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Author/s:

Grilo, C;Borda-de-Água, L;Beja, P;Goolsby, E;Soanes, K;le Roux, A;Koroleva, E;Ferreira, FZ;Gagné, SA;Wang, Y;González-Suárez, M

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CONSERVATION THREATS FROM ROADKILL IN THE GLOBAL ROAD NETWORK

Short running title: CONSERVATION THREATS FROM ROADKILL

Clara Grilo^{1,2*}, Luis Borda-de-Água^{3,4}, Pedro Beja^{3,4}, Eric Goolsby⁵, Kylie Soanes⁶, Aliza le Roux⁷, Elena Koroleva⁸, Flávio Z. Ferreira¹, Sara A. Gagné⁹, Yun Wang¹⁰, Manuela González-Suaréz¹¹

¹Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras, Lavras (MG), Brazil, CEP 37.200-900

²CESAM - Centro de Estudos do Ambiente e do Mar, Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal

³CIBIO/InBIO - Research Center in Biodiversity and Genetic Resources, Laboratório Associado, Universidade do Porto, Campus Agrário de Vairão R. Padre Armando Quintas 4485-661 Vairão, Portugal

⁴CIBIO/InBIO - Research Center in Biodiversity and Genetic Resources, Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal

⁵University of Central Florida, Orlando, FL, USA 10

⁶Clean Air and Urban Landscapes Hub, National Environmental Science Programme, School of Ecosystem and Forest Science, University of Melbourne, Australia

⁷Department of Zoology and Entomology, University of the Free State, Qwaqwa, Private Bag X13, Phuthaditjhaba, 9866 Republic of South Africa

⁸Department of Biogeography, Faculty of Geography, Moscow State Lomonosov University, 119991 Moscow, Russia

⁹Department of Geography and Earth Sciences, University of North Carolina at Charlotte 9201 University City Blvd., Charlotte, NC 28223, USA

¹⁰Research Center for Environment Protection and Water and Soil Conservation, China Academy of Transportation Sciences. 240 Huixinli, Chaoyang District, Beijing, 100029 P.R. China

¹¹Ecology and Evolutionary Biology, School of Biological Sciences, University of Reading, Reading, RG6 6AS, UK

*Corresponding author

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 **This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/GEB.13375](https://doi.org/10.1111/GEB.13375)**

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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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1 Corresponding Author Email ID: clarabentesgrilo@gmail.com

2 DR. CLARA GRILO (Orcid ID : 0000-0001-9870-3115)

3 DR. PEDRO BEJA (Orcid ID : 0000-0001-8164-0760)

4 DR. MANUELA GONZÁLEZ-SUÁREZ (Orcid ID : 0000-0001-5069-8900)

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10 **CONSERVATION THREATS FROM ROADKILL IN THE GLOBAL ROAD NETWORK**

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12

13

ABSTRACT

14

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

19 **Location** - Global

20 **Time period** – 1995 -2015

21 **Major taxa studied** – Terrestrial mammals

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

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

33 concern that concentrate species vulnerable to roadkill and high road densities in areas of South Africa,
34 central and Southeast Asia, and the Andes.

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

38

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

40 **Main text**

41 1. INTRODUCTION

42 There are at least 36 million kilometres of roads in the world currently (CIA, 2020). Roads dominate the
43 landscape in some regions, e.g., 83% of land in the USA (Riitters & Wickham, 2003) and 50% in Europe
44 (Torres et al., 2016) are within 1 and 1.5 km of the nearest road, respectively. An additional 25 million
45 kilometres of roads are expected by 2050, mostly from expanding the road networks of developing countries
46 that contain exceptional biological diversity and highly conserved ecosystems (Laurance, 2018; Meijer et al.,
47 2018; Alamjir et al., 2019). Given the potential for roads to negatively affect biodiversity, evaluating the
48 current and future impacts of the global road network on wildlife is critical (van der Ree et al., 2015). Wildlife
49 mortality through collisions with vehicles (hereafter roadkill) is often considered one of the most serious
50 impacts of roads, being a significant source of anthropogenic mortality for some species (Loss et al., 2015;
51 Hill et al., 2019; Morelli et al., 2020). Roadkill impacts have been well documented for a wide range of
52 vertebrates and regions, with estimates of millions of individuals dying annually in roads across Europe (e.g.
53 Erritzoe et al., 2003; Wembridge et al., 2016; Grilo et al., 2020), the Americas (e.g. Loss et al., 2014; Baxter-
54 Gilbert et al., 2015; González-Suaréz et al., 2018) and Australia (Ehmann & Cogger, 1985), and roadkill
55 being identified as a problem also in Africa (Collinson et al., 2019; Gandiwa et al., 2020) and Asia (Seo et al.,
56 2015; Silva et al., 2020). While numbers killed are high, the actual impact of that added mortality at the
57 population level is poorly understood, but at least for some species it can be high (Benítez-López et al.,
58 2010). For instance, roadkill is responsible for 35% of annual deaths in Florida panthers *Puma concolor coryi*
59 (Taylor et al., 2002) and 49% in badgers *Meles meles* in Britain (Harris et al., 1992, Harris et al., 1995). Also,
60 roadkill annually removes 10% of the Iberian lynx *Lynx pardinus* population (Simón et al., 2012), 10% of
61 black bears *Ursus americanus* in Ocala National Forest (FFWCC, 2012) and may have reduced the density
62 of hedgehogs *Erinaceus europaeus* in the Netherlands by 30% (Huijser & Bergers, 2000). Overall, it is likely
63 that roadkill can increase the risk of local extinction by reducing effective population size and genetic
64 diversity, and by limiting demographic and genetic rescue (Jackson & Fahrig, 2011). There is, therefore, a
65 critical need to identify the species and regions that are most vulnerable to the rapid expansion of roads and
66 traffic worldwide (Laurance et al., 2014). A challenge to achieve this goal is that wildlife populations do not
67 respond equally to additional mortality, which makes evaluation of roadkill effects on population persistence
68 challenging (Gibbs & Shriver, 2005; Row et al., 2007; Diniz & Brito, 2013, Ceia-Hasse et al., 2017). These
69 effects may vary depending not only on the proportion of the population killed on roads each year (Jaeger et
70 al., 2005; Jacobson et al., 2016) but also on demographic processes (e.g., density dependent fecundity or
71 immigration) that affect the ability of the population to offset increased mortality (Purvis et al., 2000; Pearson
72 et al., 2014). Species characteristics can help us predict these variable effects. For example, species with

