











Tayra (*Eira barbara*) landscape use as a function of cover types, forest protection, and the presence of puma and free-ranging dogs

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Abstract

The tayra (*Eira barbara*) is a common and broadly distributed Neotropical carnivore, yet is not well-studied. While this species is apparently associated with forested habitats, it also appears tolerant of some anthropogenic disturbance. We deployed 57 unbaited camera traps ($n = 4923$ trap-days) in and around a protected area (Furnas do Bom Jesus State Park, São Paulo, Brazil) to survey for tayra and two potentially interactive species: puma (*Puma concolor*) and free-ranging dogs (*Canis familiaris*). We used encounter histories generated from photographs and occupancy models to quantify tayra landscape use in the human-dominated landscape composed of the protected area that was near a city and surrounded by agricultural lands dominated by small farms. We fit co-occurrence models to understand whether puma and free-ranging dogs affected landscape use by tayra. We detected tayra at 44% of sites and found that tayra landscape use increased with the proportion of forest cover within 500 m of the sampling site. Other factors predicting tayra landscape use included whether the sampling site was within the protected area, its distance to water, and slope. Dogs, which are common on the periphery of the protected area, seem to have a weak negative effect on tayra landscape use. Because of the concentration of forest within the park, this is an important protected area for the carnivore population within this human-modified landscape. Thus, environmental variables, such as forest cover, distance to water, as well as administrative protection status, are important for understanding local-scale tayra distribution.

Abstract in Portuguese is available with online material.

KEYWORDS

Brazilian Cerrado, *Canis familiaris*, carnivore interactions, habitat use, Neotropical carnivores, *Puma concolor*

1 | INTRODUCTION

Mid-sized mammalian Carnivora can have important influences on community structure and function. Their relative abundance, resilience to human-dominated or fragmented landscapes, and diverse dietary habits can result in relatively deep trophic penetrance (Prugh et al., 2009; Roemer et al., 2009). Yet our understanding of the ecology of many common mesocarnivores, such as the tayra (*Eira barbara*), remains underdeveloped, hindering management and conservation efforts. The tayra is a mid-sized (3–7 kg), scansorial, omnivorous mustelid and is distributed from the coasts of central Mexico to northern Argentina (Larivière & Jennings, 2009; Presley, 2000). Yet despite its prevalence across this large range, basic aspects of tayra ecology remain unknown.

There have been few formal studies of tayra resource selection and habitat use, and what knowledge does exist has been based on studies with very small sample sizes. Research in Venezuela, Belize, and Brazil described tayra resource selection from a just 1–2 radio-collared individuals. In the Venezuelan llanos, one radio-collared female showed a strong association with closed canopy forests (Sunkuist et al., 1989). In Belize ($n = 2$), a monitored female was found more often in old fields (open habitat), while a male was more often located in early second growth forest (Konecny, 1989). One female in Brazil used secondary forest and *Eucalyptus* plantations and incorporated less grassland than available in the surrounding study area (Michalski et al., 2006). There are also reports of tayra moving through the canopy, resting in trees (Camargo & Ferrari, 2007; Konecny, 1989) and even hunting arboreal species such as primates (Asensio & Gómez-Marín, 2002; Camargo & Ferrari, 2007; Galef et al., 1976; Hughes et al., 2017; Luna et al., 2010; Sáenz-Bolaños et al., 2019). Yet despite their apparent strong association to forest cover types, tayra are also found in human-modified landscapes (Dotta & Verdade, 2011; Timo et al., 2014), including agroforestry plantations (Soley & Alvarado-Díaz, 2011). When landscape complexity is reduced, as in coffee plantations without arboreal strata, or as human disturbance increases (e.g., roads, settlements, reduced protected status of landscapes), then arboreal and scansorial mammals such as tayra may be negatively affected (Cassano et al., 2014; Gallina et al., 1996; Naughton-Treves et al., 2003).

Thus, tayra resource selection might focus primarily on forest availability at a local scale. However, recent studies of Carnivora emphasize the potential importance of not only habitat preferences, but also intraguild interactions, to community structure (Oliveira & Pereira, 2014). Larger carnivores may sometimes, although not always, limit the ability of smaller carnivores to persist in seemingly high-quality habitat (Gompper et al., 2016; Lesmeister et al., 2015; Rich et al., 2018). For example, in a diverse carnivore community in North America, small mustelid (*Mustela* spp.) habitat occupancy patterns were associated with both environmental metrics and coyote (*Canis latrans*) abundance, while for fisher (*Pekania pennanti*), a mustelid similar in size and basic ecology to tayra, the occupancy and abundance patterns of larger carnivores were of little predictive value for understanding occupancy (Gompper et al., 2016). Similarly,

in a Neotropical felid community, prey abundance was considered more important than interspecific interactions in governing the local occurrence and spatial distribution of species (Santos et al., 2019).

Therefore, assessments of carnivore landscape use will be more complete when considering both environmental metrics and the potential influence of co-occurrence with larger members of the carnivore community. As a mesopredator, tayra may be affected by top predators in Neotropical forest, particularly, puma (*Puma concolor*) and free-ranging domestic dogs (*Canis familiaris*). The latter is an invasive exotic predator-competitor, which commonly occurs in and around protected areas in Brazil (Lessa et al., 2016; Paschoal et al., 2016; Silva et al., 2018) and across the globe (Gompper, 2014). Large felids including puma, are likely to have an impact on the structure of the Neotropical Carnivora guild and are a presumed tayra predator (Elbroch & Kusler, 2018; Oliveira & Pereira, 2014). The potential consequences of dog-tayra interactions are largely unknown, although increases in dog detections were associated with reduced detection rates of tayra and crab-eating raccoon (*Procyon cancrivorus*), and decreased occupancy rates of spotted-cats (*Leopardus* spp.) in an agro-forest region in Brazil (Cassano et al., 2014). Similarly, the abundance of free-ranging domestic dogs was negatively associated with ocelot abundance in protected areas in Minas Gerais, Brazil (Massara et al., 2015, 2018).

