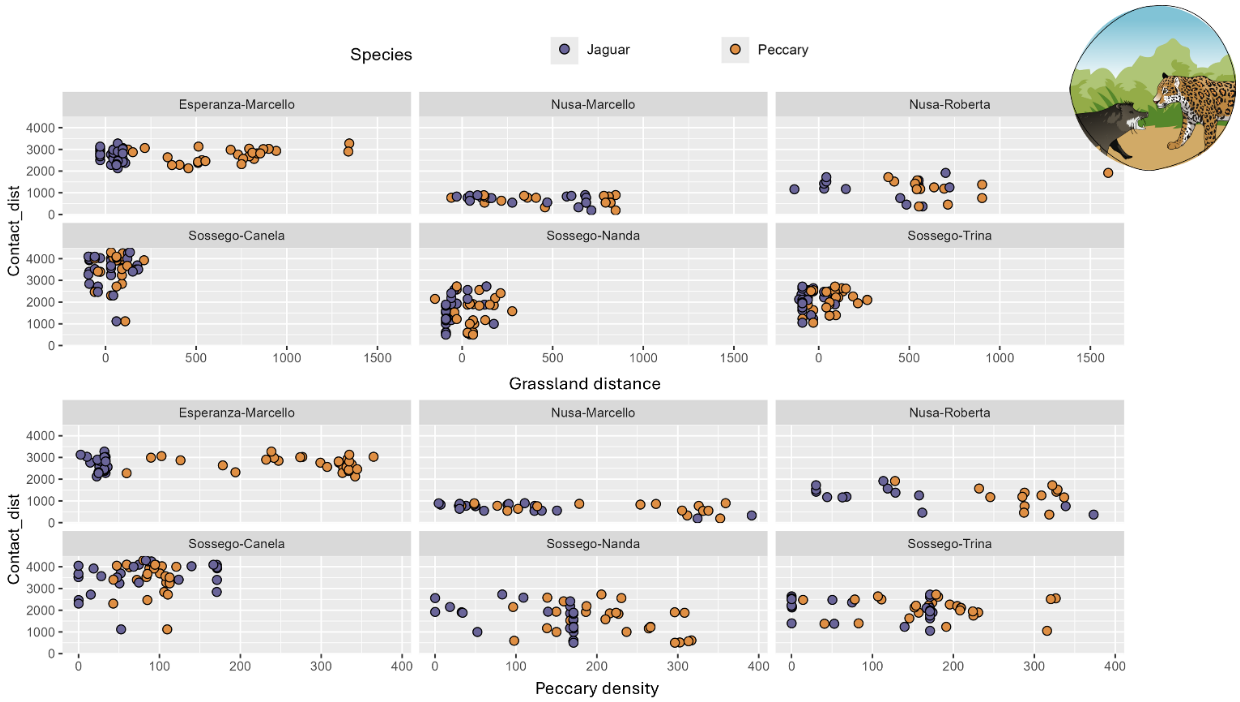

Figure 4: The shortest distance of the first calculated quarter of each interaction distance versus the significant variables of the DII model. The first set of plots shows variation through distance from the grassland, and the second set of plots shows variation through the density of white-lipped peccaries in the area.