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Giant anteater (*Myrmecophaga tridactyla*) conservation in Brazil: Analysing the relative effects of fragmentation and mortality due to roads

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ABSTRACT

Road networks can have serious ecological consequences for many species, mainly through habitat fragmentation and mortality due to collisions with vehicles. One example of a species impacted by roads is the giant anteater (*Myrmecophaga tridactyla*), currently listed as Vulnerable by IUCN. Here we analysed the relative effect of fragmentation and mortality due to roads on giant anteater populations and show the critical areas for their persistence in Brazil. We estimated minimum patch size and maximum road density to evaluate the impact of the road network and observed road-kills on this species. We explored different scenarios by varying values of dispersal capacity to estimate the minimum patch size, and also of population densities to estimate maximum road density for giant anteater persistence. Our findings indicated that the minimum patch size can be from 498 to 247 km^2 and the maximum road density can vary between 0.21 and 0.55 km/km^2 in pessimist and optimistic scenarios, respectively. In Brazil, habitat fragmentation seemed to have a major impact over giant anteater populations. Habitat fragmentation due to roads seemed to have a more negative effect than mortality due to collisions with vehicles. Critical areas for the species persistence can represent 32% of its range in the optimistic scenario with 18% of suitable patches below the minimum size and 0.1% above the maximum road density. This study provides insights and implications for road networks on giant anteater populations in Brazil and guidance on road density and patch size thresholds for land managers and road agencies charged with planning ecologically sustainable roads in Brazil.

1. Introduction

Habitat fragmentation constitutes a serious threat for mammals worldwide (Crooks et al., 2017) as 27% of mammals are at risk of extinction, and 40% of those at risk due to habitat loss (Schipper et al., 2008). Road networks are one of the primary anthropogenic contributors to habitat loss and fragmentation, and have been highlighted as primary drivers of biodiversity decline and species extinction (Rands et al., 2010; Crooks et al., 2017). Fragmentation can create adverse edge effects on the boundaries of habitat patches (Haddad et al., 2015), decrease landscape connectivity (Cushman, 2006; Jackson and Fahrig, 2011), act as a barrier for animal movement and gene flow (Chen and Koprowski, 2016), and reduce genetic diversity (Balkenhol et al., 2013), all of which can lead to local declines of populations (Bender et al., 1998; Gibbon et al., 2000).

Mortality from collisions with vehicles is a major negative effect of roads on wildlife (Mumme et al., 2000; Gibbs and Shriver, 2002). In general, high mobility species have higher chances of encountering roads compared to less mobile species, and thus, are more affected by road-related mortality (Rytwinski and Fahrig, 2012). The loss of individuals by road mortality can have a strong effect on population viability especially for species with low reproductive rates (Ferreras et al., 2001; Haines et al., 2006; Medici and Desbiez, 2012; Diniz and Brito, 2013).

The importance of road networks to species ecology (e.g. reproduction, behaviour, habitat use) has motivated work on minimum road density estimation. For example, wolves (*Canis lupus*) and pumas (*Puma concolor*) do not maintain breeding groups in areas with road densities > 0.6 km/km^2 (Thiel, 1985; Van Dyke et al., 1986). Basille et al. (2013) observed that Eurasian lynx (*Lynx lynx*) in southern Norway avoided using areas with a road density > 0.41 km/km^2. While these studies provided a road density threshold that can influence the

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species ecology, they did not evaluate the impact of road density on population viability. In fact, few studies have taken this next step. A Canadian study found a positive relation between risk of extinction of birds and mammals and a road density > 0.3 km/km^2 (Anderson et al., 2011). Further, Ceia-Hasse et al. (2017) identified road density thresholds above which carnivore species cannot persist, for example: puma (0.77 km/km^2), jaguar (*Panthera onca*, 0.14 km/km^2), Darwin's fox (*Lycalopex fulvipes*, 0.11 km/km^2).

Population viability analysis has been commonly used to evaluate the impact of human activities on wildlife populations (Beaudry et al., 2008; Brook et al., 2000; Row et al., 2007). Understanding the causes of population declines and ultimately processes contributing to extinction is particularly important to strategically focus actions on populations most at risk (Cardillo et al., 2005; Pereira et al., 2010). Spatially-explicit population models have been extensively used in conservation planning as they combine population dynamic with the spatial structure of landscapes (Ceia-Hasse et al., 2017; Schumaker et al., 2014). Assessing the relative role of habitat fragmentation and additional mortality due to collision with vehicles on population viability is crucial to provide guidance to road managers and help implement more effective mitigation measures.

One species considered particularly vulnerable to roads is the giant anteater, *Myrmecophaga tridactyla* (Miranda et al., 2014). Classified as a Vulnerable species, giant anteater populations show a current decrease trend with records of extinctions in Central America and in the southern parts of its range (IUCN, 2018). According to Freitas et al. (2014), the species exhibits road avoidance when traffic is > 2600 vehicles/day, potentially increasing habitat fragmentation effects and population isolation. Furthermore, road-kill studies regularly detect this species, with road-kill rates up to 0.19 ind/km/year (Fischer, 1997). Although road mortality events are well documented in the literature (de Carvalho et al., 2014; de Souza et al., 2015; Ascensão et al., 2017), little is known about how road networks affect the viability of giant anteater populations (Diniz and Brito, 2013, 2015). Assessing road network effects on persistence of giant anteater populations will inform transportation planning decisions by the Brazilian government as they expand national road networks over the next 20 years (DNIT, 2013; Bager et al., 2015).

In this study, we analysed the effects of habitat fragmentation and mortality due to roads on giant anteater populations in Brazil. We estimated the minimum habitat patch size and maximum road density required for giant anteater persistence under six scenarios. Four scenarios to estimate minimum patch size using all combinations between low and high dispersal capacity with roads as barriers and without roads, and two scenarios to estimate maximum road density thresholds using the minimum and maximum giant anteater population densities. Our findings will identify which of the two road effects are more important for giant anteater persistence, thereby providing road density and patch size thresholds for land managers and road agencies responsible for planning ecologically sustainable road networks in Brazil.

