



# Spatial patterns of carnivore roadkill in a high-traffic-volume highway in the endangered Brazilian Atlantic Forest

Isabel Marques da Cruz Costa<sup>1,2</sup> · Mariana Silva Ferreira<sup>1,2</sup> · Claudio Lacet Belfort Mourão<sup>1,2</sup> · Cecília Bueno<sup>1,2</sup>

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## Abstract

In the past decade, we have been witnessing an unprecedented expansion of roads and other transportation infrastructure, especially in developing countries in South America and southeastern Asia. However, comprehensive information on roadkills is not available for many countries. Mammalian carnivores are especially vulnerable to roadkill events due to their relatively large body size, high dispersion capacity, and low density. In this way, we analysed the spatial patterns of roadkills of four medium-sized carnivorous mammals, including two threatened species (the crab-eating fox, *Cerdocyon thous*; the maned wolf, *Chrysocyon brachyurus*; the ocelot, *Leopardus pardalis* and the jaguarundi, *Herpailurus yagouaroundi*), at a high-traffic road immersed in the Atlantic Forest biome, a globally recognized biodiversity hotspot. We aimed at identifying whether roadkills were spatially clustered forming hotspots and analysed which landscape characteristics (percentage of urban areas, forest cover, herbaceous cover, crop fields, and proximity to water bodies) explained roadkill distribution over 12 years. Roadkills were concentrated in two areas of the BR-040 highway and were associated with areas with high percentage of herbaceous vegetation (except for the crab-eating fox). Overall, species avoided altered areas such as crop fields and urban areas, and only the ocelot had roadkills directly associated with continuous forest areas. The present study demonstrates the importance of long-term monitoring programs in evaluating the pattern of roadkills in a complex landscape and, for the first time, we were able to identify areas with a high probability of roadkill for two felid species, the ocelot and the jaguarundi.

**Keywords** Landscape · Mammal · Matrix · Road mortality · Tropical forest · Vehicle collision

## Introduction

In the past decades, we have been witnessing an unprecedented expansion of roads and other transportation infrastructure, especially in developing countries in Equatorial Africa, South America, and Southeast Asia (Laurance et al. 2017; Sloan et al. 2018; Laurance 2019). These new roads in tropical areas not only have strong negative effects on biodiversity (Laurance et al. 2009), but also open the so-called Pandora's box, providing easy access to previously out of reach areas, allowing other forms of forest exploitation, and

the spawn of unofficial roads (Laurance 2015; Pinto et al. 2020). As a consequence, roadkill have increased in recent decades (Groot Bruinderink and Hazebroek 1996; Huijser et al. 2008; Schwartz et al. 2020; Abra et al. 2021), driving biodiversity loss and acting as barriers to dispersal as well as access to food and mates (Parris and Schneider 2009; Ware et al. 2015), limiting gene flow (Ascensão et al. 2016), affecting individual survival, and the long-term persistence of populations (van der Ree et al. 2015). These impacts are not restricted to major paved roads and even small unpaved roads can have an impact on wildlife (Laurance 2015).

Comprehensive information on roadkills is not available for many countries worldwide (Schwartz et al. 2020). The lack roadkill data are even higher for the most biodiverse countries, which preclude researchers and managers to evaluate the effect of roads on wildlife, as well as develop mitigation measures (Rytwinski et al. 2016). Roadkill can be driven by several factors such as road characteristics (type of road, traffic noise, and volume) (Parris and Schneider 2009; Ware et al. 2015), drivers behaviour (Secco et al. 2014), and

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✉ Mariana Silva Ferreira  
msferreira84@gmail.com

<sup>1</sup> Mestrado Profissional em Ciências do Meio Ambiente, Universidade Veiga de Almeida, Rio de Janeiro, Brazil

<sup>2</sup> Núcleo de Estudos de Vertebrados Silvestres, Universidade Veiga de Almeida, Rio de Janeiro, Brazil

landscape characteristics (van der Ree et al. 2015). Factors related to landscape characteristics and composition determines the presence/absence of wildlife on roads and, therefore, the probability of wildlife–vehicle collisions. In the particular case of tropical forest mammals, the probability of wildlife–vehicle collisions seems to be associated with the proximity of watercourses (Bueno et al. 2015; Freitas et al. 2015), the amount of tree cover, or continuous preserved forests in the landscape (Ascensão et al. 2017). Thus, understanding how spatial patterns of wildlife–vehicle collisions relate to the surrounding landscape can help identify areas with a high probability of roadkill and provide valuable information to decide where to implement mitigation measures, such as the use of fences and crossing structures or both combined (Rytwinski et al. 2016).

Mammalian carnivores are especially vulnerable to vehicle collisions due to the relative large body size, high dispersal ability, wide home range, low density, and dependence on prey availability (Cardillo et al. 2004; Crooks 2002). In heterogeneous and fragmented landscapes, the amount of habitat available for wildlife is severely reduced and forest remnants may become too isolated, forcing individuals to explore new, low-quality areas and exposing them to the risks of roads (van der Ree et al. 2015). Besides, vehicles colliding with large- and medium-sized mammals are also a threat to human safety, causing serious accidents, including loss of human lives and substantial material damages (Abra et al. 2019; Bueno et al. 2013).

In this way, we analysed the spatial patterns of wildlife–vehicle collisions of four medium-sized carnivorous mammals (the crab-eating fox, *Cerdocyon thous*; the maned wolf, *Chrysocyon brachyurus*; the ocelot, *Leopardus pardalis*; and the jaguarundi, *Herpailurus yagouaroundi*) at a high-traffic-volume road in the state of Rio de Janeiro, Brazil. Specifically, we aimed at (1) identifying whether wildlife–vehicle collisions are spatially clustered forming roadkill hotspots and (2) analysing which landscape characteristics [percentage of urban areas, forest cover (native forest and reforestation), herbaceous cover (grassy-woody savannas, floodplains, and grasslands), crop fields, and proximity to water bodies] explain the roadkill distribution for these four carnivorous species.