The outcome of predator interactions may vary on a case-by-case basis as a function of the natural history of the interacting taxa as well as the setting of interactions (e.g., the resource availability, landscape complexity, and diversity of the predator community). The structural complexity of some environments may reduce negative interactions between predators by providing refuges that allow mesopredators to avoid direct encounters with top predators (Ritchie & Johnson, 2009). For example, the ability of gray foxes (*Urocyon cinereoargenteus*) to climb trees may reduce the likelihood of antagonistic encounters with larger predators (Lesmeister et al., 2015; Rich et al., 2018), a strategy that may also be used by tayra for reducing encounters with puma and free-ranging dog in tropical forests.

Mesocarnivores make up the majority of species in the order Carnivora, but our understanding of their ecology is superficial (Gittleman & Gompper, 2005) and the tayra is an emblematic example of the scarcity of information about an important component of Neotropical communities. Our goal was to understand tayra landscape use within and around a forested reserve in close proximity to a city and within a landscape dominated by agricultural lands with small farms where free-ranging dogs are common. This focal landscape is similar to that of other protected areas in Brazilian biodiversity hotspots, and indeed, is likely typical of many Neotropical landscapes containing protected areas. We also quantified the effect of puma and free-ranging dog presence on tayra site use. We predicted that: (1) tayra would be strongly and positively associated with forest, water, and prey and would avoid human infrastructure (e.g., areas with high road or building density) and areas of high slope, and (2) tayra would have reduced use of areas that are also used by pumas and free-ranging dogs.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area included the Furnas do Bom Jesus State Park (20°11'14" to 20°16'34"S and 47°22'13" to 47°29'17" W; hereafter, Furnas; Figure 1), a 2069 ha protected area within in a cerrado landscape in the municipality of Pedregulho, São Paulo State, Brazil. The park and surrounding landscape are topographically rugged and dominated by the Pedregulho River basin running through the center of the park. The lands inside of the park are characterized primarily by escarpment slopes covered with Cerrado and Atlantic forest remnants, while outside of the park, the land is flat with little slope and has been primarily converted to coffee plantations and pasture lands (Branco et al., 1991). The cover type in the escarpment region and valley riparian area is mainly low secondary vegetation and primary semi-deciduous seasonal forests; the higher elevations have fragments of old fields, grasslands, and savanna *stricto sensu* (Sasaki & De Mello-Silva, 2008). The climate is defined as tropical of altitude, with average annual minimum, maximum, and average

temperatures of 13.7°C, 26.5°C, and 20.1°C, respectively, and annual average rainfall of 1545 mm (Cepagri, 2016). The carnivore community in the park is composed of puma, ocelot (*Leopardus pardalis*), margay (*L. wiedii*), jaguarundi (*Herpailurus yagouaroundi*), maned-wolf (*Chrysocyon brachyurus*), crab-eating fox (*Cerdocyon thous*), hoary fox (*Lycalopex vetulus*), striped hog-nosed skunk (*Conepatus semistriatus*), coati (*Nasua nasua*), and crab-eating raccoon and tayra. The domestic dog population is comprised of both owned and unowned rural and urban free-ranging animals.

2.2 | Data collection

We used unbaited camera traps (Bushnell® Trophy Cam 6.0 Mpxl and Scoutguard® SG 550) to survey for tayra, puma, and free-ranging dogs at 60 sampling sites between January and August 2017. We placed the camera traps at each intersection of a 1 km² grid extending inside ($n = 44$) and outside of Furnas ($n = 16$) (Figure 1) totaling 4815 ha of sampled area. Three of the camera traps failed, so our final sample of surveyed sites was 57. We affixed cameras to