73 high adult survival and low fecundity, typically have low population growth rates, and are more likely to
74 experience declines with added anthropogenic mortality (Sparkman et al., 2011). The link between species
75 demographic variables and risk of extinction due to additional mortality has been established for some
76 sources of human impacts (Owens & Bennet, 2000; Crooks et al., 2017) but not for roadkill (but see Grilo et
77 al., 2020 that estimated the incidence of roadkill based on species trait-models and estimated population
78 vulnerability in Europe).

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

89

90 **2. MATERIAL AND METHODS**

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

95

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

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

112 assumes that larger mammals killed during the survey period would always be detected, but that some small
113 species could be missed as they could disappear between survey intervals. The two methods are equivalent
114 for daily surveys.

115 For a target group of species for which roadkill rates were available we then estimated the fraction of the
116 population roadkilled in the study areas, selecting estimates from the site with the highest observed roadkill
117 rate if multiple estimates were available. The target group included all mammalian species of conservation
118 concern (i.e., Near Threatened, Vulnerable, Endangered, or Critically Endangered species classified by
119 IUCN Red List 2016) and those species with high roadkill rates: the three small-sized (<1kg) and the three
120 large-sized (>1kg) mammals with the highest roadkill rates in each continent [North America (Canada, USA
121 and Mexico), Central/South America, Europe, Africa, Asia and Oceania]. For each species, we assumed
122 observed roadkill rates were representative of all paved roads (excluding urban areas) in the *study site*,
123 which was defined by using a buffer around the centroid of the actual surveyed road. The buffer was defined
124 to potential encompass a local population considering species area requirements vary with body size (Jetz et
125 al. 2004). We considered a 5km radius buffer for species with body mass <1kg, and a 50km radius for mass
126 >1kg.

127 The fraction of a population lost to roadkill was calculated as $F_{\text{Roadkill}} = N_{\text{roadkilled}}/N_{\text{pop}}$, where $N_{\text{roadkilled}}$ is the
128 estimated total number of roadkilled individuals of the species in the *study site* (ind/km), calculated by
129 multiplying the observed roadkill rate by the total length of paved roads in the study site. Road length was
130 estimated using Google Earth (Digital Globe 2016. <http://www.earth.google.com> [2015-2016]). N_{pop} is an
131 estimate of the total population of the species in the *study site* calculated by multiplying observed population
132 density (ind/km²) by study site area (km²). Population density estimates were obtained from within or near
133 the *study site* when possible; otherwise we used published species-level estimates (see SM2 for references).
134 Although we had a single observed roadkill rate for each species in each study site, we often found multiple
135 estimates of population density from different sources. We used the minimum and maximum estimates of
136 population densities to calculate several F_{Roadkill} values and reflect uncertainty.

137

138 **Step 2 Risk of extinction from roadkill for the target species**

139 We used a spatially implicit age-structured stochastic population model based on Borda-de-Água et al. (2014)
140 to estimate the increased probability of extinction in 50 years (based on 600 simulations) for each selected
141 species in its study site under simulated scenarios of F_{Roadkill} values ranging from 0.01 to 0.9 at 0.01
142 increments (methodological details and code in SM3; Figure 1). Without roadkill all species had stable
143 populations with no risk of extinction within 50 years. These simulations allowed us to estimate the increased
144 probability of extinction given the observed F_{Roadkill} for each selected species. For species with multiple F_{Roadkill}
145 we reported the range based on the minimum and maximum fractions. In addition, we defined a threshold
146 value, $F_{\text{RiskExt10}}$, to represent the proportion of the population that if roadkilled would result in an increase in the
147 probability of extinction of 0.1. $F_{\text{RiskExt10}}$ could be higher or lower than the observed F_{Roadkill} . We propose
148 $F_{\text{RiskExt10}}$ as an indicator of vulnerability to roadkill, with species in which loss of small fractions of a population
149 can result in increased risk of extinction (small $F_{\text{RiskExt10}}$) being more vulnerable and more likely to be
150 threatened by roadkill.