We expect (1) the crab-eating fox to be the most road-killed species, based on previous studies with mammal road-kills in Brazil (Coelho et al. 2008; Cunha et al. 2010; Pereira et al. 2006; Zanzini et al. 2018; Ferregueti et al. 2020); (2) high roadkill numbers associated with both continuous forest areas and herbaceous cover, because of species opportunistic habitat use and landscape composition (Eisenberg and Redford 1999); and, (3) hotspots located near continuous forest areas, because of the species habits registered in the Atlantic forest (except for the maned wolf, an species typical of open habitats).

## Materials and methods

### Study species

We studied four medium-sized mammals of the Order Carnivora (Family Canidae and Felidae): *Cerdocyon thous*, *Chrysocyon brachyurus*, *Leopardus pardalis*, and *Herpailurus yagouaroundi*. These species were chosen because of their high dispersal ability, wide home range, and opportunistic habitat use, becoming more susceptible to wildlife–vehicle collisions (Cardillo et al. 2004; Crooks 2002). Besides, the maned wolf and the jaguarundi are listed as threatened according to the national list (ICMBio-Instituto Chico Mendes de Conservação da Biodiversidade 2018) and the maned wolf as Near Threatened in the IUCN Red List (Paula and DeMateo 2015).

(a) Crab-eating fox, *Cerdocyon thous* (Linnaeus, 1766)

*Cerdocyon thous* is a medium-sized (4–7 kg) insectivorous/omnivorous canid (Bueno and Motta-Junior 2004) with the most widespread geographical distribution among neotropical canids (Eisenberg and Redford 1999). It can be found from southern Panama to northern Argentina and Uruguay, outside the lowlands of the Amazon Basin (Eisenberg and Redford 1999). It has opportunistic habits, occupying forests, savannas, and disturbed areas such as cultivated fields, forest fragments, and areas around human settlements (Eisenberg and Redford 1999; Ferraz et al. 2010; Michalski et al. 2006). Its home range varies greatly among habitats and between sexes (Michalski et al. 2006). In a mosaic of vegetation in the Atlantic Forest biome in southeastern Brazil, the home range of male and female crab-eating fox were estimated 10.53 km<sup>2</sup> and 0.48 km<sup>2</sup>, respectively (Michalski et al. 2006), and the longest average distance covered was 793 m (Faria-Corrêa et al. 2009).

(b) Maned wolf, *Chrysocyon brachyurus* (Lliger, 1815)

*Chrysocyon brachyurus* is the largest South American canid (20–26 kg) (Bueno and Motta-Junior 2004), typical of open habitats such as grasslands and other open vegetation types of the Cerrado, a Brazilian savanna biome (Massara et al. 2012; Vynne et al. 2011), and also found in other countries of central South America (Eisenberg and Redford 1999). The maned wolf is omnivorous, eating fruits (especially wolf's fruit, *Solanum lycocarpum*), small mammals, and other small vertebrates (Bueno and Motta-Junior 2004). Predominantly solitary, territorial and monogamous, its home range area can reach 115 km<sup>2</sup> (Bueno and Motta-Junior 2004; Carvalho and Vasconcellos 1995; Jácomo et al. 2009). The maned wolf has been registered in several areas of the Atlantic Forest in southeastern and southern Brazil, outside its original distribution, especially in the states of São Paulo, Minas Gerais, Rio de Janeiro, and Paraná (Xavier et al. 2017).

Range expansion has been aided by human activities, due to deforestation, which opens new and altered areas for cultivation and pasture (Bereta et al. 2017).

(c) Ocelot, *Leopardus pardalis* (Linnaeus, 1759)

*Leopardus pardalis* is the largest of the small-spotted cats (11–16 kg) (Murray and Gardner 1997), found from the southern United States to Paraguay and northern Argentina (Eisenberg and Redford 1999). Ocelots occur in a variety of habitats, from tropical–humid forests, mangroves, and swampy savannas to grasslands, seasonally dry tropical forest, and scrub vegetation (Murray and Gardner 1997). They will take any vertebrate they can handle, from small to large mammals, reptiles, and fishes (Murray and Gardner 1997). Ocelot home range size varies considerably between sites and sexes (Oliveira et al. 2010). According to Oliveira et al. (2010), the home range of male and female ocelots vary between  $22.63 \text{ km}^2 \pm 24.16$  (standard deviation; SD) and  $14.41 \text{ km}^2 \pm 20.84$ , respectively.

(d) Jaguarundi, *Herpailurus yagouaroundi* (Geoffroy Saint-Hilaire, 1803)

*Herpailurus yagouaroundi* is a medium-sized (4.5–6 kg) carnivorous cat, widely distributed in Brazil, and found from southern Texas to the province of Buenos Aires, Argentina (Eisenberg and Redford 1999). It uses primary and secondary forest environments, shrub savannas, mangroves, grasslands, and altered environments (Giordano 2016). Its home range varies greatly among habitats and between sexes (Giordano 2016). In the same disturbed vegetation mosaic in the Atlantic Forest studied by Michalski et al. (2006), the male home range was of  $20.47 \text{ km}^2$ , while females,  $1.88 \text{ km}^2$ . However, females can move long distances. In a protected subtropical forest in southern Brazil, a female occupied an area of  $19.6 \text{ km}^2$  (Crawshaw Jr 1995).