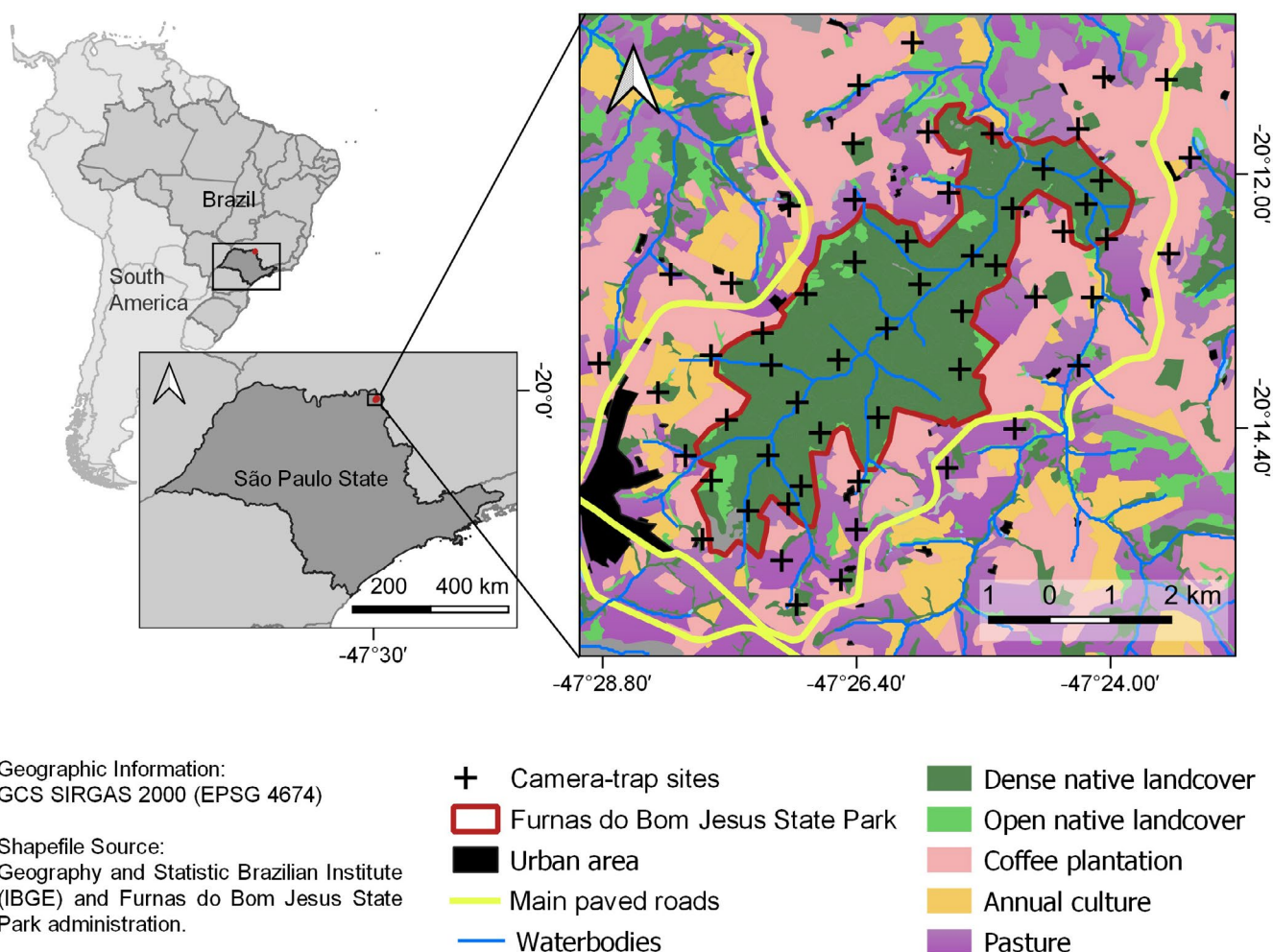


FIGURE 1 The distribution of camera traps ($n = 57$) in Furnas do Bom Jesus State Park and associated landscape features, Pedregulho, São Paulo State, Brazil

tree trunks approximately 30–40 cm above ground and programmed for continuous operation (24 hr/day), capturing three photographs at each triggering event with a 10 s interval between events. We deployed camera traps for 60 to 132 days at each sampling point and checked camera operation every 15–20 days. Camera trapping is a continuous form of monitoring, so we subdivided the survey period for each camera into discrete intervals representing sampling occasions (Sollmann, 2018). We generated encounter histories for each species at each camera with detections and non-detections dividing data into nine 12-day sampling occasions.

We used previous studies of tayra and other mid-sized Carnivora (Blomdahl et al., 2019; Davis et al., 2011; Konecny, 1989; Michalski et al., 2006) to identify environmental variables predicted to influence tayra resource selection including: slope, prey index (based on Azevedo et al., 2008; Campos et al., 2007; Presley, 2000; Taber et al., 1997; Table S1), distance to road, distance to urban areas, distance to water, density of buildings, and proportions of natural dense areas (forest), natural open areas (open), pasture, and coffee plantations (Table 1). We generated the land cover covariates using a land cover map provided by the park administration using cover classes defined according to the Brazilian Institute of Geography and Statistics. The land cover map was verified using Landsat 8 images (<https://earthexplorer.usgs.gov/>) (Figure 1). We summarized the proportion of each land cover metric within buffers of 100, 200 and 500 m. We also measured the linear distance from each camera trap to the closest water body using “Rede de Drenagem do Estado de São Paulo” (<https://www.ambiente.sp.gov.br/cpla/mapa-da-rede-de-drenagem-do-estado-de-sao-paulo/>). We calculated the slope at each camera with “Modelo Digital de Elevação do Estado de São Paulo” (<https://www.infraestruturameioambiente.sp.gov.br/cpla/modelo-digital-de-elevacao-mde-do-estado-de-sao-paulo/>). Land cover and slope were estimated using ArcMap® 10.2.1 (ESRI, 2016). Distances from cameras to nearest roads and to nearest urban land cover were calculated using satellite images in Google Earth Pro (<http://earth.google.com/>).

Weather patterns may have impacted the ability of cameras to detect animals, so we summarized the mean monthly temperature and mean total precipitation over each 12-day sampling occasion (Available at: <http://www.ciiagro.sp.gov.br>) to evaluate the influence of weather on detection probability (Kays et al., 2017; Lesmeister et al., 2015).

2.3 | Data analysis

We used a three-stage approach to model (1) single-species detection probabilities (p), (2) single-species landscape use for tayras, dogs, and pumas, and (3) two-species (i.e., co-occurrence) use patterns of tayra-puma and tayra-dog using the top models from single-species models. We used the RPresence package in R (R Development Core Team, 2020) and Program PRESENCE 2.12.26 (Hines, 2006) for all analysis and ranked models based on their Akaike's Information Criterion adjusted for small sample size (AIC_c)

and model weights (w) (MacKenzie et al., 2018). We ran all models with 100 random initial value vectors to ensure that models did not converge at local maxima. We considered models comprising 0.90 cumulative w (i.e., the 90% confidence set) as competitive. We based inference on top models that ranked higher than the constant (\cdot) model and did not add uninformative parameters (Arnold, 2010). We considered covariates with 90% coefficient confidence intervals (CI) not overlapping zero adequately supported (informative) and those with 95% CI not overlapping zero strongly supported. We calculated the c -hat value of top models in program Presence using 1000 bootstraps; all top models had a c -hat <1 . We standardized all continuous covariates (x -mean/ SD) prior to analysis. Correlated covariates were not used in the same model (Spearman rank correlation >0.60), Table S3).