151 The Borda-de-Água et al. (2014) model assumes that population growth is determined by age at first birth,
152 interval between births, litter size, period of recruitment (the average interval in months between two births by

153 an adult female), number of litters per year, natural survival rates for nine variables: newborns/youngest
154 individuals, juveniles, and adults (categories reflect those in the study from which survival data were obtained,
155 see below), and maximum longevity. Estimates for these variables were obtained from available compilations
156 (Jones et al., 2009; Myhrvold et al., 2015; Myers et al., 2016; WildScreen Arkive, 2016; IUCN, 2016) and
157 dedicated literature searches (SM2). For survival rates we used any available data, and in some cases we
158 applied the single estimate available to all age-stages. When data were not available for a species we used
159 the median from all available estimates from closely related taxa/species or from the most closely related
160 species (same genus). A total of 68 cases out of 710 ((population density + nine variables) * 71 populations)
161 were missing data being the majority on survival rates (details in SM2). We used empirical estimates of
162 variance for all variables when available; otherwise we used a 10% variance.
163 The Borda-de-Água et al. (2014) model incorporates density dependence using the Beverton-Holt
164 relationship between the number of births and juveniles (Beverton & Holt, 1957). By applying this model we
165 assumed that: roadkill rates were constant over time in each study site, the available data reflected
166 dynamics reasonably well even if obtained from other regions, and the population in the study site was not
167 part of a metapopulation.

168

169 **Step 3. Global assessment of mammalian vulnerability to roadkill**

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

184

185 **Validation**

186 Step 2 generated estimates of risk of extinction from roadkill (anthropogenic mortality) for local populations.
187 Ideally, those estimates could be compared with population trends in those locations for validation, but those
188 data are simply not available. Instead, we conducted a qualitative validation searching the literature for
189 independent evidence from population viability analyses or other modelling approaches showing the effects
190 of anthropogenic mortality on risk of extinction. We considered mortality from roadkill and other human-
191 driven sources, as analyses of roadkill impacts are very limited. The comparison focused on evidence from
192 those species identified as most vulnerable in our assessment ($F_{\text{RiskExt10}} < 0.20$, $n=9$) and those identified as
193 least vulnerable ($F_{\text{RiskExt10}} > 0.90$, $n=15$). For step 3, we validated model estimates of $F_{\text{RiskExt10}}$ using leave-

194 one-out cross-validation (LOO-CV) (Bruggeman, 2009) as well as 2-fold and 5-fold cross-validation blocked
195 by phylogenetic distance (Roberts et al., 2017) (see SM4 for further details).

196

197 **3. RESULTS**

198 **3.1 Roadkill rates and population responses to roadkill**

199 We compiled a total of 1,310 roadkill rate records for 392 different mammalian species representing 184
200 references and personal communications (SM1). We found high inter- and intra-specific variability in roadkill
201 rates (SM1). Roadkill rates varied from fewer than 0.005 ind/km/year ($n=16$ species) to more than 10
202 ind/km/year ($n=10$ species). The large mammal with the highest number of records (moose (*Alces alces*);
203 $n=45$) had roadkill rates ranging between 0.00015 and 1.17 ind/km/year (SM1), while the small mammal with
204 the highest number of records (guinea pig (*Cavia aperea*); $n=9$) had roadkill rates ranging between 0.004
205 and 12.82 ind/km/year.

206

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

214

215 Our population models suggest populations of four species in the target group may be at risk of extinction if
216 observed roadkill levels persist on the study sites including the maned wolf *Chrysocyon brachyurus* in
217 Uberlândia-Uberada (Brazil), little spotted cat *Leopardus tigrinus* in western Santa Catarina (Brazil), brown
218 hyena *Hyaena brunnea* in Mapungubwe Transfrontier conservation area (Southern Africa), and leopard
219 *Panthera pardus* in Rajaji National Park and the Hariwar Conservation area (North India) (Figure 2; details in
220 SM5 and SM6). Among the 71 populations analysed, we classified 10 as most vulnerable to roadkill ($F_{\text{RiskExt10}} < 0.2$),
221 31 had intermediate vulnerability ($0.2 < F_{\text{RiskExt10}} < 0.5$), 15 had low vulnerability ($0.5 < F_{\text{RiskExt10}} < 0.9$), and
222 15 had very low vulnerability ($F_{\text{RiskExt10}} > 0.9$) (Figure 2, SM6).

223 Results from the qualitative validation largely supported our assessment: while 60% of the nine most
224 vulnerable species ($F_{\text{RiskExt10}} < 0.20$) had published studies showing non-natural mortality can increase risk of
225 extinction for those species, only 13% of the 15 species with very low risk ($F_{\text{RiskExt10}} > 0.90$) had published
226 studies showing non-natural mortality can pose a threat (SM7).

