Spatial and species-level predictions of road mortality risk using trait data

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Spatial and species-level predictions of road mortality risk using trait data

Running title: Trait-based predictions of roadkill risk

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Biosketch

Manuela González-Suárez is a lecturer at the University of Reading interested in understanding how species' traits influence vulnerability to extinction and anthropogenic threats from a local to a global scale. She has recently become interested in road ecology working in Africa and South America. Flavio Zanchetta completed his MSc in road ecology working to understand the factors that affect wildlife-vehicle collision risk in Portugal and Brazil. Clara Grilo is currently a researcher at Federal University of Lavras, Brazil. Her primary interest is applied ecological research namely examining role of human activities on landscape and wildlife. In recent years, her research has focused on road ecology, mainly the effects of roads on the relative abundance, behaviour, mortality risk and implications on genetic structure and population viability of birds and mammals in Portugal, Spain and Brazil.

Abstract

Aim: Wildlife-vehicle collisions are recognized as one of the major causes of mortality for many species. Empirical estimates of road mortality show that some species are more likely to be killed than others but to what extend this variation can be explained and predicted using intrinsic species characteristics remains poorly understood. This study aims to identify general macroecological patterns associated to road mortality and generate spatial and species-level predictions of risks.

Location: Brazil

Time period: 2001-2014

Major taxa: Birds and mammals

Methods: We fitted trait-based random forest regression models (controlling for survey characteristics) to explain 783 empirical road mortality rates from Brazil, representing 170 bird and 73 mammalian species. Fitted models were then used to make spatial and species-level prediction of road mortality risk in Brazil considering 1775 birds and 623 mammals which occur within the country's continental boundaries.

Results: Survey frequency and geographic location were key predictors of observed rates, but mortality was also explained by species' body size, reproductive speed and ecological specialization. Spatial predictions revealed high potential standardized (per km road) mortality risk in Amazonia for birds and mammals, and additionally high risk in Southern Brazil for mammals. Given the existing road network, these predictions mean more than 8 million birds and 2 million mammals could be killed per year in Brazilian roads. Furthermore, predicted rates for all Brazilian endotherm uncovered potential vulnerability to road mortality of several understudied species which are currently listed as threatened by the IUCN.

Conclusion: With a fast-expanding global road network, there is an urgent need to develop improved approaches to assess and predict road-related impacts. This study illustrates the potential of trait-based models as assessment tools to better understand correlates of vulnerability to road mortality across species, and as predictive tools for difficult to sample or understudied species and areas.

Introduction

Roads are increasingly prevalent features in global landscapes (Laurance & Balmford, 2013; Ibisch, Hoffmann, Kreft, Pe'er, Kati, Biber-Freudenberger, ..., & Selva, 2016) leading to growing concerns about their impacts on wildlife (Alamgir, Campbell, loan, Goosem, Clements, Mahmoud, & Laurance, 2017). Wildlife-vehicle collisions are one of the most visible road-related impacts (Coffin, 2007), which can reduce population abundance, limit dispersal, decrease genetic diversity, and ultimately threaten population viability (e.g., Fahrig & Rytwinski, 2009; Borda-de-Água, Grilo, & Pereira, 2014; Grilo C, Del Cerro, Centeno-Cuadros, Ramiro, Román, Molina-Vacas, Fernández-Aguilar, …, & Godoy, 2016). However, not all species appear to be equally affected by road-associated risks (Fahrig & Rytwinski, 2009). Variation among species can reflect methodological issues: small species degrade faster and are less conspicuous, which can reduce their detectability once collision has occurred, leading to underestimated rates (Santos, Carvalho, & Mira, 2011; Teixeira, Coelho, Esperandio, & Kindel, 2013). Differences may also occur due to true variability in collision risk associated to local abundance, more common species being more likely to suffer high mortality rates (Ford & Fahrig, 2007; Santos, Mira, Salgueiro, Costa, Medinas, & Beja, 2016). However, detectability and abundance do not appear to be the only sources of variation. For example, the lowland tapir *Tapirus terrestris* and the crab-eating fox *Cerdocyon thous* have similar detectability and observed population densities in the Brazilian Pantanal region (0.4 ind/km² - Desbiez, Bodmer, & Tomas, 2010), yet estimated mortality rates vary considerably (fox: 0.24 ind/km/year; tapir: 0.01 ind/km/year. Souza, Cunha, & Markwith, 2014). An explanation is that variability in road mortality rates among species is also explained by species' traits related to ecological habits, behaviour, and life-history traits.

Species' traits can influence mortality risk via one or more of the processes that lead to collision. First, the probability of encountering roads can be influenced by how the animal moves on the landscape and acquires resources (Grilo, Molina-Vacas, Fernández-Aguilar, Rodríguez, Ramiro, Porto-Peter, & Revilla, 2018). Previous studies have shown higher risks for passerine birds that forage on foliage or bark and inhabit woodlands (Santos et al., 2016), for herbivorous and omnivorous mammals (Barthelmess & Brookes, 2010; Cook & Blumstein, 2013), and for more habitat generalist mammals (Núñez-Regueiro, Branch, Fletcher Jr, Marás, Derlindati, & Tálamo, 2015). Second, the probability of crossing an encountered road may be affected by how the road is perceived and the animal's mobility

(Jaeger, Bowman, Brennan, Fahrig, Bert, Bouchard, …, Toschanowitz, 2005). For example, nocturnal species appear to have higher risk because low traffic volume at night may prevent roads from being perceived as a threat (Grilo, Sousa, Ascensão, Matos, Leitão, Pinheiro, …, & Revilla 2012). Conversely, species exposed to regular hunting or poaching may be more aware of the human-associated risks often linked to roads, which lead them to avoid roads and thus reduce the risk of collision (Laurance, Croes, Tchignoumba, Lahm, Alonso, Lee, Campbell, & Ondzeano, 2006). Finally, the probability of being hit if crossing can be influenced by the animals' agility, behaviour, and its visibility to drivers (Legagneux & Ducatez, 2013). Collectively these previous results have shown that individual traits can be useful to understand road mortality risk, but to gain a comprehensive understanding and develop valuable predictive tools we need to simultaneously evaluate multiple ecological, behavioural and life-history traits for a diverse group of species.

Trait-based models are powerful tools commonly used in macroecological studies to assess the mechanisms underlying the response of species to impacts and predict risks for unstudied or difficult-to-detect organisms (González-Suárez, Gómez, & Revilla, 2013; Bland, Collen, Orme, & Bielby, 2015). Here we used machine-learning trait-based models to assess the role of a wide range of species' traits on estimated road mortality rates for bird and mammalian species in Brazil. We focused on birds and mammals because these are well-studied groups that provide a suitable empirical dataset (e.g. Coelho, Kindel, & Coelho, 2008). Brazil is also an interesting case study because in the last two decades economic and social growth has led to a 20% increase in the road network, increasing impacts on wildlife (DNIT, 2015) and this growth is likely to continue and expand into regions of exceptional biological diversity and global ecological importance like the Cerrado and the Amazon (Hoorn, Wesselingh, TerSteege, Bermudez, Mora, Sevink, …, Antonelli, 2010; Lahsen, Bustamante & Dalla-Nora, 2016). Therefore, there is an urgent need to better understand and predict road risks within Brazil to guide infrastructure planning and mitigation measures, including the protection of those species that are most susceptible to road impacts. To achieve this goal we fitted trait-based models to predict road mortality rates for all Brazilian birds and mammals including the many species for which roadkill estimates are not currently available (unstudied or undetected organisms). These predictions allowed us to identify unstudied species with high vulnerability to road-related mortality, and revealed areas where road impact is likely high. Our study provides a first comprehensive evaluation of the key intrinsic risk factors associated with road impacts in endotherms, and demonstrates the potential of using macroecological approaches for road ecology to define predictive trait-based models that can identify potentially vulnerable species and high risk areas.

Methods

Data

Empirical road mortality rates for birds and mammals were collected from unpublished databases (made available by individual researchers contacted via the *Lattes* platform http://lattes.cnpq.br), grey literature sources (technical reports, proceedings of scientific conferences, MSc and PhD theses), and scientific papers from peer-reviewed journals. Published sources were located using the following keywords in English and their translations to Portuguese: ("roadkills" OR "road mortality") AND ("birds" OR "mammals" OR "vertebrates"). We considered only rates from areas of Brazil in which systematic surveys had been conducted at least once a week for a minimum period of three months to minimize the bias on roadkill rates among studies. From each study, road mortality rates per species were calculated as the number of individual carcasses detected standardized per kilometre of surveyed road per year (ind/km/year). Rates may be underestimated because not all carcasses persist equally in the pavement. In addition, in some studies not all carcases were identified or reported at the species level. The calculated rates were modified using a correction for carcass persistence estimated by Santos, Carvalho, & Mira (2011) that aims to reduce bias from variable detection rates among species (see Appendix S1 in Supporting Information). Both corrected and uncorrected rates were tested to evaluate consistency of results. We present the corrected rates in the main text, but results did not change qualitatively when using uncorrected rates (see Appendix S2). We characterized the study location using the geographic coordinates of the surveyed road(s) midway point (Appendix S3, Fig. S3.1). Taxonomic names used by each study were matched to the current IUCN taxonomy (IUCN 2017). One mammalian species with empirical road mortality data (*Guerlinguetus ingrami*) was not recognized by the IUCN and was not considered in the analyses. *Coendou spinosus* was listed as two different species (*Coendou villosus* or *Coendou spinosus*) in separate studies but treated as one species in our analyses.

We identified Brazilian birds and mammals based on overlap of distribution range maps (IUCN 2017) with the continental Brazilian territory (based on the IUCN country boundary map). We used distribution range polygons classified as presence “Extant” or “Possible extant” and included all origins and seasonalities. These range polygons were also overlapped with a 1º x 1º grid (equivalent to ~110 x 110 km near the equator) covering the continental Brazilian territory.

We considered 12 species’ traits as potentially important to predict the vulnerability of species to road mortality and used published trait databases to find information on all Brazilian birds and mammals (see Table 1 for details).

Data analysis

We modelled empirical road mortality rates using random forest regression trees, a machine learning technique that uses bootstrapped data samples to generate multiple regression trees from which the importance of the predictors is defined (Breiman, 2001). Regression trees have high predictive accuracy and the capacity to deal with complexity in relationships including non-linearities and interactions (Cutler, Edwards, Beard, Cutler, Hess, Gibson, & Lawler, 2007). Regression trees have also been show to offer comparable results to phylogenetic methods that explicitly account for the fact that related species may share similar traits due to shared evolutionary history (Bielby et al., 2009). While incorporating phylogenetic information into regression trees is not possible, to capture the potential importance of phylogeny we included taxonomic order (following the classification of the IUCN, 2017) as a predictor in our models.