In stage 1, when modeling single-species detection probabilities, we held the landscape use parameter constant ($\psi(\cdot)$) and allowed detection to be constant ($p(\cdot)$), or to vary with: minimum ordinal date ($p(\text{Day})$; number of days since January 1st), mean precipitation ($p(\text{Prec})$), and mean temperature ($p(\text{Temp})$) for each occasion. We used ordinal date rather than an occasion trend since camera traps were not deployed at the same time (deployed from January 18th to August 24th).

We used a two-step approach for modeling the landscape use (ψ) of each species, holding p as the top model(s) from Stage 1. Since animals can differ in their association with resources measured at different scales (Johnson, 1980), we first fit and ranked single covariate models of each multi-scale covariate. We considered the highest ranked scale as most useful for each species and then developed another model set to quantify predictors of landscape use for each species. We allowed ψ to vary as a function of either a single covariate or a combination of two (only additive effects) uncorrelated combinations (Spearman rank correlation <0.60), Table S3) of land cover and landscape metrics which ranked above the constant ψ model ($\psi(\cdot)$). We did not include protected area (park) in models with any landscape metric that was statistically different in and out of park (Table S2).

In stage 3, we used the two-species single-season occupancy modeling approach (MacKenzie et al., 2018) to explore our hypothesis that tayra landscape use was negatively influenced by dogs and pumas. We used the ψ BA parameterization in PRESENCE software, which estimates ψ A (occupancy of dominant species [dog or puma]), ψ BA (occupancy of subordinate species [tayra] when the dominant species is present), and ψ Ba (occupancy of subordinate species [tayra] when the dominant species is absent). We modeled ψ A, ψ BA, and ψ Ba incorporating the top ranked single-species models for each species to account for possible differences in landscape preferences (Gompper et al., 2016; Lesmeister et al., 2015). We built and ranked models where the occupancy of the subordinate species was influenced by the dominant species (ψ BA \neq ψ Ba) or was independent of the dominant species (ψ BA = ψ Ba). We allowed detection probabilities to differ between species (p A \neq p B) but assumed detection probability was not affected by the presence of other species (p Ba = p BA).

TABLE 1 Description of variables used to quantify tayra landscape use (ψ) and detection probability (p) in and around Furnas do Bom Jesus State Park, São Paulo State, Brazil

Variable	Description	Model
Temp	Average monthly temperature of the municipality where the protected area is located	p
Prec	Average monthly rainfall of the municipality where the protected area is located.	p
Day	Ordinal day of year at start of occasion	p
Slope	Index of slope for which zero corresponds to a flat ground and seven corresponds to high declivity.	ψ
Prey	Number total prey photographs for each species in sampling point multiplied by one hundred and divided by number total photographs in sampling area.	ψ
Road	Linear distance, in meters, to nearest paved road.	ψ
Urban	Linear distance, in meters, to 'urban' land cover.	ψ
Water	Linear distance, in meters, to nearest water body.	ψ
Forest100	Proportion of dense natural land cover within 100 m of camera.	ψ
Forest200	Proportion of dense natural land cover within 200 m of camera.	ψ
Forest500	Proportion of dense natural land cover within 500 m of camera.	ψ
Open100	Proportion of open natural land cover within 100 m of camera.	ψ
Open200	Proportion of open natural land cover within 200 m of camera.	ψ
Open500	Proportion of open natural land cover within 500 m of camera.	ψ
Pasture100	Proportion of pasture land cover within 100 m of camera.	ψ
Pasture200	Proportion of pasture land cover within 200 m of camera.	ψ
Pasture500	Proportion of pasture land cover within 500 m of camera.	ψ
Coffee100	Proportion of coffee land cover within 100m of camera.	ψ
Coffee200	Proportion of coffee land cover within 200 m of camera.	ψ
Coffee500	Proportion of coffee land cover within 500 m of camera.	ψ
Builds100	Proportion of builds within 100 m of camera.	ψ
Builds200	Proportion of builds within 200 m of camera.	ψ
Builds500	Proportion of builds within 500 m of camera.	ψ

3 | RESULTS

We detected 12 species of carnivores at our 57 camera traps, of which tayra was the most commonly photographed native carnivore. Due to equipment issues, 92 of our 627 12-day occasions were missing data. We detected tayra on 45 occasions at 25 camera traps (naive occupancy = 0.44), dogs on 55 occasions at 28 camera traps (naive occupancy = 0.49), and puma on 13 occasions at 9 camera traps (naive occupancy = 0.16). Within Furnas, we detected both tayra and dogs on two occasions at nine camera traps. Puma were only detected within the park and five camera traps detected both tayra and puma on one occasion. Two camera traps within Furnas detected all three focal species but during different occasions.