227

228 **3.2 Terrestrial mammals potentially threatened by roadkill**

229 Phylogenetic predictive model showed that high reproductive rates, represented by low age of maturity, high
230 numbers of litters per year and large litter sizes, were key predictors of high $F_{\text{RiskExt10}}$ (details in SM8). The
231 use of the proposed phylogenetic predictive models was supported during validation, with a strong
232 correlation ($R^2=0.69$) between observed and imputed $F_{\text{RiskExt10}}$ risk (SM). Predicted $F_{\text{RiskExt10}}$ identified 2.7% of
233 mammals (124 species out of 4,677) as most vulnerable to roadkill ($F_{\text{RiskExt10}} < 0.2$) including 83 species
234 Threatened or Near Threatened by other human activities, but also 18 Least Concern species (23 species

235 were not evaluated) (see SM9 for complete list of species vulnerability). Surprisingly, IUCN only considered
236 roadkill as a threat to only 10 out of 5940 mammalian species which, according to our estimates are not
237 among those most vulnerable to roadkill ($F_{\text{RiskExt10}} < 0.20$). Particularly vulnerable species ($F_{\text{RiskExt10}} < 0.10$)
238 included: wild yak *Bos mutus* (listed as Vulnerable by the IUCN), Bohor reedbuck *Redunca redunca* (Least
239 Concern), Amur tiger *Panthera tigris altaica* (Endangered), African elephant *Loxodonta africana* (Vulnerable),
240 sun bear *Helarctos malayanus* (Vulnerable), African buffalo *Syncerus caffer* (Near Threatened), Asian
241 elephant *Elephas maximus* (Endangered) and Sumatran rhinoceros *Dicerorhinus sumatrensis* (Critically
242 Endangered) (SM8).

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

252

253 **DISCUSSION**

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

267 Global assessments such as the one presented here provide the opportunity to identify unstudied or
268 undetected species potentially vulnerable to road mortality impacts and generate a priority map that reveal
269 areas where mammalian biodiversity could be negatively affected by existing and future roads. Applying our
270 framework at a global scale, we identified more than 100 mammals as very vulnerable to roadkill and
271 revealed several areas where mammalian biodiversity may be lost due to the impact of existing road
272 infrastructure. While our results emphasize global findings, the proposed framework can inform conservation

273 prioritization and mitigation efforts both at regional and broad scales as it produces output at local scales
274 already and step 3 could be easily adapted to different spatial and taxonomic scales.

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

292 Our study presents a new framework for identifying, ranking and predicting species and areas vulnerable to
293 roadkill impacts. This can be a powerful tool to understand risk but there are data and modelling limitations
294 that need to be considered. First, the majority of road surveys only indicated the number of carcasses
295 recorded overall. These estimates can be biased by low carcass detectability and high removal rates (e.g.
296 Santos et al., 2016). Several studies have proposed correction indexes for specific taxa based on the time
297 interval between surveys, the taxonomic group and the species body mass (e.g., Santos et al., 2011;
298 Teixeira et al., 2013). However, it is not clear whether these regional corrections can be extrapolated for
299 mammals worldwide. Second, the modelling approach applies the highest observed roadkill rate for a
300 specific surveyed area (one or several roads) to the entire paved road network in our defined study area,
301 which for large body mass mammals could cover over 7,854 km². Currently, there is no scientific consensus
302 regarding how different types of paved roads and associated traffic influence roadkill risk (see Seiler, 2003;
303 Bissonette & Kassir, 2008, Grilo et al, 2015; Sadleir & Linklater, 2016). Further research is needed to
304 determine how varying traffic volume, road widths and types of roadside vegetation influence roadkill rates
305 for a wide range of species. Third, our modelling approach does not consider that roadkill may impact some
306 groups of individuals within a species more than others. Given the same fraction of a population removed by
307 roadkill, population persistence would be different if those removed are primarily reproductive adults vs. older
308 animals. For some species there is a high incidence of mortality of juveniles and sub adults while for other
309 species no distinct vulnerability was found among individuals (Grilo et al., 2009). Fourth, for many
310 mammalian species, non-natural mortality includes sources other than road mortality such as legal hunting
311 and poaching (Hill et al., 2019), but our model only considers road mortality. To better understand overall
312 extinction risk for particular populations and species we need to understand all sources of mortality and
313 explore whether non-natural mortality sources may be compensated. Finally, our approach relied on trait

314 data that was largely obtained from global datasets that do not reflect regional and local variation. One
315 example is population density, which was critical to estimate the fraction of the population roadkilled at the
316 regional level. While we cannot overcome this limitation, our approach explicitly included this uncertainty by
317 considering both the minimum and maximum densities observed, which allowed us to estimate a range of
318 fractions of the population roadkilled and, therefore, a broad-spectrum of extinction risks.

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

326 **CONCLUSIONS**

327 Results of this study have implications for mammalian conservation and road mitigation worldwide. Our
328 analyses bring attention to Sub-Saharan Africa and south-eastern Asia as regions where roads can lead to
329 loss of mammalian biodiversity and thus, areas where future road development and road mitigation need to
330 be carefully considered. The positive news is that these areas (as well as Latin America) have been
331 identified as threat refugia for vertebrates where conservation actions are likely to succeed (Allan et al.,
332 2019).

