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Do the roadkills of different mammal species respond the same way to habitat and matrix?

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Abstract
While road network expansion connects human settlements between themselves, it also leads to deforestation and land use changes, reducing the connectivity between natural habitat patches, and increasing roadkill risk. More than 30% of registered mammal roadkills in Brazil are concentrated in four species: *Cerdocyon thous* (crab-eating fox); *Euphractus sexcinctus* (six-banded armadillo); *Tamandua tetradactyla* (collared anteater) and *Myrmecophaga tridactyla* (giant anteater), the latter being categorized as vulnerable by IUCN redlist. Our aim was to understand how these animals' roadkills could be related to the land use proportions on landscapes all over the Brazilian territory, and investigate if the roadkill patterns differ among species. We collected secondary data on mammal roadkills (N = 2698) from several studies in different regions of Brazil. Using MapBiomas' data on land use and land cover, we extracted landscape composition around each roadkill sample. Through the proportion of land use and land cover in the area of influence where the roadkill occurred, we built binomial GLM models and selected the best ones by Akaike Information Criteria. For crab-eating fox and the six-banded armadillo, the best models include matrix coverage resulting in increased roadkill risk, while both anteaters' species have a habitat and a matrix component in their best models, with an interaction between the variables. These four species seem to be roadkilled in different landscape arrangements, but in all scenarios, anthropic areas had an important influence over the models. For habitat-dependent and more sensible

species, such as *Tamandua tetradactyla* and *Myrmecophaga tridactyla*, the amount of matrix influencing the roadkill risk depends on habitat availability in the landscape. It changes the strength and direction of the effect according to the proportion of natural areas in the region, while with generalist species such as *Cerdocyon thous* and *Euphractus sexcinctus*, the quantity of human-modified coverage increases the risk.

Keywords
Conservation biology, environmental impact assessment, landscape ecology, road ecology, tropics

Introduction

Road ecology is a research area that aims to understand the impact of highways and railways on natural ecosystems, economics, and society. Many studies on this subject focus on one of the most conspicuous effect of roads: wildlife mortality by vehicle collisions (Forman and Alexander 1998; Forman et al. 2003; Laurance et al. 2009; Van Der Ree et al. 2015; Pinto et al. 2020; Teixeira et al. 2020). In temperate regions, such as North America, special attention is given to large mammals, because of the risk associated with collisions, causing fatalities, and human and economic injuries (Huijser et al. 2009). In tropical regions, on the other hand, attention is mostly paid to the high rates of wildlife mortality (Pinto et al. 2020), since the high diversity and high density of natural populations in these habitats lead to an elevated risk of biodiversity loss.

Changes in landscape composition and its structure are some of the main factors leading to biodiversity loss (Dirzo et al. 2014). Roads induce several landscape changes: firstly, the roads are by themselves one type of matrix on the landscape; secondly, this type of matrix causes both population isolation and mortality; and thirdly, roads provide access to remote areas, allowing expansion of agricultural frontiers, causing other major landscape changes (Nagendra et al. 2003; Jaeger et al. 2005; Fahrig and Rytwinski 2009; Laurance et al. 2009; Freitas et al. 2010). All those factors together lead to biodiversity loss (Teixeira et al. 2020). In order to better understand the impact of roads on ecosystems, we need to evaluate the effects of those linear infrastructures from a landscape perspective, searching for patterns that allow us to make guided decisions for biodiversity conservation strategies on large scales.

The majority of studies on road mortality focus on a small region, studying a road or a portion of it. Those studies are important to understand the local impacts of roads, and to search for patterns on specific landscape configuration. When we search for similar studies in Brazil, it is notable that some species are constantly found on roadkill registers (Dornas et al. 2012; Cirino and Freitas 2018; González-Suárez et al. 2018; Grilo et al. 2018). Many mammals in Brazil have large distribution areas, covering a great part of the national territory, and therefore, making it one of the most studied groups (Pinto et al. 2020). It happens because of their response to landscape changes, and their relative risk to human life, since collisions with larger animals can cause human injuries (Huijser et al. 2013; Abra et al. 2019). Landscape influence on mammal road mortality has been accessed by some studies in local scales (Bueno et al.

2013, 2015; Ascensão et al. 2019), but broader scales studies are scarce and needed to identify how different land uses affect the most frequent roadkill mammals on a national scale. Some species have high roadkill rates, such as *Cerdocyon thous* (Linnaeus, 1766), *Euphractus sexcinctus* (Linnaeus, 1758), *Tamandua tetradactyla* (Linnaeus, 1758) and *Myrmecophaga tridactyla* (Linnaeus, 1758) – the latter being considered as Vulnerable (VU) by IUCN, and locally extinct in some regions of Brazil (Miranda et al. 2014a). Those four species are among the most roadkilled animals in the Brazilian territory (Ribeiro et al. 2017; Cirino and Freitas 2018; Grilo et al. 2018). However, they have different degrees of sensitivity to landscape changes and configuration.