The uniform tayra detection probability model ranked higher than models including precipitation, day of year, or temperature (Table 2;

Figure 2). The logit scale intercept indicated an average detection probability of 0.17 for tayra (95% CI: 0.13, 0.22). Twelve models of tayra use represented the 90% confidence model set (Table 2). Within the top confidence set, six models added informative environmental parameters whose 95% or 90% confidence intervals did not include zero (ψ [Park + water], ψ [Forest500], ψ [Park], ψ [Pasture200 + slope], ψ [Pasture200 + road], and ψ [Pasture200 + water]; Table S4). Metrics in each of these models were related to variables in other top models; Forest500 was inversely correlated with Pasture200. Forest500, Pasture200, slope, and distance to road were significantly different at sites inside and outside of the park (Table S2). Tayra landscape use was higher in Furnas compared with outside of the park and use increased near water sources ($\beta = 3.41$, 95% CI: -1.98 , 0.09 ; Figure 3a). At the average distance from water (319 m), the probability of landscape use within the park was 0.70 (95% CI: 0.02, 1.0) compared with 0.07 (95% CI: 0.01, 0.40) outside of the park. The likelihood of tayra

Model	npar ^a	$\Delta AICc^b$	neg2ll ^c	w ^d	cum w ^d
Tayra					
$p(.) \psi(\text{Forest500} + \text{water})$	4	0.000	253.902	0.217	0.217
$p(.) \psi(\text{Water} + \text{park})^*$	4	0.526	254.428	0.167	0.383
$p(.) \psi(\text{Forest500})^*$	3	1.119	257.337	0.124	0.507
$p(.) \psi(\text{Forest500} + \text{road})$	4	2.017	255.919	0.079	0.586
$p(.) \psi(\text{Forest500} + \text{slope})$	4	2.201	256.103	0.072	0.658
$p(.) \psi(\text{Forest500} + \text{prey})$	4	2.360	256.262	0.067	0.724
$p(.) \psi(\text{Park})^*$	3	3.046	259.264	0.047	0.772
$p(.) \psi(\text{Slope} + \text{road})$	4	3.327	257.229	0.041	0.813
$p(.) \psi(\text{Prey} + \text{park})$	4	3.890	257.792	0.031	0.844
$p(.) \psi(\text{Pasture200} + \text{slope})^*$	4	4.316	258.218	0.025	0.869
$p(.) \psi(\text{Pasture200} + \text{road})^*$	4	5.115	259.017	0.017	0.885
$p(.) \psi(\text{Pasture200} + \text{water})^*$	4	5.372	259.273	0.015	0.900
$p(.) \psi(.)$	2	12.215	270.663	0.001	0.999
$p(\text{Prec}) \psi(.)$	3	14.074	270.293	0.000	1.000
$p(\text{Temp}) \psi(.)$	3	14.421	270.639	0.000	1.000
$p(\text{Day}) \psi(.)$	3	14.226	270.644	0.000	1.000
Puma					
$p(\text{Day}) \psi(\text{forest500})$	4	0.000	90.879	0.231	0.231
$p(\text{Day}) \psi(.)$	3	0.873	94.068	0.149	0.381
$p(\text{Day}) \psi(\text{open100})$	4	1.081	91.960	0.135	0.515
$p(\text{Day}) \psi(\text{slope})$	4	1.352	92.231	0.118	0.633
$p(\text{Day}) \psi(\text{coffee100})$	4	2.001	92.880	0.085	0.718
$p(\text{Day}) \psi(\text{pasture500})$	4	2.609	93.488	0.063	0.780
$p(\text{Day}) \psi(\text{urban})$	4	2.766	93.645	0.058	0.838
$p(\text{Day}) \psi(\text{park})$	4	2.913	93.792	0.054	0.892
$p(\text{Temp}) \psi(.)$	3	6.727	99.923	0.008	1.000
$p(.) \psi(.)$	2	14.409	109.835	0.000	1.000
$p(\text{Prec}) \psi(.)$	3	16.538	109.733	0.000	1.000
Domestic dog					
$p(.) \psi(\text{Water} + \text{prey})^*$	4	0	294.454	0.716	0.716
$p(.) \psi(\text{Water} + \text{urban})^*$	4	4.408	298.862	0.079	0.796
$p(.) \psi(\text{Water} + \text{forest200})$	4	4.443	298.897	0.078	0.873
$p(.) \psi(.)$	2	13.395	312.397	0.001	0.996
$p(\text{Temp}) \psi(.)$	3	13.885	310.655	0.001	0.997
$p(\text{Day}) \psi(.)$	3	14.445	311.215	0.001	0.997
$p(\text{Prec}) \psi(.)$	3	15.561	312.332	0.000	1.000

^aNumber of model parameters.

^bDifference in Akaike's Information Criterion for small samples compared to top ranked model. Top tayra model AICc = 262.679. The top puma model AICc = 99.648. The top dog model AICc = 303.22

^cModel deviance, estimated as $-2\text{Log}(\text{Likelihood})$.

^dAkaike's model weight (w) and cumulative model weight (cum w).

TABLE 2 Top ranked single-species landscape use models with null models included for comparison for tayra, puma, and domestic dogs surveyed in and around Furnas do Bom Jesus State Park, São Paulo State, Brazil. Models with asterisks added ψ coefficients with 90% confidence limits not including zero

use increased with the proportion of dense natural cover at 500 m ($\beta = 5.90$, 95% CI: -1.12 , 12.91 ; Figure 3b) and declined with the proportion of pasture cover at 200m ($\beta = -0.97$, 95% CI: -1.82 , -0.07 ; Figure 3c). The probability of use was also greater farther from roads

($\beta = 0.84$, 95% CI: 0.01 , 1.67) and increased in areas with higher slope values ($\beta = 0.86$, 95% CI: 0.09 , 1.63 ; Figure 3c).