## Study area

The monitoring program took place in the BR-040 highway, from km 125.2 to km 0 in the state of Rio de Janeiro (RJ; UTM 23K 675,461.77/7,477,535.14) and km 828.7 to km 773.5 in the state of Minas Gerais (MG; UTM 23K 661,842.40/7,605,888.64), in southeastern Brazil (Fig. 1). The highway includes 2 and 4-lane paved roads, with an average width of 6 and 12 m, respectively. The highway has a maximum speed of 110 km/h (70 km/h in the mountain range) and the mean traffic volume during the study period was 42,028 vehicles/day. The topography varies from the lowlands near Duque de Caxias city (19 m asl, UTM 23K 673,284.52/7,479,190.58), through the mountain range ( $\approx 1000 \text{ m asl}$ ) and Petrópolis city (838 m asl, UTM 23K 687,326.94/7,510,126.52) up to Juiz de Fora city (715 m asl, UTM 23K 671,276.13/7,600,685.07). The BR-040 highway crosses six other cities: Areal (RJ), Petrópolis (RJ), Comendador Levy Gasparian (RJ), Três Rios (RJ), Matias Barbosa

(MG), and Simão Pereira (MG), and is surrounded by urban areas, rivers, protected forests, and agriculture. Along this 180.4 km stretch, BR-040 highway cross three protected areas [Área de Proteção Ambiental de Petrópolis (from km 89 to km 59; towards MG and from km 59 to km 82; towards RJ), Reserva Biológica do Tinguá (from km 83 to km 85; towards RJ) and Refúgio da Vida Silvestre Estadual da Serra da Estrela (from km 91 to km 84; towards MG)], which are part of the Serra do Mar Biodiversity Corridor, whose main native vegetation cover is composed of tropical rainforest (Veloso et al. 1991). The most adjacent landscape of BR-040 highway is composed by the herbaceous cover (pasture and grasslands, 42.7%), followed by forest cover (29.9%) and urban areas (21.6%).

The study area is characterized by hot (17–27 °C) summers and mild (4–20 °C) winters with occasional frost. The mean annual rainfall is 278 mm, but can be as low as 154 mm during dry years and as high as 451 mm during wetter years. During the rainy season, from October to March, the area receives 90% of its total annual rainfall.

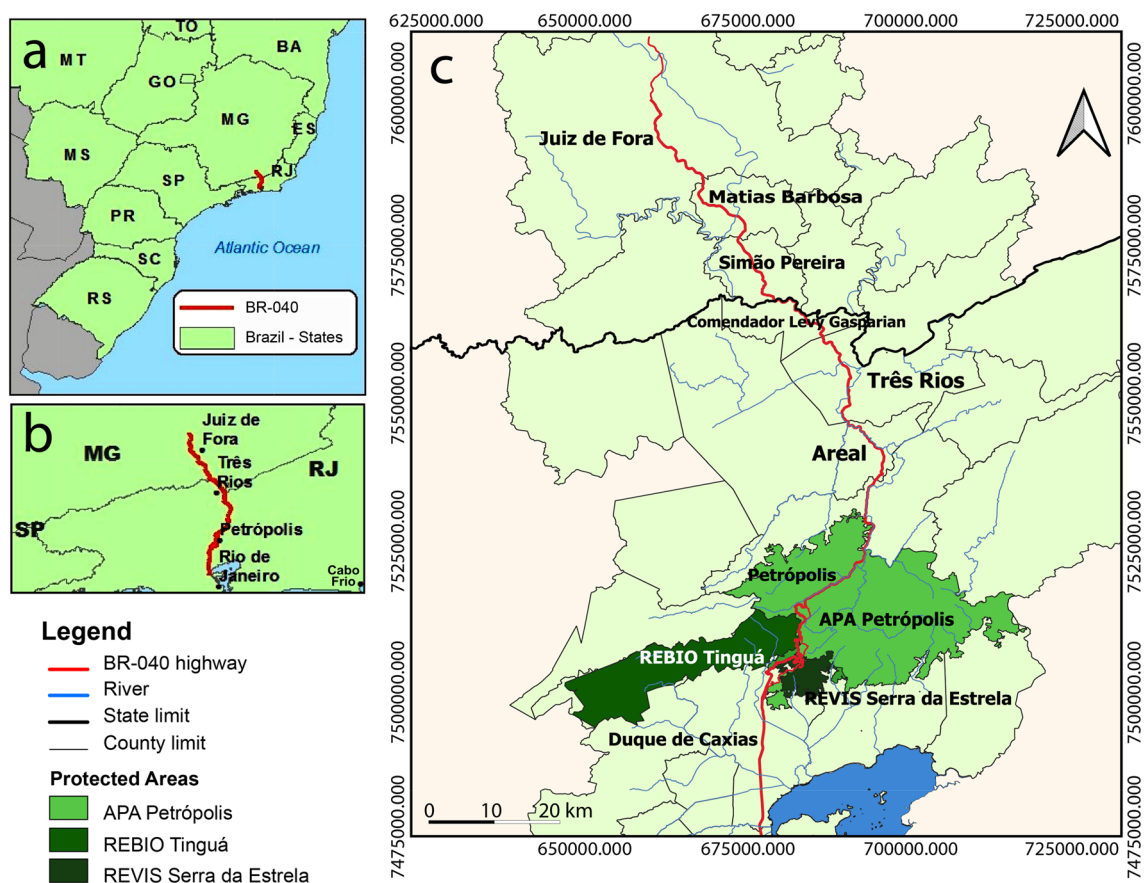
## Data collection and identification

Wildlife roadkill was registered in a 24/7 type schedule from January 2006 to June 2018 by car on estimated average speed between 40 and 60 km/h. As the highway includes two and four lanes, being the opposite lanes separated by a median strip, it was monitored in both directions (towards Minas Gerais and Rio de Janeiro). Concer staff (Companhia de Concessão Rodoviária Juiz de Fora-Rio—traffic inspectors and biologists) were trained by the coordinator of the Caminhos da Fauna (“Wildlife Pathways”) program, Dr Cecilia Bueno, employing standard protocol of forms and techniques, which included records of time and location, photographs, carcasses removal, and storage in freezers. Fortnightly the specimens collected were taken to the Laboratory of Ecology of the Veiga de Almeida University (RJ), identified and prepared as study skins, skeletons, or stored whole in the spirits collection depending on the conditions of the material. Species were deposited in the National Museum of Rio de Janeiro collection.

