CONSERVATION THREATS FROM ROADKILL IN THE GLOBAL ROAD NETWORK

Short running title: CONSERVATION THREATS FROM ROADKILL

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BIOSKETCH

Clara Grilo is particularly interested in applied ecological questions to provide scientific underpinnings for the preservation, management, or restoration of wildlife and landscapes. Over the last years, much of her research focused on the effects of road network on birds and mammals such as behaviour, relative abundance, genetic structure, risk of mortality and population viability. The research interests of this team include road ecology, macroecology, macroevolution, extinction risk and global change biology. The shared interests in these fields were combined to advance our understanding of the impact of roadkill on wildlife populations.

AUTHOR CONTRIBUTIONS

C.G. and P.B. conceived the idea. C.G., K.S., A.R., E.K., F.Z.F, S.A.G. and Y. W. collected the data. C.G, L.B.A. and E.G. designed the methods. C.G and E.G. analyzed the data. M.G.S. prepared the final map. C:G. led the writing of the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

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ABSTRACT

Aim – The road network is increasing globally but the consequences of roadkill on the viability of wildlife populations are largely unknown. We provide a framework that allows us to estimate how risk of extinction of local populations increases due to roadkill and to generate a global assessment that identifies which mammalian species are most vulnerable to roadkill and the areas where they occur.

Location - Global

Time period – 1995 -2015

Major taxa studied – Terrestrial mammals

Methods – We introduce a framework to quantify the effect of roadkill on terrestrial mammals worldwide that includes three steps: 1) compilation of roadkill rates to estimate the fraction of a local population killed on the roads, 2) prediction of population risk of extinction based on observed roadkill rates (for a target group of species of conservation concern and non-threatened species with high roadkill rates), and 3) global assessment of vulnerability to roadkill for 4,677 terrestrial mammalian species estimated using phylogenetic regression models that link extinction risk to demographic parameters.

Results – We identified four populations among the 70 species in the target group which could become extinct in 50 years if observed roadkill levels persist in the study areas: maned wolf *Chrysocyon brachyurus* (Brazil), little spotted cat *Leopardus tigrinus* (Brazil), brown hyena *Hyaena brunnea* (Southern Africa) and leopard *Panthera pardus (*North India). The global assessment revealed roadkill as an added risk for 2.7% (n=124) terrestrial mammals, including 83 species Threatened or Near Threatened. We identified regions of concern that concentrate species vulnerable to roadkill and high road densities in areas of South Africa, central and Southeast Asia, and the Andes.

Main conclusions – Our framework revealed populations of threatened species that require special attention and can be incorporated into management and planning strategies informing road managers and conservation agencies.

Keywords: Mammals; roadkill; life-history; risk of extinction; road mitigation; road network;

Main text

1. INTRODUCTION

There are at least 36 million kilometres of roads in the world currently (CIA, 2020). Roads dominate the landscape in some regions, e.g., 83% of land in the USA (Riitters & Wickham, 2003) and 50% in Europe (Torres et al., 2016) are within 1 and 1.5 km of the nearest road, respectively. An additional 25 million kilometres of roads are expected by 2050, mostly from expanding the road networks of developing countries that contain exceptional biological diversity and highly conserved ecosystems (Laurance, 2018; Meijer et al., 2018; Alamjir et al., 2019). Given the potential for roads to negatively affect biodiversity, evaluating the current and future impacts of the global road network on wildlife is critical (van der Ree et al., 2015). Wildlife mortality through collisions with vehicles (hereafter roadkill) is often considered one of the most serious impacts of roads, being a significant source of anthropogenic mortality for some species (Loss et al., 2015; Hill et al., 2019; Morelli et al., 2020). Roadkill impacts have been well documented for a wide range of vertebrates and regions, with estimates of millions of individuals dying annually in roads across Europe (e.g. Erritzoe et al., 2003; Wembridge et al,. 2016; Grilo et al., 2020), the Americas (e.g. Loss et al., 2014; Baxter-Gilbert et al., 2015; González-Suaréz et al., 2018) and Australia (Ehmann & Cogger, 1985), and roadkill being identified as a problem also in Africa (Collinson et al., 2019; Gandiwa et al., 2020) and Asia (Seo et al., 2015; Silva et al., 2020). While numbers killed are high, the actual impact of that added mortality at the population level is poorly understood, but at least for some species it can be high (Benítez-López et al., 2010). For instance, roadkill is responsible for 35% of annual deaths in Florida panthers *Puma concolor coryi* (Taylor et al., 2002) and 49% in badgers *Meles meles* in Britain (Harris et al., 1992, Harris et al., 1995). Also, roadkill annually removes 10% of the Iberian lynx *Lynx pardinus* population (Simón et al., 2012), 10% of black bears *Ursus americanus* in Ocala National Forest (FFWCC, 2012) and may have reduced the density of hedgehogs *Erinaceus europaeus* in the Netherlands by 30% (Huijser & Bergers, 2000). Overall, it is likely that roadkill can increase the risk of local extinction by reducing effective population size and genetic diversity, and by limiting demographic and genetic rescue (Jackson & Fahrig, 2011). There is, therefore, a critical need to identify the species and regions that are most vulnerable to the rapid expansion of roads and traffic worldwide (Laurance et al., 2014). A challenge to achieve this goal is that wildlife populations do not respond equally to additional mortality, which makes evaluation of roadkill effects on population persistence challenging (Gibbs & Shriver, 2005; Row et al., 2007; Diniz & Brito, 2013, Ceia-Hasse et al., 2017). These effects may vary depending not only on the proportion of the population killed on roads each year (Jaeger et al., 2005; Jacobson et al., 2016) but also on demographic processes (e.g., density dependent fecundity or immigration) that affect the ability of the population to offset increased mortality (Purvis et al., 2000; Pearson et al., 2014). Species characteristics can help us predict these variable effects. For example, species with high adult survival and low fecundity, typically have low population growth rates, and are more likely to experience declines with added anthropogenic mortality (Sparkman et al., 2011). The link between species demographic variables and risk of extinction due to additional mortality has been established for some sources of human impacts (Owens & Bennet, 2000; Crooks et al., 2017) but not for roadkill (but see Grilo et al., 2020 that estimated the incidence of roadkill based on species trait-models and estimated population vulnerability in Europe).

In this study, we present a framework that allows us to generate the first global assessment of vulnerability to roadkill in mammals (Figure 1). Within this framework we first analysed a unique global dataset of observed roadkill rates using spatially implicit population models to estimate the increase in risk of extinction due to roadkill in multiple local populations. We then use trait data and phylogenetic predictive regressions to identify mammalian species most vulnerable to roadkill and the areas where they occur. Our findings offer insights into the risks that roads pose to wildlife currently and identifies areas where roadkill can lead to loss of mammalian biodiversity. This information can provide initial guidance to prioritize conservation and mitigation efforts to meet sustainable development goals in countries with high biodiversity. More generally, the proposed framework could be integrated into existing risk assessment protocols and expanded to other taxonomic groups.

2. MATERIAL AND METHODS

Our framework includes three steps which we explain in detail below. In summary, the first step generated estimates of the fraction of a local population killed in vehicle-wildlife collisions; the second step predicted the risk of extinction from that added mortality for target populations; and the third step used identified relationships in the target group to predict vulnerability to roadkill for 4,677 terrestrial mammals.