Rates from birds and mammals were analysed separately to reflect the intrinsic differences between these groups. For each imputed version (15 per taxonomic group) we fitted a random forest model with 2000 trees using the randomForest procedure from the randomForest library (Liaw & Wiener, 2002) in R version 3.4.1 (R Core Team 2017). Model predictors included traits (Table 1), taxonomic order, and the three survey related predictors for each study: survey interval (time between surveys in days), and latitude and longitude of the surveyed road(s) midway point.

Trait data were not available for all species (data limitations are common in comparative studies, see González-Suárez, Lucas, & Revilla, 2012). To avoid excluding observations, which can lead to biases, we estimated missing values for each taxonomic group using nonparametric imputation based on random forest regression trees (Stekhoven & Bühlmann, 2012). Since this imputation approach results in slightly different values each time it is run, we imputed and analysed 15 datasets for each taxonomic group to capture uncertainty in the imputation process and assess sensibility of results to that uncertainty. To facilitate reproducibility and encourage open science the code (R script) and data used in this study will be available at https://dx.doi.org/ 10.6084/m9.figshare.6237608 on 9 November 2018.

We assessed overall model performance using the total variance explained. We also calculated the importance of each variable by permuting all observed values within each variable across observations and evaluating the effect on model performance (changes in variance explained). The permutation of important variables decreases significantly the model performance whereas the permutation of less important variables should have little effect on the model performance.

Fitted models were subsequently used to generate predicted values for each Brazilian species in each of its occupied 1º x 1º grid cells, representing a hypothetical systematic survey across all Brazil (cells treated as studies sites). Geographic coordinates were defined as those of the grid cell centroid. The survey interval was set to the observed median value (3.5 days between surveys for both birds and mammals). Different survey intervals did not qualitatively affect results (Appendix 3 figure S3.2). We used the median prediction from the 15 models based on the different imputed datasets for each cell and species combination. Predicted risk for each species (species-level predictions) was then calculated as the median of the predicted rates over all its occupied grid cells; thus, reflecting intrinsic vulnerabilities and spatial risks within the species' distribution range. Spatial predictions were generated by aggregating predicted values for each grid cell, thus, summarizing risk associated to geographic location and to the intrinsic vulnerabilities of co-occurring species. We calculated a standardized risk based on ind/km/year, and a predicted total risk (ind/year) obtained by multiplying the standardized risk by the total kilometres of paved road within each grid cell. Road network data were obtained from the Openstreetmap available at https://www.openstreetmap.org. As there is limited knowledge on the responses of the different species to roads, our approach assumes no specific road avoidance.

Results

We located 38 studies that reported road mortality rates in different areas of Brazil and met our criteria of minimum frequency and period of survey (Figure S3.1). From these studies we obtained 417 mortality rates for 170 bird species, and 366 road mortality rates for 73 mammal species. Based on current distribution range maps we identified 1831 birds and 623 mammals as present in Brazil. We made predictions for all mammals, but had to exclude 56 bird species classified in taxonomic orders not represented in our empirical dataset (predictions cannot be made for new levels in a categorical variable). All data are available on (to be deposited on online repository upon acceptance, and made available as supplementary files for review).

Some species were reported by multiple studies, for example the smooth-billed ani *Crotophaga ani* was the most frequently detected bird (16 studies), while the crab-eating fox was the most frequently reported mammal (32 studies). However, many species were only observed in one study (90 bird species and 26 mammals). Observed (corrected) road mortality rates ranged from 0.001 to 7.61 ind/km/year for birds (highest rate was observed for *Crotophaga ani*). For mammals rates ranged from 0.0007 to 18.52 ind/km/year (highest rate was reported for the capybara *Hydrochoerus hydrochaeris*).

Fitted models explained 61.7% of the observed variance in road mortality rates for birds (median value, range across imputed datasets 61.1-62.4%) and 51.8% for mammals (range 51.2-52.4%). As expected survey predictors were important in both groups (Fig. 1). In particular, survey interval was the most important predictor with intervals of 1-2 day generally associated with higher estimates both for birds and mammals (Figs. 2 and 3). Geographic location also explained observed road mortality rates (Fig. 1) with partial dependence plots showing higher rates associated to western locations for both birds and mammals, but contrasting patterns for latitude, with locations closer to the equator associated with higher risk in birds but with lower risk in mammals (Figs. 2 and 3). Taxonomic order was an important predictor for birds with higher rates found among cuckoos and anis (Cuculiformes, eight species) and flightless birds (Cariamiformes, one species; Struthioniformes, four species). Order was also important for mammals, with higher rates among anteaters and sloths (Pilosa, 6 species) and armadillos (Cingulata, six species).

The analyses also revealed several species' traits as predictors of road mortality rates in both birds and mammals with high consistency among models based on the different imputed datasets (Fig. 1). Partial dependence plots show higher road mortality rates in birds associated to larger body mass (>2 kg), earlier maturity ages, shorter lifespans, ground foraging behaviour, and habitat and diet generalism (Fig. 2). For mammals, higher rates were associated with scavenging behaviour, early maturity, smaller home range sizes, intermediate body masses (3-50 kg), and habitat generalism (Fig. 3).

Model predictions matched empirical data well for mammals, but showed a tendency to overestimate low values for birds (Fig. S3.3). Both observed and predicted rates showed considerable within-species variation. Overall, median observed and predicted road mortality rates per species were lower among species with more threatened conservation status as defined by the global IUCN Red List status (Fig. S3.4).

Median predicted rates for all Brazilian species ranged from 0.02 to 0.37 ind/km/year for birds and from 0.02 to 1.08 ind/km/year for mammals. Among species without empirical data, the blue-black grassquit *Volatinia jacarina* and Reig's grass mouse *Akodon reigi* had the highest predicted rates (0.37 and 1.08 respectively, data available at – online repository). High rates were also predicted for several unstudied species of conservation concern, including the white-lined antbird *Myrmoborus lophotes* and the rufous-fronted antthrush *Formicarius rufifrons*, both birds listed as Near Threatened by the IUCN Red List (predicted median rates of 0.30 and 0.28 ind/km/year, respectively), and the greater Wilfred's mouse *Wilfredomys oenax* (Endangered status, predicted median rates of 0.93 ind/km/year) and the Lami tuco-tuco *Ctenomys lami* (Vulnerable status, predicted median rates of 0.44 ind/km/year).

The map of standardized predicted spatial risk (the sum of all predicted mortalities per kilometre of road per year for species co-occurring in a given grid cell) showed high expected roadkill rates in the western Amazon region for both birds and mammals, and also high mammalian rates in the Pampas region (southern Brazil), with the lowest values generally found in eastern Brazil (Fig. 4a, b). These patterns were consistent when representing median standardized predicted risk, the rates expected for an average species in each cell per kilometre of road (Fig. S3.5). Areas with high predicted risk generally also showed high variability among species (high standard deviation. Fig S3.5), reflecting differences in intrinsic vulnerabilities of the local fauna. These spatial standardized risk patterns did not solely reflect species richness. For example, the highest road mortality rates for mammals were predicted in southern Brazil where mammalian richness is lowest (Fig. 4e, f).

When considering the existing road network to estimate total mortality (number of mortalities per year in each grid cell, Fig. 4c, d), the patterns, as expected, changed, and revealed higher total predicted risk in coastal areas where most roads are found (Fig. S3.6). However, total mortality did not exclusively reflect existing roads. For example, risk was high in Western areas (Mato Grosso and Rondonia) where there are relatively few roads, and relatively low in the Northeast region where road density is high. Worryingly, in some areas total risk was very high with expected rates of over 96,000 individual birds and over 53,000 individual mammals killed per year in some 1º x 1º areas. Adding all predicted rates across the country our results suggest that as many as 8,351,120 birds and 2,225,101 mammals could be killed per year in Brazilian roads. Considering potential impacts of additional planned paved roads (Fig. 3.7) we find increased risk in the Amazon, which we identify as a sensitive area (with high standardized and median risk rates).

Mapping predicted rates only for threatened species we found a slightly different spatial pattern with highest risk found in the eastern Amazon (Fig S3.8). The predicted total risk suggests as many as 179,601 threatened birds and 73,031 threatened mammals could be killed per year in Brazilian roads.

Discussion

Our results provide evidence that road-associated mortality risk is not randomly distributed among species and can be partly explained by ecological, behavioural and life-history traits in avian and mammalian species. Previous studies explored the role of individual traits (e.g. Ford & Fahrig, 2007; Cook & Blumstein, 2013), but our results reveal that road mortality is associated to a combination of multiple predictors that reflect diverse characteristics of the studied species. Although analyses were conducted separately, we found that several traits explained vulnerability to traffic for both bird and mammal species suggesting generalized intrinsic sources of risk for endotherms, for example associated with body size. Our study also identified distinct sources of vulnerability, which highlight idiosyncrasies of the studied species and/or distinct mechanisms associated with vulnerability for birds and mammals. In addition, road mortality also varied among taxonomic groups, potentially reflecting untested characteristics. For example, for mammals we found higher rates among relatively slow moving species like armadillos and sloths, while for birds flightless groups exhibited higher rates. As expected survey-related variables were also important predictors of risk. Although we used a correction factor, survey interval remained a key predictor for both groups. Our results suggest that 1-2 days intervals between surveys may be optimal to assess risks for these species (those intervals were associated with the higher rates - see also Santos et al., 2011). Survey location was also important for both birds and mammals, with higher predicted risk towards the west in both groups but contrasting latitudinal gradients that identified distinct risk regions within Brazil for birds and mammals.

We observed that species with weights above 2-3 kg had higher risk of being roadkilled, although for mammals the risk decreased again for species above ~50 kg. Generally, larger species tend to be more mobile (Sutherland, Harestad, Price, & Lertzman, 2000), which increases the probability of encountering and crossing roads. However, for the largest mammals, collision risk may be reduced due to earlier detection by drivers, which provides more time for response, and also due to more active avoidance responses by drivers seeking to prevent potentially dangerous collisions. Lower risk among smaller species could be partly explained by variation in detectability during surveys (methodological limitations). Smaller species are more difficult to see, and degrade faster, and this could result in potentially underestimated mortality rates. However, we actually found some increases in risk predicted for some small species, suggesting detectability during surveys does not fully explain this pattern. A previous study also reported a trend for higher mortality rates in smaller birds based on species <1.2 kg (Santos et al., 2016).

