

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

Article

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

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3 Running title: Trait-based predictions of roadkill risk

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10

11 **Keywords:** bird, Brazil, life-history, machine-learning models, mammal, random forest, road-
12 associated mortality, species' traits.

13

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21

22 **Biosketch**

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

33 **Abstract**

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

40 *Location:* Brazil

41 *Time period:* 2001-2014

42 *Major taxa:* Birds and mammals

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

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

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

61 **Introduction**

62 Roads are increasingly prevalent features in global landscapes (Laurance & Balmford, 2013;
63 Ibisch, Hoffmann, Kreft, Pe'er, Kati, Biber-Freudenberger, ..., & Selva, 2016) leading to
64 growing concerns about their impacts on wildlife (Alamgir, Campbell, Ioan, Goosem,
65 Clements, Mahmoud, & Laurance, 2017). Wildlife-vehicle collisions are one of the most
66 visible road-related impacts (Coffin, 2007), which can reduce population abundance, limit
67 dispersal, decrease genetic diversity, and ultimately threaten population viability (e.g., Fahrig
68 & Rytwinski, 2009; Borda-de-Água, Grilo, & Pereira, 2014; Grilo C, Del Cerro, Centeno-
69 Cuadros, Ramiro, Román, Molina-Vacas, Fernández-Aguilar, ..., & Godoy, 2016). However,
70 not all species appear to be equally affected by road-associated risks (Fahrig & Rytwinski,
71 2009). Variation among species can reflect methodological issues: small species degrade
72 faster and are less conspicuous, which can reduce their detectability once collision has
73 occurred, leading to underestimated rates (Santos, Carvalho, & Mira, 2011; Teixeira, Coelho,
74 Esperandio, & Kindel, 2013). Differences may also occur due to true variability in collision
75 risk associated to local abundance, more common species being more likely to suffer high
76 mortality rates (Ford & Fahrig, 2007; Santos, Mira, Salgueiro, Costa, Medinas, & Beja,
77 2016). However, detectability and abundance do not appear to be the only sources of
78 variation. For example, the lowland tapir *Tapirus terrestris* and the crab-eating fox *Cerdocyon*
79 *thous* have similar detectability and observed population densities in the Brazilian Pantanal
80 region (0.4 ind/km² - Desbiez, Bodmer, & Tomas, 2010), yet estimated mortality rates vary
81 considerably (fox: 0.24 ind/km/year; tapir: 0.01 ind/km/year. Souza, Cunha, & Markwith,
82 2014). An explanation is that variability in road mortality rates among species is also
83 explained by species' traits related to ecological habits, behaviour, and life-history traits.

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

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

105 Trait-based models are powerful tools commonly used in macroecological studies to
106 assess the mechanisms underlying the response of species to impacts and predict risks for
107 unstudied or difficult-to-detect organisms (González-Suárez, Gómez, & Revilla, 2013; Bland,
108 Collen, Orme, & Bielby, 2015). Here we used machine-learning trait-based models to assess
109 the role of a wide range of species' traits on estimated road mortality rates for bird and
110 mammalian species in Brazil. We focused on birds and mammals because these are well-
111 studied groups that provide a suitable empirical dataset (e.g. Coelho, Kindel, & Coelho,
112 2008). Brazil is also an interesting case study because in the last two decades economic and
113 social growth has led to a 20% increase in the road network, increasing impacts on wildlife
114 (DNIT, 2015) and this growth is likely to continue and expand into regions of exceptional
115 biological diversity and global ecological importance like the Cerrado and the Amazon
116 (Hoorn, Wesselingh, TerSteege, Bermudez, Mora, Sevink, ..., Antonelli, 2010; Lahsen,
117 Bustamante & Dalla-Nora, 2016). Therefore, there is an urgent need to better understand and
118 predict road risks within Brazil to guide infrastructure planning and mitigation measures,
119 including the protection of those species that are most susceptible to road impacts. To achieve
120 this goal we fitted trait-based models to predict road mortality rates for all Brazilian birds and
121 mammals including the many species for which roadkill estimates are not currently available
122 (unstudied or undetected organisms). These predictions allowed us to identify unstudied
123 species with high vulnerability to road-related mortality, and revealed areas where road
124 impact is likely high. Our study provides a first comprehensive evaluation of the key intrinsic

125 risk factors associated with road impacts in endotherms, and demonstrates the potential of
126 using macroecological approaches for road ecology to define predictive trait-based models
127 that can identify potentially vulnerable species and high risk areas.