For puma, detection probabilities declined throughout the study period ($\beta = -2.13$, 95% CI: -3.53 , -0.73 ; Table 2; Figure 2). Eight

landscape use models, including the constant ($\Psi(.)$) model, comprised the puma 90% confidence set. $\Psi(\text{Forest500})$ was ranked above the constant model, suggesting that there was some support that puma landscape use was associated with dense natural cover ($\beta = 1.75$, 95% CI: -1.35 , 4.84). However, none of the puma use models

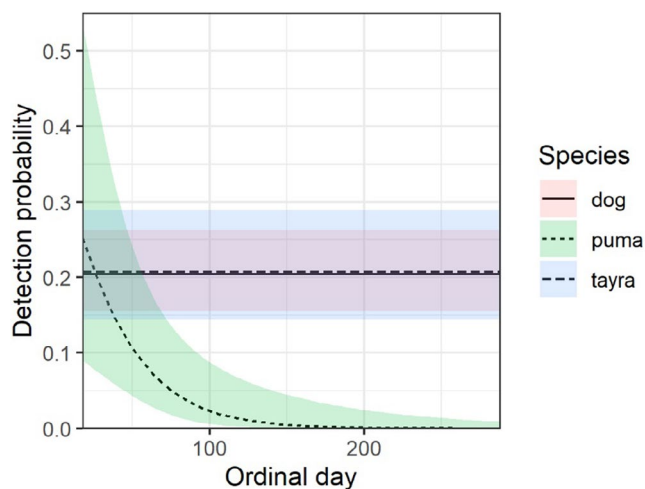


FIGURE 2 Detection probability by ordinal day of year for tayra, puma, and domestic dog in 2017 at camera traps at Furnas do Bom Jesus State Park. Predicted values (with 95% confidence intervals) were generated from top ranked single-species models

included an environmental parameter whose 90% coefficient confidence interval did not include zero (Table S5). Thus, we did not include any puma-specific landscape covariates in co-occurrence models.

The uniform detection probability model ranked higher than models including precipitation, day of year, or temperature for free-ranging dogs (Table 2; Figure 2). There were three models in the landscape use 90% confidence set, two of which (the model $\Psi(\text{Prey} + \text{water})$ and $\Psi(\text{urban} + \text{water})$) added informative landscape variables whose 90% and 95% confidence intervals did not include zero (Table S6). Dog landscape use was more likely closer to water sources ($\beta = -1.72$, 95% CI: -3.32 , -0.13) and was positively associated with the prey index (i.e., potential dog prey availability; $\beta = 3.67$, 95% CI: 0.74 , 6.62 ; Table 2; Table S6). Dog presence was higher closer to urban areas ($\beta = -0.96$, 95% CI: -1.72 , -0.20). We considered distance to water and the prey index in dog-tayra co-occurrence models.

We did not find evidence that puma affected the landscape use of tayra based on co-occurrence model rankings (Table 3). The model allowing tayra landscape use to vary with dog landscape use ($\psi_{BA} \neq \psi_{Ba}$) ranked above the model for which tayra use was independent of dogs ($\psi_{BA} = \psi_{Ba}$; Table 3). Holding distance to water at the mean, the probability of tayra landscape use was higher at sites outside of the park without free-ranging dogs ($\Psi = 0.20$ 95% CI = 0.022 , 0.749) than at sites outside of the park with free-ranging dogs ($\Psi = 0.02$

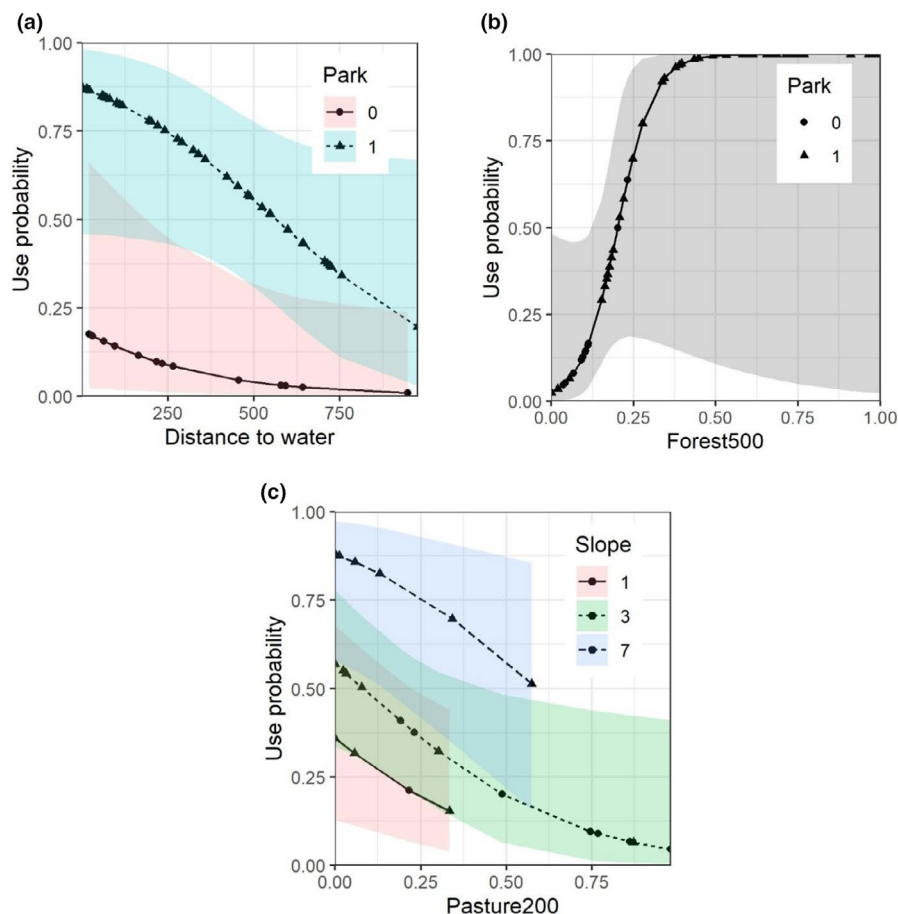


FIGURE 3 Predicted values (with 95% confidence intervals) illustrating covariate relationships from top three tayra single-species landscape use (Ψ) models that added informative parameters (a = distance from water in meters; b = percentage of forest in 500 m buffer; c = percentage of pasture in 200 m buffer) for tayra (*Eira barbara*) inside (triangles) and outside (circles) of Furnas do Bom Jesus State Park in 2017. Predictions of use for pasture within 200m for high (slope = 7), moderate (slope = 3), and low (slope = 1) slope values