Step 1: Roadkill rates and estimated fraction of the population roadkilled per year

To estimate roadkill rates, we conducted a systematic literature search and located unpublished data to compile roadkill counts for mammals collected between 1995 and 2015 in any areas of the world (Figure 1). Peer-reviewed and grey literature were located searching the Web of Knowledge, Science Direct and Google Scholar using combinations of the following search terms: “mammal*” and all related taxonomic orders combined with “roadkill* or “road-kill” or “road mortality” in five languages (Chinese, English, Portuguese, Russian and Spanish). We only compiled roadkill counts from surveys completed before the end of 2015 that surveyed more than 3 km of road for a minimum period of one month (SM1). For each species and study we used these counts (reported number of roadkilled individuals) to calculate annual roadkill rates (roadkilled individuals per km of road surveyed per survey effort in days) using two different approaches to account for the lower detectability and persistence in roads of small sized carcasses (small carcasses do not persist in the road as long as larger ones, Santos et al., 2016). For species with average body size <1 kg, we calculated annual roadkill rates as: (count/km of road sampled /number of surveys)*365 days, where the number of surveys is the total number of days in which surveys were completed. For species with average body size > 1kg we calculated annual roadkill rates as: (count/km of road sampled /total survey period)*365 days, where total survey period is the number of days between the first and the last survey day. This assumes that larger mammals killed during the survey period would always be detected, but that some small species could be missed as they could disappear between survey intervals. The two methods are equivalent for daily surveys.

For a target group of species for which roadkill rates were available we then estimated the fraction of the population roadkilled in the study areas, selecting estimates from the site with the highest observed roadkill rate if multiple estimates were available. The target group included all mammalian species of conservation concern (i.e., Near Threatened, Vulnerable, Endangered, or Critically Endangered species classified by IUCN Red List 2016) and those species with high roadkill rates: the three small-sized (<1kg) and the three large-sized (>1kg) mammals with the highest roadkill rates in each continent [North America (Canada, USA and Mexico), Central/South America, Europe, Africa, Asia and Oceania]. For each species, we assumed observed roadkill rates were representative of all paved roads (excluding urban areas) in the *study site*, which was defined by using a buffer around the centroid of the actual surveyed road. The buffer was defined to potential encompass a local population considering species area requirements vary with body size (Jetz et al. 2004). We considered a 5km radius buffer for species with body mass <1kg, and a 50km radius for mass >1kg.

The fraction of a population lost to roadkill was calculated as $F_{Roadkill} = N_{roadkilled}/N_{pop}$, where $N_{roadkilled}$ is the estimated total number of roadkilled individuals of the species in the *study site* (ind/km), calculated by multiplying the observed roadkill rate by the total length of paved roads in the study site. Road length was estimated using Google Earth (Digital Globe 2016. http://www.earth.google.com [2015-2016]. N_{pop} is an estimate of the total population of the species in the *study site* calculated by multiplying observed population density (ind/km^2) by study site area (km^2). Population density estimates were obtained from within or near the *study site* when possible; otherwise we used published species-level estimates (see SM2 for references). Although we had a single observed roadkill rate for each species in each study site, we often found multiple estimates of population density from different sources. We used the minimum and maximum estimates of population densities to calculate several $F_{Roadkil}$ values and reflect uncertainty.

Step 2 Risk of extinction from roadkill for the target species

We used a spatially implicit age-structured stochastic population model based on Borda-de-Água et al. (2014) to estimate the increased probability of extinction in 50 years (based on 600 simulations) for each selected species in its study site under simulated scenarios of $F_{Roadkill}$ values ranging from 0.01 to 0.9 at 0.01 increments (methodological details and code in SM3; Figure 1). Without roadkill all species had stable populations with no risk of extinction within 50 years. These simulations allowed us to estimate the increased probability of extinction given the observed $F_{Roadkill}$ for each selected species. For species with multiple $F_{Roadkill}$ we reported the range based on the minimum and maximum fractions. In addition, we defined a threshold value, $F_{RiskExt10,}$ to represent the proportion of the population that if roadkilled would result in an increase in the probability of extinction of 0.1. $F_{RiskExt10}$ could be higher or lower than the observed $F_{Roadkill}$. We propose $F_{RiskExt10}$ as an indicator of vulnerability to roadkill, with species in which loss of small fractions of a population can result in increased risk of extinction (small $F_{RiskExt10}$) being more vulnerable and more likely to be threatened by roadkill.

The Borda-de-Água et al. (2014) model assumes that population growth is determined by age at first birth, interval between births, litter size, period of recruitment (the average interval in months between two births by an adult female), number of litters per year, natural survival rates for nine variables: newborns/youngest individuals, juveniles, and adults (categories reflect those in the study from which survival data were obtained, see below), and maximum longevity. Estimates for these variables were obtained from available compilations (Jones et al., 2009; Myhrvold et al., 2015; Myers et al., 2016; WildScreen Arkive, 2016; IUCN, 2016) and dedicated literature searches (SM2). For survival rates we used any available data, and in some cases we applied the single estimate available to all age-stages. When data were not available for a species we used the median from all available estimates from closely related taxa/species or from the most closely related species (same genus). A total of 68 cases out of 710 ((population density + nine variables) * 71 populations) were missing data being the majority on survival rates (details in SM2). We used empirical estimates of variance for all variables when available; otherwise we used a 10% variance.

The Borda-de-Água et al. (2014) model incorporates density dependence using the Beverton-Holt relationship between the number of births and juveniles (Beverton & Holt, 1957). By applying this model we assumed that: roadkill rates were constant over time in each study site, the available data reflected dynamics reasonably well even if obtained from other regions, and the population in the study site was not part of a metapopulation.

Step 3. Global assessment of mammalian vulnerability to roadkill

The population models described above were computationally intensive and to estimate $F_{RiskExt10}$ for all terrestrial mammals (n=4,677) worldwide we used a phylogenetic predictive model fitted for the target group (see SM4 for further details). First, we identified the demographic variables that best explain $F_{RiskExt10}$ for the target group species (step 1 – n=71) fitting both (non-phylogenetic) generalized least squares regression (GLS) and phylogenetic GLS (PGLS) models (see SM4 for further details). We then applied the phylogenetic imputation method using the demographic variables that better explained $F_{RiskExt10}$ to predict the missing values of $F_{RiskExt10}$ for the remaining mammals (see Stearns 1983; Guénard et al. 2011) (SM4). To identify regions of concern, we mapped the overlap between the species most vulnerable to roadkill ($F_{RiskExt10}$ <0.2) and the global road network using a 100-km x 100-km grid cells with a Cylindrical Equal Area projection. Species presence was determined using current native distribution data (IUCN, 2019) selecting polygons classified as presence: Extant, Probably Extant and Possibly Extant; origin: Native, and Reintroduced; and seasonality: Resident, Breeding Season, and Non-breeding Season. To quantify the kilometres of roads in each grid we used data from Meijer et al. (2018) selecting all roads classified as highways and primary roads, and all roads with road surface classified as paved.

Validation

Step 2 generated estimates of risk of extinction from roadkill (anthropogenic mortality) for local populations. Ideally, those estimates could be compared with population trends in those locations for validation, but those data are simply not available. Instead, we conducted a qualitative validation searching the literature for independent evidence from population viability analyses or other modelling approaches showing the effects of anthropogenic mortality on risk of extinction. We considered mortality from roadkill and other human-driven sources, as analyses of roadkill impacts are very limited. The comparison focused on evidence from those species identified as most vulnerable in our assessment ($F_{RiskExt10}$ <0.20, n=9) and those identified as least vulnerable ($F_{RiskExt10}$ >0.90, n=15). For step 3, we validated model estimates of $F_{RiskExt10}$ using leaveone-out cross-validation (LOO-CV) (Bruggeman, 2009) as well as 2-fold and 5-fold cross-validation blocked by phylogenetic distance (Roberts et al., 2017) (see SM4 for further details).

3. RESULTS

3.1 Roadkill rates and population responses to roadkill

We compiled a total of 1,310 roadkill rate records for 392 different mammalian species representing 184 references and personal communications (SM1). We found high inter- and intra-specific variability in roadkill rates (SM1). Roadkill rates varied from fewer than 0.005 ind/km/year (n=16 species) to more than 10 ind/km/year (n=10 species). The large mammal with the highest number of records (moose (*Alces alces*); n=45) had roadkill rates ranging between 0.00015 and 1.17 ind/km/year (SM1), while the small mammal with the highest number of records (guinea pig (*Cavia aperea*); n=9) had roadkill rates ranging between 0.004 and 12.82 ind/km/year.