The crab-eating-fox (*Cerdocyon thous*) is one of the most frequent species in roadkill registers according to the "Banco de Dados Brasileiro de Atropelamentos de Fauna Selvagem" – BAFS (http://cbee.ufla.br/portal/sistema_urubu/urubu_map.php) and other published researches (Vieira 1996; Prada 2004; Rosa and Mauhs 2004; Cherem et al. 2007; Coelho et al. 2008; Rezini 2010; Lemos et al. 2011; Dornas et al. 2012; Cirino and Freitas 2018). In the evaluation of *C. thous*' extinction risks, one major threat is the roadkill (Beisiegel et al. 2013). Freitas et al. (2014) associated the roadkill of this species to *Pinus* sp. forestry cover in a road in a savanna region of southeastern Brazil. The elevated numbers of *C. thous* roadkill records might be a reflection of its high abundance, generalist habits, and the fact that its occurrence range is in the entirety of Brazil with the exception of the center of the Amazon forest (Lucherini 2015).

The six-banded-armadillo (*Euphractus sexcinctus*) is also a frequent species on roadkill records (Carvalho et al. 2015; Ribeiro et al. 2017). It is a species with fossorial habits, active predominantly at daytime, and mainly inhabiting open areas and forest edges (Medri et al. 2006). The occurrence of this species on forest edges can be an aggravating factor to its high run-over rate, since roads generate edge effect and discontinuities on native vegetation. In a published evaluation of the risks to six-banded-armadillo conservation, the impact of roadkill was listed as a needed research topic for this taxon (Silva et al. 2015).

Both anteater species (*Tamandua tetradactyla* and *Myrmecophaga tridactyla*) are more exigent in terms of habitat quality than the other two species studied in this research. They are less abundant, but also highly roadkilled. The giant-anteater (*Myrmecophaga tridactyla*) is a terrestrial Xernarthra that can move long distances by ground, which can aggravate the roadkill rate of this species. On the other hand, its roadkill is associated with native vegetation proximity to roads in a Cerrado area (Freitas et al. 2014), and to their own movement behavior associated with the proximity of roads to their home ranges and crossing habits (Noonan et al. 2021). The collared-anteater (*Tamandua tetradactyla*) has semi-arboreal habits, and can move both by ground and on tree canopies. It has been recorded in several road monitoring reports (Grilo et al. 2018). The landscape associated with the roadkill of this species in Mato Grosso do Sul state, Brazil, was riparian areas and grassland pastures (Ascensão et al. 2017).

Most road impacts mitigation measures focus on general recommendations, such as implementation of underpasses or fencing in roadkill hotspots, which usually comes in association with native or riparian vegetation, assuming that most animals would use those areas to move and cross the road. However, we cannot assume that all species have the same habitat requirements and patterns of space usage, since it is known that the rate of underpasses usage differs among species (Abra et al. 2020). Furthermore, the roadkill hotspot differs between vertebrate taxa, according to traits such as body size, type of locomotion and time of activity (Teixeira et al. 2013) and such hotspots might change its locations over time (Lima Santos et al. 2017; Teixeira et al. 2017). For a better mitigation of the impacts of roads on animal mortality, patterns and landscape characteristics associated with species' roadkill risk and habitat requirements must be investigated, since species differ in their abundance, occurrences and roadkill rates.

Understanding the landscape patterns linked to road mortality of those species can provide guidance for protection and conservation efforts aiming to mitigate the road impacts on wildlife. Together, these four species presented here represent between 34,7% and 38,8% of the total roadkills of medium-large sized mammals in Brazil (Cirino and Freitas 2018). Most studies on roadkills in Latin America focus on mortality, but just a few focus on how habitat and landscape patterns influence those roadkills occurrences (Pinto et al. 2020). Our aim is to analyze at a national level the effects of habitat and matrix amount on the mortality of those highly roadkilled species, while assessing the year and scale according to each occurrence. Our central hypothesis is that road mortality of different species responds differently to habitat and matrix proportions in the landscape.

Methods

Roadkill data collection

We collected a sample of georeferenced roadkill data from two main sources: (1) monitoring studies across the country; and (2) the "Banco de Dados Brasileiro de Atropelamento de Fauna Selvagem" (**BAFS**). The first one consists of previously published systematic studies in roads of different regions of Brazil; such data was provided by collaborators (see Acknowledgements – Coelho et al. 2008; Freitas 2009; Caceres 2011; Teixeira et al. 2013; Dornelles 2015; Freitas et al. 2015; Ascensão et al. 2017). The second is a dataset obtained at the Brazilian Center of Road Ecology of the University of Lavras, which gathers geo-referenced and validated citizen science roadkill data from a mobile phone app and from other studies across the country. The app works as follows: the user takes a photo of the roadkilled animal, the app then records the location of the photo that is sent for identification down to species level by an expert in the taxonomic group (Castro and Bager 2019). The records used in our analysis were those with adequate species identification, which depended on the quality of the photo and the degradation degree of the carcass. We selected the roadkill data of the four species focused in this study – *Cerdocyon thous*, *Euphractus sexcinctus*, *Tamandua tetradactyla*, and *Myrmecophaga tridactyla* – ranging from 2002 to 2015. We chose these species because they present high rates of mortality in Brazilian roads. For each roadkill occurrence, we created a random point in the same road segment, thus representing the pseudo-absence of roadkill. Thereafter, we used these data to build a roadkill presence (ones) and absences (zeros) matrix for each species, with the same number of absences and presences.

Landscape data and scale of analysis

For land cover and land use, we utilized the serial time data from MapBiomas (Projeto MapBiomas 2021), with a pixel size of 30 m, between 2002 and 2015. To access the exact landscape composition at the time of each roadkill occurrence, we used the land cover map of the correspondent year of the roadkill register. For example, if a *C. thous* was registered as roadkilled in 2006, we would collect the data from MapBiomas of the corresponding year and for the correspondent region. This process was performed to all evaluated species registers throughout the 14 years analyzed.