2. Material and methods

2.1. Study area

Our study area comprises the giant anteater range in Brazil (IUCN, 2014), which represents almost 90% (7.5 million km^2) of the entire Brazilian territory (Fig. 1). Forested areas encompass almost 65% (4.8 million km^2) of the study area, followed by open and sparse vegetated areas (shrubs and grasslands) with 17% (1.3 million km^2), croplands 14% (1.1 million km^2), water bodies 1.5% (109,000 km^2), herbaceous vegetation (aquatic or regularly flooded) with 1% (77,000 km^2), and urban areas with 0.5% (30,000 km^2) (GLC (Global Land Cover Share) et al., 2014). The study area covers all of the Brazilian biomes except Pampas in the extreme south. The Amazon, Pantanal and Cerrado biomes are totally represented, while the Caatinga and Atlantic forest are partially represented where the species is considered possibly extinct in southern portions of the latter biome (Miranda et al., 2014).

The study area encompasses nearly 35% (~70 million inhabitants) of the Brazilian human population, where the most populated region is the southeast (IBGE, 2017). The mean paved road density ± SD in the giant anteater range is 0.02 ± 0.07 km/km^2, with the highest value in the south-southeast portions (0.05 ± 0.07 km/km^2) and the lowest in the northern region (0.004 ± 0.03 km/km^2).

2.2. Model parameterization

To model the impact of road networks on giant anteater population persistence we followed the approach of Borda-de-Água et al. (2011). The authors used the reaction-diffusion equation proposed by Skellam (1951) (Appendix information A) to derive two simple formulas (Eqs. (1) and (2)) where the main forces driving population dynamics are dispersal and population growth. The Borda-de-Água et al. (2011) approach assumes that a population occurs in a landscape composed of suitable habitat surrounded by unsuitable areas (e.g. roads) acting as a "sink-habitat" and will not persist when it reaches to 1/e (0.36) of its original size in a time given by the relaxation time equation (Appendix information B). The model is parameterized with the following population features: growth rate in suitable habitat (r_1), dispersal variance (σ^2), and survival on roads specified by a (negative) growth rate (r_0). Model output includes predicted minimum patch size below which populations cannot persist (P_{min}) and maximum road density above which populations cannot persist (D_{max}).

$$P_{min} = \pi^2(\sigma^2/r_1) \quad (1)$$

$$D_{max} = r_1/(r_1+|\ r_0\ |) \quad (2)$$

We estimated the three anteater population parameters using data from the literature (Table 1). We calculated intrinsic population growth rate (r_1) with a simplified version of the Euler equation (Pereira and Daily, 2006; Appendix information C), using the following parameters obtained from Miranda (2004): fecundity (*b*), the interval between litters (years), age at the first birth (years), and a constant mortality rate (μ). To estimate dispersal variance (i.e. dispersal capacity; σ^2), we used the following equation provided by Pereira and Daily (2006):

$$\sigma^2 = (\sigma m/1.18)^2 * \mu,$$

where (μ) is a constant mortality rate assumed as the inverse of lifespan (Table 1), and (σm) the median dispersal distance derived from the equation suggested by Bissonette and Adair (2008): $\sigma m = 7 * (\sqrt{HR})$, where HR is the median of home-ranges (Table 1).

Population growth rate on roads (r_0) is an approximation of the proportion of the population killed on roads and is always expressed as a negative rate. It was obtained using data on giant anteater population density and estimates of road-kill rates using the following equation:

$$r_0 = (N_{killed}/D) * year^{-1},$$

where N_{killed} is the number of individuals road-killed/km/year, D is the giant anteater population density expressed by the number of individuals/km^2 (Table 1) divided by the road width (we assumed all roads were 10 m wide). Only the highest road-kill rate was used to run the model (Table 1).

2.2.1. Minimum patch size estimation

Calculation of P_{min} requires estimation of population growth rate in suitable habitat. Studies on giant anteater habitat use revealed that four land cover types are suitable habitat for the species for foraging, resting and/or reproduction behaviours (Fig. 1): 1) Grasslands; 2) shrubland areas; 3) herbaceous vegetation, aquatic or regularly flooded and 4) forested areas (Bertassoni et al., 2017; Braga, 2010; Camilo-Alves and Mourão, 2006; Medri and Mourão, 2005). We then identified those land