The carcasses of the animals used in this study comply with and are in accordance with the SISBIO License Number: 30727-12, Operation License Number 1187/2013 and the Authorization for Capture, Collection and Transport of Biological Material—Abio (Renewal) No. 514/2014.

## Landscape characteristics

We used a land use and land cover map of the studied area using Landsat images of 2002, produced by Bueno et al. (2016), and based on the maps produced by the Instituto de Estudos Socioambientais do Sul da Bahia (Iesb 2007),



**Fig. 1** The BR-040 highway stretch, from the km 125.2, near Duque de Caxias city in Rio de Janeiro state (RJ) to the km 773.5, near Juiz de Fora city in Minas Gerais state (MG), in southeastern Brazil. The highway crosses three protected areas in the state of Rio de Janeiro:

Área de Proteção Ambiental de Petrópolis (APA Petrópolis), Reserva Biológica do Tinguá (REBIO Tinguá), and Refúgio da Vida Silvestre Estadual da Serra da Estrela (REVIS Serra da Estrela), which are part of the Serra do Mar Biodiversity Corridor

which were developed at a meso detail scale (1:250,000), with information of the native vegetation cover, forest and non-forest vegetation, and discriminating the different phytophysiognomies, as well as other uses and cover, of the Atlantic Forest biome and associated ecosystems. Maps produced by Iesb had an accuracy of 86.39% detected in the validation process. Considering the scale used, the landscape did not suffer significant changes in a decade, thus the landscape map represents well the time when road-kill data were collected. The map had four classes of landscape characteristics: percentage of the urban area, forest cover (native forest and reforestation), herbaceous cover (grassy-woody savannas, floodplains and grasslands), and crop fields. Three buffer sizes were created around each roadkill event to evaluate the effect of the landscape characteristics at different spatial scales: 1, 5, and 10 km with the software QGIS 3.6 (QGIS Development Team 2019). We also measured the distance of each roadkill event to the nearest river (in meters).

## Data analysis

### (a) Roadkill hotspots

The analysis of the spatial distribution of roadkills should begin by estimating the intensity of occurrence of the punctual process throughout the area of interest (Druck et al. 2004). To visualize the spatial distribution of the roadkill hotspots of the four mammal species in the BR-040 highway we used heatmaps (i.e., visual representation to depict areas with high point density) with kernel density estimation in a geographic information system (GIS). Kernel density is calculated based on the number of collisions per kilometer of road, with larger numbers of clustered points resulting in larger values. Point density is calculated by adding the values of all overlapping kernel surfaces within any cell of determining size. The bandwidth of the kernel exhibits a strong influence on the estimation results, since it determines the search radius in which roadkills will contribute to the hotspot identification (Bil et al. 2013). We used a

search radius of 500 m to investigate collision clusters, which has been considered a reasonable distance between mitigation measures in hotspots (Bil et al. 2013). To model kernel shape, we used a quartic kernel shape function in the 'Heatmap' plug-in for QGIS 3.6 (QGIS Development Team 2019). According to Silverman (1986), the Kernel density estimator can be set to:

$$f(x) = 1/nh^2 \sum K\{x - X_i/h\}ni = 1,$$

where  $K$  is the Kernel function,  $n$  is the number of points observed,  $h$  is the smoothing bandwidth,  $x$  is the coordinate vector that represents the location of the estimated point,  $X_i$  is the vector of the coordinated that represents each point observed in relation to the estimated.

#### (b) Model selection

Logistic regression models were designed using the presence/absence of roadkill as dependent variables and landscape characteristics as independent variables. We sorted out the same number of roadkills along the highway to represent absences in logistic regression models. Pearson's correlations were performed among independent variables. Values above 0.7 were considered highly significant and not included in the same regression model (see Supplementary Table SD1). Overall, we built 40 models for the crab-eating fox, 39 for the maned wolf, 37 for the ocelot, and 39 for the jaguarundi (see Supplementary Table SD2). Each model had one or a combination of two independent variables because of the number of records for some species (e.g. the ocelot,  $N=14$ ). We also included an intercept-only model to compare the explanatory power of predictor variables relative to other unaccounted sources of variation. The best-fitted model was obtained based on the likelihood of the binomial distribution using Generalized Linear Models (GLM). Multiple competing models were compared with the corrected version of Akaike's Information Criterion for small samples (AICc),  $\Delta$ AICc, and Akaike weight (wi). The lower the AICc and  $\Delta$ AICc, the better is the model fit to the data (Burnham and Anderson 2002). Models were considered plausible with  $\Delta$ AICc  $\leq 2$  (Richards 2005). Model selection was performed with the package MuMIn (version 1.9.11). All analyses were performed in R software version 2.14.1 (R Core Team 2015).