For each species, we considered a different influence buffer radius starting from the place of the roadkill, since each one has different home ranges, body sizes, and habits requirements. We estimated the mean home range for *C. thous* as 4.9 km^2 (Beisiegel et al. 2013), for *E. sexcinctus* as 0.7 km^2 (Silva et al. 2015), for *M. tridactyla* as 3.6 km^2 (Ohana et al. 2015), and for *T. tetradactyla* as 2.7 km^2 (Miranda et al. 2015). To assess the potential landscape influencing each individual we used a buffer with twice the radius of the home range approximated to a circle shape (A), resulting in the radius of roadkill influence (φ):

If the area of a circle is given by:

$$A = \partial r^2$$

where r is the radius of the circle, so the double of a radius of a circle of a given area is:

$$\varphi = 2\left(\sqrt{\frac{A}{\partial}}\right)$$

We used this radius size because the roadkill point may have occurred on the center of the home range, or on its border (Fig. 1); this way, considering a bigger radius of influence would prevent us from connecting the wrong area, or a smaller area, with the roadkilled individual. The radius for *C. thous* was 2.50 km, for *E. sexcinctus* 0.95 km, for *M. tridactyla* 2.14 km and for *T. tetradactyla* 1.85 km.

For each presence or absence of roadkills we calculated the proportion of land use and land cover inside the buffer based on MapBiomas land cover map for the corresponding year of the roadkill. The classes of land use and land cover considered in the analysis were: (1) forest; (2) savanna; (3) natural open areas; (4) forestry; (5) agriculture; (6) pasture; (7) farming; and (8) water. Farming represents the sum of agriculture and pasture in addition to mosaics or rotation of both classes in the same area. We conduct all landscape analysis and data extraction on ArcGIS v10.3 environment.

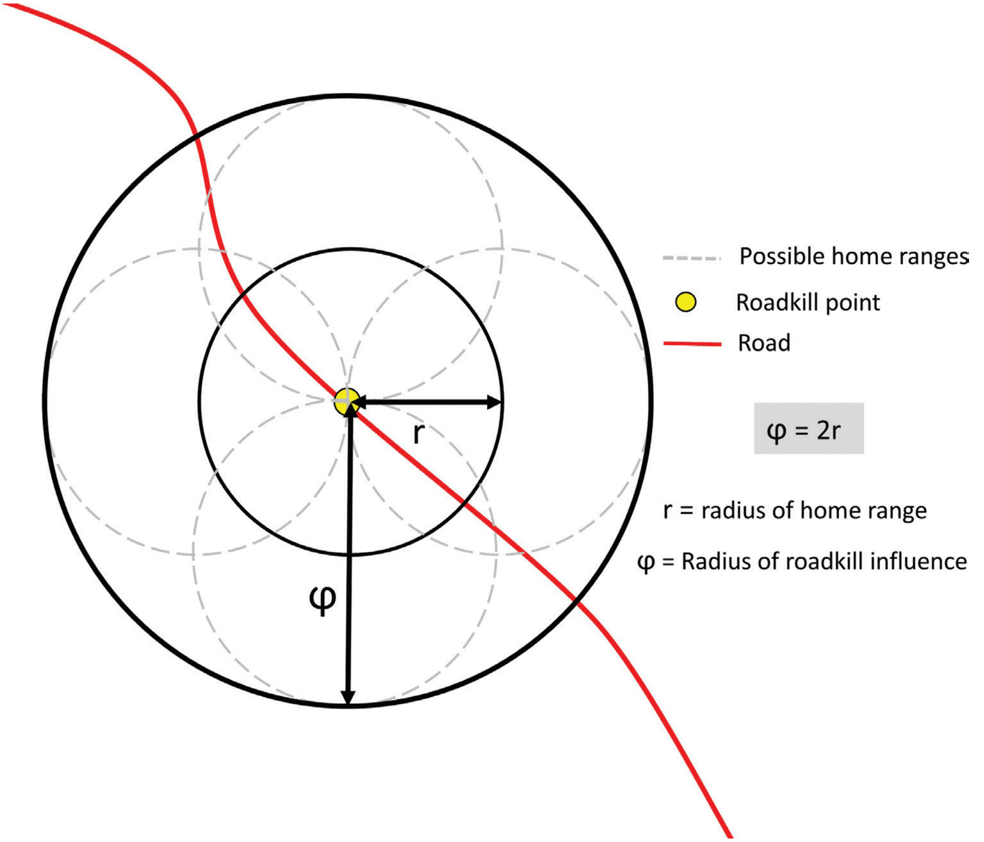

Figure 1. Scheme exemplifying the radius of roadkill influence chosen. For a given roadkill point using the simple radius of home range (r), we might exclude some of the landscape characteristics if the roadkill occurred in the border of the home range. Including the possible home ranges (approximated to a circular shape), and doubling the radius (φ), we ensure that all landscape composition associated with the roadkill occurrence is incorporated within the analysis.

Statistical analysis

To estimate the relative chance of roadkill of each species we constructed binomial generalized linear models (**GLM**), considering the matrix of presences and absences as our response variables, and the proportion of the eight landscape variables inside the radius of roadkill influence as our predictive variables. We built four groups of models, one for each species, with one or two predictive variables by model, combining variables in pairs, and considering the interaction between them. We discarded models with some degree of correlation (> 0.6 or < -0.6) between predictive variables (see Suppl. material 1: Fig. S1). Models with some level of collinearity between the two predictive variables (Variance Inflation Factor > 4.0) were excluded from the analysis (Tay 2017). Overall, we had 45 models for each species (see Suppl. material 1).