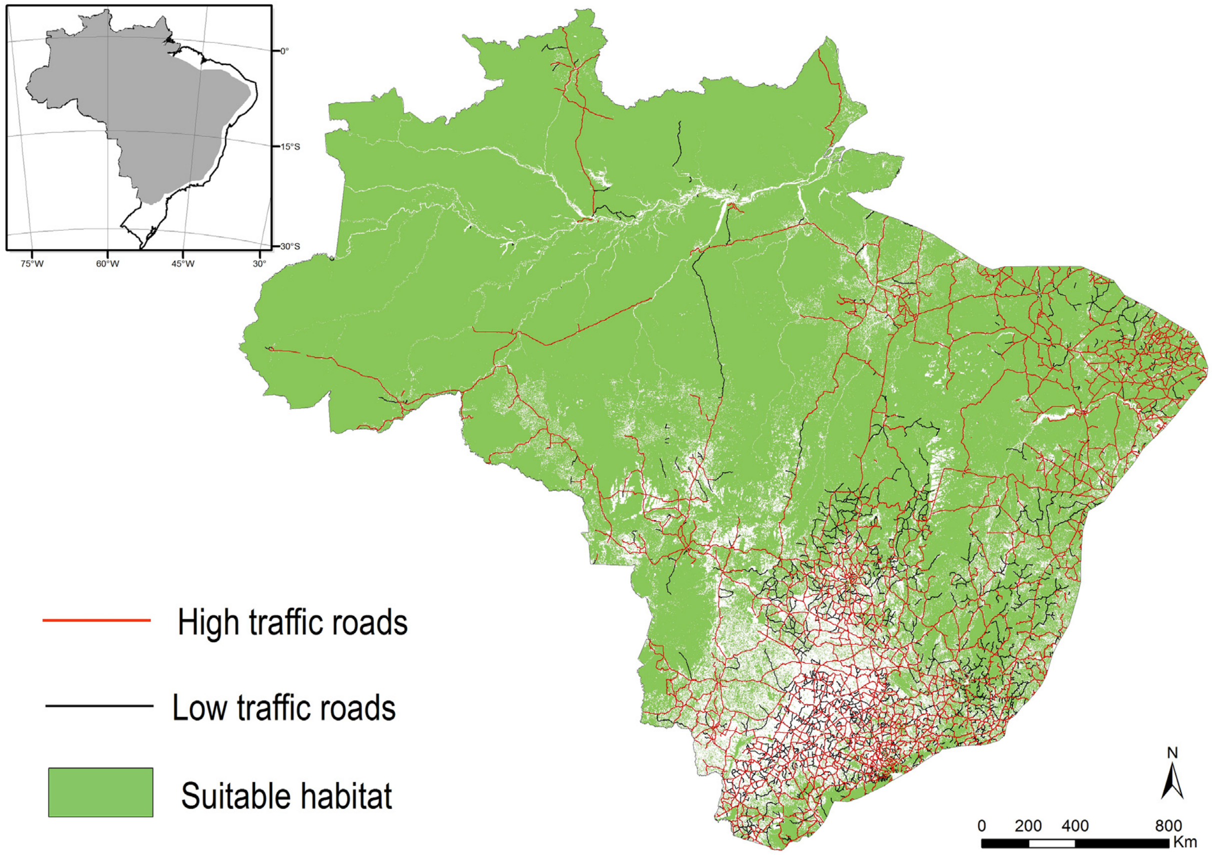

Fig. 1. Extent of suitable Giant anteater habitat in Brazil overlaid with high- and low-traffic volume roads.

cover types at the Global Land Cover spatial data with a resolution of 1 × 1 km (GLC (Global Land Cover Share) et al., 2014).

We used the Equation 1 (Eq. (1)) to estimate the minimum suitable habitat patch size (Pmin) assuming: 1) an infinite carrying capacity (k = ∞), 2) considering explicitly the location of the roads, 3) exponential growth in suitable habitats and 4) that all individuals die when crossing a road (r0 = −∞) (Borda-de-Água et al., 2011; Appendix information A). The last assumption is supported by the fact that animals move at slow speed and by the observation of high road-kill rates (Fischer, 1997; Freitas et al., 2014).

2.2.2. Maximum road density estimation

The Equation 2 (Eq. (2)) was used to estimate maximum road density (D_{max}) above which populations cannot persist, assuming 1) exponential population growth, 2) large dispersal ($\sigma^2 = \infty$), 3) ignoring the spatial location of the roads and considering only the road density, and 4) a large carrying capacity (k = ∞, so the term $1 - N(x, y, t) / K$ in the reaction-diffusion equation is not considered; Appendix information A) (Borda-de-Água et al., 2011).

For maximum road density, we created a grid square of 10 × 10 km^2 over the Brazilian giant anteater range and estimated the paved road density (km/km^2) for each square (Open Street Map, Geofabrik, 2016). We then mapped the D_{max} values in each square of 10 × 10 km^2.

Table 1
Giant-anteater life history variables used for parameterization of minimum patch size (P_{min}) and maximum road density (D_{max}) models.

Parameters used to compute P_{min} and D_{max}	Life-history parameters[a]	Values	References
Population growth rate (r_1)	Fecundity (b)	0.5	Miranda (2004)
	Interval between litters (years)	0.7	Miranda (2004)
	Age at the first birth (years)	3	Miranda (2004)
	Constant mortality (μ)	0.04 (1/25)	Miranda (2004)
Dispersal variance (σ^2)[b]	Median home range size (km^2; Min; Max)[b]	4.7; 9.5	Braga (2010), Medri (2002), Miranda (2004), Shaw et al. (1987) and Medri and Mourão (2005)
Population growth rate on roads (r_0)	Maximum road-kill rate (ind/km/yr)	0.19	Fischer (1997)
	Population density (ind/km^2; Min; Max)	0.15; 0.4	Desbiez and Medri (2010) and Miranda (2004)

[a] Fecundity: the ratio of the number of female offspring regarding to the mean litter size (50% of mean litter size); litter interval: mean interval between litters; age at first birth: age at first reproductive event; mortality: constant mortality rate (inverse of mean lifespan (25 years)).

[b] We estimated minimum and maximum dispersal variances (σ^2) for scenarios P1, P3 and P2, P4, respectively. We used the median of minimum and maximum home-range sizes found in the literature (varied between 2.7 and 11.9 km^2). First, we calculated the median of all values found for giant anteater (8.11 km^2) and then for the values below the median (2.74; 3.67; 5.7; 7.3 km^2) we calculate the median of the minimum home range and for the values above the 8.11 km^2 (8.92; 9.1; 9.83; 11.9 km^2) we calculated the median of the maximum home range.