Model	npar ^a	$\Delta AICc^b$	neg2ll ^c	AICc w ^d
Puma (A) and Tayra (B)				
$pA(day) \neq pB(.), \psi A(.) \neq \psi BA(park + water) = \psi Ba(park + water)$	7	0.000	364.786	0.000
$pA(day) \neq pB(.), \psi A(.) \neq \psi BA(park + water) \neq \psi Ba(park + water)$	8	2.604	367.390	0.049
$pA(.) \neq pB(.), \psi A(.) \neq \psi BA(.) = \psi Ba(.),$	4	24.484	389.269	0.458
$pA(.) \neq pB(.), \psi A(.) \neq \psi BA(.) \neq \psi Ba(.)$	5	26.321	391.106	0.493
Domestic dog (A) and Tayra (B)				
$pA(.) \neq pB(.), \psi A(pre + water) \neq \psi BA(park + water) \neq \psi Ba(park + water),$	9	0.000	544.9	0.572
$pA(.) \neq pB(.), \psi A(pre + water) \neq \psi BA(park + water) = \psi Ba(park + water)$	8	0.580	548.93	0.428
$pA(.) \neq pB(.), \psi A(.) \neq \psi BA(.) \neq \psi Ba(.)$	5	26.917	580.84	0.000
$pA(.) \neq pB(.), \psi A(.) \neq \psi BA(.) = \psi Ba(.),$	4	26.729	583.060	0.000

TABLE 3 Co-occurrence landscape use models used to evaluate the role of interspecific interactions of the landscape use of sympatric tayra and dogs and tayra and puma in and around Furnas do Bom Jesus State Park, São Paulo State, Brazil

Note: ψA = occupancy of dominant species; ψBA = occupancy of tayra when the dominant species is present; ψBa = occupancy of tayra when the dominant species is absent. Park = Covariate "within Park." water = Covariate "distance to water." We used "=" to designate that two or more parameters were set as equal (e.g., $\psi BA = \psi Ba$ means that the occupancy of tayra is independent of that of the dominant species). We used " \neq " to designate that two or more parameters were set as different (e.g., $\psi BA \neq \psi Ba$ models assumed that the occupancy of the tayra was not influenced by the dominant species).

^aNumber of model parameters.

^bDifference in Akaike's Information Criterion for small samples compared with top ranked model. The top puma-tayra model AICc = 364.326. The top dog-tayra model AICc = 562.90.

^cModel deviance, estimated as $-2\log(\text{Likelihood})$.

^dModel weight.

95% CI = 0.001, 0.346). However, the 90% and 95% confidence intervals for intercept estimates overlapped, suggesting weak support of a difference (Table S7).

4 | DISCUSSION

Our findings strongly support the characterization of tayra as a forest carnivore. The top predictors of tayra landscape use were the protected area itself and the proportion of the landscape comprised of forest cover within 500m of the survey site. The association of tayra with forest cover may relate to a foraging strategy of active hunting and foraging within or under tree canopies. Although tayra have been recorded hunting or foraging for fruits on the ground, for instance preying on caiman (*Caiman crocodilus*) eggs and rabbits (*Sylvilagus brasiliensis*) (Calouro, 2000; Campos & Mourão, 2015; Campos et al., 2016), their primary foraging seems to occur in the tree canopy on arboreal mammals (Asensio & Gómez-Marín, 2002; Bezerra et al., 2009; Galef et al., 1976; Luna et al., 2010; Sáenz-Bolaños et al., 2019; Sobroza et al., 2016). Complex forest structure may play a key role in predator-prey interactions (Linnell & Lesmeister, 2020) and provide important cover for rearing young for a range of species. Tayra also select hollow trees for den sites or dig burrows at the base of trees, and in captivity, tayra prefer elevated nest boxes (Poglayen-Neuwall, 1975; Presley, 2000). The availability

of suitable denning sites might be a limited resource outside of the park or outside of forest habitats (Birks et al., 2005).

Phylogenetic studies of the Mustelidae indicate that tayra are an early lineage in a clade that also gave rise to the fisher as well as the *Martes* species and the wolverine (*Gulo gulo*; Koepfli et al., 2008). Although the tayra is the only species in the clade to occur outside of North America and Eurasia, almost all taxa in the clade are predominantly forest-dwelling (Larivière & Jennings, 2009). Resource use of the similar-sized fisher has been reasonably well-studied. Fishers tend to select home ranges and resting sites in areas of complex forest structure that provide sufficient prey, escape cover, and suitable microstructures for reproduction and resting (Green et al., 2019; Matthews et al., 2019; Zielinski et al., 2013). The strong association between fisher and forest fragment size, forest density, or the presence of large or old trees may be in part a function of the need for physical structure for reproductive dens with small entries to prevent entry and predation by larger males (Blomdahl et al., 2019; Ellington et al., 2017; Green et al., 2019). Thus, while the reproductive ecology of tayra is poorly known, a reliance of forested habitats might be expected when viewed in a phylogenetic context.