Our findings also suggest generalists (those with wider habitat and diet breadths) have higher mortality rates than specialists (although for mammals diet specialization was not clearly related to road mortality risk). However, contrary to previous studies, we did not find an effect of trophic level (Ford & Fahrig, 2007; Cook & Blumstein, 2013). It is possible this difference occurs because those previous studies did not consider diet specialization. By exploring both variables we show that the degree of specialization may be more informative to predict roadkill likelihood than trophic level, at least for birds. In general, specialist species may be less likely to approach and cross roads if these are perceived as unsuitable environments. Previous studies have shown that species that are reluctant to cross open grounds avoid crossing roads due to low availability of cover, and therefore have lower likelihood of being roadkilled (Develey & Stouffer, 2001; Rytwinski & Fahrig, 2012). Moreover, the high availability of resources and refuges in road verges can attract habitat and diet generalist species to roads and increase their risk of being hit by passing vehicles (Ruiz-Capillas, Mata, & Malo, 2012; Barrientos & Bolonio, 2009). Among the resources that may be available near roads are roadkill carcasses, which attract scavengers, potentially increasing their collision risk. Although we found scavenging behaviour of mammals considerably increased mortality rates, there was no clear association for birds. A previous study by Cook

& Blumstein (2013) reported no effect of scavenging behaviour for either group. These contrasting results may be due to individual responses to traffic and risk perception (Jacobson, Bliss-Ketchum, De Rivera, & Smith, 2016) and also be influenced by road-related features including sinuosity and traffic intensity (Grilo, Ascensão, Santos-Reis, & Bissonette, 2011).

Population-level processes can also influence risk with locally abundant species being more likely to have higher mortality rates. Although we did not have abundance estimates for the studied areas, higher local abundance is often associated with faster reproductive rates (e.g., earlier maturity ages) which we found were associated with higher risk of collision in both birds and mammals. However, while consistent with predicted patterns, we note that many estimates of maturity age were imputed, particularly for bird species, thus, support should be interpreted with caution. Future studies would benefit from conducting both roadkill and abundance surveys in the same areas to better understand road-associated risks.

Besides contributing to our understanding of the general drivers of road-associated mortality, our analyses show trait-based models can be used as predictive tools for conservation assessment and management of road-related impacts. Our model predicted high roadkill rates for several species of conservation concern for which empirical estimates are not currently available. Empirical estimates may be unavailable for different reasons: 1) species only inhabit poorly sampled areas (e.g., Amazon); 2) species occur in sampled areas but avoid modified habitats including roads; and 3) species are not detected (e.g., small size bias) or are not correctly identified during surveys due to taxonomic uncertainty or cryptic characteristics. A recommendation that emerges from our study is the need for targeted survey efforts for species identified as potentially susceptible here so their true risk can be quantified and if needed adequate management and mitigation actions can be implemented.

Our results also generate spatial predictions of road mortality risks, which highlight the apparent high vulnerability of Amazonian species (higher risk per kilometre of road). Although mortality rates in this area are likely to be relatively small due to low road density, this region has high biodiversity and our analyses suggest road infrastructure development could have severe impacts on many species. Considering the existing road network, as expected, we found higher total risk in areas with higher road density. However, median risk per species was not always high in areas, like Southern Brazil, with many threatened species and high road densities, perhaps reflecting former population depression due to road mortality (Teixeira, Kindel, Hartz, Mitchell, & Fahrig, 2017). Worryingly, our results suggest that more than 8 million individual birds (nearly 180,000 from species threatened by extinction) and more than 2 million mammals (over 72,000 from threatened species) may be killed each year in existing Brazilian roads. These high values are predicted despite the fact that Brazil has a relatively high number of roadless areas (Ibisch, Hoffmann, Kreft, Pe'er, Kati, Biber-Freudenberger, ..., & Selva, 2016). Furthermore, our rates may be underestimated because we do not consider unpaved roads. We also do not account for other indirect road impacts, such as changes in spatial distribution due to road avoidance (Torres, Jaeger & Alonso, 2016), which can reduce roadkill but may in turn impact population viability in other ways. Future road development is also likely to result in increased risk, particularly in areas we identified as sensitive (with intrinsically vulnerable species), like the Amazon. These results provide a first overview of risk revealing potentially vulnerable species and areas. However, localized and refined spatial predictions (accounting for unpaved roads and traffic levels) would be useful to further describe areas in which road development is likely to have widespread impacts on the local fauna, as well as areas in which mitigation measured would be most valuable.

While our analyses offer useful insights, there are also limitations of the available data. First, missing trait data is a common problem in comparative studies (González-Suárez et al., 2012). Data imputation methods may be helpful but some limitations (e.g. handling variable correlation) need consideration (Penone, Davidson, Shoemaker, Marco, Rondinini, Brooks, …, Costa, 2014). Also imputation of large proportions of the dataset incorporate uncertainty in results, this can be quantified as done here, but results should still be interpreted with caution. In addition, to missing trait data, empirical estimates of road mortality were also not available for all species or areas. Instead, these data reflect a non-random subset of species and locations, associated to biases in research effort and methodological issues. In fact, these biases may explain the relatively abrupt geographic changes in our spatial predictions, particularly for birds. Variation in detectability during surveys is a recurrent problem in road surveys. Carcasses from small species may disappear from roads in less than 24 hours (Teixeira et al., 2013). Carcasses in hot, humid areas, and those with high traffic levels may also disappear faster. We applied corrections to the observed road mortality rates, but our results were qualitatively the same when using uncorrected rates (Appendix 1) contrary to what Santos et al. (2011) found in their study. The criteria we adopted to only include studies with a 7-day minimum survey interval may have contributed to reduce differences; intervals of one week or shorter have been found to significantly reduce bias for medium- and large-sized birds and mammals (Bager & Rosa, 2011). Ultimately, data limitations and biases can only be effectively addressed with additional research efforts. In the meantime, studies using available data should consider uncertainty in results, explore correction methods, and interpret findings with caution.

Overall, our results contribute to a better understanding of the biological drivers that make species vulnerable to road traffic collisions. Previous studies have largely focused on the importance of road characteristics (e.g. traffic, size, and design) and landscape features (e.g. vegetation type, and degree of fragmentation; Saeki & Macdonald, 2004; Grilo, Bissonette, & Santos-Reis, 2009). However, our study shows that using available knowledge on species traits and macroecological approaches can contribute to better evaluate risks and offer insights into species and spatial level risks. Obtained predictions can guide future survey efforts, pointing to poorly sampled areas with potentially susceptible species, and may also be used to plan conservation strategies, road development, and mitigation measures. These predictions also offer insights into the magnitude of the threat imposed by roads, with potentially millions of individual birds and mammals being killed each year within one country.

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Data accessibility

The R scripts and full database including available empirical road mortality rates, trait descriptors, and predicted rates for all Brazilian birds and mammals will be available at https://dx.doi.org/ 10.6084/m9.figshare.6237608 on 9 November 2018.

Table 1. Definitions, hypothesis, data sources and sample size availability for the species traits considered as predictors of road mortality in Brazilian birds and mammals in this study. Total species considered for birds data N_{all}=1831, birds with empirical roadkill rates N_{RK}=170, total mammalian species N_{all}=623, and mammals with empirical roadkill rates N_{RK}=73. Home range and sociality were only considered for mammals.

Trait	**Definition and hypothesis**	**Data source**	**Birds**		**Mammals**	
			N_{all}	N_{RK}	N_{all}	N_{RK}
Diet breadth	Total number of 10 possible dietary categories consumed by each species. Diet generalist are more likely to use resources on road verges and thus, approach roads leading to higher roadkill rates.	Wilman et al., 2014	1527	153	454	70
Scavenger behaviour	Binary descriptor to identify species with diet consisting of ≥10% carrion. Scavengers can forage on roadkill, and thus will spend time on and near roads leading to higher roadkill rates.	Wilman et al., 2014	1700	168	585	72
Trophic level	Trophic level described as: Herbivore (>80% plant diet), Carnivore (>80% animal diet), or Omnivore (<80% animal or plant diet). We used 80% thresholds as some diet data may include accidentally ingested material.	Wilman et al., 2014	1700	168	585	72

	Herbivores are more likely to utilize road verges, where vegetation can benefit from run-off, leading to higher roadkill rates.					
Habitat breadth	Total number of ecoregions within Brazil overlapping the current geographic range area of each species. Habitat specialists are likely to avoid novel environments like roads, leading to reduced roadkill rates.	Dinerstein et al., 2017	1831	170	544	70
Ground foraging	Prevalence of foraging on ground estimated as percentage of use of that substrate for birds. For mammals a categorical variable describing species classified as "ground foragers". Species that forage in arboreal or aerial environments are less likely to be on roads, leading to reduced roadkill rates.	Wilman et al. 2014	1646	167	623	73
Activity cycle	The main period a species is active defined as: nocturnal, diurnal or other. Nocturnal species are active at times with less traffic (which can reduce their perception of risk) and also when visibility is limited for drivers (affecting collision avoidance behaviours), both mechanisms can lead to higher roadkill rates.	Jones et al., 2009; Wilman et al. 2014	1700	168	585	72

Exploitation	Binary descriptor to identify species classified as at risk from direct exploitation based on the IUCN (species classified as affected by categories 5.1 and/or 5.4). Hunted species are more likely to perceive roads as risks and avoid them, leading to reduced roadkill rates.	IUCN Threats Classification Schemes, category 5.1 (Version 3.2).	1643	166	617	73
Body mass	Average body mass in grams of an adult individual. Median values per species based on all available sources. Large species are generally more mobile which could increase roadkill rates.	Jones et al., 2009, Paglia et al., 2012, Wilman et al. 2014,	1664	170	546	72
Home range	Average home range size in km^2. Species with wider home ranges are more likely to overlap with roads, leading to increased roadkill rates.	Jones et al. 2009	*NA*	*NA*	85	30
Lifespan	The maximum recorded age of an individual of the species in days. Median values per species based on all available sources. Species with longer lifespans may be more likely to learn about road risks, leading to reduced roadkill rates.	Jones et al., 2009; Myhrvold et al., 2015	230	36	254	68
Maturity age	Average age in years at which individuals reach sexual maturity. Median values per species based on all available sources.	Jones et al., 2009; Myhrvold et al., 2015	177	30	197	50

	Species with delayed maturation are more likely to prioritize survival, which can lead to greater perception of risk from roads and reduced roadkill rates.					
Sociality	Binary descriptor to identify species in which individual spend most of their lives in a group. Defined as groups size=1 for solitary. Social species can benefit from collective vigilance and learning experienced that can reduce roadkill rates.	Jones et al., 2009	*NA*	*NA*	136	33

Figures and their legends

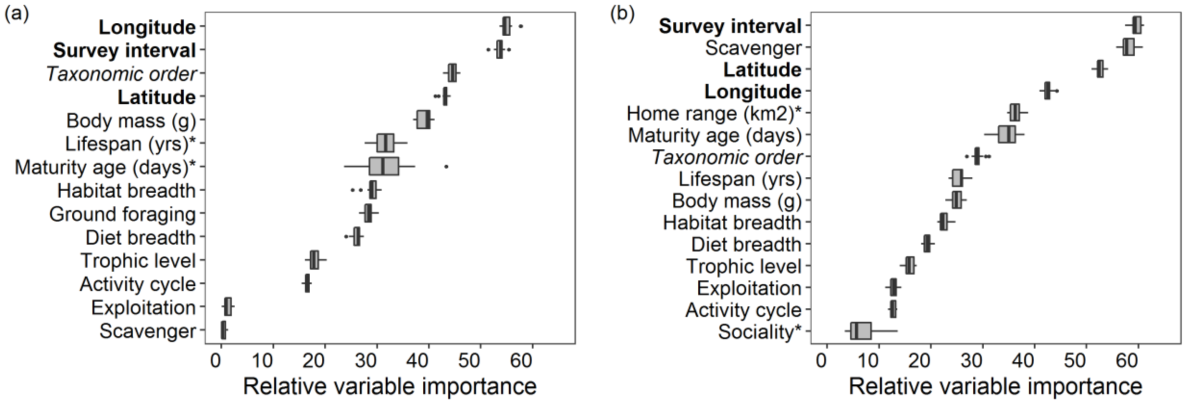

Figure 1. Relative importance of predictors associated with empirical road mortality based on random forest regression models for birds (a) and mammals (b). Boxplots show results for the 15 imputed datasets for each taxonomic group. Study predictors (representing study site coordinates and survey sampling frequency) are in bold, taxonomic predictor (order) is in italics, traits with <50% empirical data are marked with an asterisk.

