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RESEARCH ARTICLE

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Conservation threats from roadkill in the global road network

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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: (a) compilation of roadkill rates to estimate the fraction of a local population killed on the roads, (b) 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 (c) 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 that 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 have species vulnerable to roadkill with 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

life history, mammals, risk of extinction, road mitigation, road network, roadkill

1 | INTRODUCTION

There are at least 36 million km of roads in the world currently (CIA, 2020). Roads dominate the landscape in some regions, for example, 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 km of roads are expected by 2050, mostly from expanding the road networks of developing countries that contain exceptional biological diversity and highly conserved ecosystems (Alamgir et al., 2019; Laurance, 2018; Meijer et al., 2018). 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 (Hill et al., 2019; Loss et al., 2015; 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., 2012; Grilo et al., 2020; Wembridge et al., 2016), the Americas (e.g., Baxter-Gilbert et al., 2015; González-Suárez et al., 2018; Loss et al., 2014) 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, 1995). Also, roadkill annually removes 10% of the Iberian lynx *Lynx pardinus* population (Simón, 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 achieving this goal is that wildlife populations do not respond equally to additional mortality, which makes evaluation of roadkill effects on population persistence challenging (Ceia-Hasse et al., 2017; Diniz & Brito, 2013; Gibbs & Shriver, 2005; Row et al., 2007). These effects may vary depending not only on the proportion of the population killed on roads each year (Jacobson et al., 2016; Jaeger et al., 2005) but also on demographic processes (e.g., density dependent fecundity or immigration) that affect the ability of the population to offset increased mortality (Pearson et al., 2014; Purvis et al., 2000). 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 (Crooks et al., 2017; Owens & Bennet, 2000) but not for roadkill (but see Grilo et al., 2020, which 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 identify 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.