We also found that tayra landscape use was higher near water sources. Such patterns are relatively common for diverse mammals. Areas close to water may be cooler than other areas and may be important to animals such as tayra, who are diurnal and have high

metabolic rates (Bianchi et al., 2020; McNab, 1995), similar to many other forest-dwelling species (Kalle et al., 2013). Yet, in contrast to the association with forested areas and water bodies, tayra in our study were negatively associated with open areas such as pasture and roads. Tayra can traverse large non-forest landscapes and are frequently recorded in roadkill surveys (Ciochetti et al., 2017), and are able to persist in agricultural mosaics retaining some forest cover (Dotta & Verdade, 2011; Timo et al., 2014). Nonetheless, despite water availability, our findings suggest such open areas are not used when forested landscapes are available. In more human-modified landscapes, tayra have been reported to subsidize their diet with human-derived foods such as papaya and banana, and by preying on small livestock such as chickens (Michalski & Peres, 2005; Soley & Alvarado-Díaz, 2011). Such foraging habits may allow tayra occurrence in areas that would not otherwise be suitable for the species (Michalski & Peres, 2005, 2007).

The importance of forested protected areas is reinforced by the strong association of tayra with Furnas do Bom Jesus State Park. Despite its relatively small size, the reserve is a vital Brazilian Cerrado remnant and was important not just for tayra but also for puma. Furnas has the highest carnivore species richness identified to date within the remaining Cerrado in São Paulo State (Bianchi, RC unpublished data). For many carnivore species, protected areas alone cannot guarantee carnivore survival in the long term (Di Minin et al., 2016), but they are nonetheless critical and several protected areas have now become indispensable for ensuring the persistence of many mammal species (Nagy-Reis et al., 2019; Pacifici et al., 2020). Maintaining protected areas such as Furnas in Brazil, and particularly in states such as São Paulo State that have very high rates of landscape conversion, is crucial to maintaining a diversity of species.

While our study was not focused foremost on puma and dog landscape use, it nonetheless provided important insights into the landscape ecology of these species. As a large felid, we expect that pumas would range widely, but we still found that they used areas with forest cover more than other landcover types. The mechanism for this association may have been that forested areas provide enhanced hunting opportunity for ambush predators as well as dense cover for concealment from humans. Our results support findings from a variety of other studies indicating strong associations of puma with natural habitats and protected areas, and lower probability of occurrence and relative abundance per unit area in smaller and more isolated forest patches, as well as the avoidance of urban areas (Boron et al., 2018; Di Bitetti et al., 2010).

In contrast to puma, free-ranging dogs generally have lower use in forest areas, occupying areas close to urban settings and water and prey sources. Globally, dogs are spatially associated with humans (Gompper, 2014), and as a subsidized predator, most dog populations are highly dependent on human-derived food (Vanak & Gompper, 2009). In rural settings around Furnas, free-ranging dogs fit the general pattern (Morin et al., 2018; Farris et al., 2014) of being kept by people for herding, hunting, guarding of livestock and homesteads, and general companionship. Nonetheless, the large number of people and dogs in the region supports the occurrence

of dogs throughout both unprotected and protected areas. Free-ranging dogs were detected at 49% of survey sites within the park and the likelihood of use decrease with distance to urban structures. Although dog populations are centralized on areas where there are more people, many individuals travel widely and venture into protected areas searching for resources water and prey (Doherty et al., 2017; Ritchie et al., 2014).

In Furnas, free-ranging dogs weakly influenced the landscape use of tayra, and this effect was higher outside of the park. Free-ranging dogs are known to negatively affect mesocarnivore species (Doherty et al., 2017; Vanak et al., 2014). In cocoa plantations in Bahia State Brazil, higher rates of domestic dog detection were associated with decreased site detectability of tayra (Cassano et al., 2014) and dogs have been documented to negatively influence an array of other carnivore taxa in Neotropics (Espartosa, 2009; Massara et al., 2018; Lacerda et al., 2009; Silva-Rodriguez et al., 2010; Zapata-Ríos & Branch, 2016). In the presence of dogs, mesocarnivores can alter vigilance behavior, reduce food consumption, and change space use or activity patterns (Gerber et al., 2012; Vanak & Gompper, 2009; Vanak & Gompper, 2010; Zapata-Ríos & Branch, 2016). Tayras do not appear to alter activity patterns in the presence of dogs (Bianchi et al., 2020), but our finding suggests they may reduce use of areas with dogs. Furthermore, the structural complexity of the native forests may mediate the potential negative effects of dogs on tayra, especially where arboreal strata provide refugia from dogs.

At the scale of our analysis, we found no evidence that tayra avoided areas used by puma. In multi-species carnivore communities, the relationships between pairs of species can be strongly context dependent (Brashares et al., 2010; Pasanen-Mortensen & Elmhagen, 2015). In high diversity communities, individual linkages among species tend to be weaker than in less complex communities, such as high latitude or island communities. Underlying this interaction variability may be factors such as resource availability, landscape complexity, and the composition and diversity of the broader predator communities (Estes et al., 2011; Ritchie & Johnson, 2009; Roemer et al., 2009). For instance, for some co-occurring competitive carnivore species that might be expected to interact negatively, measures of cover types were nonetheless more important in predicting the landscape use than was the presence of potential competitors (Gompper et al., 2016). Yet in other communities, such intraguild interactions were strong predictors of the presence of some taxa (Lesmeister et al., 2015; Rich et al., 2018). Thus, context-specific explanations may underpin the lack of an observed effect of puma on tayra in Furnas.

While we did not find strong support for effects of puma on tayra, in Amazonia, tayra were more likely to occur in patches where ocelot, jaguarundi and crab-eating fox were negatively affected by poaching (Michalski & Peres, 2005, 2007). Such observations suggest that tayra are not immune to the intraguild interactions observed in other systems without an exotic predator. Thus, our findings should not be interpreted to imply that spatial partitioning between tayra and puma does not occur. Nor should the findings be construed to

suggest that puma do not influence tayra. Rather, in the Cerrado setting where we worked, tayra occurrence is best predicted by forest protection and associated negatively by an exotic predator.

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DISCLOSURE STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.0cfxpnw2g> (Bianchi et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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