Average roadkill rates were lower for species of conservation concern (0.09 ind/km/year) than for least concern species (0.44 ind/km/year). We obtained roadkill estimates for 61 species of conservation concern (four species in North America, 14 in Central/South America, eight in Europe, six in Africa, 23 in Asia, and six in Oceania; SM1). Thirty-six species were identified as top-roadkilled in the six continents resulting in a selected subset of 97 species. We obtained population density estimates for 70 of these species (SM2). Since we obtained roadkill records of leopard *Panthera pardus* in Africa and Asia, we analysed 71 populations of 70 species (SM2).

Our population models suggest populations of four species in the target group may be at risk of extinction if observed roadkill levels persist on the study sites including the maned wolf *Chrysocyon brachyurus* in Uberlândia-Uberada (Brazil), little spotted cat *Leopardus tigrinus* in western Santa Catarina (Brazil), brown hyena *Hyaena brunnea* in Mapungubwe Transfrontier conservation area (Southern Africa), and leopard *Panthera pardus* in Rajaji National Park and the Hariwar Conservation area (North India) (Figure 2; details in SM5 and SM6). Among the 71 populations analysed, we classified 10 as most vulnerable to roadkill ($F_{RiskExt10}$ <0.2), 31 had intermediate vulnerability (0.2< $F_{RiskExt10}$<0.5), 15 had low vulnerability (0.5< $F_{RiskExt10}$<0.9), and 15 had very low vulnerability ($F_{RiskExt10}$>0.9) (Figure 2, SM6).
Results from the qualitative validation largely supported our assessment: while 60% of the nine most vulnerable species ($F_{RiskExt10}$ <0.20) had published studies showing non-natural mortality can increase risk of extinction for those species, only 13% of the 15 species with very low risk ($F_{RiskExt10}$ >0.90) had published studies showing non-natural mortality can pose a threat (SM7).

3.2 Terrestrial mammals potentially threatened by roadkill

Phylogenetic predictive model showed that high reproductive rates, represented by low age of maturity, high numbers of litters per year and large litter sizes, were key predictors of high $F_{RiskExt10}$ (details in SM8). The use of the proposed phylogenetic predictive models was supported during validation, with a strong correlation (R^2=0.69) between observed and imputed $F_{RiskExt10}$ risk (SM). Predicted $F_{RiskExt10}$ identified 2.7% of mammals (124 species out of 4,677) as most vulnerable to roadkill ($F_{RiskExt10}$<0.2) including 83 species Threatened or Near Threatened by other human activities, but also 18 Least Concern species (23 species were not evaluated) (see SM9 for complete list of species vulnerability). Surprisingly, IUCN only considered roadkill as a threat to only 10 out of 5940 mammalian species which, according to our estimates are not among those most vulnerable to roadkill ($F_{RiskExt10} < 0.20$). Particularly vulnerable species ($F_{RiskExt10} < 0.10$) included: wild yak *Bos mutus* (listed as Vulnerable by the IUCN), Bohor reedbuck *Redunca redunca* (Least Concern), Amur tiger *Panthera tigris altaica* (Endangered), African elephant *Loxodonta africana* (Vulnerable), sun bear *Helarctos malayanus* (Vulnerable), African buffalo *Syncerus caffer* (Near Threatened), Asian elephant *Elephas maximus* (Endangered) and Sumatran rhinoceros *Dicerorhinus sumatrensis* (Critically Endangered) (SM8).

Mapping richness of species identified as most vulnerable to roadkill and existing road densities together revealed several areas of concern where high numbers of most vulnerable species coincide with high road densities, including parts of South Africa, Ghana, central and Southeast Asia, the Malay archipelago and the Andean region (Figure 3). Parts of Sub-Saharan Africa, Amazon, Mongolian plateau, and the Palearctic tundra concentrate vulnerable species but currently have low densities of paved roads (“future risk zones”). Europe, North America and many areas of central and South America and coastal Australia represent human-dominated areas with high road density but low numbers of species particularly vulnerable to roadkill. Finally, deserts and the Artic appear as “untouched” areas with no species particularly vulnerable to roadkill and few paved roads.

DISCUSSION

Preventing the impact of roadkill on wildlife requires identifying which species could have increased risk of extinction from the added risk of road mortality. Here, we proposed a framework that produces two key outputs: local evaluations of extinction risk associated with observed roadkill, and a global assessment of vulnerability to roadkill. This framework goes beyond quantifying numbers of roadkill individuals and moves the field of road ecology towards a more comprehensive understanding of the long-term consequences of observed road mortality for multiple species. We show that local high roadkill rates do not necessarily mean that a high fraction of the population will be lost, and that, even with relatively high roadkill rates, populations may be able to persist into the future (Cardillo et al., 2004; Borda-de-Água et al., 2014). However, road projects can pose an additional threat to species of conservation concern that are particularly vulnerable to traffic due to their characteristics and behaviour towards roads (Jacobson et al., 2016; González-Suaréz et al., 2018). Our analyses identified populations of several species of conservation concern (IUCN, 2018) that could become extinct if observed roadkill rates persist in their respective study areas, including the maned wolf and little spotted cat in South America, brown hyena in Africa, and leopard in Asia.

Global assessments such as the one presented here provide the opportunity to identify unstudied or undetected species potentially vulnerable to road mortality impacts and generate a priority map that reveal areas where mammalian biodiversity could be negatively affected by existing and future roads. Applying our framework at a global scale, we identified more than 100 mammals as very vulnerable to roadkill and revealed several areas where mammalian biodiversity may be lost due to the impact of existing road infrastructure. While our results emphasize global findings, the proposed framework can inform conservation prioritization and mitigation efforts both at regional and broad scales as it produces output at local scales already and step 3 could be easily adapted to different spatial and taxonomic scales.

We found that variation among species in their vulnerability to roadkill was in part associated with reproductive traits. Traits associated with faster, more frequent reproduction predicted population resilience to additional mortality, with less impact for species that mature early and have multiple large litters per year (see also Rytwinsky & Fahrig, 2012). Our model predicts these species will have increased risk of extinction only if there is a very high proportion of individual loss (>0.90), a pattern also suggested by previous studies focused on other sources of non-natural mortality (e.g. Garcia et al., 2008, Hurchings et al., 2012; Wang et al., 2018). This is consistent with the hypothesis that faster life histories can protect species from increased mortality risk, suggesting species with slow reproductive rates, and regions were these species are found, should receive more attention when considering roadkill mitigation strategies (e.g. Ceia-Hasse et al., 2017; Pinto et al., 2018). Combining species vulnerabilities with existing road maps, we identified areas where road infrastructure can result in important loss of biodiversity. In particular, Sub-Saharan Africa and south-eastern Asia are areas of concern, where many species vulnerable to roadkill co-occur. These regions also have a high number of threatened mammalian species with declining population (Ceballos et al., 2017) and are already impacted by widespread deforestation (Kleinschroth et al., 2019), commercial poaching (Steinmetz et al., 2006) and mineral exploitation (Laurance et al., 2015). The added impact of mortality due to roads for many mammalian species reveals the need to include the effect of roadkill on cumulative road impact assessments to biodiversity conservation (e.g. Alamgir et al., 2019; Kleinschroth et al., 2019).