All models were ranked by Akaike Information Criteria (AIC) and selected by their corrected AIC value (AICc), with lower values of AICc representing the best models (Burnham and Anderson 2002). Models with AICc distance equal or lower than two (ΔAICc $\leq$ 2), and evidence ratio lower than 2 are considered equally plausible. The statistical analysis was performed on the software R 4.0.2 (R Core Team 2020) using the packages 'bbmle', 'numDeriv', 'effects', 'ggplot2' and 'corrplot' (Fox and Hong 2009; Wickham 2016; Wei and Simko 2021).

Results

Distribution of roadkill occurrences

We collected a total of 2698 georeferenced roadkill records across the country (*Cerdocyon thous* (N = 1282); *Euphractus sexcinctus* (N = 589); *Myrmecophaga tridactyla* (N = 422) and *Tamandua tetradactyla* (N = 405)) (Fig. 2). Overall, the distribution of the observations reflects a potential occurrence and abundance of the four species. Some biases can occur, since the data came from previous studies and citizen science, but to assess the landscape composition in the radius of roadkill influence, we had enough data in terms of quantity and spatial distribution, given the potential distribution of each species.

Model selection

For *Cerdocyon thous* and *Tamandua tetradactyla* only one model was selected as the best model by AIC criteria (ΔAICc $\leq$ 2 and evidence $\leq$ 2), while the remaining studied species had two equally plausible models. For *Cerdocyon thous* the best model shows a positive effect of agriculture and pasture proportion inside the buffer on the chance of roadkill: for each 10% of pasture cover in landscape the roadkill risk increases by 2.7%, while for agriculture it increases by 4.6%. (Table 1, Fig. 3). For *Euphractus sexcinctus* one selected model shows a positive relationship of roadkill risk with farming and forestry. On the other hand, the other models show a positive relationship with pasture and agriculture, these variables made up the farming class, so we only considered the first model, in which the relative risk of roadkill of *Euphractus sexcinctus* increases 6,5% and 14,7% for each 10% of land cover increment of farming and forestry, respectively (Table 1, Fig. 5). Both anteaters' best models include habitat land cover, matrix land cover and the interaction between them, which will be discussed in the next section (Table 1). For *Myrmecophaga tridactyla*, the best model includes an interaction between pasture and forest areas (Fig. 6), while for *Tamandua tetradactyla* the selected model includes the interaction between savanna and agriculture areas (Fig. 7). The other selected model for *Myrmecophaga tridactyla* includes an interaction between forest and savanna areas, but the effect of both variables on roadkill risk was not significant ($p > 0.05$).

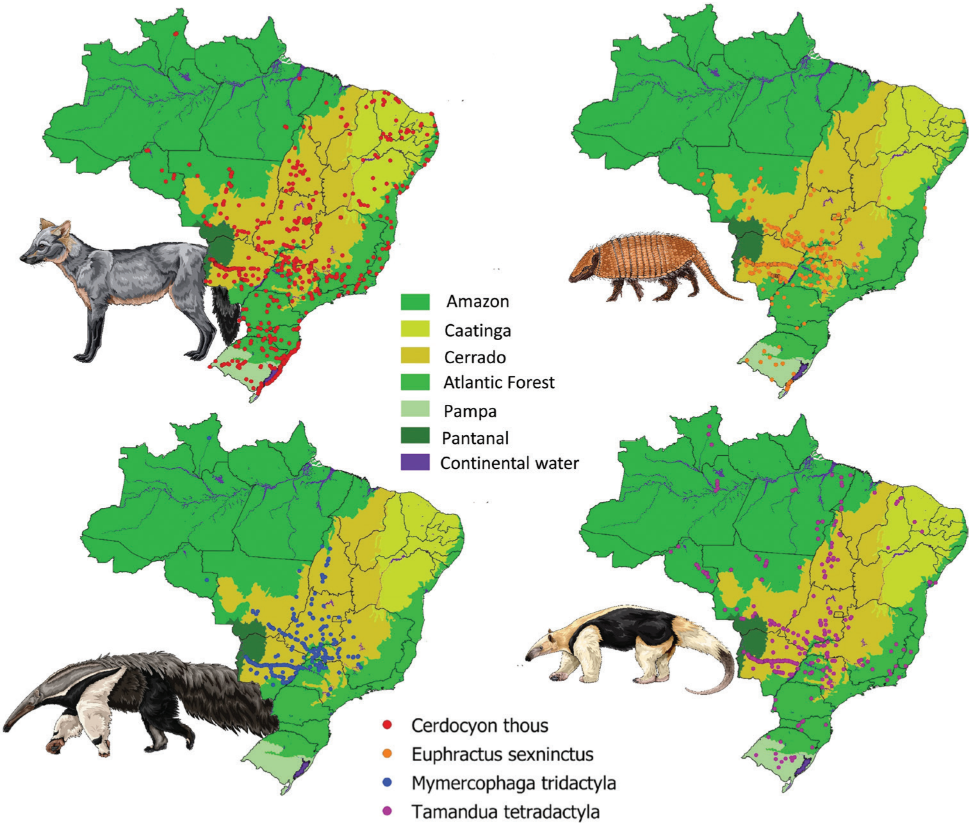

Figure 2. Roadkill samples distribution for the species studied. *Cerdocyon thous* represents the majority of roadkill samples, covering the entire territory. The other three species have samples aggregated in central Brazil, mostly in the Cerrado ecosystem.