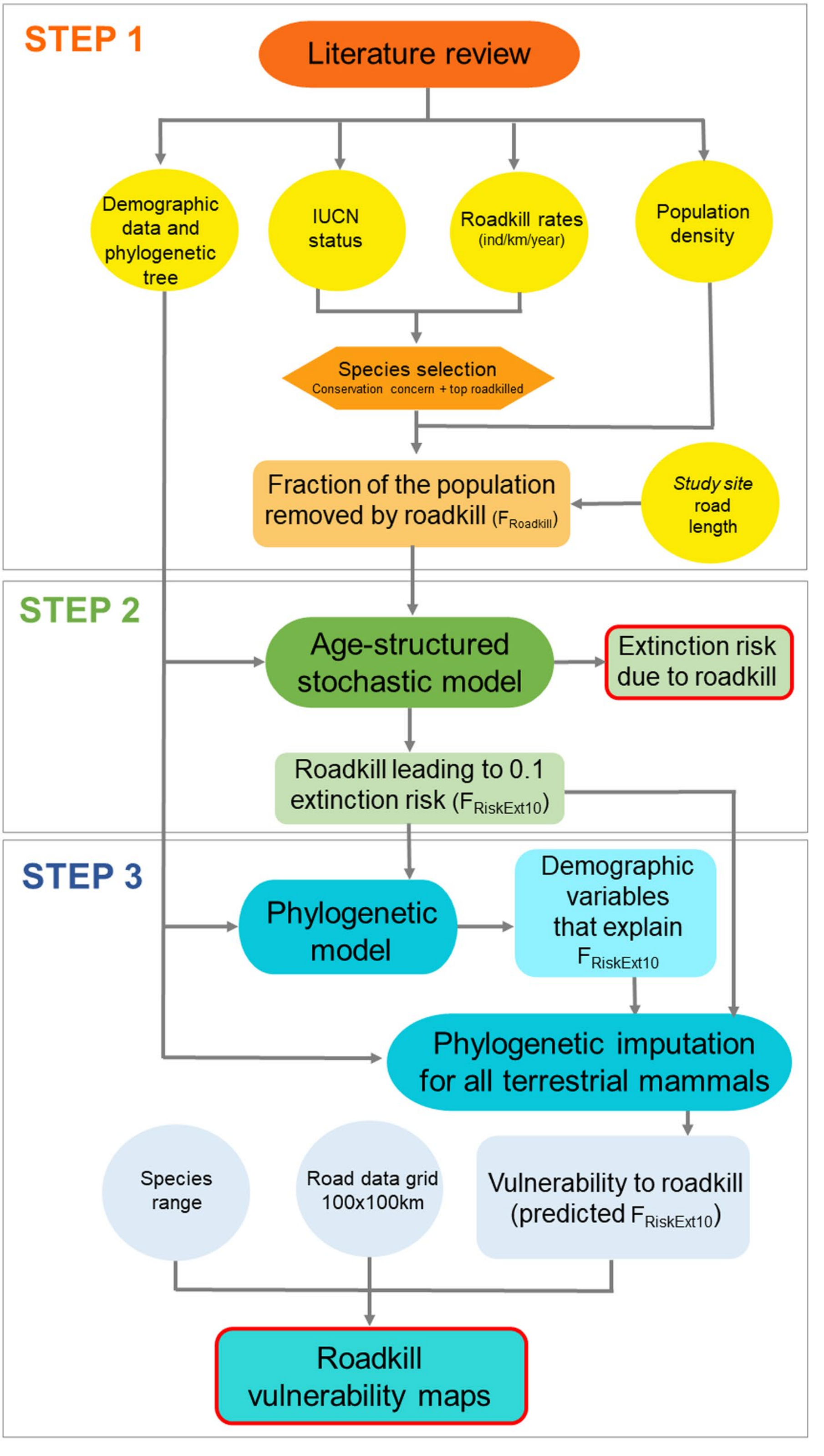

FIGURE 1 Our proposed framework to quantify roadkill impacts on mammals worldwide. The framework includes three steps: step 1 – roadkill rates and estimated fraction of the population roadkilled per year; step 2 – risk of extinction from roadkill for the selected species, and step 3 – global assessment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

2 | MATERIAL AND METHODS

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

2.1 | 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 1 month (Supporting Information Appendix S1). 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 on roads of small-sized carcasses (small carcasses do not persist on the road as long as larger ones, R. A. 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 on which surveys were completed. For species with average body size > 1 kg 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 International Union for Conservation of Nature (IUCN) Red List 2016] and those species with high roadkill rates: the three small-sized (< 1 kg) and the three large-sized (> 1 kg) 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 potentially encompass a local population considering species area requirements vary with body size (Jetz et al., 2004). We considered a 5-km-radius buffer for species with body mass < 1 kg, and a 50-km radius for mass > 1 kg.

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 (ind) 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. https://earth.google.com/web/ (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 Supporting Information Appendix S2 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 $F_{Roadkill}$ values and reflect uncertainty.

2.2 | 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 .01 to .9 at 0.01-increments (methodological details and code in Supporting Information Appendix S3; 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 .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: 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 (IUCN, 2016; Jones et al., 2009; Myers et al., 2016; Myhrvold et al., 2015; WildScreen Arkive, 2016) and dedicated literature searches (Supporting Information Appendix S2). 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, the majority being on survival rates (details in Supporting Information Appendix S2). 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.

2.3 | 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 Supporting Information Appendix S4 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 Supporting Information Appendix S4 for further details). We then applied the phylogenetic imputation method using the demographic variables that best explained $F_{RiskExt10}$ to predict the missing values of $F_{RiskExt10}$ for the remaining mammals (see Guénard et al., 2011; Stearns, 1983) (Supporting Information Appendix S4). To identify regions of concern, we mapped the overlap between the species most vulnerable to roadkill ($F_{RiskExt10} < .2$) and the global road network using 100-km × 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.

2.4 | 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 ($F_{RiskExt10} < .20$, $n = 9$) and those identified as least vulnerable ($F_{RiskExt10} > .90$, $n = 15$). For step 3, we validated model estimates of $F_{RiskExt10}$ using leave-one-out cross-validation (LOO-CV) (Bruggeman, 2009) as well as twofold and fivefold cross-validation blocked by phylogenetic distance (Roberts et al., 2017) (see Supporting Information Appendix S4 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 (Supporting Information Appendix S1). We found high inter- and intraspecific variability in roadkill rates (Supporting Information Appendix S1). 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 (Supporting Information Appendix S1), 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 (4 species in North America, 14 in Central/South America, 8 in Europe, 6 in Africa, 23 in Asia and 6 in Oceania; Supporting Information Appendix S1). 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 (Supporting Information Appendix S2). Since we obtained roadkill records of leopard *Panthera pardus* in Africa and Asia, we analysed 71 populations of 70 species (Supporting Information Appendix S2).