Our study presents a new framework for identifying, ranking and predicting species and areas vulnerable to roadkill impacts. This can be a powerful tool to understand risk but there are data and modelling limitations that need to be considered. First, the majority of road surveys only indicated the number of carcasses recorded overall. These estimates can be biased by low carcass detectability and high removal rates (e.g. Santos et al., 2016). Several studies have proposed correction indexes for specific taxa based on the time interval between surveys, the taxonomic group and the species body mass (e.g., Santos et al., 2011; Teixeira et al., 2013). However, it is not clear whether these regional corrections can be extrapolated for mammals worldwide. Second, the modelling approach applies the highest observed roadkill rate for a specific surveyed area (one or several roads) to the entire paved road network in our defined study area, which for large body mass mammals could cover over 7,854 km^2. Currently, there is no scientific consensus regarding how different types of paved roads and associated traffic influence roadkill risk (see Seiler, 2003; Bissonette & Kassar, 2008, Grilo et al, 2015; Sadleir & Linklater, 2016). Further research is needed to determine how varying traffic volume, road widths and types of roadside vegetation influence roadkill rates for a wide range of species. Third, our modelling approach does not consider that roadkill may impact some groups of individuals within a species more than others. Given the same fraction of a population removed by roadkill, population persistence would be different if those removed are primarily reproductive adults *vs*. older animals. For some species there is a high incidence of mortality of juveniles and sub adults while for other species no distinct vulnerability was found among individuals (Grilo et al., 2009). Fourth, for many mammalian species, non-natural mortality includes sources other than road mortality such as legal hunting and poaching (Hill et al., 2019), but our model only considers road mortality. To better understand overall extinction risk for particular populations and species we need to understand all sources of mortality and explore whether non-natural mortality sources may be compensated. Finally, our approach relied on trait data that was largely obtained from global datasets that do not reflect regional and local variation. One example is population density, which was critical to estimate the fraction of the population roadkilled at the regional level. While we cannot overcome this limitation, our approach explicitly included this uncertainty by considering both the minimum and maximum densities observed, which allowed us to estimate a range of fractions of the population roadkilled and, therefore, a broad-spectrum of extinction risks.

Detailed local data are rarely available, but we do acknowledge that population density variation can be important to understand dynamics and extinction risk (González-Suárez & Revilla, 2013; González-Suárez et al., 2015) with the exploration of scenarios for those species we identified as most vulnerable to roadkill impacts. While compiling improved datasets for all species will not be possible, our study offers some guidance for prioritization of data collection: fundamental research for reliable estimation of the size or density of animal populations and survival rates are critical to improve the accuracy of the population model outputs.

CONCLUSIONS

Results of this study have implications for mammalian conservation and road mitigation worldwide. Our analyses bring attention to Sub-Saharan Africa and south-eastern Asia as regions where roads can lead to loss of mammalian biodiversity and thus, areas where future road development and road mitigation need to be carefully considered. The positive news is that these areas (as well as Latin America) have been identified as threat refugia for vertebrates where conservation actions are likely to succeed (Allan et al., 2019).

The local scale output from our framework provides a first step to highlight populations which might be currently under risk of extirpation and areas where local studies are needed to ultimately make site-specific recommendations for road mitigation. This local scale analysis could be directly used in environmental impact studies applied to target areas and species to provide estimates of risk of extinction and potential scenarios given data uncertainty and alternative management plans (Alamgir et al., 2017; Ceballos et al., 2017). "Since IUCN Red List assessments describe ongoing and future threats to each species, our study can directly inform these descriptions by providing information about which species are affected by roadkill and about the severity of that threat. Combining our approach with information on planned infrastructures could additionally identify and quantify the severity of future threats. In addition, the global scale output of our proposed framework could be part of strategic environmental, social and economic assessments by national infrastructure planning agencies, environmental governance agencies, global financing institutions, international NGOs. Projecting risk of extinction across broader areas and taxonomic groups could support decisions towards infrastructure that remains more sustainable throughout its life cycle. Our approach could be directly integrated into existing assessment frameworks, adding a relatively unstudied dimension. For example, the World Bank is the largest source of financing for development and has recently updated its Environmental and Social framework (ESA) to minimize the negative impacts of the projects it finances (Morley et al., 2020). Frameworks such as the ESA could incorporate our approach as an additional module to identify vulnerable areas and species and guide strategies to minimize long-term impacts of proposed road projects. In addition, we generate output for mammals that can be valuable. The global list of mammals vulnerable to roadkill generated here may be used by road managers and conservation agencies in the design of surveys, monitoring, and mitigation measures. The global map identifies regions that deserve special attention and can be particularly relevant for large-scale projects, such as the Belt and Road Initiative, providing information to facilitate addressing all impacts before projects begin (Ascensão et al., 2018).

Predictions and management implications of our framework can be refined once additional roadkill, population density data and demographic become available. The development of tools for global spatial prioritization and strategic road planning, such as the framework presented here for the impact of mortality, are critical to ensure wildlife protection and achieve sustainable transport infrastructure development and should complement other negative road effects on wildlife.

REFERENCES

Alamjir, M., Campbell, M. J., Suhardiman, A., Supriatna, J., & Laurance, W. F. (2019). High-risk infrastructure projects pose imminent threats to forests in Indonesian Borneo. *Scientific Reports* 9,140.

Allan, J. R., Watson, J. E. M., Di Marco, M., O'Bryan, C. J., Possingham, H. P., Atkinson, S. C., & Venter O. (2019). Hotspots of human impact on threatened terrestrial vertebrates. *PLoS Biol* 17(3): e3000158.

Ascensão, F., Fahrig, L., Clevenger, A. P., Corlett, R. T., Jaeger, J., … Pereira H.M. (2018). Environmental challenges for the Belt and Road Initiative. *Nature Sustainability*,1, 206-209.

Baxter-Gilbert, J. H., Riley, J. L., Neufeld, C. J. H., Litzgus, J. D., & Lesbarrères, D. (2015). Road mortality potentially responsible for billions of pollinating insect deaths annually. *Journal of Insect Conservation*, 19, 1029-1035.

Benitez-Lopez, A., Alkemade, R., & Verweij, P. A. (2010). The impacts of roads and other infrastructure on mammals and bird populations: A meta-analysis. *Biological Conservation*, 143, 1307-1316.

Beverton, R. J. H., & Holt S. J. (1957). On the Dynamics of Exploited Fish Populations. Fishery Investigations Series 2: Sea Fisheries. MAFF, London, UK.

Bissonette, J. A., & Kassar, C. A. (2008). Locations of deer–vehicle collisions are unrelated to traffic volume or posted speed limit. *Human–Wildlife Conflicts*, 2,122-130.

Borda-de-Água, L., Grilo, C., & Pereira, H. M. (2014). Modeling the impact of road mortality on barn owl (Tyto alba) populations using age-structured models. *Ecological Modelling*, 276, 29-37.

Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., & Mace, G.M. (2004). Human Population Density and Extinction Risk in the World's Carnivores. *PLoS Biol*, 2(7), e197.

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *PNAS*, 114 (30), E6089-E6096.

Ceia-Hasse, A., Borda-de-Água, L., Grilo, C., & Pereira, H. M. (2017). Global exposure of carnivores to roads. *Global Ecology and Biogeography,* 26, 592–600.

CIA (2020) The World Factbook. Available at: https://www.cia.gov/library/publications/the-world-factbook/rankorder/2085rank.html. Last accessed 8 December 2020.

Collinson, W., Davies-Mostert, H., Roxburgh, L., & van der Ree, R. (2019). Status of Road Ecology Research in Africa: Do We Understand the Impacts of Roads, and How to Successfully Mitigate Them? *Frontiers Ecology and Evolution,* 7, 479.

Crooks, K. R., Burdett, C. L., Theobald, D. M., King, S. R. B., Di Marco, M., … Boitani L. (2017). Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *PNAS,* 114, 7635-7640.

Diniz, M. F., & Brito, D. (2013). Threats to and viability of the giant anteater, *Myrmecophaga tridactyla* (Pilosa: Myrmecophagidae), in a protected Cerrado remnant encroached by urban expansion in central Brazil. *Zoologia*, 30, 151–156.

Ehmann, H., & Cogger H. (1985). Australia's endangered herpetofauna: a review of criteria and policies. In: Biology of Australasian Frogs and Reptiles. Grigg G, Shine R, Ehmann H. Surrey Beatty: Sydney, pp. 435–447.