333 The local scale output from our framework provides a first step to highlight populations which might be
334 currently under risk of extirpation and areas where local studies are needed to ultimately make site-specific
335 recommendations for road mitigation. This local scale analysis could be directly used in environmental
336 impact studies applied to target areas and species to provide estimates of risk of extinction and potential
337 scenarios given data uncertainty and alternative management plans (Alamgir et al., 2017; Ceballos et al.,
338 2017). "Since IUCN Red List assessments describe ongoing and future threats to each species, our study
339 can directly inform these descriptions by providing information about which species are affected by roadkill
340 and about the severity of that threat. Combining our approach with information on planned infrastructures
341 could additionally identify and quantify the severity of future threats. In addition, the global scale output of our
342 proposed framework could be part of strategic environmental, social and economic assessments by national
343 infrastructure planning agencies, environmental governance agencies, global financing institutions,
344 international NGOs. Projecting risk of extinction across broader areas and taxonomic groups could support
345 decisions towards infrastructure that remains more sustainable throughout its life cycle. Our approach could
346 be directly integrated into existing assessment frameworks, adding a relatively unstudied dimension. For
347 example, the World Bank is the largest source of financing for development and has recently updated its
348 Environmental and Social framework (ESA) to minimize the negative impacts of the projects it finances
349 (Morley et al., 2020). Frameworks such as the ESA could incorporate our approach as an additional module
350 to identify vulnerable areas and species and guide strategies to minimize long-term impacts of proposed
351 road projects. In addition, we generate output for mammals that can be valuable. The global list of mammals
352 vulnerable to roadkill generated here may be used by road managers and conservation agencies in the
353 design of surveys, monitoring, and mitigation measures. The global map identifies regions that deserve

354 special attention and can be particularly relevant for large-scale projects, such as the Belt and Road Initiative,
355 providing information to facilitate addressing all impacts before projects begin (Ascensão et al., 2018).

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

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530

FIGURES

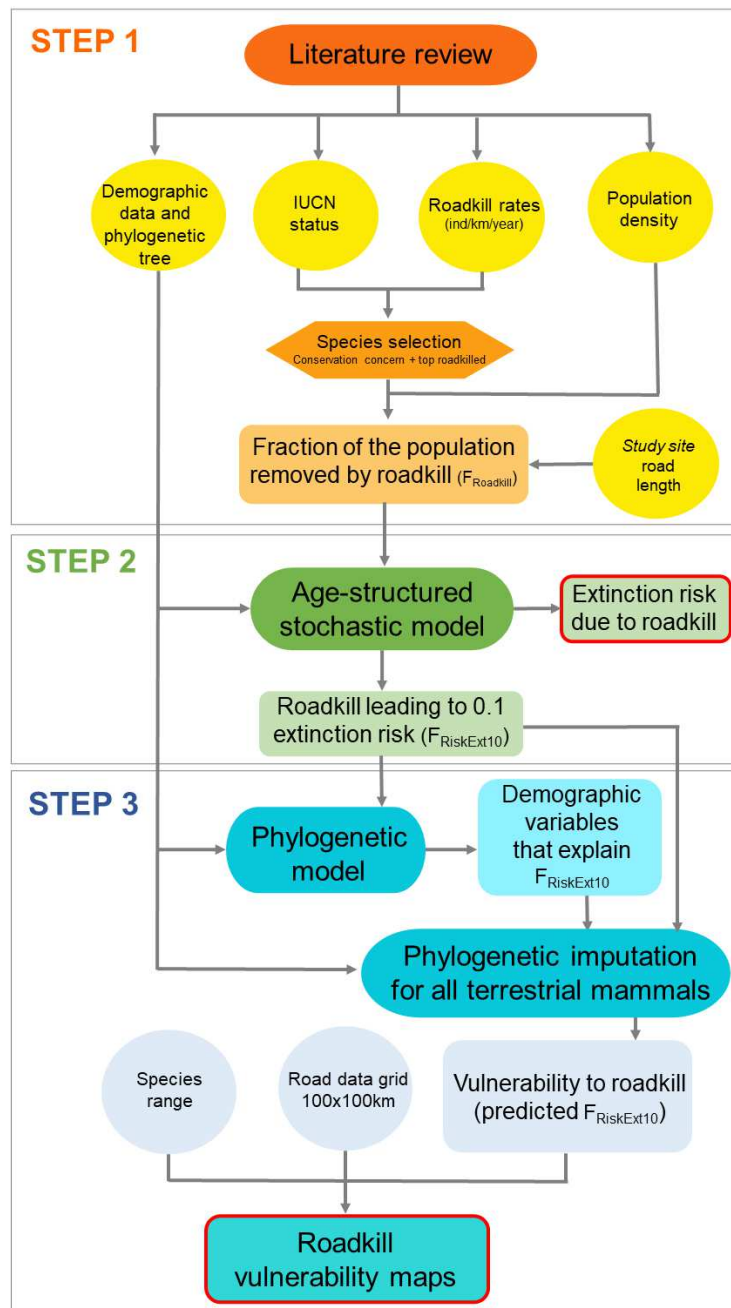


Figure 1 – Our framework to quantify roadkill impacts on mammals. The framework includes three steps: step 1 - roadkill

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.

proposed framework roadkill impacts on worldwide. The includes three steps: rates and estimated