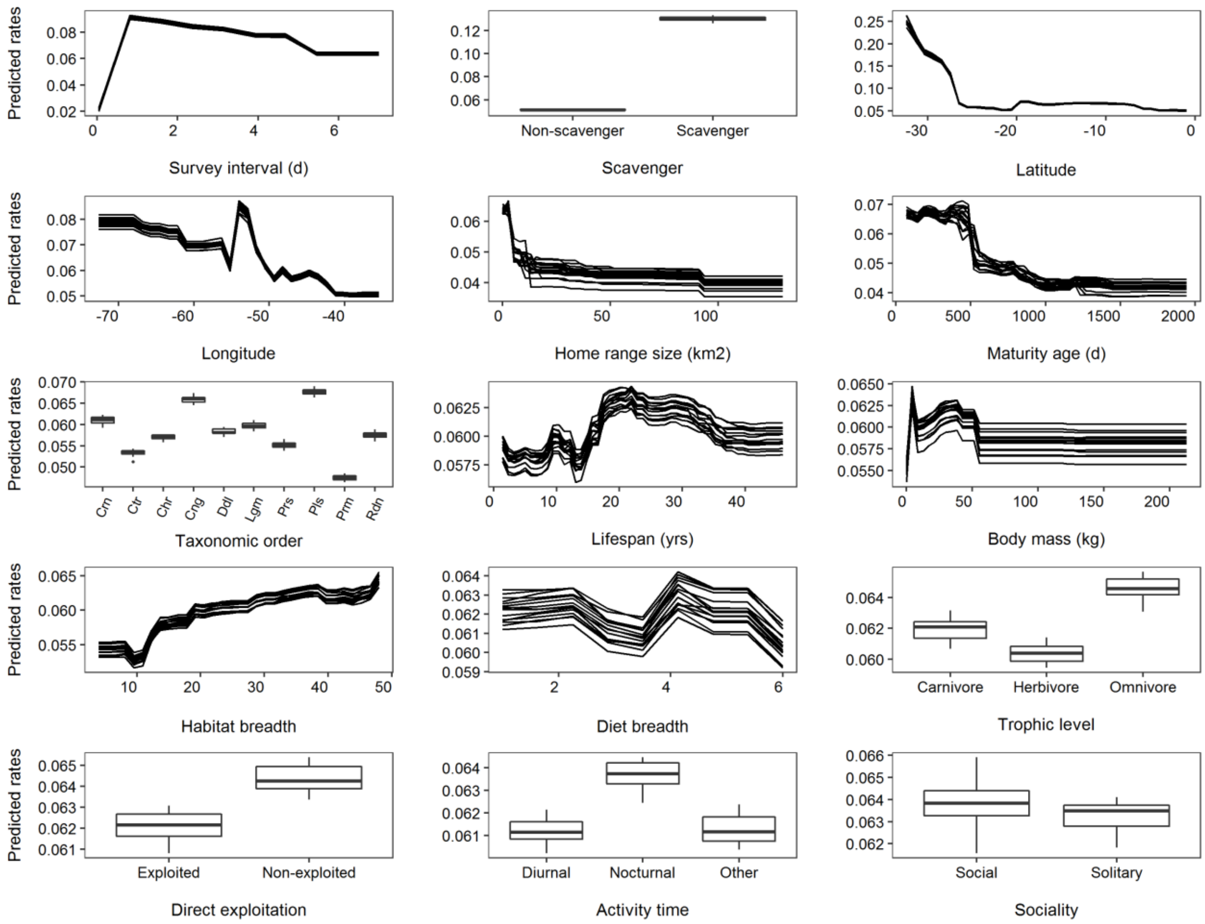

Figure 2. Partial dependence plots for all tested predictors on the predicted road mortality rates of Brazilian birds. Predictors are in descending variable importance order (see Fig. 1a). Showing results for the 15 imputed datasets. Note that y-scales differ among plots. Taxonomic orders are abbreviated as follows: Acc (Accipitriformes), Ans (Anseriformes), Ccl (Cuculiformes), Chr (Charadriiformes), Clm (Columbiformes), Cpr (Caprimulgiformes), Crc (Coraciiformes), Crm (Cariamiformes), Cth (Cathartiformes), Flc (Falconiformes), Gll (Galliformes), Grf (Gruiformes), Pcf (Piciformes), Plc (Pelecaniformes), Pss (Passeriformes), Pst (Psittaciformes), Slf (Suliformes), Strg (Strigiformes), Strt (Struthioniformes).

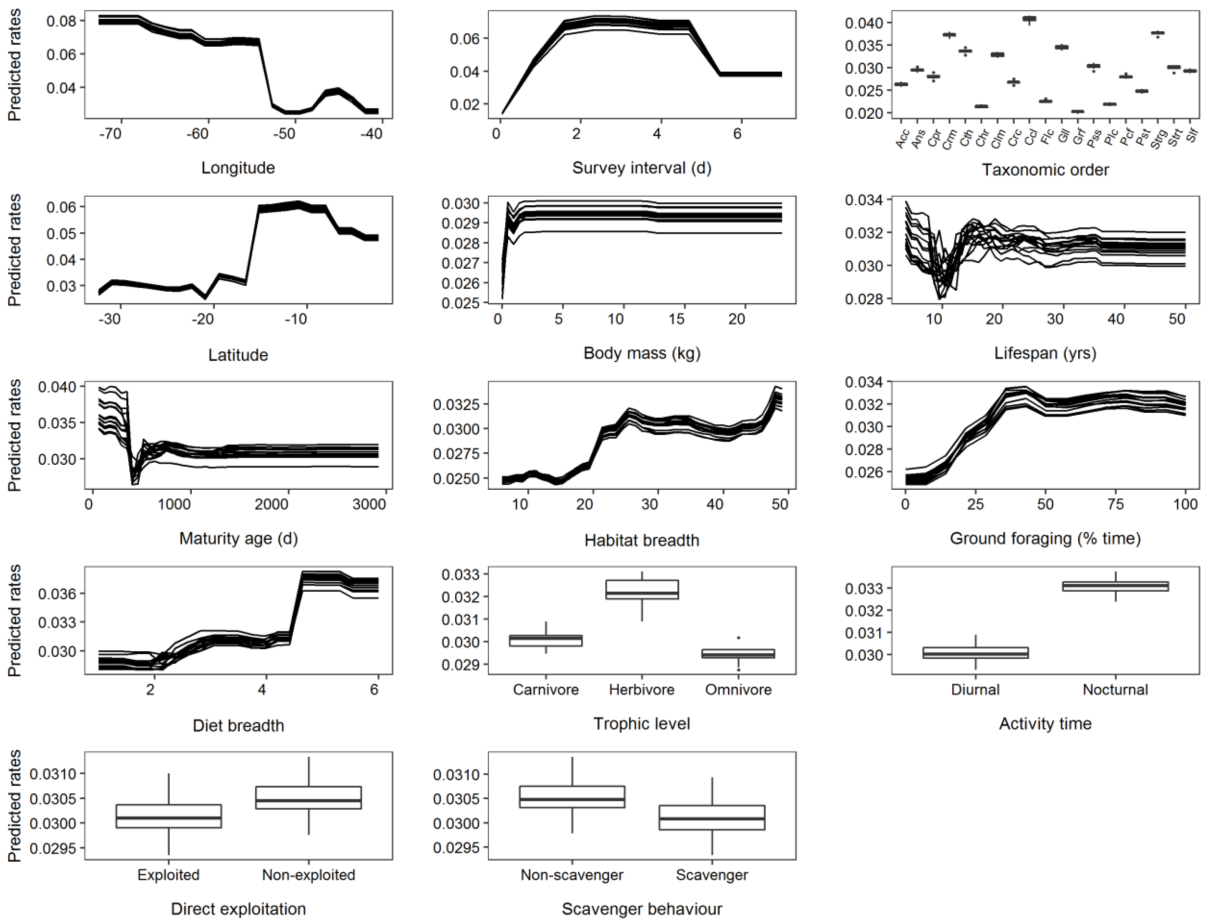

Figure 3. Partial dependence plots for all tested predictors on the predicted road mortality rates of Brazilian mammals. Predictors are in descending variable importance order (see Fig. 1b). Showing results for the 15 imputed datasets. Note that y-scales differ among plots. Taxonomic orders are abbreviated as follows: Crn (Carnivora), Ctr (Cetartiodactyla), Chr (Chiroptera), Cng (Cingulata), Ddl (Didelphimorphia), Lgm (Lagomorpha), Prs (Perissodactyla), Pls (Pilosa), Prm (Primates), Rdn (Rodentia).