Erritzoe, J., Mazgajski, T.D., & Rejt, L. (2012). Bird Casualties on European Roads - A Review. *Acta Ornithologica*, 38, 77-93.

FFWCC (2012). Florida Fish and Wildlife Conservation Commission. Florida black bear management plan. Available at: https://myfwc.com/media/13666/bear-management-plan.pdf. Last accessed 14 February 2019.

Gandiwa, E., Mashapa, C., Muboko, N., Chemurab, A., Kuvaoga, P, & Mabikad, C.T. (2020). Wildlife-vehicle collisions in Hurungwe Safari Area, northern Zimbabwe. *Scientific Africa*, 9, e00518

García, V. B., Lucifora, L. O., & Myers, R. A. (2008). The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proceedings of the Royal Society B: Biological Sciences*, 275, 83-89.

Gibbs, J. P., & Shriver, W. G. (2005). Can road mortality limit populations of pool-breeding amphibians? *Wetlands Ecology and Management* 13, 281-289.

González-Suaréz, M., & Revilla, E. (2013). Variability in life-history and ecological traits is a buffer against extinction in mammals. *Ecology Letters,* 16, 242-251.

González-Suárez, M., Bacher, S., & Jeschke, J. M. (2015). Intraspecific trait variation is correlated with establishment success of alien mammals. *American Naturalist,* 185, 737-746.

González-Suaréz, M., Zanchetta Ferreira, F. & Grilo, C. (2018). Spatial and species-level predictions of road mortality risk using trait data. *Global Ecology and Biogeography*, 27, 1093-1105.

Grilo, C., Koroleva, E., Andrášik, R., Bíl, M. & González-Suárez, M. (2020). Roadkill risk and vulnerability in European birds and mammals. *Frontiers in Ecology and Environment,* 18, 323-328.

Grilo, C., Bissonette, J. A., & Santos-Reis, M. (2009). Spatial-Temporal patterns in Mediterranean carnivore road casualties: Consequences for Mitigation. *Biological Conservation,* 142, 301-313.

Grilo, C., Zanchetta Ferreira, F., & Revilla, E. (2015). No evidence of a threshold in traffic volume affecting road-kill mortality at a large spatio-temporal scale. *Environmental Impact Assessment Review,* 55,54-58.

Guénard, G., von der Ohe, P. C., Zwart, D., Legendre, P., & Lek, S. (2011). Using phylogenetic information to predict species tolerances to toxic chemicals. *Ecological Applications,* 21, 3178-3190

Harris, S., Cresswell, W., Reason, P., & Cresswell, P. (1992). An integrated approach to monitoring badger (*Meles meles*) population changes in Britain. In: Wildlife 2001: Populations, McCullough, D.R., Barrett, R.H. Elsevier Applied Science, London.

Harris, S., Morris, P., Wray, S. & Yalden, D. (1995). A Review of British Mammals: Population Estimates and Conservation Status of British Mammals Other Than Cetaceans. Joint Nature Conservation Committee, Peterborough.

Hill, J., DeVault, T. L., & Belant, J. L. (2019). Cause-specific mortality of the world's terrestrial vertebrates. *Global Ecology and Biogeography*, 28, 680-689.

Huijser, M. P., & Bergers, P. J. M. (2000). The effect of roads and traffic on hedgehog (*Erinaceus europaeus*) populations. *Biological Conservation,* 95,111-116.

Hurchings, J. A., Myers, R. A., Garcia, V. B., Lucifora, L. O., & Kuparinen, A. (2012). Life-history correlates of extinction risk and recovery potential. *Ecological Applications,* 22, 1061-1067.

IUCN (2016). The IUCN Red List of Threatened Species Available at: http://www.iucnredlist.org. Last accessed at 22 January 2016.

IUCN (2019). The IUCN Red List of Threatened Species. Version 6.2. Available at: https://www.iucnredlist.org. Last accessed at 20 March 2019.

Jackson, N. D., & Fahrig, L. (2011). Relative effects of road mortality and decrease connectivity on population genetic diversity. *Biological Conservation*,144, 3143–3148.

Jacobson, S. L., Bliss-Ketchum, L. L., de Rivera, C. E., & Smith, W. P. (2016). A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere,* 7:e01345.

Jaeger, J. A. G., Bowman, J., Brennan, J., Fahrig L., Bert, D., Bouchard J., & Toschanowitze K. T. (2005). Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling*, 185, 329-348.

Jetz, W., Carbone, C., Fulford J, & Brown, J. H. (2004). The scaling of animal space use. *Science,* 306, 266-268.

Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L. … Purvis, A. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90, 2648-2648.

Kleinschroth, F., Laporte, N., Laurance, W.F., Goetz, S., & Ghazoul, J. (2019). Road expansion and persistence in forests of the Congo Basin. *Nature Sustainability,* 2, 628-634.

Laurance, W. F. (2018). If you can't build well, then build nothing at all. *Nature*, 563, 295-295.

Laurance, W. F., Clements, G. R., Sloan, S., O'Connell, C. S., Mueller, N. D., Goosem, M., … Arrea I. B. (2014). A global strategy for road building. *Nature*, 513, 229-239.

Laurance, W. F., Peletier-Jellema, A., Geenen B., Koster H., Verweij P., Van Dijck P., … Kuijk M. V. (2015). Reducing the global environmental impacts of rapid infrastructure expansion*. Current Biology*, 25, R259-R262

Loss, S. R., Will, T., & Marra, P. P. (2015). Direct Mortality of Birds from Anthropogenic Causes. *Annual Review of Ecology, Evolution and Systematics*, 46, 99-120.

Loss, S. R., Will, T., & Marra, P. P. (2014). Estimation of bird-vehicle collision mortality on U.S. roads. *Journal of Wildlife Management*, 78, 763:771.

Kao, J., Songsasen N., Ferraz, K., Traylor-Holzer, K. (Eds.) (2020). Range-wide Population and Habitat Viability Assessment for the Dhole, *Cuon alpinus*. IUCN SSC Conservation Planning Specialist Group, Apple Valley, MN, USA.

Meijer, J. R., Huijbregts, M. A. J., Schotten, K. C. G. J., & Schipper, A.M. (2018). Global patterns of current and future road infrastructure. *Environmental Research Letters*, 13: 064006.

Morelli F., Benedetti Y., & Delgado J. D. (2020). A forecasting map of avian roadkill-risk in Europe: A tool to identify potential hotspots. *Biological Conservation*, 249, 108729

Myers, P., Espinosa, R., Parr, C. S., Jones, T., Hammond, G. S., & Dewey, T. A. (2016). The Animal Diversity Web Available at: Accessed at http://animaldiversity.org. Last accessed 13 June 2016.

Myhrvold, N. P., Baldridge, E., Chan, B., Sivam, D., Freeman D. L., & Ernest, S. K. M. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, 96, 3109.

Owens, I. P. F., & Bennet P. M. (2000). Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. *PNAS*, 97, 12144-12148.

Pearson, R. G., Stanton, J. C., Shoemaker, K. T., Aiello-Lammens, M., Ersts, P. J., Horning, N.,… Akçakaya H. R. (2014). Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, 4, 217-221.

Pinto, F. A. S., Bager, A., Clevenger, A. P., & Grilo, C. (2018). Giant anteater (*Myrmecophaga tridactyla*) conservation in Brazil: Analysing the relative effects of fragmentation and mortality due to roads. *Biological Conservation*, 228, 148-157.

Purvis, A., Gittleman, J. L., Cowlishaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society B*, 267, 1947–1952.

Riitters, K. H., & Wickham, J. D. (2003). How far to the nearest road? *Frontiers in Ecology and Environment,* 1, 125-129.