## Results

We recorded a total of 152 roadkill events from January 2006 to June 2018. Of these, 94 (61.8%) individuals were of the crab-eating fox, 29 (19.1%) of the maned wolf, 15 (9.8%) of the jaguarundi, and 14 (9.2%) of the ocelot (Fig. 2). Crab-eating fox roadkills were distributed throughout the road, while the other three species were recorded mainly in the

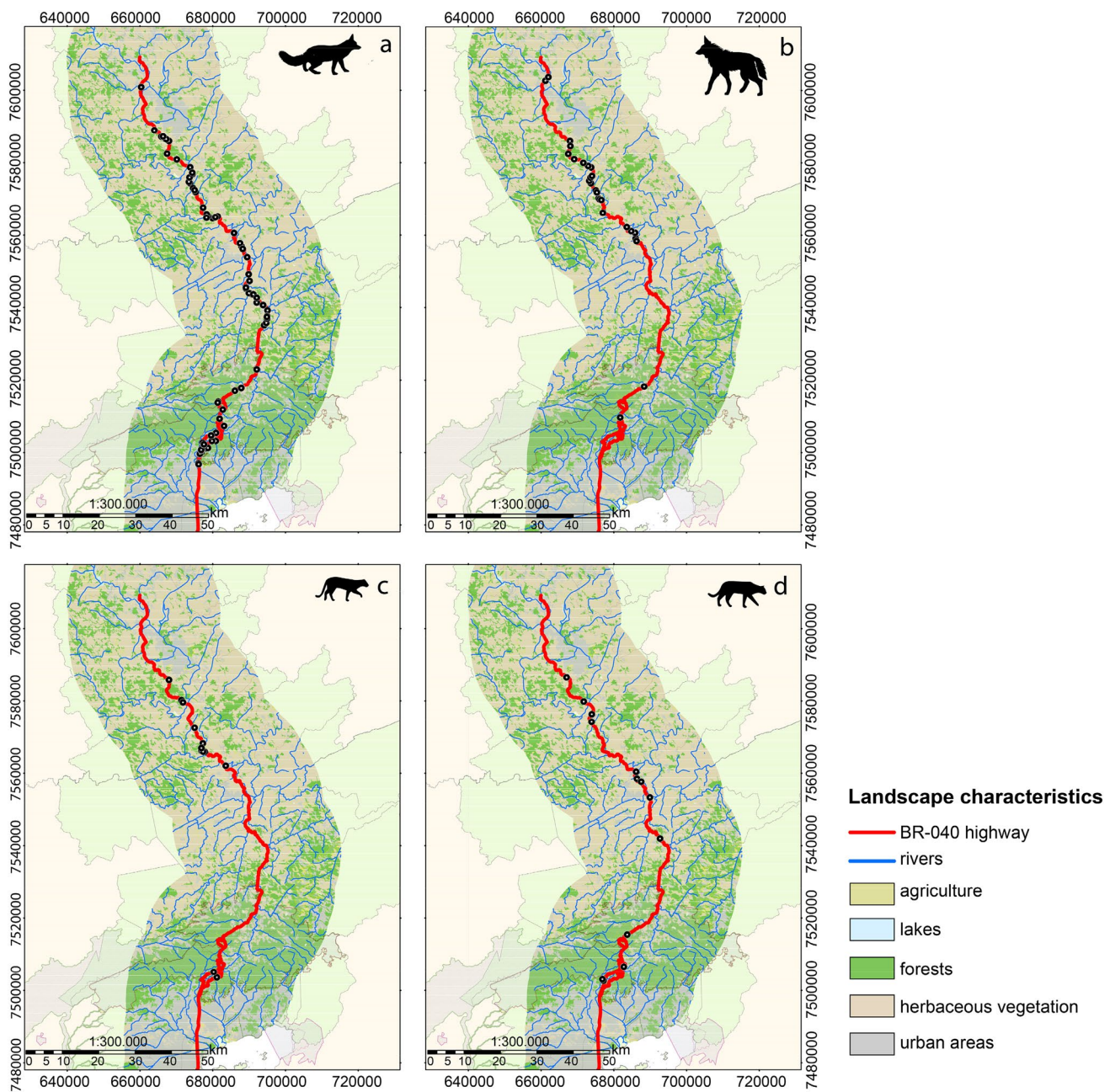
northern section of the road (Fig. 2). We found two regions of increased roadkill density: a larger one spread over the northern section of the road, around the border between the states of Minas Gerais and Rio de Janeiro (from km 796 to 828 in MG and from km 1 to 20 in RJ), and another at southern section of the road (from km 97 to 104 in RJ), in the vicinity of three protected areas (Fig. 3). Overall, the cluster of roadkill identified in the southern section of the road was due to the high roadkill numbers of the crab-eating fox (see also Fig. 2a). The other three species were recorded only five times in this section ( $N=1$ , maned wolf;  $N=2$ , the jaguarundi;  $N=2$ , the ocelot).

Different landscape characteristics explained roadkill events for each species and at different scales (Tables 1 and 2). For the crab-eating fox, roadkills were less likely to occur in areas with a high percentage of crop fields, urban areas, and herbaceous vegetation, at 5 km buffer size (Tables 1 and 2). For the maned wolf, roadkills were less likely to occur in areas with a high percentage of crop fields and more likely to occur in areas with high percentage of herbaceous vegetation, at 1 km buffer size (Tables 1 and 2). For the jaguarundi, roadkills were more likely to occur in areas with high percentage of herbaceous vegetation and lower percentage of crop fields, at all buffer sizes (Tables 1 and 2). For the ocelot, roadkills were positively associated with the percentage of forest and crop fields at 5 km buffer size. At the same time, the second and third-ranked models also have both positive and negative effects of the percentage of forest, herbaceous vegetation, and urban areas at different scales (Tables 1 and 2).