128

129 **Methods**

130 *Data*

131 Empirical road mortality rates for birds and mammals were collected from unpublished
132 databases (made available by individual researchers contacted via the *Lattes* platform
133 <http://lattes.cnpq.br>), grey literature sources (technical reports, proceedings of scientific
134 conferences, MSc and PhD theses), and scientific papers from peer-reviewed journals.
135 Published sources were located using the following keywords in English and their translations
136 to Portuguese: (“roadkills” OR “road mortality”) AND (“birds” OR “mammals” OR
137 “vertebrates”). We considered only rates from areas of Brazil in which systematic surveys had
138 been conducted at least once a week for a minimum period of three months to minimize the
139 bias on roadkill rates among studies. From each study, road mortality rates per species were
140 calculated as the number of individual carcasses detected standardized per kilometre of
141 surveyed road per year (ind/km/year). Rates may be underestimated because not all carcasses
142 persist equally in the pavement. In addition, in some studies not all carcasses were identified or
143 reported at the species level. The calculated rates were modified using a correction for carcass
144 persistence estimated by Santos, Carvalho, & Mira (2011) that aims to reduce bias from
145 variable detection rates among species (see Appendix S1 in Supporting Information). Both
146 corrected and uncorrected rates were tested to evaluate consistency of results. We present the
147 corrected rates in the main text, but results did not change qualitatively when using
148 uncorrected rates (see Appendix S2). We characterized the study location using the
149 geographic coordinates of the surveyed road(s) midway point (Appendix S3, Fig. S3.1).
150 Taxonomic names used by each study were matched to the current IUCN taxonomy (IUCN
151 2017). One mammalian species with empirical road mortality data (*Guerlinguetus ingrami*)
152 was not recognized by the IUCN and was not considered in the analyses. *Coendou spinosus*
153 was listed as two different species (*Coendou villosus* or *Coendou spinosus*) in separate studies
154 but treated as one species in our analyses.

155 We identified Brazilian birds and mammals based on overlap of distribution range maps
156 (IUCN 2017) with the continental Brazilian territory (based on the IUCN country boundary

157 map). We used distribution range polygons classified as presence “Extant” or “Possible
158 extant” and included all origins and seasonalities. These range polygons were also overlapped
159 with a 1° x 1° grid (equivalent to ~110 x 110 km near the equator) covering the continental
160 Brazilian territory.

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

164

165 *Data analysis*

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

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

184 Trait data were not available for all species (data limitations are common in
185 comparative studies, see González-Suárez, Lucas, & Revilla, 2012). To avoid excluding
186 observations, which can lead to biases, we estimated missing values for each taxonomic group
187 using nonparametric imputation based on random forest regression trees (Stekhoven &
188 Bühlmann, 2012). Since this imputation approach results in slightly different values each time

189 it is run, we imputed and analysed 15 datasets for each taxonomic group to capture
190 uncertainty in the imputation process and assess sensibility of results to that uncertainty. To
191 facilitate reproducibility and encourage open science the code (R script) and data used in this
192 study will be available at [https://dx.doi.org/ 10.6084/m9.figshare.6237608](https://dx.doi.org/10.6084/m9.figshare.6237608) on 9 November
193 2018.

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

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

217

218 **Results**

219 We located 38 studies that reported road mortality rates in different areas of Brazil and met
220 our criteria of minimum frequency and period of survey (Figure S3.1). From these studies we

221 obtained 417 mortality rates for 170 bird species, and 366 road mortality rates for 73 mammal
222 species. Based on current distribution range maps we identified 1831 birds and 623 mammals
223 as present in Brazil. We made predictions for all mammals, but had to exclude 56 bird species
224 classified in taxonomic orders not represented in our empirical dataset (predictions cannot be
225 made for new levels in a categorical variable). All data are available on (to be deposited on
226 online repository upon acceptance, and made available as supplementary files for review).