Row, J. R., Blouin-Demers, G., & Weatherhead, P. J. (2007). Demographic effects of road mortality in black ratsnakes (*Elaphe obsolete*). *Biological Conserv*ation, 137,117-124.

Rytwinsky, T., & Fahrig, L. (2012). Do species life history traits explain population responses to roads? A meta-analysis. *Biological Conservation*, 147, 87-98.

Sadleir, R. F. M. S., & Linklater W. L. (2016). Annual and seasonal patterns in wildlife road-kill and their relationship with traffic density. *New Zealand Journal of Zoology*, 43, 275-291.

Santos, S. M., Carvalho, F., & Mira, A. (2011). How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS One*, 6(9), e25383.

Santos, R. A., Santos, S. M., Santos-Reis, M., Picanço de Figueiredo, A., Bager, A., Aguiar, L.M., ... Ascensão, F. (2016). Persistence and Detectability: Reducing the Uncertainty Surrounding Wildlife-Vehicle Collision Surveys. *PloS One*, 11(11), e0165608.

Seiler, A. (2003). The toll of the automobile: wildlife and roads in Sweden. PhD thesis. Swedish University of Agricultural Sciences.

Seo, C., Thorne, J. H., Choi, T., Kwon, H., & Park, C-H. (2015). Disentangling roadkill: the influence of landscape and season on cumulative vertebrate mortality in South Korea. *Landscape and Ecological Engineering*, 11(1), 87-99.

Silva, I., Crane, M., & Savini, T. (2020). High roadkill rates in the Dong Phayayen-Khao Yai World Heritage Site: conservation implications of a rising threat to wildlife. *Animal Conservation*, 23, 466-478.

Simón, M. (Ed) (2012). Ten years conserving the Iberian lynx. Seville: Consejería de Agricultura, Pesca y Medio Ambiente. Junta de Andalucía: Sevilla.

Sparkman, A. M., Waits, L. P., & Murray, D. L. (2011). Social and Demographic Effects of Anthropogenic Mortality: A Test of the Compensatory Mortality Hypothesis in the Red Wolf. *PLoS One* 6(6):e20868.

Stearns, S. C. (1983). The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, 41, 173-187.

Steinmetz, R., Chutipong, W., & Seuaturien, N. (2006). Collaborating to conserve large mammals in Southeast Asia. *Conservation Biol*ogy, 20, 1391-401.

Taylor, S. K., Buergelt, C. D., Roelke-Parker, M. E., Homer, B. L., & Rotstein, D.S. (2002). Causes of mortality of free-ranging Florida panthers. *Journal of Wildlife Diseases,* 38,107-14 (2002).

Teixeira F. Z., Coelho, A. V. P., Esperandio, I. B., & Kindel, A. (2013). Vertebrate road mortality estimates: Effects of sampling methods and carcass removal. *Biological Conservation,* 157, 317-323.

Torres, A, Jaeger, J. A. G., & Alonso, J. C. (2016). Assessing large-scale wildlife responses to human infrastructure development. *PNAS,* 113, 8472-8477.

van der Ree, R., Smith, D. J., & Grilo, C. (2015). Handbook of Road Ecology. Chichester, UK: John Wiley & Sons.

Wang, Y., Si, X., Bennett, P.M., Chen C, Zeng, D., Zhao, Y., Wu, Y., & Ding, P. (2018). Ecological correlates of extinction risk in Chinese birds. *Ecography*, 41,782-94.

Wembridge, D. E., Newman, M. R., Bright, P. W. & Morris, P. A. (2016). An estimate of the annual number of hedgehog (*Erinaceus europaeus*) road casualties in Great Britain. *Mammal Communications*, 2, 8-14.

Wildscreen Arkive (2016). Available at: http://archive.org. Last accessed 23 March 2016.

FIGURES

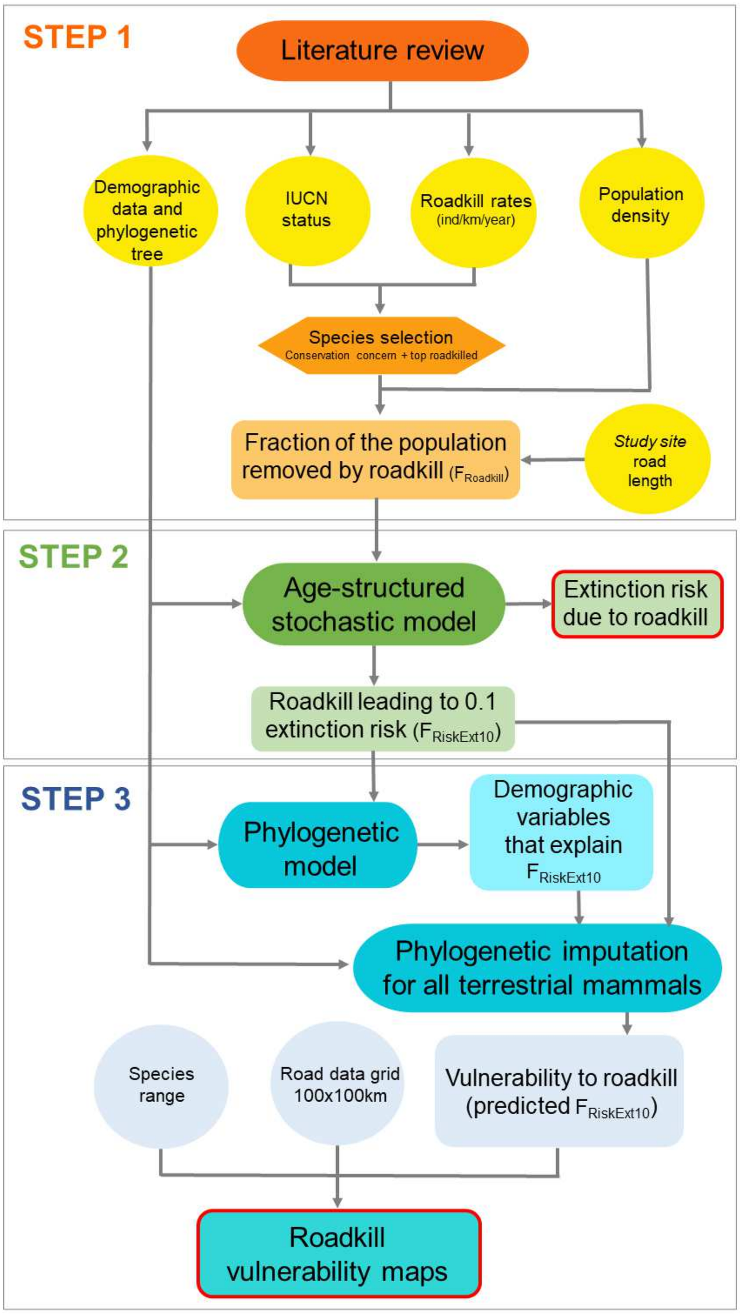


Figure 1 – Our proposed framework to quantify roadkill impacts on mammals worldwide. The framework includes three steps: step 1 - roadkill rates and estimated fraction of the population roadkilled per year; step 2 – risk of extinction from roadkill for the selected species, and step 3 -global assessment of mammal species vulnerability to roadkill. The two boxes framed in red are the main outputs.