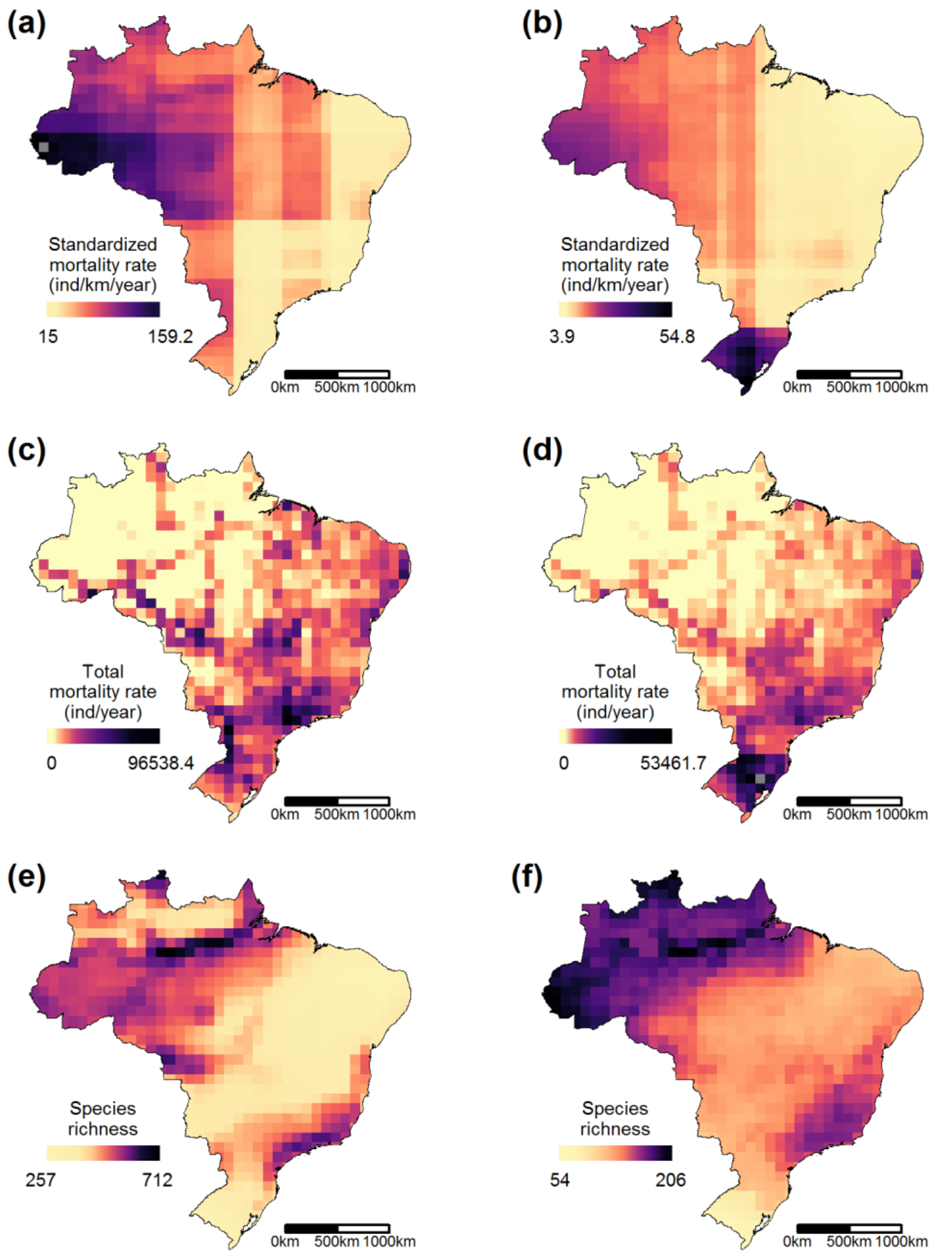

Figure 4. Predicted standardized road mortality rates (in ind/km/year) for birds (a) and mammals (b) in Brazil. Total road mortality rates based on existing paved roads (ind/year) for birds (c) and mammals (d). Total bird (e) and mammalian (f) species richness.

Supplementary information for González-Suárez, M; Zanchetta Ferreira, F; Grilo, C. Spatial and species-level predictions of road mortality risk using trait data. *Global Ecology and Biogeography*

[Appendices S1-S3]

Appendix S1. Correction of mortality rates

We used a correction factor derived from estimates of carcass persistence described in Santos, Carvalho, & Mira (2011). They estimated persistence probability (*S*), which we converted into a correction factor = 1+(1-*S*) adapting their estimates for survey intervals of 1, 2 and 7 days to our observed ranges, and combining some species groups to match our data (Table S1.1). Estimates from studies with survey intervals <1 day (ranging from twice a day to 16 times a day) were not corrected. Body mass was given priority when defining groups (e.g. rates for a bird of prey of 130 g were corrected based on the "Small birds" factor).

Groups	**Survey intervals**		
	1.0-1.4	1.5-3.0	3.0-7.0
Small birds (4-200 g)	1.634	1.797	1.968
Large birds (200-23000 g, excluding birds of prey)	1.283	1.391	1.717
Birds of prey (175-1600 g)	1.255	1.327	1.555
Small mammals (29-300 g)	1.611	1.759	1.970
Large mammals (1100-170000 g)	1.196	1.294	1.457
Bats (20-60 g)	1.854	1.963	2.000

Appendix S2. Results based on uncorrected road mortality rates

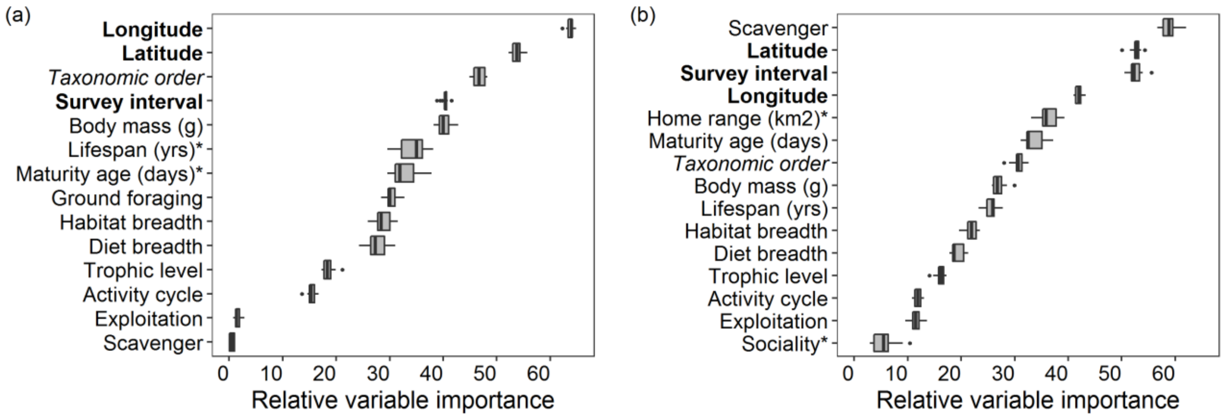

Figure S2.1. Relative importance of predictors associated with empirical uncorrected road mortality based on random forest regression models for bird (a) and mammal (b). Boxplots show results for the 15 imputed datasets for each taxonomic group. Study predictors (representing study site coordinates and survey sampling frequency) are in bold, taxonomic predictor (order) is in italics, traits with <50% empirical data are marked with an asterisk.

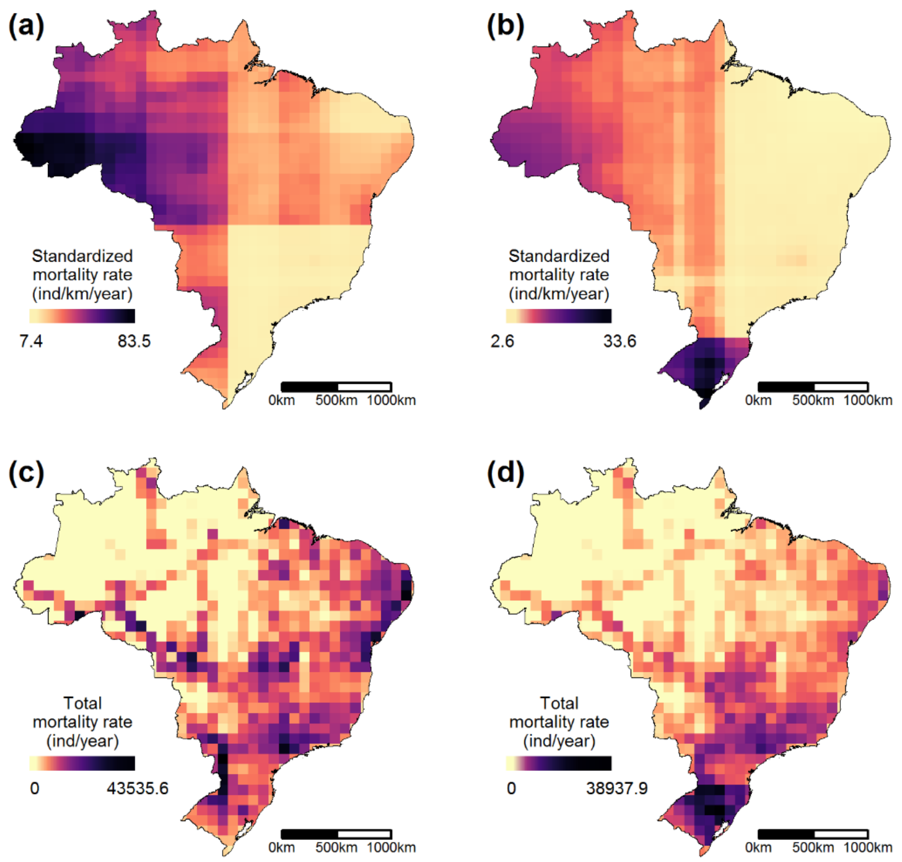

Figure S2.2. Predicted standardized road mortality rates (in ind/km/year) for birds (a) and mammals (b) in Brazil. Total road mortality rates based on existing paved roads (ind/year) for birds (c) and mammals (d). Values based on models fitted for uncorrected road-kill rates.