## Discussion

Our extensive 12-year road survey has enabled us to unravel the spatial pattern of four medium-sized carnivorous mammal roadkills on a high-traffic road immersed in the Atlantic Forest biome, a globally recognised biodiversity hotspot. Roadkills were concentrated in two areas of the BR-040 highway: a larger one in the north and a smaller one in the south section of the road. Roadkill hotspots match among the studied species in the north section of the road. Although protected areas are often seen as custodians of biodiversity, our study showed that roadkill does occur at high rate in their vicinity. Overall, roadkills were more significant in areas with a high percentage of herbaceous vegetation (except the crab-eating fox). In general, species avoided other altered regions, such as cultivated fields and urban areas, where we registered a reduced number of carcasses. Only the ocelot had roadkill events directly associated with the continuous forest.

Based on the pattern of mammal roadkills (Ford and Fahrig 2007) and previous studies developed in Brazil

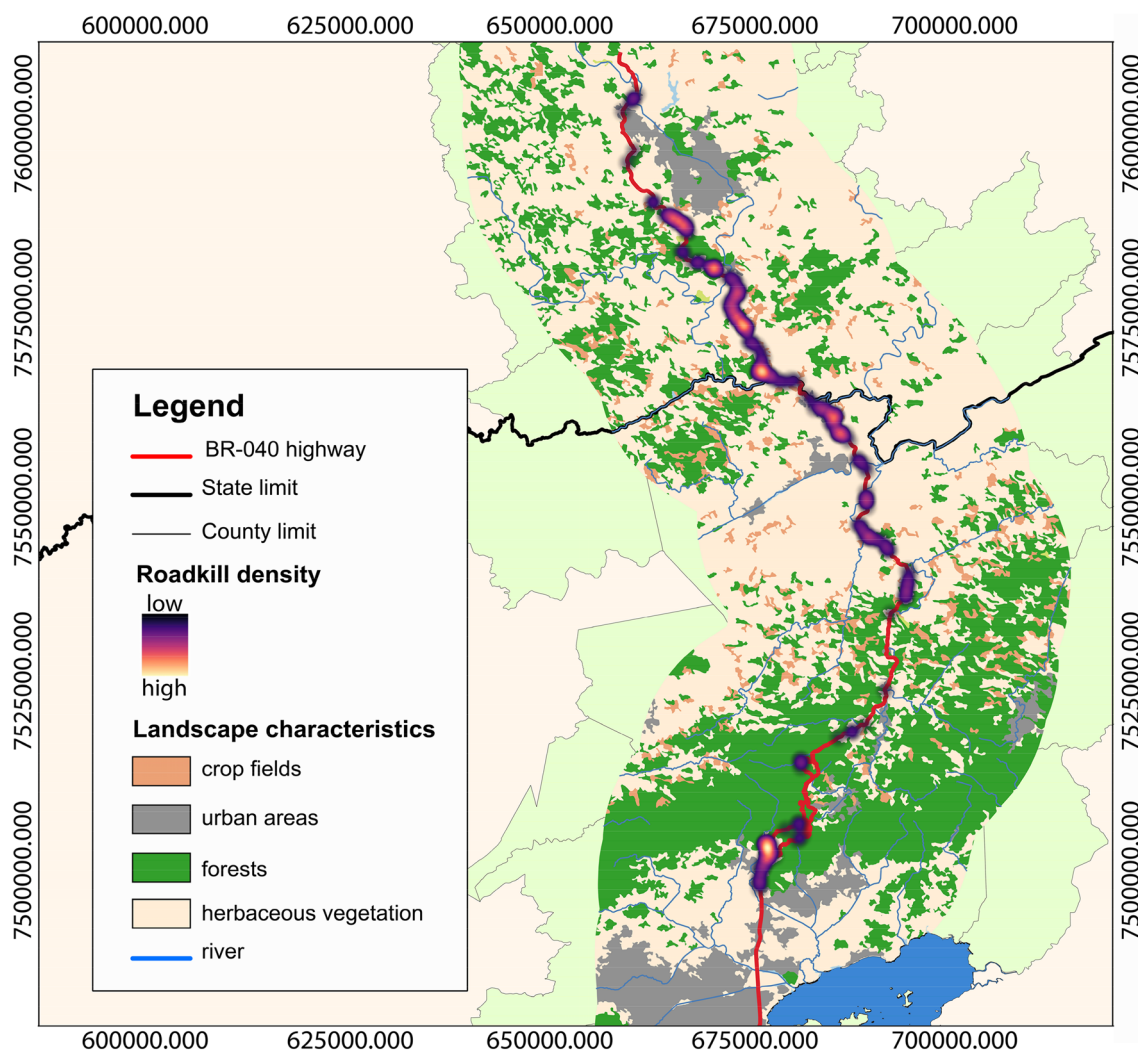


**Fig. 2** Roadkills of four medium-sized carnivorous mammals (black circles) in the BR-040 highway (red line), southeastern Brazil. **a** The crab-eating fox, *Cercdocyon thous*, **b** the maned wolf, *Chrysocyon*

*brachyurus*, **c** the ocelot, *Leopardus pardalis*, **d** the jaguarundi, *Herpailurus yagouaroundi*. Landscape characteristics 20 km around BR-040 highway are shown in detail