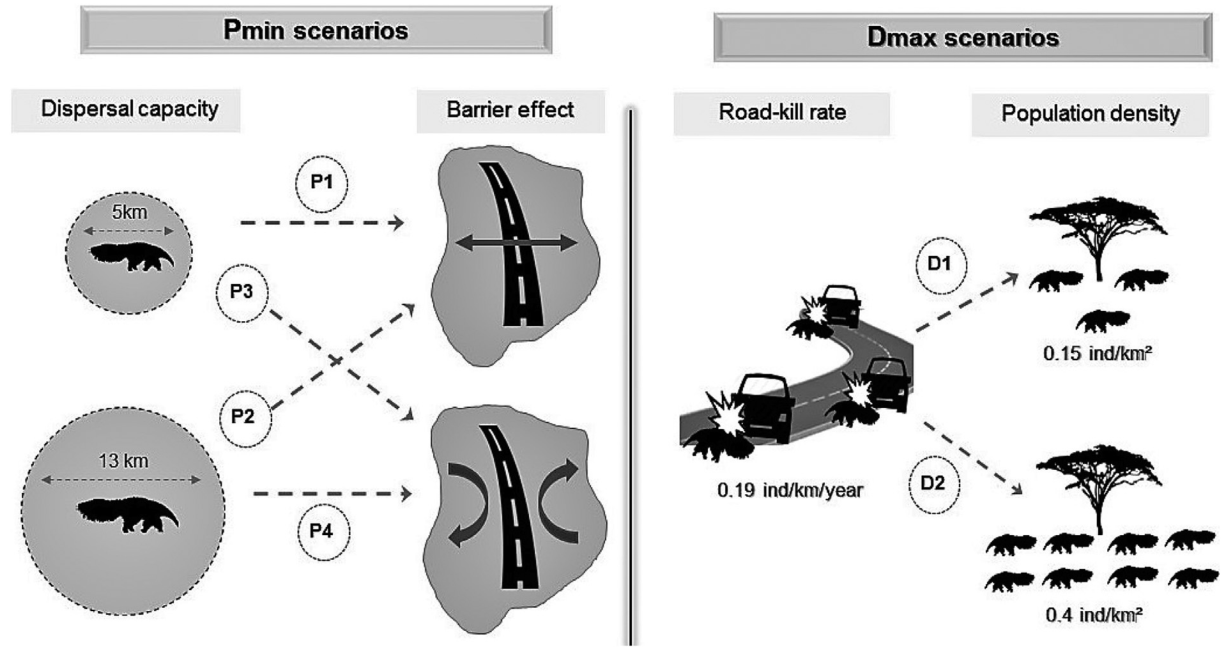

Fig. 2. Four scenarios to estimate minimum patch size (P_{min}) (P_1, P_2, P_3, P_4) and two scenarios to estimate Maximum Road Density (D_{max}) (D_1 and D_2) for giant anteater.

2.3. Scenario development and critical areas

We examined the sensitivity of P_{min} and D_{max} to giant anteater life histories, behaviour, and model assumptions. To assess sensitivity of P_{min}, we varied dispersal variance (σ^2) and barrier effect to create four scenarios: (P_1) limited dispersal capacity (4.7 km^2) and roads do not act as barriers, (P_2) high dispersal capacity (9.5 km^2) and roads are not barriers, (P_3) limited dispersal and roads are barriers, and (P_4) high dispersal and roads are barriers (Fig. 2). To simulate the no-barrier effect of roads (P_1 and P_2), we overlaid our estimated patch sizes with the giant anteater range, ignoring the presence of roads. To simulate roads as a barrier (P_3 and P_4), we intersected estimated patch size with high traffic roads (> 2600 vehicle/day, Freitas et al., 2014) and recalculated the area of each resulting patch in ArcGis. In the absence of official estimates of traffic intensity, we used Open Street Map (Geofabrik, 2016) and reclassified the "motorway", "trunk" and "primary" roads as high traffic roads, and the "secondary" as low traffic roads (Fig. 1). To assess D_{max}, we created two scenarios by combining the maximum road-kill rate (N_{killed}; 0.19 ind./km/yr) with a low and high giant anteater population density estimate (D - 0.15 ind/km^2 and 0.4 ind/km^2, respectively) (D_1 and D_2 scenarios, respectively) (Fig. 2).

We identified areas of low predicted population persistence (critical areas) by overlaying regions with values below the estimated minimum patch sizes (P_{min}) and regions above the maximum road density (D_{max}). We were specifically interested in two contrasting scenarios for critical areas: 1) an optimistic scenario that combines the better P_{min} and D_{max} scenarios ($P_1 + D_2$), and 2) a pessimistic scenario that combines the worst P_{min} and D_{max} ($P_4 + D_1$). We added unsuitable habitats at the sum of critical areas. Most of these areas are composed of anthropogenic landscapes representing poor quality habitats for species persistence (i.e. croplands, water bodies, and urban areas; see Section 2.1).

3. Results

3.1. Minimum patch size

Minimum patch size (P_{min}) for giant anteater population persistence was 247 km^2 with minimum dispersal capacity and 498 km^2 with maximum dispersal capacity. Approximately 18% (1.15 million km^2) and 20% (1.3 million km^2) of suitable habitat was below the minimum patch size considering the scenarios without road barrier (P_1 and P_2, respectively; Fig. A1). When we added roads as a barrier by splitting the patches (scenarios P_3 and P_4), 19% of suitable habitat (1.2 million km^2) and 21% (1.35 million km^2) of the suitable habitats were below the minimum estimated patch size, respectively (Fig. A1). The fragmentation process due to roads as a barrier decreased the amount of suitable patches by 3% (~200 thousand km^2), considering the differences between P1 and P4 scenarios.

3.2. Maximum road density

Our results indicate that the maximum road density (D_{max}) for giant anteater population persistence was 0.21 km/km^2 considering the lowest population density scenario (D_1), that represents 0.95% (71,756 km^2) of the giant anteater range in Brazil. Considering the highest population density scenario (D_2), the maximum road density value was 0.55 km/km^2, that represents 0.09% (6798 km^2) of the species range (Fig. A2). Most of the grid cells with D_{max} are concentrated in southeast portion of the range (Fig. A2) with 5% of the cells having road density estimates above 0.21 km/km^2 followed by the South region with 3.5% with a road density above 0.21 km/km^2.

3.3. Critical areas

The optimistic scenario ($P_1 + D_2$) showed that 32% of the giant anteater range in Brazil (2.4 million km^2) is under critical threats to their population's persistence, while 36% (2.7 millionkm2) was critical considering the pessimistic scenario ($P_4 + D_1$) (Fig. 3). Other two combinations of critical areas (P_3 and D_2; P_2 and D_1 scenarios), showed that 33% (2.5 million km^2) and 34% (2.6 million km^2) of the species range is critical for persistence respectively (Figs. A3, A4). For all combinations, the central and southern species range was the most affected areas. This coincides with the highest human population density and predominantly agricultural areas on the Brazilian landscape. In particular, the southern region of the Cerrado biome is massively fragmented and scattered in small relatively undisturbed areas, unlike the northern region that contains extensive contiguous natural areas of Amazon and Cerrado biomes.