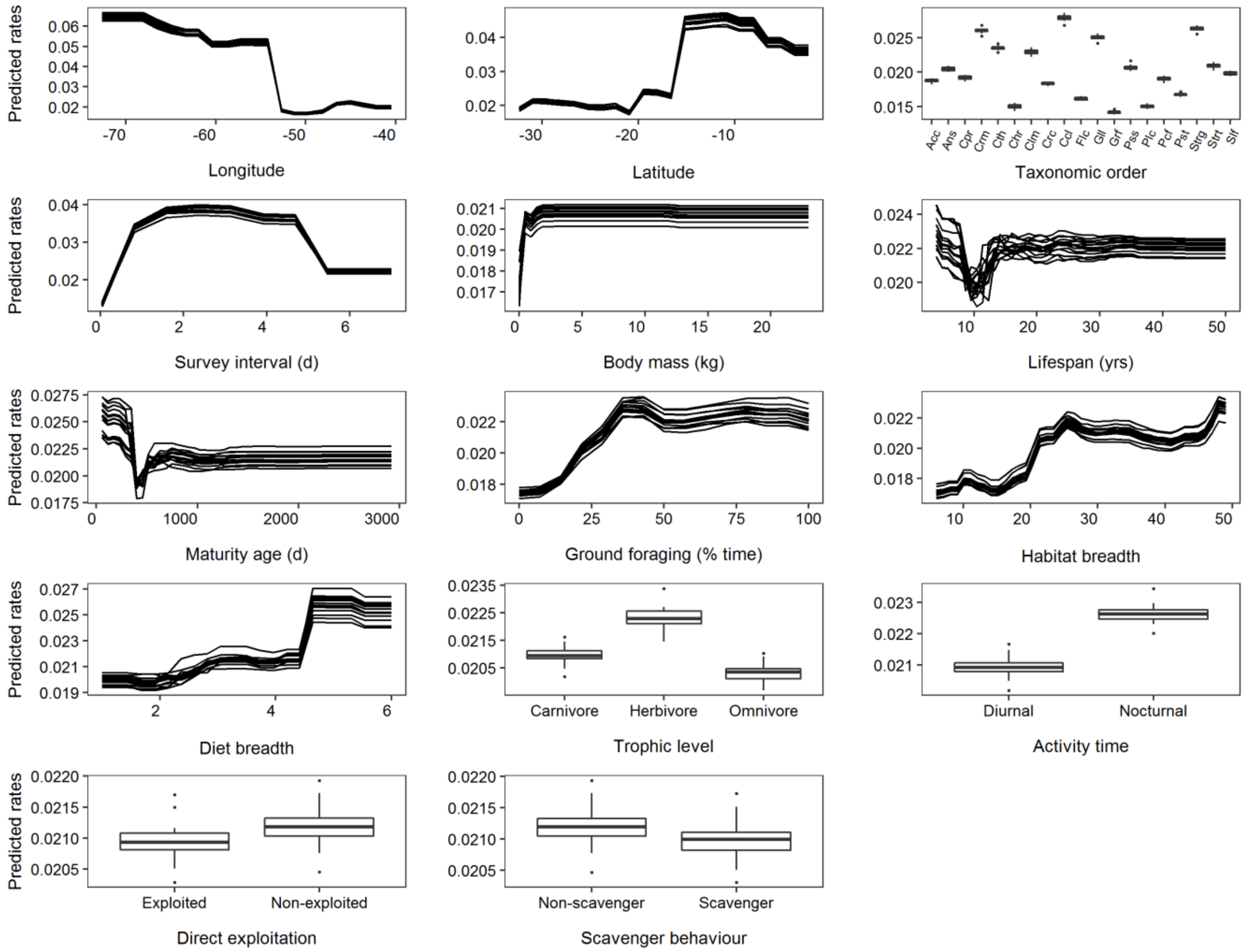

Figure S2.3. Partial dependence plots for all tested predictors on the predicted uncorrected road mortality rates of Brazilian birds. Rates are in ind/km/year. Predictors are in descending variable importance order (Fig. S2.1). Showing results for the 15 imputed datasets. Note that y-scales differ among plots. Taxonomic orders are abbreviated as follows: Acc (Accipitriformes), Ans (Anseriformes), Ccl (Cuculiformes), Chr (Charadriiformes), Clm (Columbiformes), Cpr (Caprimulgiformes), Crc (Coraciiformes), Crm (Cariamiformes), Cth (Cathartiformes), Flc (Falconiformes), Gll (Galliformes), Grf (Gruiformes), Pcf (Piciformes), Plc (Pelecaniformes), Pss (Passeriformes), Pst (Psittaciformes), Slf (Suliformes), Strg (Strigiformes), Strt (Struthioniformes).

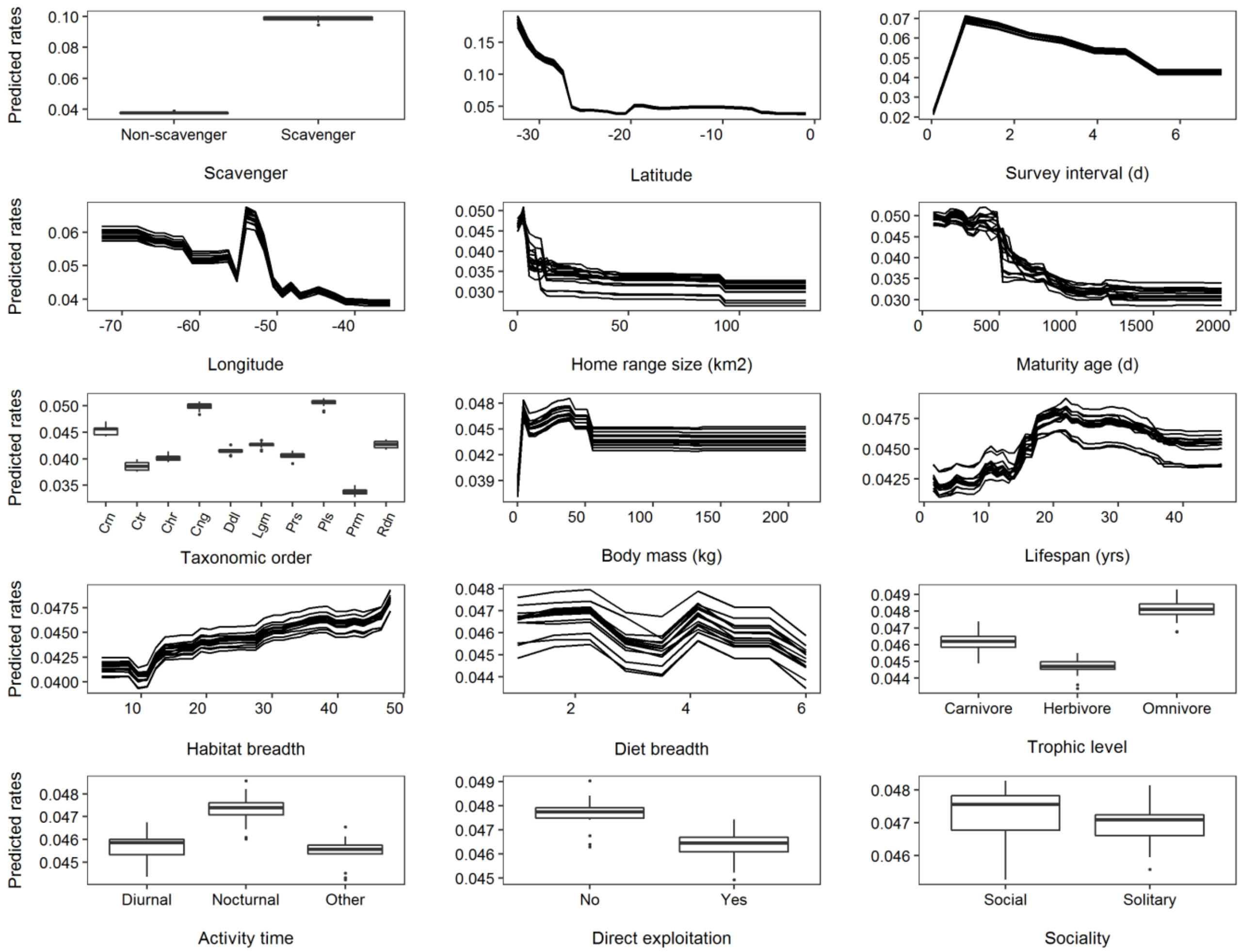

Figure S2.4. Partial dependence plots for all tested predictors on the predicted uncorrected road mortality rates of Brazilian mammals. Predictors are in descending variable importance order (Fig. S2.1). Showing results for the 15 imputed datasets. Note that y-scales differ among plots. Taxonomic orders are abbreviated as follows: Crn (Carnivora), Ctr (Cetartiodactyla), Chr (Chiroptera), Cng (Cingulata), Ddl (Didelphimorphia), Lgm (Lagomorpha), Prs (Perissodactyla), Pls (Pilosa), Prm (Primates), Rdn (Rodentia).

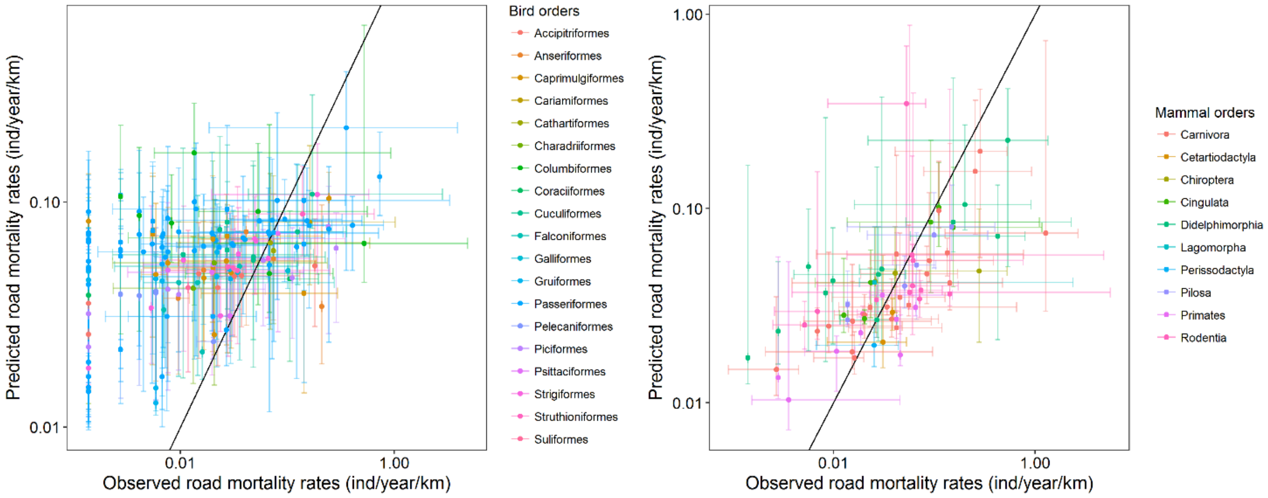

Figure S2.5. Predicted and observed uncorrected road mortality rates for 170 species of birds and 74 mammals. Symbol is the median value from all surveys for empirical data and across all predicted locations –grid cells, for predicted rates. Error bars represent the minimum and maximum range in observed and predicted values. Diagonal line indicates the 1:1 relationship.