(Coelho et al. 2008; Cunha et al. 2010; Pereira et al. 2006; Zanzini et al. 2018; Ferregueti et al. 2020), the crab-eating fox was expected to be the most roadkilled species among medium-sized mammals in the BR-040 highway. Cáceres (2010) recorded higher roadkill rates for the crab-eating fox than expected based on abundance patterns, which suggests that their population dynamics are highly influenced by roads. Most commonly inhabiting forested and edge areas in the Atlantic forest biome, the crab-eating fox can

use altered environments (Ferraz et al. 2010; Magioli et al. 2014; Monteiro-Alves et al. 2019). In the BR-040 highway, roadkill events were more likely to occur near areas with low percentage of crop fields, herbaceous vegetation, and urban regions, reinforcing the forest habits of the species in the region. Roadkill events were also associated with forest plantations (*Pinus* sp.) in a Brazilian savanna highway in southeastern Brazil (Freitas et al. 2015). In this highway, crab-eating fox roadkills were also positively associated to



**Fig. 3** Roadkill hotspots of four medium-sized carnivorous mammals (the crab-eating fox, *Cerdocyon thous*; the maned wolf, *Chrysocyon brachyurus*; the ocelot, *Leopardus pardalis* and the jaguarundi, *Her-*

*pailurus yagouaroundi*) recorded along the BR-040 highway (red line), southeastern Brazil

water bodies (10 km buffer) and negatively to distance to the nearest river; no relationship between roadkills and proximity to watercourses was observed in our study.

For the maned wolf roadkills were more likely to occur near areas with herbaceous vegetation. Typical of open habitats (Massara et al. 2012; Vynne et al. 2011), records in the Atlantic Forest could be explained by the cross-habitat spillover hypothesis which state that dispersal across habitats, including managed and natural ecosystems, is mediated by human landscape alterations, affecting landscape-wide community structure and associated processes (Tscharrntke et al. 2012). The continuous deforestation of both Cerrado (Strassburg et al. 2017) and Atlantic Forest areas (Andreacci and Marenzi 2020) may be facilitating the dispersal of the maned wolf to new open areas suitable for the species; all seven records by Xavier et al. (2017)

were in areas dominated by pastures and grasslands with reduced forest cover. Lately, there is an increase in abandonment of pasture areas in the Brazilian Atlantic Forest (Rezende et al. 2018), which have similar vegetation structure to savanna-like ecosystems when affected by fire (Sansevero et al. 2020). In a review of records also in the Atlantic Forest, Bereta et al. (2017) found most records of the maned wolf associated with open areas (agriculture and livestock— $N = 22$ , 45%; urban areas— $N = 20$ , 41%). Association with urban areas is unexpected, since the species usually inhabits grasslands and scrub forests (Freitas et al. 2015). Freitas et al. (2015) observed a positive association with the urban area at a 10 km buffer. However, this Brazilian savanna highway is immersed in a rural area, covered by agriculture and pasture, and small-sized cities mainly represent urban areas. According to Freitas et al.

**Table 1** Top-ranked models predicting roadkills of four medium-sized carnivorous mammals at three spatial scales (1, 5, and 10 km buffer size) in the BR-040 highway in southeastern Brazil

Selected models	K	$\Delta$ AICc	wi
<i>Cerdocyon thous</i>			
Crop fields (5 km)	2	0.00	0.47
Crop fields (5 km) + urban area (5 km)	3	1.75	0.19
Crop fields (5 km) + herbaceous vegetation (5 km)	3	1.95	0.18
<i>Chrysocyon brachyurus</i>			
Herbaceous vegetation (1 km) + crop fields (1 km)	3	0.00	0.54
<i>Leopardus pardalis</i>			
Forest (5 km) + crop fields (5 km)	3	0.00	0.31
Herbaceous vegetation (5 km) + urban area (5 km)	3	0.92	0.20
Herbaceous vegetation (1 km) + forest (1 km)	3	0.94	0.20
<i>Herpailurus yagouaroundi</i>			
Herbaceous vegetation (10 km) + crop fields (10 km)	3	0.00	0.26
Herbaceous vegetation (5 km) + crop fields (5 km)	3	0.45	0.21
Herbaceous vegetation (1 km)	2	1.40	0.13

K = number of parameters of the model, AICc = Akaike Information Criteria corrected for small ratio sample size/number of parameters,  $\Delta$ AICc = AICci - minimum AICc, wi = Akaike weight

(2015), the species used the urban matrix only for dispersal, not as habitat.

Most studies evaluating wildlife-vehicle collision in Brazilian roads have few records for most felid species (Coelho et al. 2008; Cunha et al. 2010; Gonçalves da Silva et al. 2014; Zanzini et al. 2018). Frequently, one or two individuals is recorded, which is probably related to their low population densities and study duration (Coelho et al. 2008; Gonçalves da Silva et al. 2014; Kasper et al. 2016; Oliveira et al. 2010). The lack of data prevents studies evaluating the effect of landscape characteristics in roadkill events in the group. The 12-year monitoring study conducted in the BR-040 highway allowed us to evaluate how this fragmented landscape affected these species, increasing or reducing the chances of wildlife-vehicle collisions. Overall, both ocelot and jaguarundi roadkills were more frequent in areas with high percentage of herbaceous vegetation. Nonetheless, differences between species were also evident; while for the jaguarundi records were less frequent in areas with higher percentage of cropfields, for the ocelot the largest numbers of roadkilled individuals were recorded in areas with high percentage of forest cover and crop fields. Overall, the ocelot's range is strongly associated with dense habitat cover (Wolff et al. 2019; Cruz et al. 2019; Oliveira et al. 2010). Even in open areas like savannas, they favor dense forests, but also use pastoral/agricultural areas, and may avoid

**Table 2** Standardized parameters of the most parsimonious models predicting roadkills of four medium-sized carnivorous mammals in the BR-040 highway in southeastern Brazil