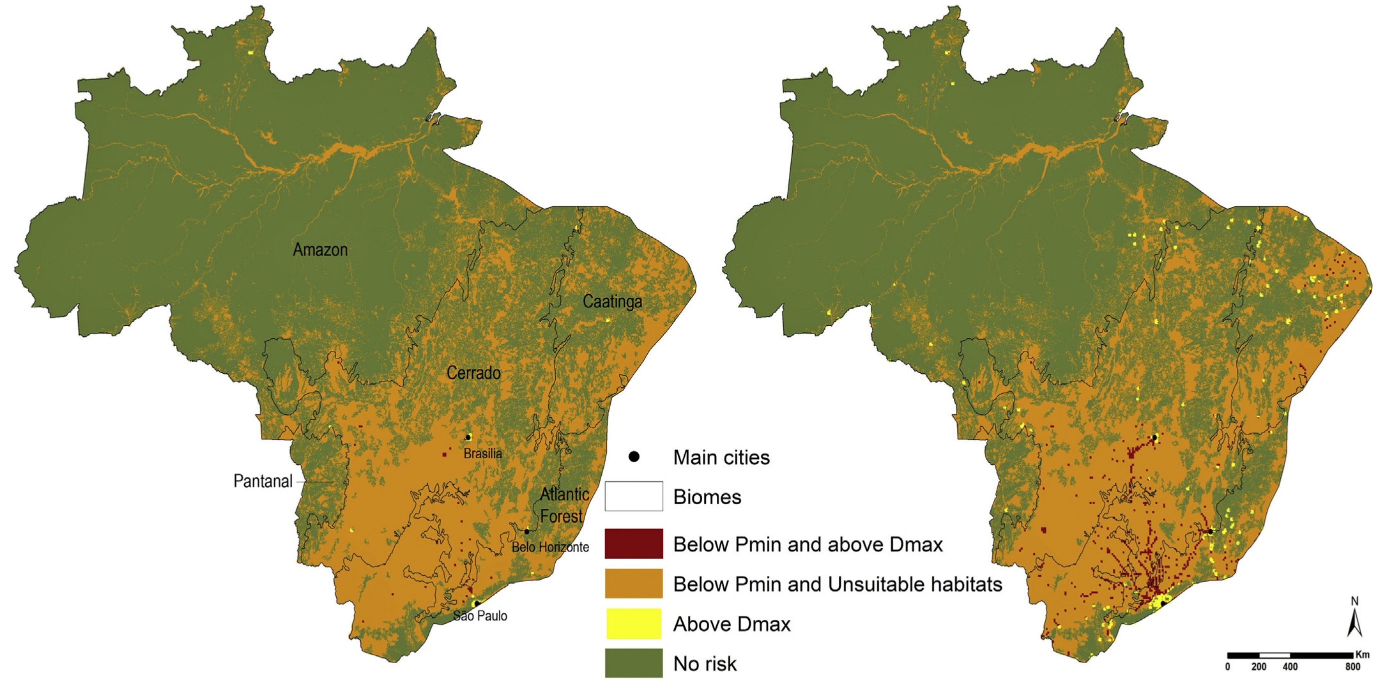

Fig. 3. Critical areas for giant anteater persistence considering the optimistic (left) and pessimistic scenario (right): P_{min} - minimum patch size; D_{max} - maximum road density; No risk - Suitable habitats above P_{min} and below D_{max}.

4. Discussion

Our findings show that habitat fragmentation has a greater impact on persistence of the giant anteater population in Brazil than the observed mortality due to vehicle collisions. Moreover, the effect of roads as a barrier to giant anteater movement, as shown by the modest change in P_{min} (200,000 km^2), seems to be minimal compared to the actual habitat fragmentation due to other human activities. The large area requirements of giant anteaters and current low road density, which does not cause a high proportion of mortality may explain this finding. Our results show that there are few natural patches over 498 km^2 bisected by roads, suggesting that areas covered by the Brazilian road network are already strongly fragmented.

Giant anteaters are flagship species in the Cerrado. This biome harbours most of the giant anteater populations (Miranda et al., 2015) and is currently under serious threat due to habitat fragmentation. Around 46% of the native Cerrado vegetation was lost in the last 60 years (88 million ha), reaching a deforestation rate of 1% per year between 2002 and 2011 and is 2.5 times higher than in the Amazon (Strassburg et al., 2017). Studies showed that maintaining native closed vegetation is crucial for giant anteater habitat use and thermoregulation (Camilo-Alves and Mourão, 2006; Mourão and Medri, 2007) and females reduce their home ranges by avoiding using altered landscapes (e.g. roads and timber plantations) (Bertassoni et al., 2017). Although we did not find a high impact of roads on populations persistence, road network expansion in tropical regions is commonly associated with an increase in others human-related impacts, e.g. urban sprawl and settlements, deforestation, land conversions, hunting (Laurance and Arrea, 2017) that can exacerbate fragmentation effects of giant anteater populations, particularly in the Cerrado biome.

Habitat fragmentation due to anthropogenic impacts affects animal movements worldwide (Cosgrove et al., 2018), reducing one-third to one-half the extent of large-bodied mammals' movement in areas with higher human footprint (Tucker et al., 2018). The establishment of undisturbed natural areas (e.g. protected areas) are important for the conservation of threatened species (Rodrigues et al., 2004), and measures of habitat patch size, shape and connectivity are needed by decision makers. Our study showed two values for the minimum patch size (247 and 498 km^2) directly related to the species dispersal capacity according to the model of Borda-de-Água et al. (2011), which appears to be in line with other predicted values for large-bodied mammals in South America. For example, 116 km^2 for minimum patch size for northern muriqui (*Brachyteles hypoxanthus*) (Brito and De Viveiros Grelle, 2004), 230 km^2 for jaguars (Zanin et al., 2015), and 400 km^2 for carnivore species like the crab-eating fox, maned wolves (*Chrysocyon brachyurus*) and pumas (Ceia-Hasse et al., 2017). Despite the differences in the methods to estimate the minimum patch size, those species have similar demographic attributes such as late sexual maturity (e.g. nine years for northern muriqui females and three years for jaguars females) and small litter size (e.g. two cubs per brood for maned wolf and 2.7 for pumas).