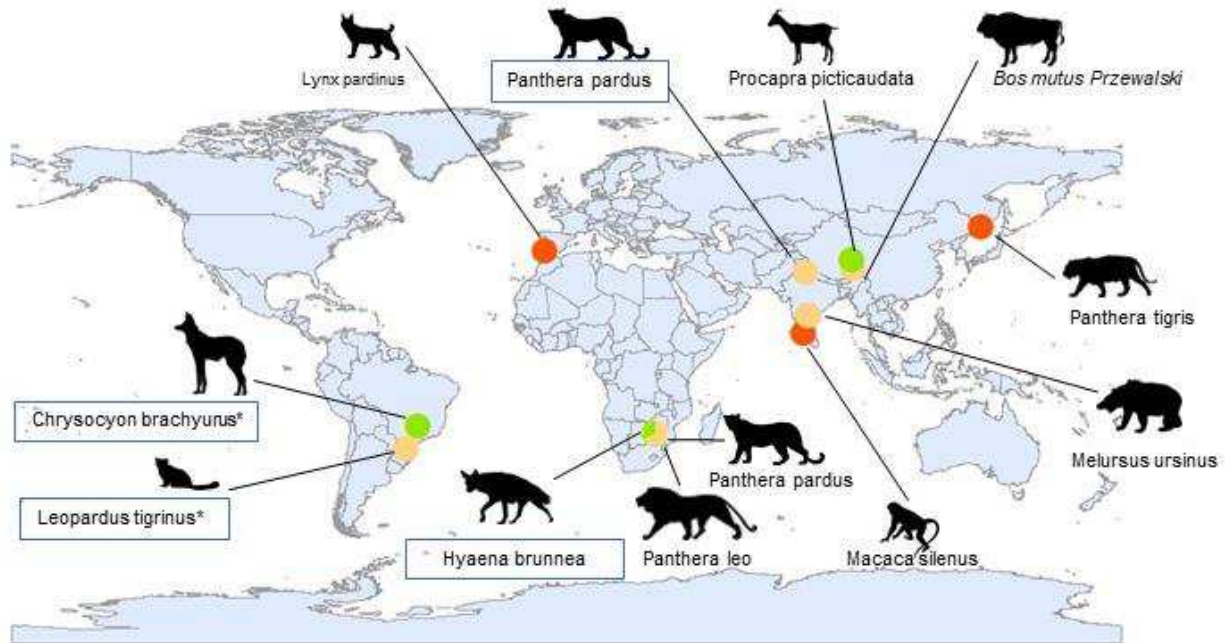


Figure 2 – Location of the species most vulnerable to roadkill ($F_{\text{RiskExt10}} < 0.2$). The scientific names framed in blue are those for which observed roadkill are estimated to lead to higher risk of extinction in 50 years if the observed roadkill persist in the region. Coloured dots are the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

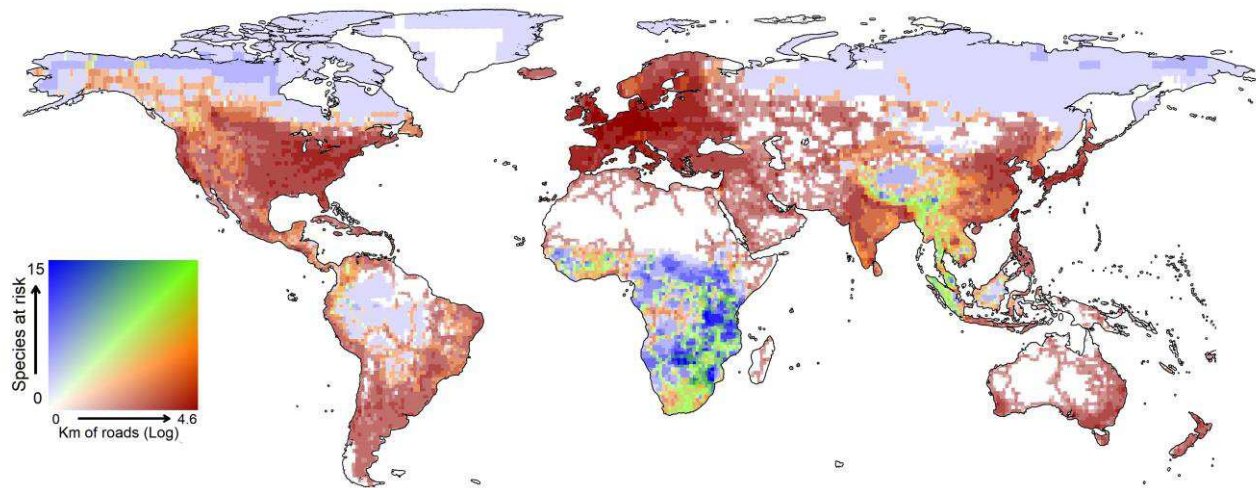


Figure 3 – Global distribution of the overlap between vulnerable species (mammal species for which roadkill of <20% of their population can lead to an additional 0.1 probability of extinction) and current paved road density (as \log_{10} kilometres of road per 100-km x100-km grid cell). Green areas indicate “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