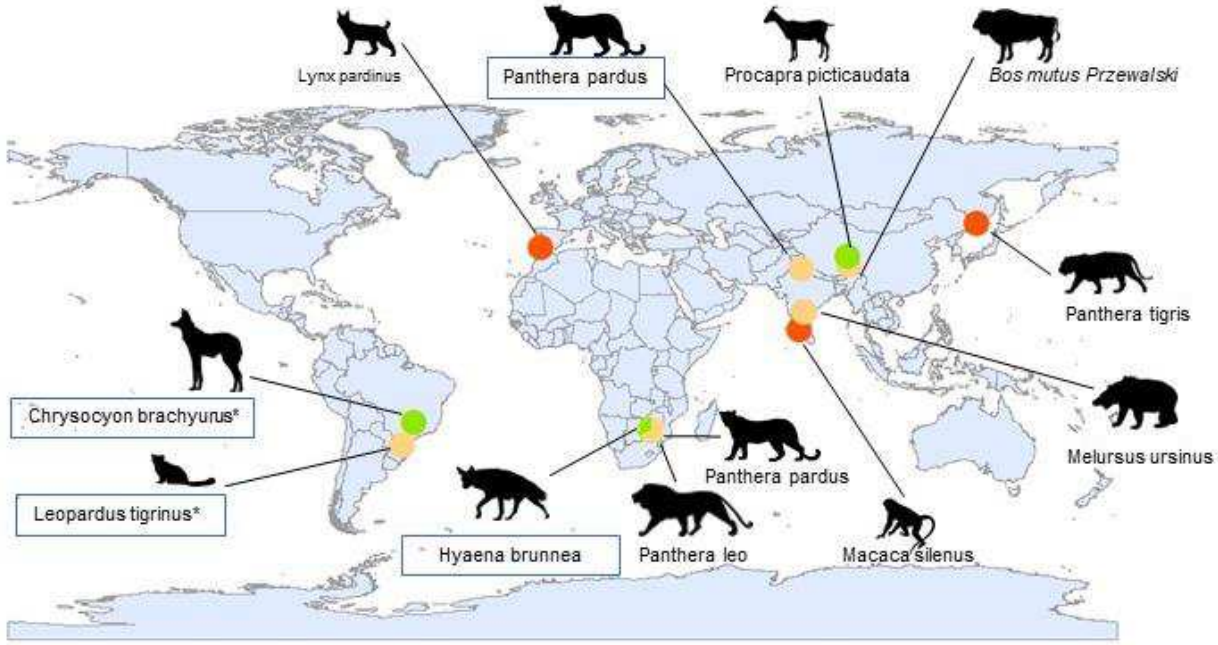


Figure 2 – Location of the species most vulnerable to roadkill ($F_{RiskExt10}$ <0.2). The scientific names framed in blue are those for which observed roadkill are estimated to lead to higher risk of extinction in 50 years if the observed roadkill persist in the region. Coloured dots are the IUCN status (Endangered – orange; Vulnerable – yellow, Near Threatened – green; Asterisks indicate species with intermediate vulnerability to roadkill ($0.2<F_{RiskExt10}<0.5$) (SM1 and SM6). Mammal species silhouettes from PhyloPic (http://phylopic.org).

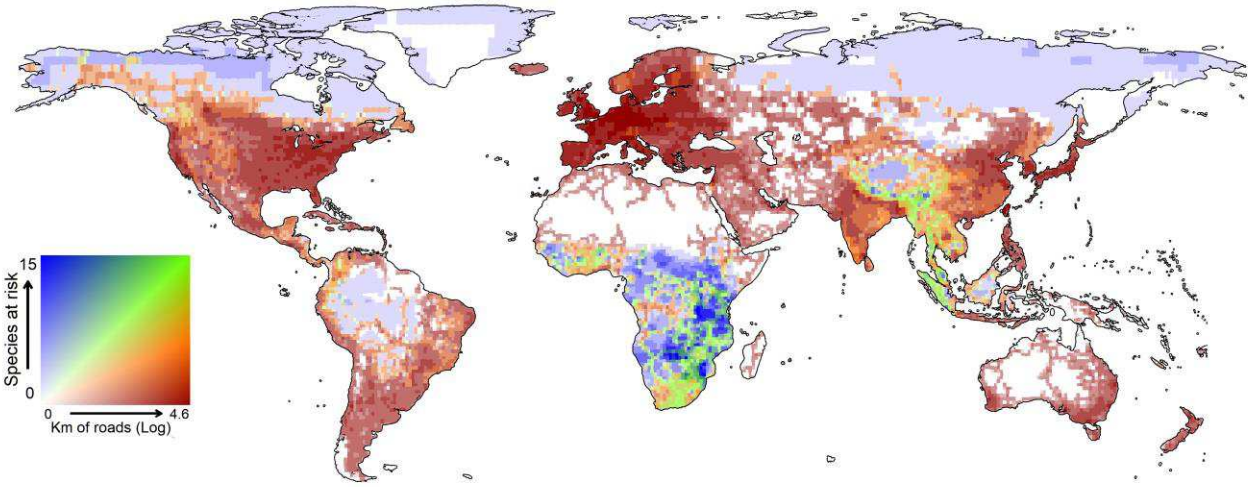


Figure 3 – Global distribution of the overlap between vulnerable species (mammal species for which roadkill of <20% of their population can lead to an additional 0.1 probability of extinction) and current paved road density (as $\log_{10}$ kilometres of road per 100-km x100-km grid cell). Green areas indicate “hot spots” of risk and exposure, blue areas represent “opportunities” for conservation with species at risk but current low road densities, brown areas are “humanized” with high road densities and few species at risk, light purple areas have both low road densities and no vulnerable species. White colour indicate no threatened species and no roads.

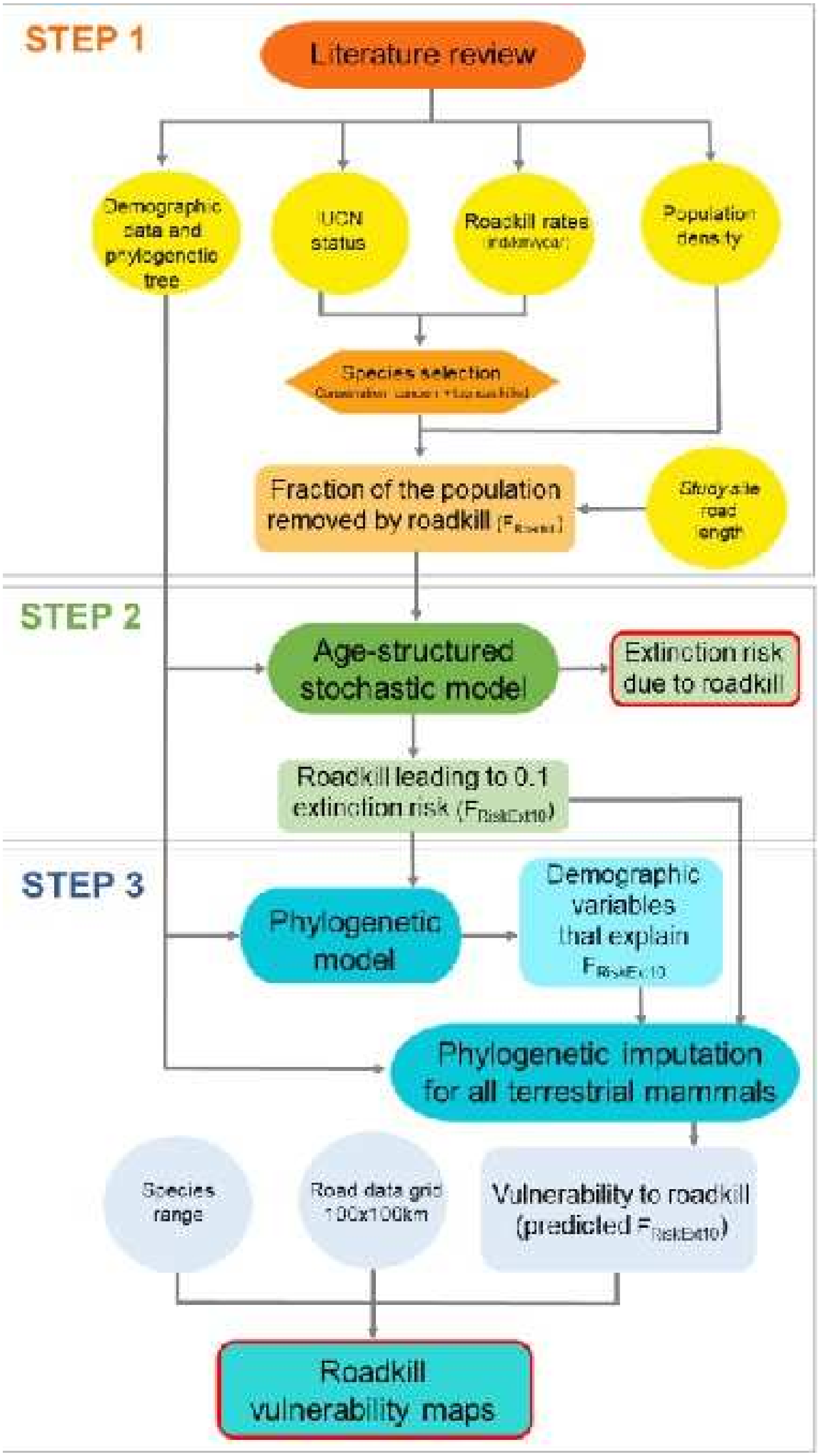
BIOSKETCH

Data accessibility

The full database of roadkill and biological traits, age structured model R scripts and outputs are available as supporting information.