Models	Variables	Estimate	Standard error
<i>Cerdocyon thous</i>			
1	Intercept	4.25	0.65
	Crop fields (5 km)	- 0.37	0.06
	Herbaceous vegetation (5 km)	- 0.36	0.06
2	Intercept	3.88	0.91
	Crop fields (5 km)	0.02	0.04
	Urban area (5 km)	- 0.36	0.06
3	Intercept	4.04	0.87
	Crop fields (5 km)	0	0.01
	Herbaceous vegetation (5 km)	- 0.37	0.05
<i>Chrysocyon brachyurus</i>			
1	Intercept	- 0.50	0.67
	Herbaceous vegetation (1 km)	0.04	0.01
	Crop fields (1 km)	- 0.15	0.05
<i>Leopardus pardalis</i>			
1	Intercept	- 6.62	2.70
	Forest (5 km)	0.11	0.04
	Crop fields (5 km)	0.55	0.23
2	Intercept	11.07	4.26
	Herbaceous vegetation (5 km)	- 0.12	0.05
	Urban area (5 km)	- 0.35	0.14
3	Intercept	- 2.41	0.99
	Herbaceous vegetation (1 km)	0.06	0.02
	Forest (1 km)	0.04	0.02
<i>Herpailurus yagouaroundi</i>			
1	Intercept	1.03	0.89
	Herbaceous vegetation (10 km)	0.05	0.02
	Crop fields (10 km)	- 0.43	0.16
2	Intercept	1.33	0.92
	Herbaceous vegetation (5 km)	0.05	0.02
	Crop fields (5 km)	- 0.56	0.21
3	Intercept	- 1.18	0.59
	Herbaceous vegetation (1 km)	0.04	0.01

grasslands (Oliveira et al. 2010). The ocelot has also been recorded using heavily disturbed areas, but less frequently than other smaller felids such as the jaguarundi (Cruz et al. 2019). However, in agricultural landscapes, the ocelot has a great association with the remnants of natural vegetation, without which it disappears (Oliveira et al. 2010). In the BR-040 highway, the ocelot was also recorded in proximity to open areas (as in other parts of its distribution; Oliveira et al. 2010), but it was the only species with high roadkill numbers in forested areas.

The jaguarundi also occupies a diversity of habitats throughout its range, from dense undergrowth to open areas (Giordano 2016). According to Oliveira et al. (2010), in altered environments, the jaguarundi can be observed using



the surrounding non-forest matrix, such as sugarcane, soy, and corn as long as it is associated with forested areas (Oliveira et al. 2010). Stone et al. (2009) also reported on the ability of the jaguarundi to use very small Atlantic Forest fragments, typical of the adjacent areas of the BR-040 highway. In our study area, we found a negative relationship between jaguarundi roadkills and cropfields. Thus, jaguarundis explore open areas such as grassy-woody savannas, floodplains, and grasslands in the BR-040 highways, but avoids cropfields, leading to the low number of records in these areas.

Except for the maned wolf, all three mammals showed an association with landscape characteristics at intermediate (5 km) and large (10 km) scales. Their wide home ranges and high dispersal abilities explain these associations (Crawshaw Jr. 1995; Giordano 2016; Michalski et al. 2006; Oliveira et al. 2010). For the crab-eating fox and the ocelot the landscape was perceived at a 5 km radius, while for the jaguarundi, at a 10 km radius. For the latter, the percentage of herbaceous vegetation, the dominant landscape feature (42.7%), was also perceived at smaller scales (1 and 5 km radius). As the other three mammalian carnivores, the maned wolf also has a large home range area and a good dispersal capacity (Bueno and Motta-Junior 2004; Carvalho and Vasconcellos 1995; Jácomo et al. 2009). However, in the study area the landscape was perceived by the maned wolf at a smaller scale (1 km). The only study that also evaluated the effects of landscape characteristics on the species found that broader area is perceived by them (10 km) (Freitas et al. 2015). Thus, evaluating the effect of landscape characteristics at different scales is extremely relevant to predict roadkill of the four mammalian carnivores.

Medium-sized carnivorous mammal roadkills were not distributed randomly and we identify two important hotspots in the BR-040 highway. In the north section of the road, roadkill density was spread over a considerable large area and all four carnivorous mammals were recorded. This region has a high percentage of herbaceous vegetation and some small forest fragments, which explain the high rates of collisions. In the south section of the road, however, the roadkill hotspot is a consequence of the high number of roadkills of the crab-eating fox. The hotspot is in the vicinity of three important protected areas. At this region, the road divides into two routes, one uphill and one downhill. The high number of wildlife–vehicle collisions occurred on the downhill route. This is probably a consequence of the increased speed when driving in this mountainous region.

## Conclusion

In Brazil and in several other developing countries, data on wildlife roadkill are scarce and punctual. Therefore, long-term monitoring of roads is essential to support

investigations aimed at reducing the direct and indirect effects of roads on wildlife and to prevent accidents, with loss of human life and substantial material damages. The data gathered during the 12-year monitoring study allowed us to evaluate the effect of the fragmented landscape with different matrix types in four medium-sized mammalian carnivores, including two threatened species (the maned wolf and the jaguarundi). The analysis of the effect of the landscape characteristics revealed that roadkills were related to the use of a similar matrix by species and, for the first time, we identified areas with a high probability of roadkill for two feline species, the ocelot and the jaguarundi. The total impact of roads and other transportation infrastructure on wildlife cannot be assessed without considering a broader landscape context. Thus, future studies should not only evaluate the effect of landscape characteristics on the spatial pattern of roadkills, but also include different scales in the landscape analysis.

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## Declarations

**Conflict of interest** We declare no conflict of interest.

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