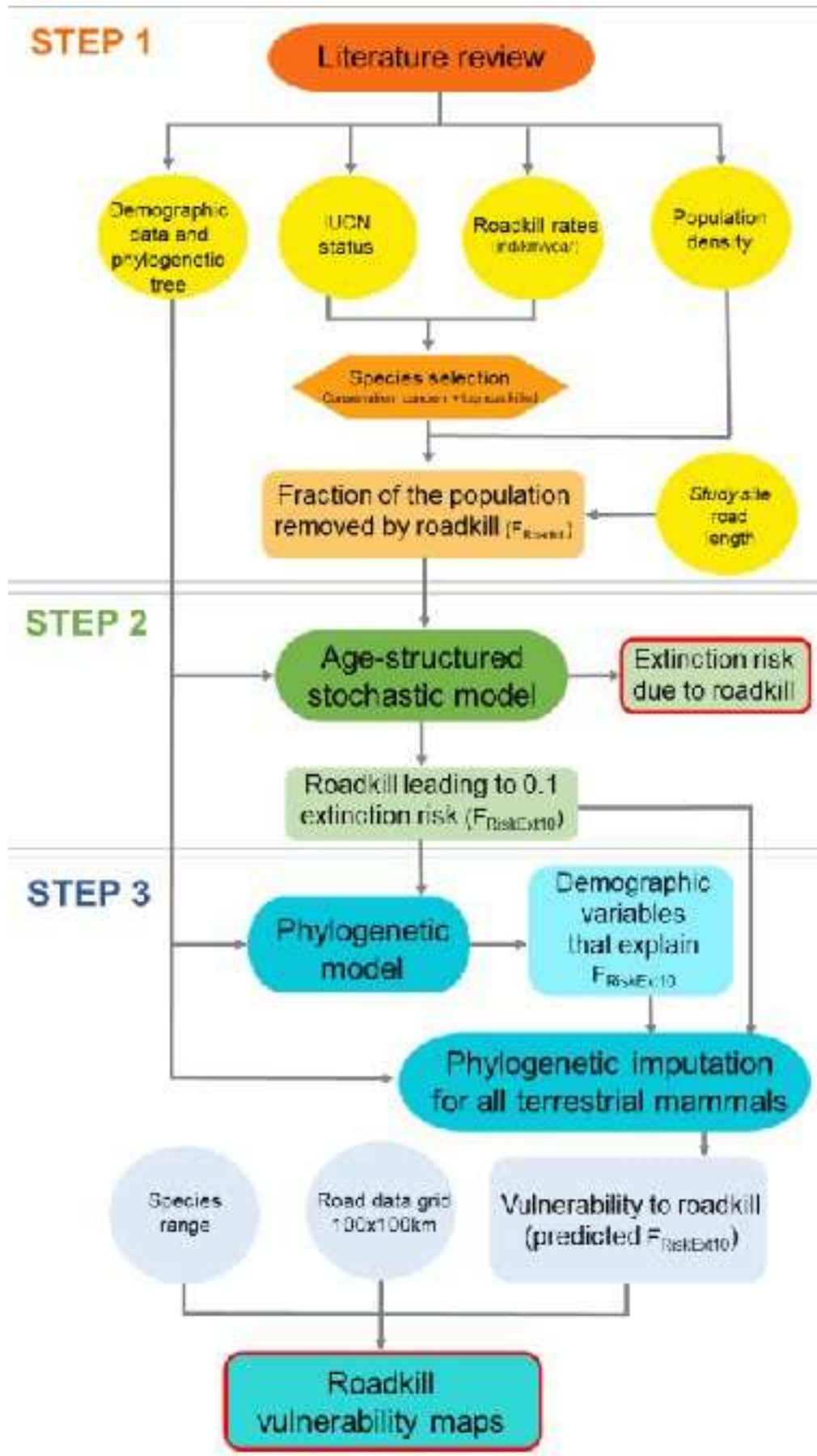
SM5 - Risk of extinction when the fraction of the population is removed due to observed roadkill for four species' populations