Appendix 3. Additional results with corrected road mortality rates

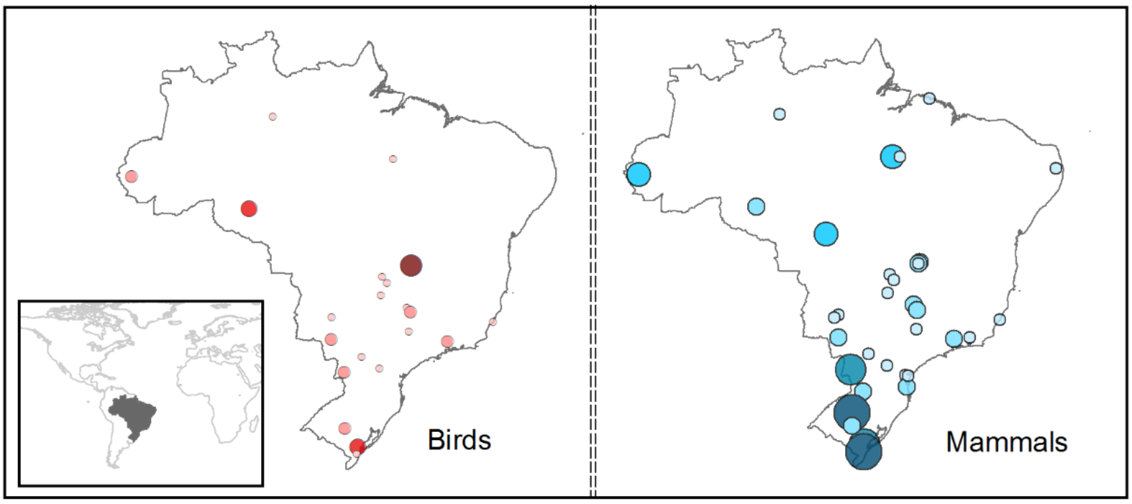

Figure S3.1. Location of the surveyed roads in Brazil represented in the 41 studies with road mortality data for birds and mammals (note that some studies provided mortality rates for both groups). The size of the symbols represent the median road mortality rates for each taxonomic group. In birds the values range from 0.001 to 1.68 ind/km/year, while in mammals values range from 0.003 to 18.5 ind/km/year.

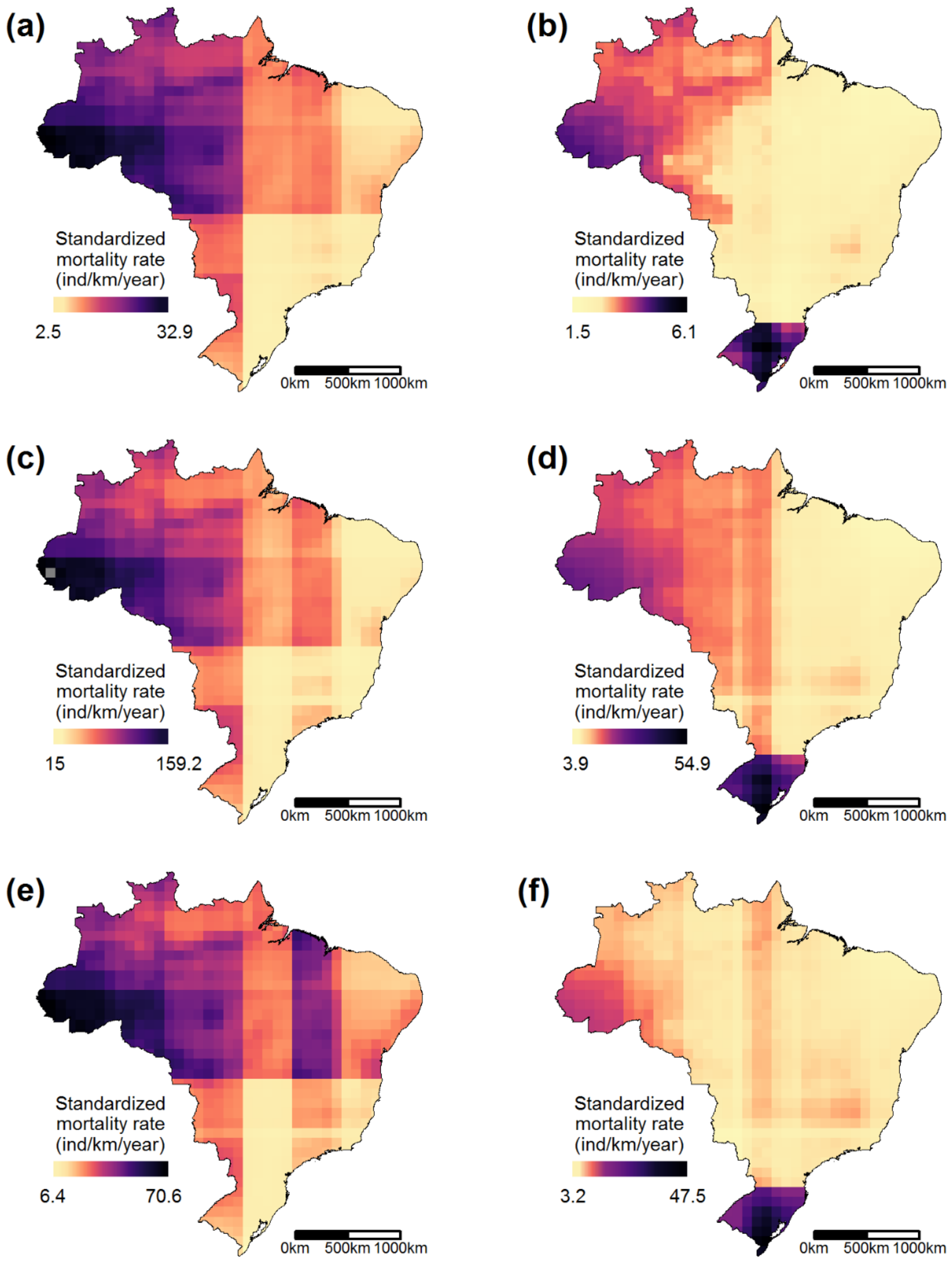

Figure S3.2. Predicted standardized road mortality rates (in ind/km/year) in Brazil assuming the minimum observed survey interval [(a) birds, (b) mammals, both 0.0417 days between surveys], mean observed interval [(c) birds 3.40 days between surveys, (d) mammals 3.64 days between surveys], and maximum observed interval [(e) birds, (f) mammals, both 7 days between surveys, which was the maximum interval we considered for our study).

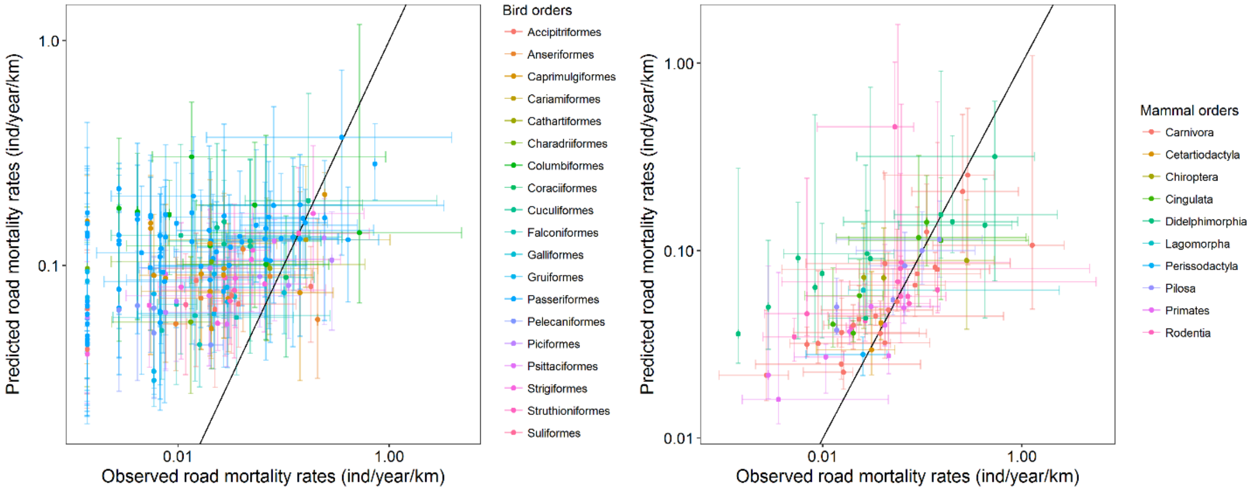

Figure S3.3. Predicted and observed road mortality rates for 170 species of birds and 74 mammals. Symbol is the median value from all surveys for empirical data and across all predicted locations –grid cells, for predicted rates. Error bars represent the minimum and maximum range in observed and predicted values. Diagonal line indicates the 1:1 relationship.

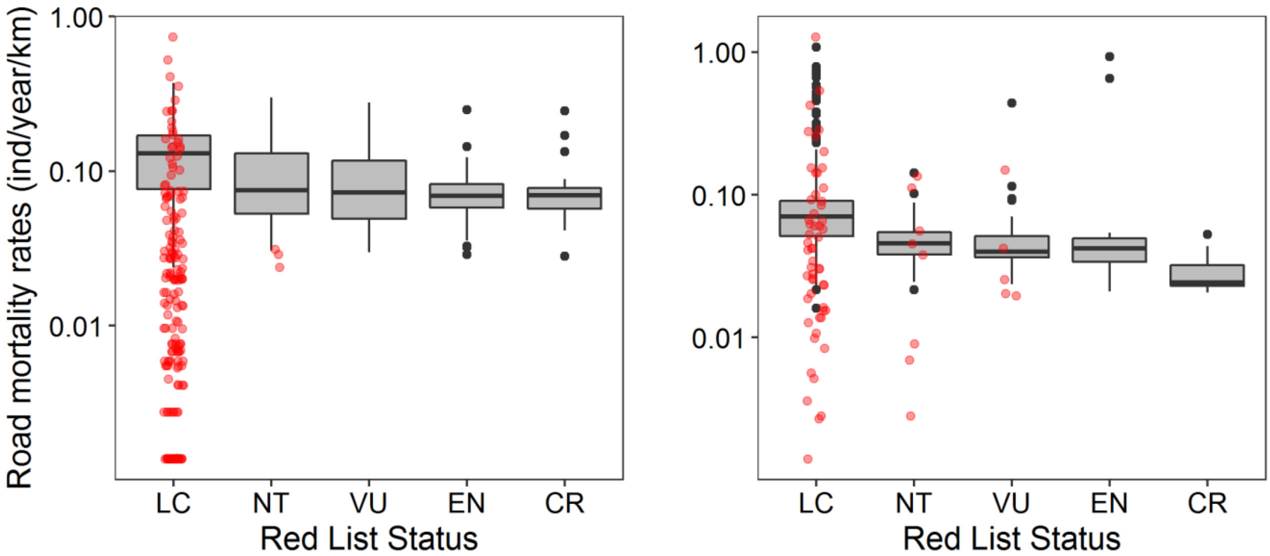

Figure S3.4. Median predicted (grey boxplot) and observed (red symbols) road mortality rates for birds (left panel) and mammals (right panel) classified in the different IUCN Red List status categories.