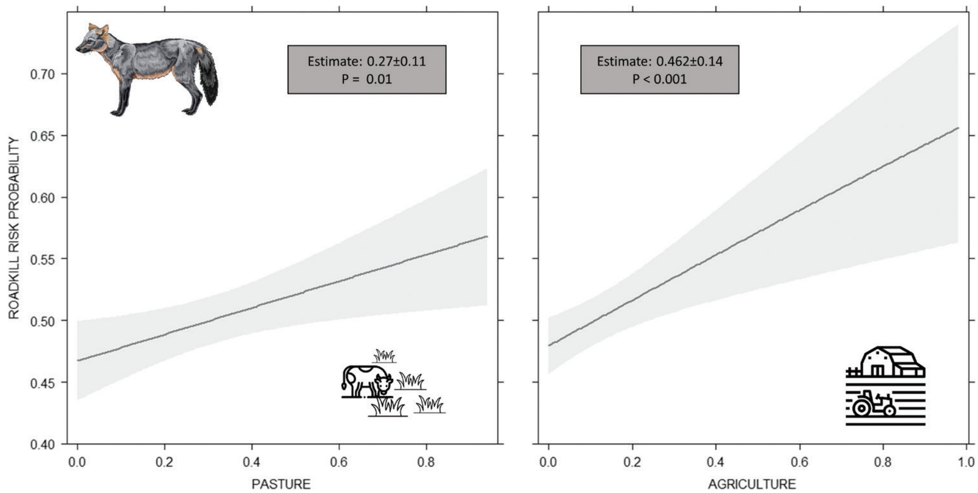

Figure 3. Best model selected by AIC for *C. thous* and its estimated coefficients. A model with two variables responded better to *C. thous* roadkill risk, being pasture and agriculture positively related to roadkill risk.

Table 1. Model selected by species according to Akaike criteria. dAICc represents the AIC distance; df represents degrees of freedom; weight represents how much the model explain de variables related to all other models; evidence is the highest weight model divided by the weight of the focal model. We just considered models with evidence lower or equal to two.

Species	Model	AICc	dAICc	df	Weight	Evidence
Cerdocyon thous	Pasture + Agriculture	3545.9	0.0	3	0.3080	1.00
Euphractus sexcinctus	Farming + Forestry	1612.4	0.0	3	0.3772	1.00
	Pasture + Agriculture	1612.8	0.3	3	0.3173	1.19
Myrmecophaga tridactyla	Forest + Pasture + Forest:Pasture	1170.6	0.0	4	0.2057	1.00
	Forest + Savanna + Forest:Savanna	1171.5	0.9	4	0.1309	1.57
Tamandua tetradactyla	Savanna + Agriculture + Savanna:Agriculture	1111.4	0.0	4	0.8495	1.00

Discussion

Landscape features – habitat, matrix and species dependency

Cerdocyon thous – The roadkill of this species responds positively to two matrix land-uses, pasture, and agriculture in the landscape (Fig. 3). Since it is a generalist species, it can occur in habitat borders, explore vast areas of human-modified landscapes and even use those regions as home ranges (Ferraz et al. 2010; Bueno et al. 2015). The use of those human-modified habitats by *C. thous* serves to show that habitat quality can also be an important factor when predicting roadkill risk. In those modified regions, the resources availability is scarcer and diffuser in the space than in preserved landscapes, making individuals move more in search of them (Regolin et al. 2021), thus increasing the chance of road encounter and, consequently, the roadkill risk.

Besides giving information on the studied animal mortality, roadkill records are also useful for assessing a species occurrence. We found registers of *C. thous* roadkill occurrences out of its original geographical distribution (Lucherini 2015) (Fig. 4). Originally, the crab-eating-fox had its habitat range limited by the dense Amazon forest, but the high-intensity of land use and land cover changes in the region led to the conversion of this forest into open areas, such as pasture and agriculture. That way, *Cerdocyon thous* may have had its geographical distribution expanded by the land use changes and deforestation in the Amazon forest. The growing agribusiness in the region has synergies with road expansion, which leads to several impacts on local ecosystems (Laurance et al. 2002), leading to fish-bone deforestation patterns (Laurance et al. 2002; Pfaff et al. 2007). These might be related to the savannization phenomena of the Amazon Rainforest (Sales et al. 2020). The fish-bones in the landscape resulted from roads being an arrow of habitat loss, and it was exactly in such regions that our data collection found roadkill registers of *Cerdocyon thous* (Fig. 4), as did other works on this species' roadkills (Gumier-Costa and Sperber 2009; Turci and Bernarde 2009).