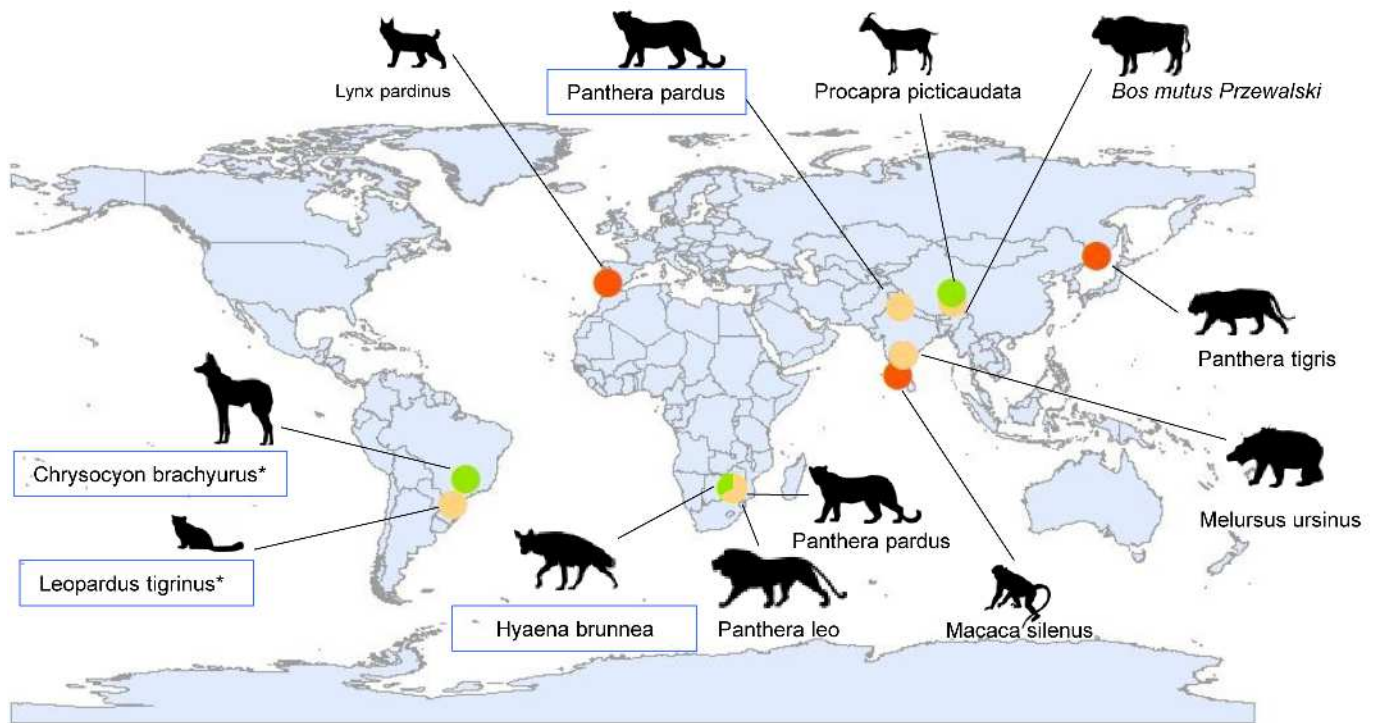
SM6 - Results from the spatially implicit age-structured stochastic models

SM7 - Qualitative validation of results from the spatially-implicit age-structured stochastic models for species predicted to be most ($F_{\text{RiskExt10}} < 0.20$) and least vulnerable ($F_{\text{RiskExt10}} > 0.90$)

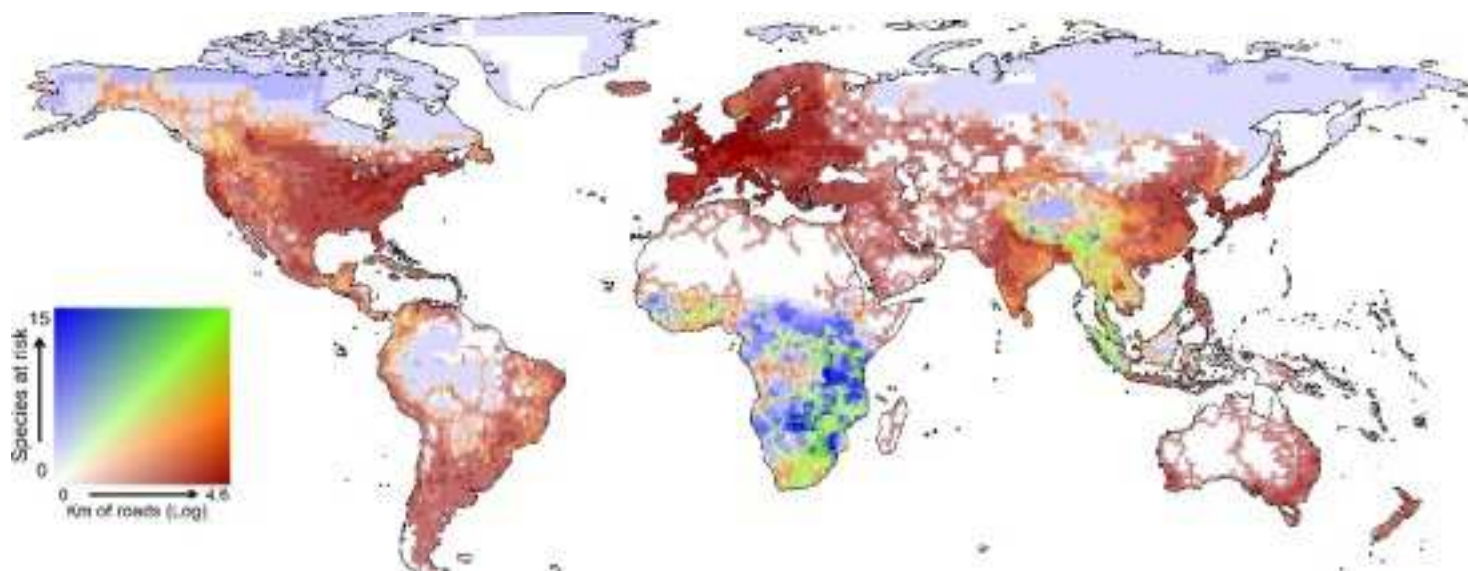
SM8 - Relative importance of each variable from GLS and PGLS model sets and averaged model coefficients with confidence intervals for each variable

SM9 - Vulnerable species to roadkill





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