Our population models suggest populations of four species in the target group may be at risk of extinction if observed roadkill levels persist at 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 Supporting Information Appendices S5 and S6). Among the 71 populations analysed, we classified 10 as most vulnerable to roadkill ($F_{RiskExt10} < .2$), 31 had intermediate vulnerability ($.2 < F_{RiskExt10} < .5$), 15 had low vulnerability ($.5 < F_{RiskExt10} < .9$) and 15 had very low vulnerability ($F_{RiskExt10} > .9$) (Figure 2, Supporting Information Appendix S6).

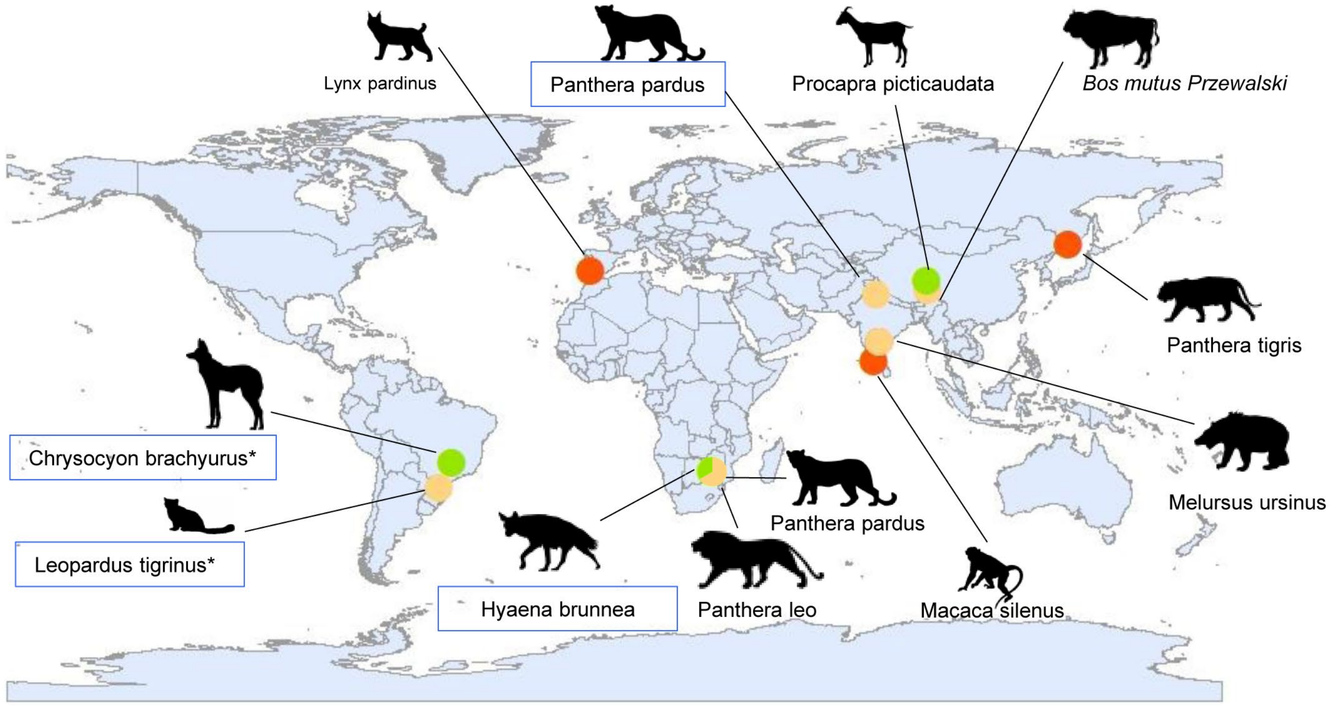

FIGURE 2 Location of the species most vulnerable to roadkill ($F_{RiskExt10} < .2$). The scientific names framed in blue are those for which observed roadkill rates are estimated to lead to an increase risk of extinction in 50 years if the observed roadkill rates persist in the region. Coloured dots are the International Union for Conservation of Nature (IUCN) status (Endangered – orange; Vulnerable – yellow, Near Threatened – green). Asterisks indicate species with intermediate vulnerability to roadkill ($.2 < F_{RiskExt10} < .5$) (Supporting Information Appendices S1 and S6). Mammal species silhouettes from PhyloPic (http://phylopic.org)