As a generalist species, *Cerdocyon thous* occurs, and is roadkilled in fragmented human-modified landscapes with agricultural and pasture uses. As reported for *Chrysocyon brachyurus* (Maned-wolf) in the Atlantic Forest (Bereta et al. 2017) and in Amazon Rainforest (Silva-Diogo et al. 2020), the occurrence of carnivores from open

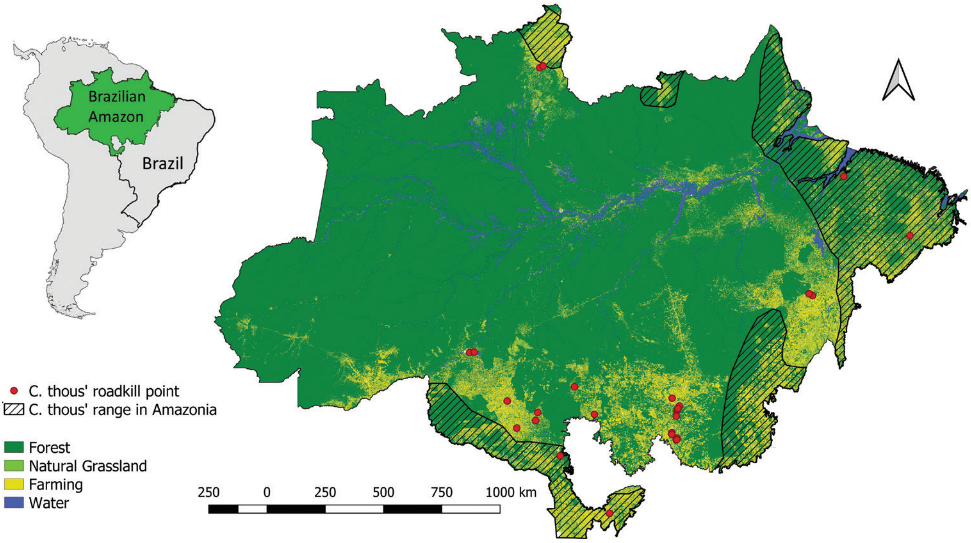

Figure 4. Roadkill records of *C. thous* in Amazon ecosystem. Red dots represent roadkill records of *C. thous* and the hashed area is the original species' range on Amazon. It is possible to notice some registers out of the crab-eating-fox's range according IUCN (Lucherini, 2015), specifically in areas where forests (dark green areas) were converted into farming areas (yellow areas).

environments in forest areas is a result of deforestation, that causes savanna species to expand its occurrence to previously dense forested regions. The creation of those novel ecosystems (Lindenmayer et al. 2008) is related to human-induced modification, and can lead to biotic homogenization (McKinney and Lockwood 1999), when forest dependent species can be replaced for generalist species, compromising the ecosystem functioning. *C. thous* is a generalist species, and its occurrence in Amazon Rainforest can compromise, by competition, populations and the conservation of other niche-equivalent carnivores, like *Atelocynus microtis* (short-eared-dog), a more habitat specialist and forest dependent species (Pitman and Beisiegel 2013).

Euphractus sexcinctus – Like *C. thous*, for this species two land use matrixes are included in the selected model, showing a positive relationship between farming and forestry with roadkill risk (Fig. 5). As all selected models have the same variables (Table 1), we considered, as the most appropriate model, using the one with less complexity to explain the roadkill risk (Table 1, Fig. 5).

This species inhabits a vast number of natural formations, but also human-modified landscapes, such as sugar cane plantations (Dalponte and Tavares-Filho 2004) or even pastures (Anacleto 2007). In the analysis of its threats, the expansion of road network and roadkill is cited as a risk factor (Silva et al. 2015). Since it has generalist habits, its occurrence and roadkill can be associated with commercial tree species in forestry areas, hence its roadkill elevated rates. Forestry regions can be areas of dry soil and low understory coverage, resembling the open dry forests of its original occurrence. The species shows a high density of individuals in the north of São Paulo State, where there is a high landscape coverage of sugar cane, pasture, *Pinus* sp. and *Eucalyptus* sp. cultivation

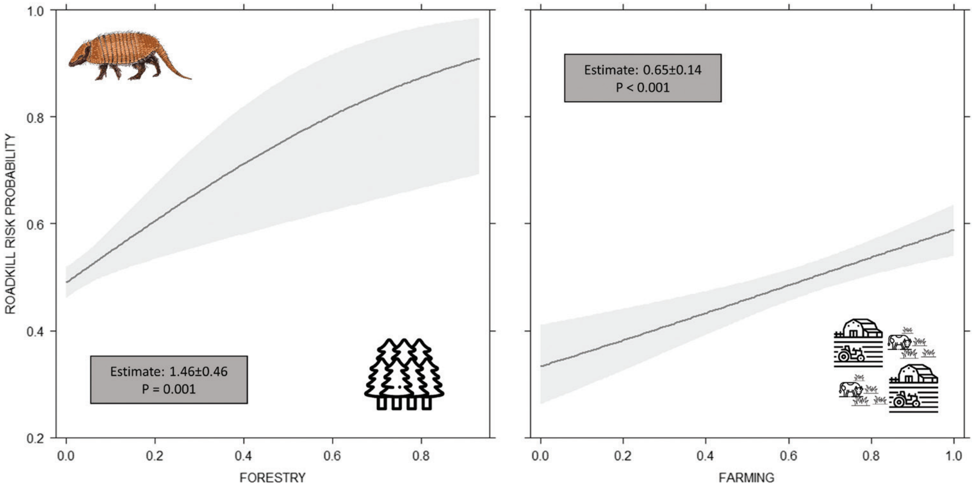

Figure 5. Best model selected by AIC for *E. sexcinctus* and its estimated coefficients. For the six-banded armadillo the best model represents forestry and farming positively related to roadkill risk, showing that the roadkill of this species is related to human modified landscapes.