The observed road-kills, per se, did not appear to impose serious risks for giant anteater persistence as only 1% of the Brazilian giant anteater range is above the maximum road density (0.21 km/km^2). This fact may be explained by the low density of paved roads in the study area (0.02 ± 0.07 km/km^2). However, the southeast region with its high road density may threaten the species persistence over the long-term. For example, São Paulo is the most populated and economically developed Brazilian state. Here, 13% of the giant anteater range has an average road density above 0.21 km/km^2. The species is classified regionally as Endangered in São Paulo state (Chiquito and Percequillo, 2009) where remnant Cerrado habitat represents only 1% of the original area and is currently surrounded by pastures, sugarcane fields and road networks (Durigan et al., 2007). Since the Brazilian government intends to increase the road network by adding 129,000 km in the next 20 years (DNIT, 2013; Teixeira et al., 2016) the new areas that exceed the maximum road density could seriously jeopardize giant anteaters persistence in the short or medium term.

Conservation opportunities occur mostly in the central-northern area that encompasses the Amazon Biome and some portions of Cerrado, and the western Pantanal. Most of these regions are roadless or undisturbed areas and still have a considerable amount of suitable patches for giant anteaters persistence according to our model. Undisturbed areas are important to maintain or increase the genetic diversity (Miraldo et al., 2016), that has been observed more diverse to giant anteaters populations living in large protected areas (e.g. Canastra and Emas National Parks and Pantanal biome) when compared to fragmented areas (Clozato et al., 2017). The central and southern portion of the species range, that encompass mainly the Cerrado Biome and some portions of Atlantic Forest, is in more urgent need of conservation efforts as only 2% of the Cerrado is under legal protection (Klink and Machado, 2005). Conservation actions consist of increasing habitat connectivity (Diniz and Brito, 2015; Paviolo et al., 2016), protection of the remnant natural Cerrado habitats (Durigan et al., 2007) and creation of new protected areas.

This study is a first attempt to assess the implications of road networks on giant anteater populations at national scale. A similar approach has been used to assess global exposure of carnivores to roads using a spatially-explicit model and life-history traits (Ceia-Hasse et al., 2017). Demographic parameters were obtained exclusively from giant anteater studies avoiding generalizations using allometric relations (Pereira and Daily, 2006). Similarly, we classified suitable habitats based on the scientific literature rather than using just the species range. The effect of roads as barriers and road-related mortality on this species were analysed by exploring different scenarios of road-kill rates, population densities, dispersal capacity and road avoidance (Diniz and Brito, 2015, 2013). With this approach, we were able to make more precise and informed inferences regarding the limitations of the model.

Our results, however, should be interpreted with caution. For example, giant anteaters do not avoid low traffic volume roads (Freitas et al., 2014) and can use unpaved roads for dispersal (Vynne et al., 2011; Braga, 2010); we considered only paved roads in the model. Paved roads represent about 12% of the Brazilian road network (DNIT, 2013). With this model we may be underestimating the impact of roads on this species. On the other hand, we assumed the highest observed road-kill was constant over the entire study area and giant anteaters used the most suitable habitat. In this case, we may be overestimating the impact of roads on giant anteaters. Due to lack of information on population densities near roads, we used values from undisturbed areas (Desbiez and Medri, 2010; Miranda, 2004). Population densities can decrease near roads (e.g. Benítez-López et al., 2010; Torres et al., 2016), which can be another reason the impact of road networks in our study may be underestimated. Further, the demographic parameters used were the same over the species range, although studies indicated these can vary regionally (Medri, 2002; Miranda, 2004; Shaw et al., 1987) depending on the amount of suitable habitat available and level of fragmentation (Bertassoni et al., 2017; Desbiez and Medri, 2010; Braga, 2010).

The critical values for patch size and road density presented here can be useful for land managers and road planners charged with protected area conservation and minimizing transportation impacts. The minimum patch size presented in our model can be interpreted as a minimum reserve size to serve as a basis for creation of protected areas or increasing their size for giant anteater conservation. The location of critical areas can provide guidance for land managers to target efforts to promote wildlife corridors or stepping stones. Corridors and stepping stones can be a key strategy to maintain continuity between small habitat patches for giant anteater populations (Carvalho et al., 2009; Vynne et al., 2011). This is important because currently protected areas, particularly on Cerrado biome, may not be large enough or effective in conserving and maintaining populations of large-bodied terrestrial mammals (Diniz and Brito, 2015; Eduardo et al., 2012). Moreover, the results presented here for the giant anteater are broadly informative about the risk for other threatened mammals that share similar life histories and high exposure to roads, such as maned wolf, puma (Ceia-Hasse et al., 2017), and Brazilian tapir (*Tapirus terrestris*) (Medici and Desbiez, 2012). Using critical road density threshold areas, transportation practitioners are then able identify where populations of giant anteaters would be impacted by future transportation infrastructure projects in Brazil, including the clearing of habitat for new roads and also prioritizing road segments for mitigation (Teixeira et al., 2016; Ciocheti et al., 2017). Future research on giant anteater life history parameters such as demography, habitat use, dispersal capacities and even road-kill rates will be valuable for refining and improving the model. This will be important for applying the model at a smaller, regional scale for informing transportation project planning and design. Studies that evaluate the genetic differentiation or gene flow (Balkenhol and Waits, 2009; Herrmann et al., 2017) on giant anteaters populations in roaded landscapes could also be an important means of validating the efficacy of our model.

5. Conclusions

Our results contribute to understanding the effects of the Brazilian road network on populations of giant anteater. We highlighted the negative effect of habitat fragmentation showing that large portions of giant anteater habitats are below the minimum patch size for sustaining viable populations. The proportion of areas above the maximum road density is low and concentrated on central-southern areas, which may increase given Brazil's ambitious plan to expand their transportation infrastructure network. The critical values for minimum patch size and maximum road density shown here can be important for transportation practitioners, land managers and decision makers responsible for mitigating transportation impacts and giant anteater conservation. It will also be useful for conservation non-governmental organizations to hold agencies accountable for using the best science available in planning transportation projects and protected areas in giant anteater range. Our framework can be applied at different spatial scales, e.g., examining regional differences in the role of road networks on giant anteater populations. We also encourage further research on the ecology and population biology of giant anteaters, which will help strengthen model inference capability.