A short title for each numbered item in the supplementary material:

SM1 - List of species with roadkill and references
SM2 - Biological traits for the selected species and references
SM3 - Spatial implicit age-structured stochastic models
SM4 - Identifying species potentially threatened by roadkill
SM5 - Risk of extinction when the fraction of the population is removed due to observed roadkill for four species' populations
SM6 - Results from the spatially implicit age-structured stochastic models
SM7 - Qualitative validation of results from the spatially-implicit age-structured stochastic models for species predicted to be most ($F_{RiskExt10}$ <0.20) and least vulnerable ($F_{RiskExt10}$ >0.90)
SM8 - Relative importance of each variable from GLS and PGLS model sets and averaged model coefficients with confidence intervals for each variable
SM9 - Vulnerable species to roadkill



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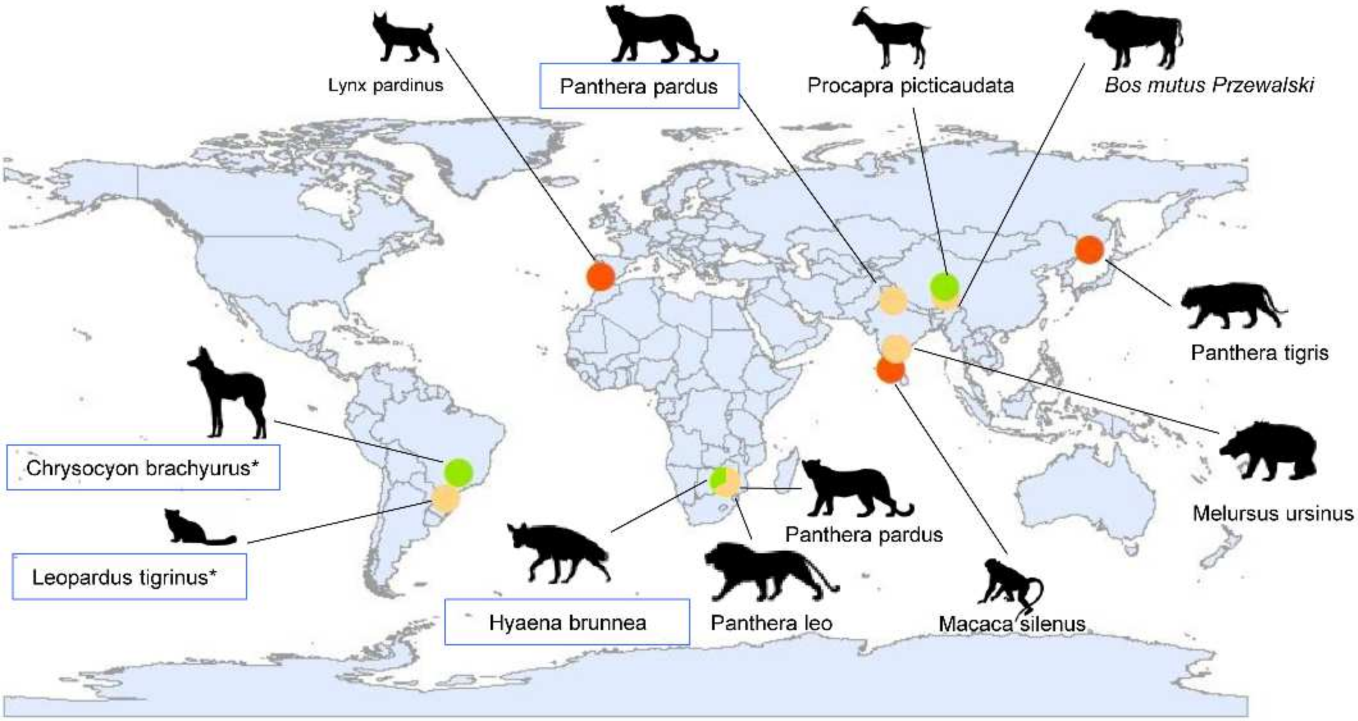

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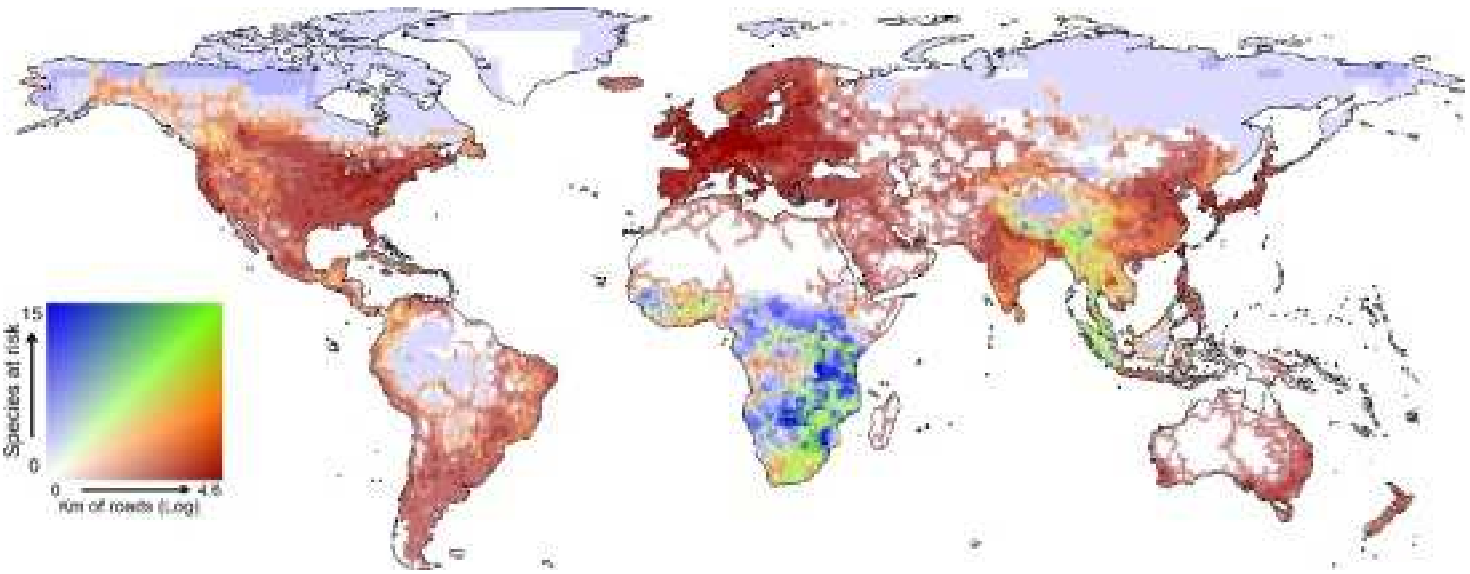

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