(Dalponte and Tavares-Filho 2004; Silva et al. 2015), reflecting the areas where these animals are roadkilled. Furthermore, armadillos provide plenty of ecosystem services (Rodrigues et al. 2020), such as soil bioturbation, seed dispersal, and the construction of borrows, which show an important role in sheltering other species for heat control, nesting, and movement (Rodrigues et al. 2020). That indicates the importance of understanding the occurrence and threats to *E. sexcinctus* which can affect other species.

Myrmecophaga tridactyla – the best model to predict the relative risk of roadkill for this species matches with its behavior, including its relationship with pasture, forests and the interaction between these variables (Fig. 6). Among the studied species, this is the only one that is threatened according to national and international sources, considered Vulnerable (VU) in the IUCN red list (Miranda et al. 2014a) and in the national red list of Brazilian threatened fauna (ICMBio 2018). The giant anteater is locally extinct in some Brazilian states, such as Espírito Santo, Santa Catarina and Rio de Janeiro (Bergallo et al. 2000; Passamani and Mendes 2007; FATMA 2011) and it is Critically Endangered (CR) in Rio Grande do Sul (Marques et al. 2002). The main threats to this species are habitat loss and land-conversion to agriculture and pasture (Miranda et al. 2015), as well as the expansion of road network, which causes habitat fragmentation and road mortality. Despite the giant-anteater being frequently associated with savannas, like the Cerrado biome, this animal inhabits a wide range of formation types, such as forests, grass-fields and even pasture and agricultural fields, mainly because its main diet consists of ants and termites, which are very abundant in open areas, but it also has a dependency on shaded areas, like forests and understories (Miranda et al. 2015). Camilo-Alves and Mourão (2006) related this activity to a thermoregulatory behavior (Rodrigues et al. 2008), using open areas in milder temperature during the day and sheltering from the sun in warmer weather (Miranda et al. 2015).

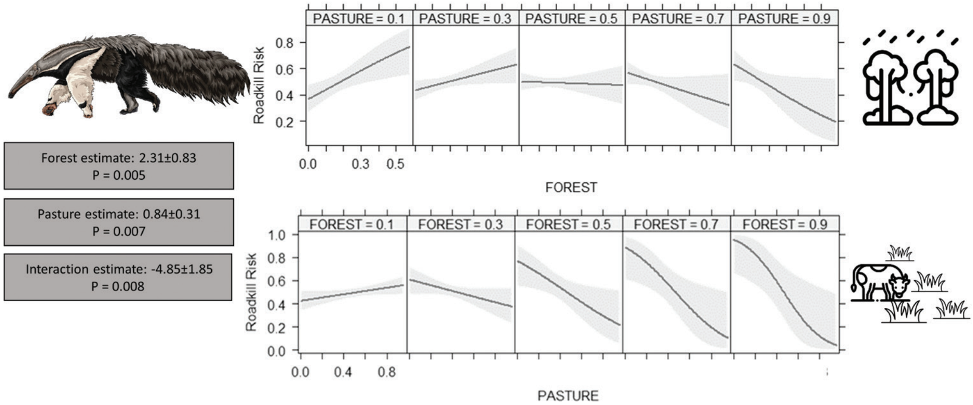

Figure 6. Best model selected by AIC for *M. tridactyla* and its estimated coefficients. The best model shows an interaction between forest and pasture, both variables positively related to roadkill risk, but the size and effect of direction changes according to the proportion of the other variable.

Depending on the amount of matrix in the landscape, the direction of the effect of habitat on roadkill risk changes. In other words, when there are small quantities of forest, the effect of pasture is positive to predict the roadkill, while when there is an increased proportion of forest in the region the effect changes, and the roadkill risk decreases with the increase of pasture areas. This could be related to the species' habits: when the landscape is mostly composed of pastureland, the animals need to move more in search of shaded shelter. This movement decreases in frequency when there are some forested areas in the landscape, allowing the individuals to rest, and therefore, decreasing the chance of encountering a road and consequently being roadkilled. This shows the importance of maintaining habitat patches in the landscape, such as riparian forests or even native vegetation fragments inside private rural property, as established by the Brazilian Forest Code (Metzger 2010). Thereby, we hypothesize that the giant-anteater roadkill risk is associated with larger extensions of monoculture or pasture, without natural formations or habitat patches (Noonan et al. 2021; Versiani et al. 2021).

Tamandua tetradactyla – The roadkill risk of the collared-anteater is strongly related to savanna and agriculture patches, and its interaction (Fig. 7). This species, considered as common in Brazil, is listed as Least Concerned in the IUCN (Miranda et al. 2014b), but in Rio Grande do Sul state it is considered Vulnerable (VU) (Marques et al. 2002). Despite occurring in a wide range of habitats (it can be found in all Brazilian vegetation formations), it has a dependence on areas with tree formation, since it is a semi-arboreal animal that feeds on termites and ants in tree canopies, and finds shelter in hollow trees (Ohana et al. 2015). It is considered a forest dependent species, unlike *C. thous* and *E. sexcinctus*, and is more closely related in terms of habitat needs with *M. tridactyla* (Desbiez and Medri 2010).