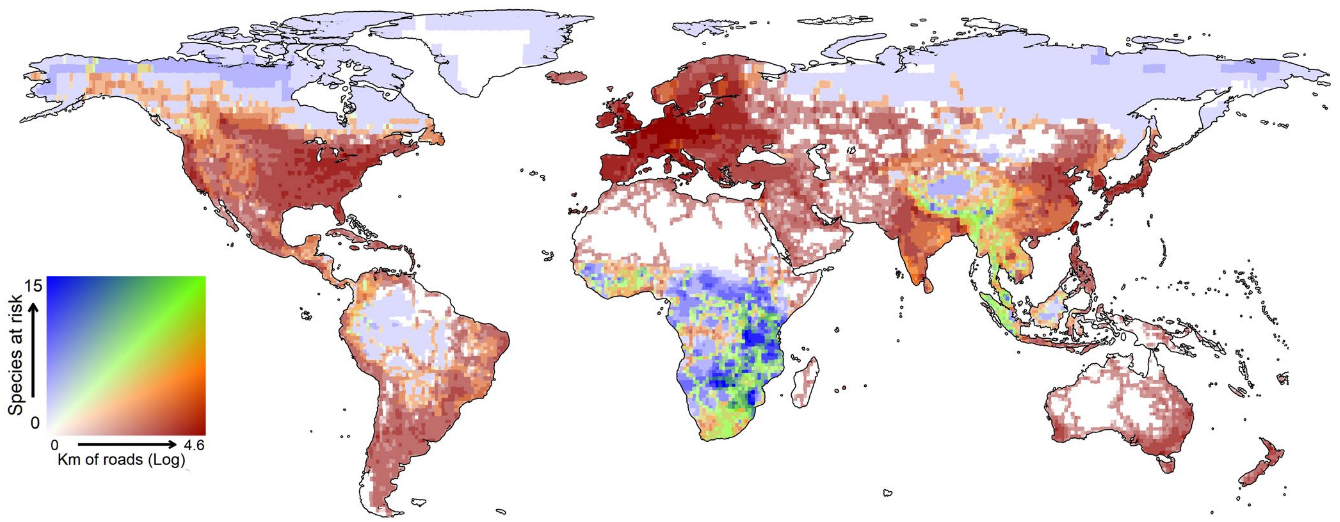

FIGURE 3 Global distribution of the overlap between vulnerable species (mammal species for which roadkill of < 20% of their population can lead to an additional .1 probability of extinction) and current paved road density (as $\log_{10}$ km of road per 100-km × 100-km grid cell). Green areas indicate 'hotspots' 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 indicates no threatened species and no roads

Results from the qualitative validation largely supported our assessment: while 60% of the nine most vulnerable species ($F_{RiskExt10}$ < .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 ($F_{RiskExt10}$ > .90) had published studies showing non-natural mortality can pose a threat (Supporting Information Appendix S7).

3.2 | Terrestrial mammals potentially threatened by roadkill

The 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 Supporting Information Appendix S8). The use of the proposed phylogenetic predictive models was supported during validation, with a strong correlation (R^2 = .69) between observed and imputed $F_{RiskExt10}$ risk (Supporting Information Appendix S9). Predicted $F_{RiskExt10}$ identified 2.7% of mammals (124 species out of 4,677) as most vulnerable to roadkill ($F_{RiskExt10}$ < .2) including 83 species Threatened or Near Threatened by other human activities, but also 18 Least Concern species (23 species were not evaluated) (see Supporting Information Appendix S9 for complete list of species vulnerability). Surprisingly, IUCN considered roadkill as a threat to only 10 out of 5,940 mammalian species, which, according to our estimates are not among those most vulnerable to roadkill ($F_{RiskExt10}$ < .20). Particularly vulnerable species ($F_{RiskExt10}$ < .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) (Supporting Information Appendix S8).

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, the Amazon, Mongolian plateau, and the Palaearctic tundra have vulnerable species but currently with 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.

4 | 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 (Borda-de-Água et al., 2014; Cardillo et al., 2004). 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 (González-Suárez et al., 2018; Jacobson et al., 2016). Our analyses identified populations of several species of conservation concern (https://www.iucnredlist.org/) 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 reveals 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 (> .90), a pattern also suggested by previous studies focused on other sources of non-natural mortality (e.g., Garcia et al., 2008, Hutchings 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 where 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 populations (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 (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., R. A. 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., S. M. 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 Bissonette & Kassar, 2008; Grilo et al., 2015; Sadleir & Linklater, 2016; Seiler, 2003). 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 versus 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 were 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.

5 | 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 that 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., 2019; 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., 2021). 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 and demographic data 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 tools to investigate other negative road effects on wildlife.

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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. analysed 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.

DATA AVAILABILITY STATEMENT

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

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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 recent years, much of her research has 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.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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