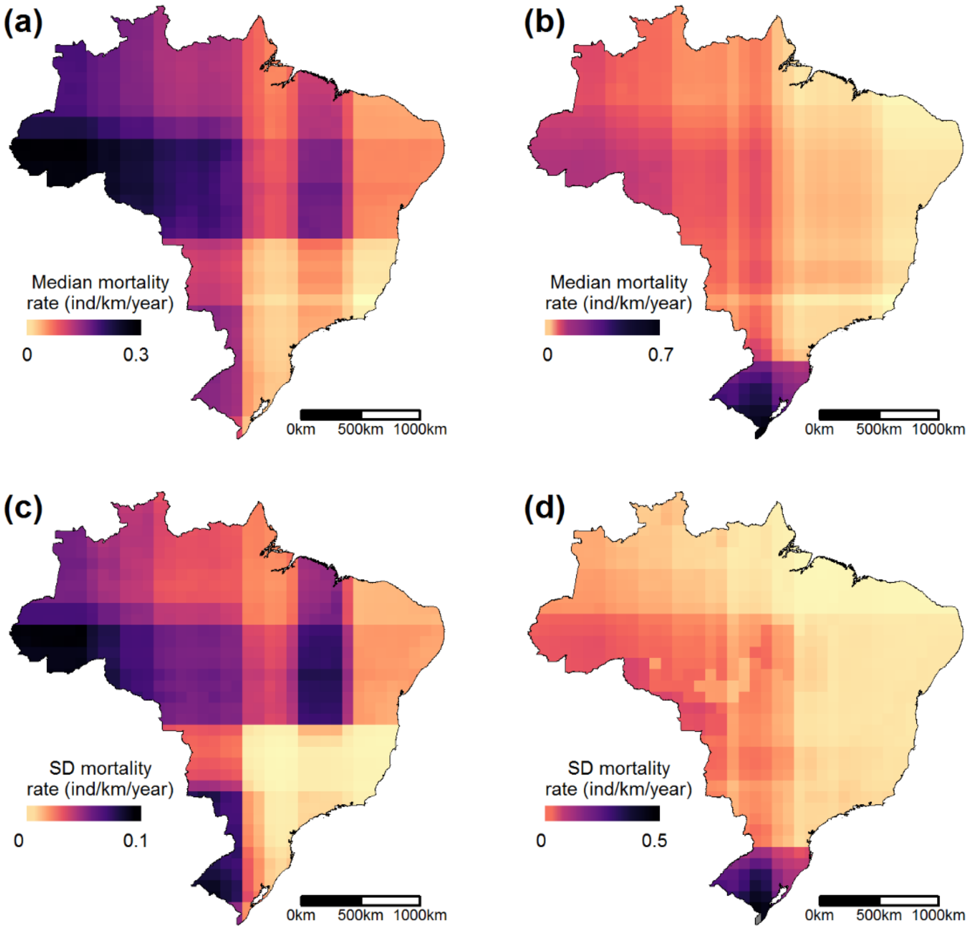

Figure S3.5. Predicted standardized road mortality rates (in ind/km/year) for birds [(a) median rates, (c) standard deviation among species within each cell] and mammals [(a) median rates, (c) standard deviation among species within each cell] in Brazil.

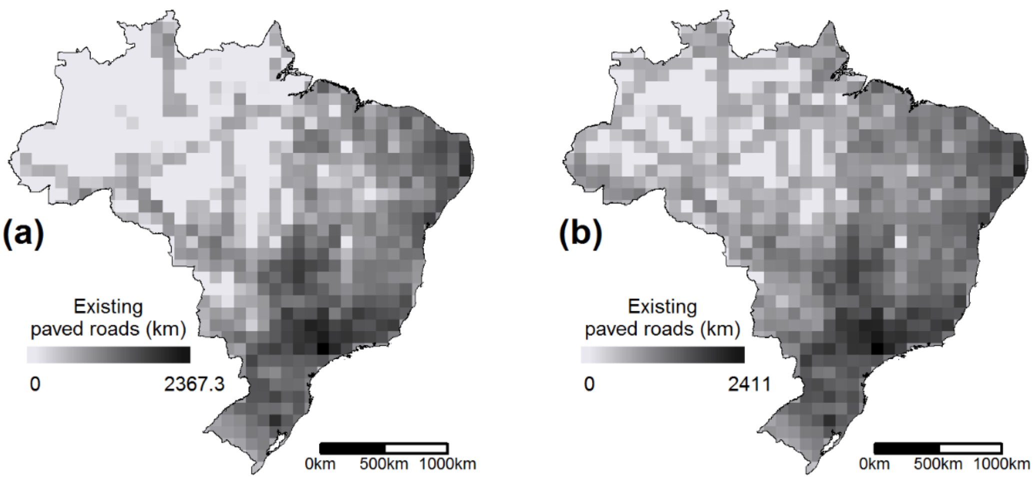

Figure 3.6. Road density map for Brazil reflecting current paved roads (panel a) and current and planned paved roads (b). Road data from https://www.openstreetmap.org.

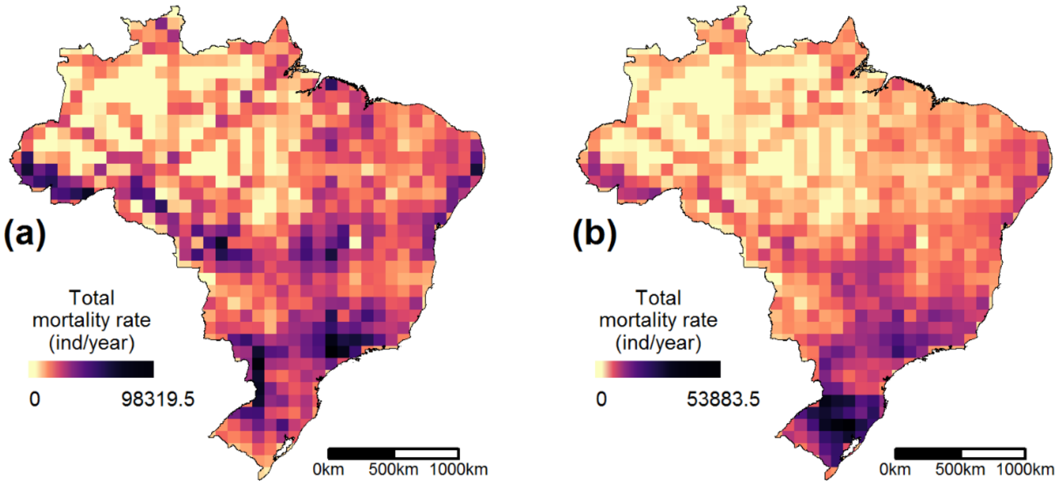

Figure S3.7. Predicted total road mortality rates (in ind/year) for birds (a) and mammals (b) given the existing and planned paved road network in Brazil. Road data from https://www.openstreetmap.org.

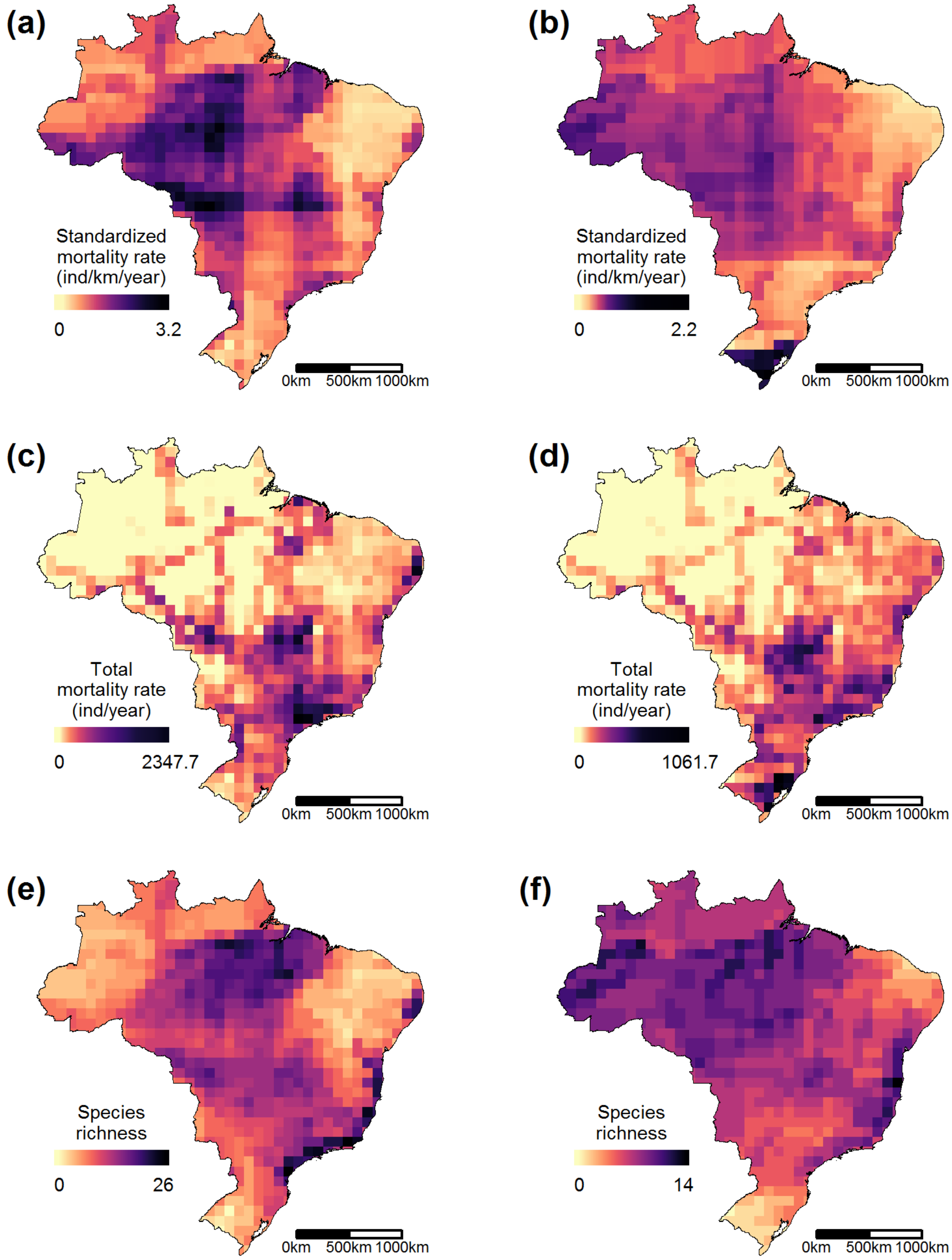

Figure S3.8. Predicted standardized road mortality rates (in ind/km/year) for threatened birds (a) and threatened mammals (b) in Brazil. Total road mortality rates based on existing paved roads (ind/year) for threatened birds (c) and threatened mammals (d). Total threatened bird (e) and threatened mammalian (f) species richness.