This habitat dependence reflects on the best model selected to predict the collared-anteater roadkill risk: the presence of savanna formations modulates the effect of agriculture. When a landscape has no natural formations cover, the effect of agriculture is

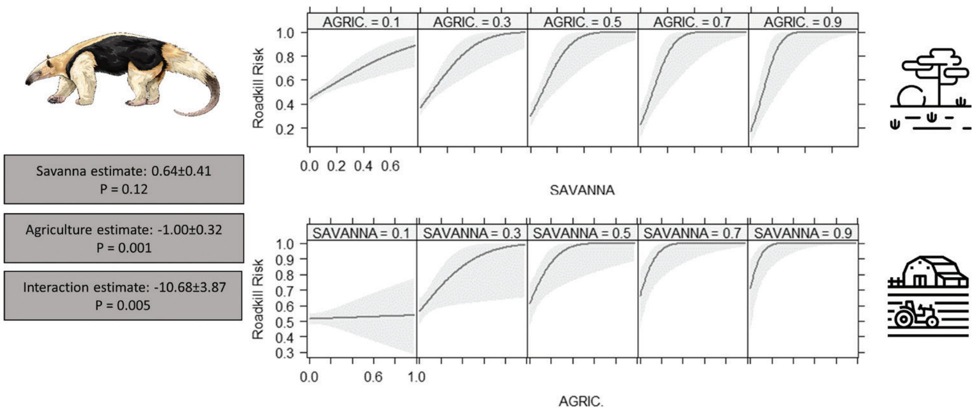

Figure 7. Best model selected by AIC for *T. tetradactyla* and its estimated coefficients. The roadkill risk is negatively related to agriculture. However, the interaction between agriculture and savanna was significant, which changes the effect direction of agriculture in the presence of more savanna areas, increasing the risk of roadkill with the increment of agriculture, in other words, landscapes with savanna and agriculture mosaics are more likely to have collared-anteaters roadkills.

negative, since the species probably do not occur in the area; and with the increment of habitat areas, the roadkill risk increases rapidly, reaching our model's peak when we have at least 40% of savanna and 50% of agriculture.

On the other hand, the roadkill risk when the landscape is entirely comprised of savanna, without agriculture, is very low, and it increases very fast when there is an increase of agricultural coverage. As it is a forest dependent animal, it was unexpected that its roadkill response was better suited to savanna than to dense forests, but that can be explained by this animal's movement pattern. In areas with continuous dense forests the locomotion of individuals occurs mainly through canopies, but in areas with low density of trees, as open areas, savannas and monocultures, it moves by ground. It can also move more often in search for sheltering trees, therefore increasing the chance of being roadkilled.

Limitations and directions for future researches

It is already known that many factors affect the roadkill risk of a species, such as species density and movement patterns (Rytwinski and Fahrig 2013). We also recognize that the home range for each species varies according to each study area, mainly due to differences in habitat quality (Ofstad et al. 2016; Viana et al. 2018). In this research, we aimed to relate roadkill risk with landscape composition in a national scale in a country with continental properties – Brazil, so there is a limitation on the availability of data to better control those factors. We preferred to use the most accurate data we had, which was mean home range for each species, rather than other inaccurate or non-existent data. Others aspects can also affect the roadkill, as nocturnal or diurnal habits; the flux and speed of vehicles in roads; the presence of crossing opportunities, as underpasses and overpasses; the season and weather; and as discussed above, the population density and habitat quality. All those factors can be considered in further research that can compare roads or road segments between themselves, use roadkill rates and model space and time to have more accurate responses. Here, we search for general patterns in large scale considering only space; future research in smaller scales should make an effort to include these variables in the modelling process and analyze how each of them influence the roadkill risk.

Conclusions

For habitat dependent and more sensitive species like anteaters, the effect of the matrix on the roadkill risk depends on habitat availability in the landscape. It changes the strength and direction of the effect according to the proportion of natural areas in the region. As for generalist species, the quantity of human-modified land uses increases the roadkill risk regardless of the habitat availability or natural formations. It also indicates the occurrence of these species in those anthropic areas.

Therefore, the habitat and matrix composition impacts the studied species differently, depending on their demand and habitat dependence. Each species showed different prediction factors regarding their roadkill risk. Overall, all four target species had some dependency on the habitat, but two of them (*Cerdocyon thous* and *Euphractus sexcinctus*) are more tolerant to landscape cover changes, using some human-modified areas as habitat areas. However, the proportion and quality of natural areas should be determinant factors for *Cerdocyon thous* and *Euphractus sexcinctus*' rate of movement, since it influences the chance of crossing a road and dying by roadkill. This movement ecology component needs to be addressed in further studies that relate the type and quality of habitat with species' movement and roadkill rates. Currently, there is not much information regarding those common species with high roadkill rates, especially for *C. thous*, that can potentially cause great amounts of accidents and human injuries on Brazilian roads.

The habitat dependent species have more complex models predicting their roadkill risk, including an interaction component between habitat and matrix. It shows the importance of maintaining the natural coverage of rural properties that, as indicated by Brazilian Forest Code, can potentially decrease the risk of roadkill, connect habitat areas, and increase habitat quality. Given that, areas with vast cover of monoculture and pasture can both decrease the natural populations' size and increase the movement of individuals that can be roadkilled while they are searching for best habitats on the landscape. Since we have shown that not only riparian corridors or continuous habitats are associated with roadkill, but also areas out of protected areas we suggest that more studies investigating the effect of movement in roadkill should be performed. We also highlight the need to consider the landscape as a whole while assessing species protection.

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Supplementary material 1

Correlation plot and R script for building and selecting best models

Authors: Douglas William Cirino

Data type: R script (text file)

Explanation note: Plot of correlations between predictor variables. The script used for reading variables, building statistical models and selecting the best model by Akaike Information Criteria.

Link: https://doi.org/10.3897/natureconservation.47.73010.suppl1