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Appendix A. Reaction-diffusion equation

The population dynamics and dispersal given by (Skellam, 1951; Borda-de-Água et al., 2011):

$$\frac{\partial N(x,y,t)}{\partial t} = \begin{cases} \frac{\partial 2}{2}\nabla 2\ \mathrm{N}\,(\mathrm{x,y,t}) + \mathrm{r1N(x,y,t)}\left(1 - \frac{N(x,y,t)}{K}\right) & \text{if } (\mathrm{x,y}) \notin \text{road} \\ \frac{\partial 2}{2}\nabla 2\ \mathrm{N}\,(\mathrm{x,y,t}) + \mathrm{r0N}\,(\mathrm{x,y,t}) & \text{if } (\mathrm{x,y}) \in \text{roa} \end{cases}$$

where $N(x,y,t)$ is the population density on location (x,y) at time t, and K the carrying capacity; the symbol Δ^2 stands for $(\partial^2/\partial\ x^2 + \partial^2/\partial^2\ y^2)$. The first term on the right-hand side of the equation describes the changes in time and space of the density of a population on the basis of its dispersal distance, assuming a Gaussian distribution. The second term on the top branch corresponds to logistic growth (outside roads) and n the bottom branch corresponds to population decay on roads (assumed by a negative growth rate where $r_0 < 0$) (Borda-de-Água et al., 2011). r_0 is interpreted here as an instantaneous mortality rate when an individual cross a road, measuring the loss of individuals from a specific population.

Appendix B. Relaxation time equation

We can determine the time to extinction of a population in a nonviable patch, that is, one with area, A, smaller than that of the minimum patch size, P_{min} (Borda-de-Água et al., 2011). The relaxation time, t_{rel}, defined as the time a population takes to reach 1/e of its original size, because it obviates the need to define the density threshold below which the population is extinct, which can be different for different populations. Counting from the moment roads were built, t = 0, the time the population takes to reach 1/e of its original abundance is:

$$\mathrm{trel} = \frac{1}{\frac{\partial 2}{2}k2 - r1},$$

where $k^2 = \pi^2 / L^2 + \pi^2 / (\alpha L)^2$.

Appendix C. Intrinsic population growth equation

The intrinsic population growth rate (r_1) follows the methodological approach made by Pereira and Daily (2006), that used a simplified version of Euler equation based on life history species-specific parameters that includes: Age at first breeding (β) (year); Inter-litter interval, (Δ) (year); Fecundity (b); and Constant mortality rate (μ). So, the implicit equation for (r_1) is then:

$$b\,X \int_0^{\infty} \sum_{y=0}^{\infty} \delta(x - y\Delta - \beta) e^{-(r1+\mu)x}\, dx = 1,$$

where δ(x) is the birth pulse function, which has a value of 1/T for x between 0 and T and 0 elsewhere. This equation can be solved numerically to determine r_1.

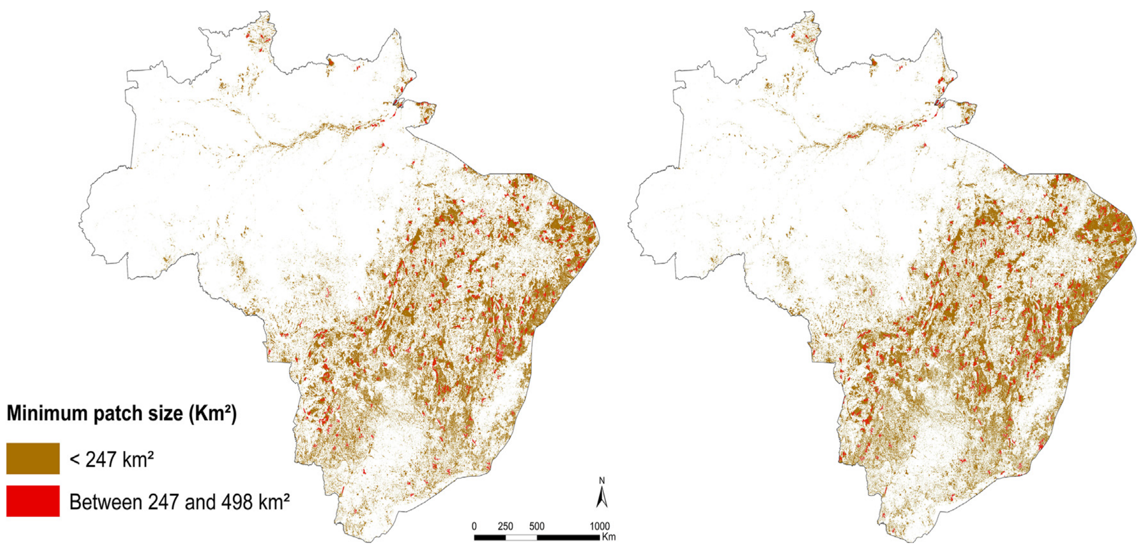

Fig. A1. Maps showing areas below the minimum patch size (P_{min}) for each of the four scenarios. P_1 and P_2 scenarios (left) - Areas below 247 km^2 and areas between 247 and 498 km^2 (that represents the amount of area below the P_{min} added by P_2 scenario) considering the low and high dispersal capacity respectively. P_3 and P_4 scenarios (right) - Areas below 247 km^2 and areas between 247 and 498 km^2 (that represents the amount of area below the P_{min} added by P_4 scenario) considering the limited and high dispersal capacity when roads acting as a barrier.

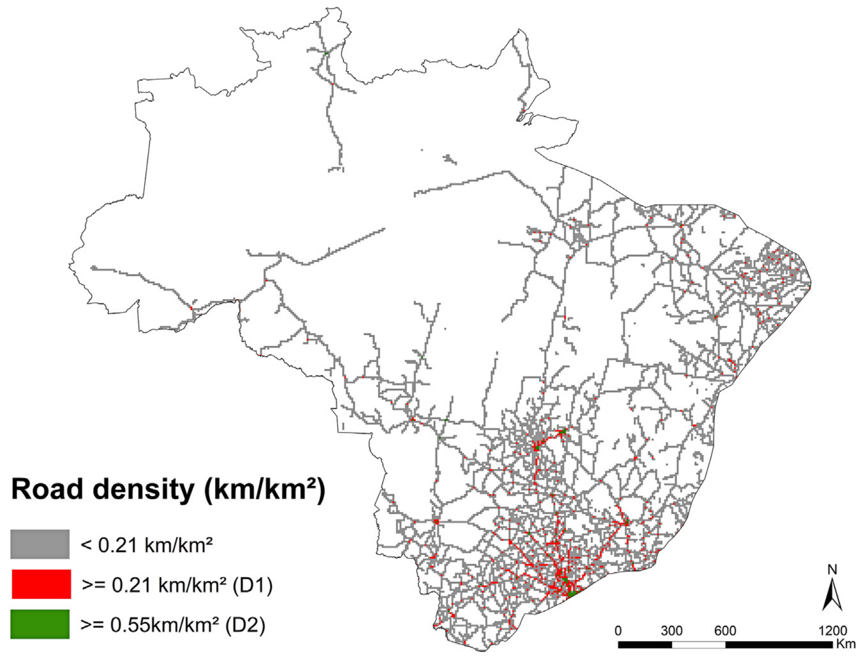

Fig. A2. Paved road density per 10 km × 10 km grid cell over Brazilian giant anteater range showing the results of the scenarios D1 and D2.

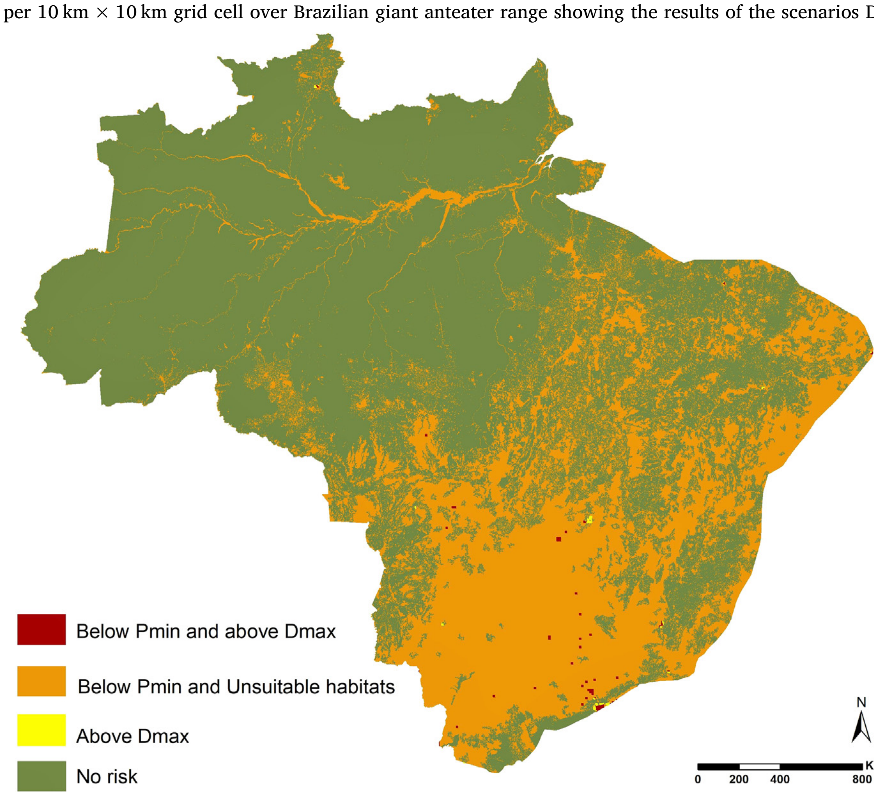

Fig. A3. Critical areas with combined D_2 and P_3 scenarios.

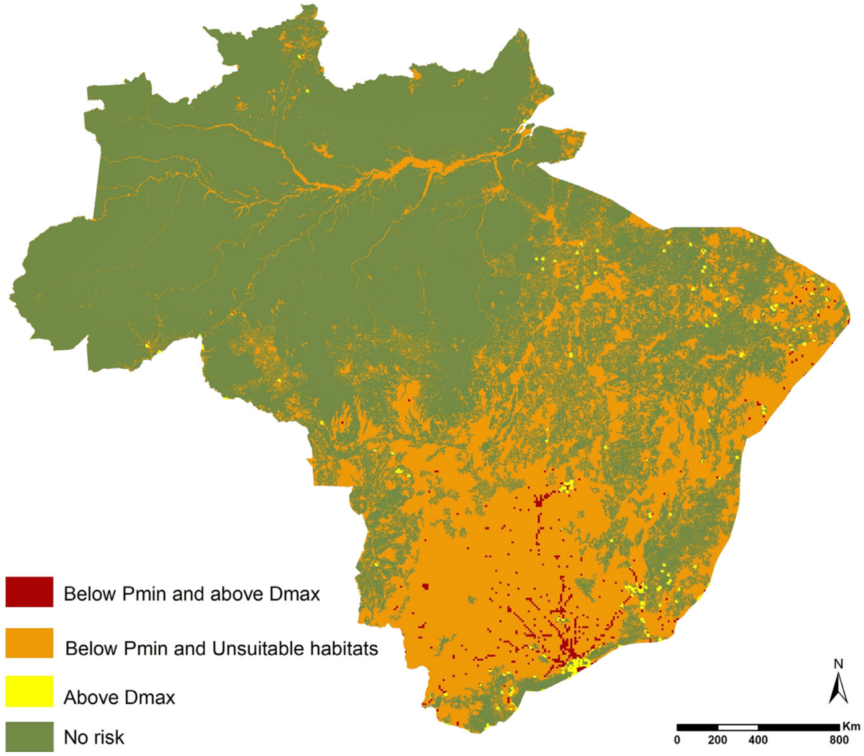

Fig. A4. Critical areas with combined D_1 and P_2 scenarios.

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