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

234 Fitted models explained 61.7% of the observed variance in road mortality rates for birds
235 (median value, range across imputed datasets 61.1-62.4%) and 51.8% for mammals (range
236 51.2-52.4%). As expected survey predictors were important in both groups (Fig. 1). In
237 particular, survey interval was the most important predictor with intervals of 1-2 day
238 generally associated with higher estimates both for birds and mammals (Figs. 2 and 3).
239 Geographic location also explained observed road mortality rates (Fig. 1) with partial
240 dependence plots showing higher rates associated to western locations for both birds and
241 mammals, but contrasting patterns for latitude, with locations closer to the equator associated
242 with higher risk in birds but with lower risk in mammals (Figs. 2 and 3). Taxonomic order
243 was an important predictor for birds with higher rates found among cuckoos and anis
244 (Cuculiformes, eight species) and flightless birds (Cariamiformes, one species;
245 Struthioniformes, four species). Order was also important for mammals, with higher rates
246 among anteaters and sloths (Pilosa, 6 species) and armadillos (Cingulata, six species).

247 The analyses also revealed several species' traits as predictors of road mortality rates in
248 both birds and mammals with high consistency among models based on the different imputed
249 datasets (Fig. 1). Partial dependence plots show higher road mortality rates in birds associated
250 to larger body mass (>2 kg), earlier maturity ages, shorter lifespans, ground foraging
251 behaviour, and habitat and diet generalism (Fig. 2). For mammals, higher rates were

252 associated with scavenging behaviour, early maturity, smaller home range sizes, intermediate
253 body masses (3-50 kg), and habitat generalism (Fig. 3).

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

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

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

280 When considering the existing road network to estimate total mortality (number of
281 mortalities per year in each grid cell, Fig. 4c, d), the patterns, as expected, changed, and
282 revealed higher total predicted risk in coastal areas where most roads are found (Fig. S3.6).
283 However, total mortality did not exclusively reflect existing roads. For example, risk was high

284 in Western areas (Mato Grosso and Rondonia) where there are relatively few roads, and
285 relatively low in the Northeast region where road density is high. Worryingly, in some areas
286 total risk was very high with expected rates of over 96,000 individual birds and over 53,000
287 individual mammals killed per year in some 1° x 1° areas. Adding all predicted rates across
288 the country our results suggest that as many as 8,351,120 birds and 2,225,101 mammals could
289 be killed per year in Brazilian roads. Considering potential impacts of additional planned
290 paved roads (Fig. 3.7) we find increased risk in the Amazon, which we identify as a sensitive
291 area (with high standardized and median risk rates).

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

296

297 **Discussion**

298 Our results provide evidence that road-associated mortality risk is not randomly distributed
299 among species and can be partly explained by ecological, behavioural and life-history traits in
300 avian and mammalian species. Previous studies explored the role of individual traits (e.g.
301 Ford & Fahrig, 2007; Cook & Blumstein, 2013), but our results reveal that road mortality is
302 associated to a combination of multiple predictors that reflect diverse characteristics of the
303 studied species. Although analyses were conducted separately, we found that several traits
304 explained vulnerability to traffic for both bird and mammal species suggesting generalized
305 intrinsic sources of risk for endotherms, for example associated with body size. Our study also
306 identified distinct sources of vulnerability, which highlight idiosyncrasies of the studied
307 species and/or distinct mechanisms associated with vulnerability for birds and mammals. In
308 addition, road mortality also varied among taxonomic groups, potentially reflecting untested
309 characteristics. For example, for mammals we found higher rates among relatively slow
310 moving species like armadillos and sloths, while for birds flightless groups exhibited higher
311 rates. As expected survey-related variables were also important predictors of risk. Although
312 we used a correction factor, survey interval remained a key predictor for both groups. Our
313 results suggest that 1-2 days intervals between surveys may be optimal to assess risks for
314 these species (those intervals were associated with the higher rates - see also Santos et al.,
315 2011). Survey location was also important for both birds and mammals, with higher predicted

316 risk towards the west in both groups but contrasting latitudinal gradients that identified
317 distinct risk regions within Brazil for birds and mammals.

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

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

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

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

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

371 Our results also generate spatial predictions of road mortality risks, which highlight
372 the apparent high vulnerability of Amazonian species (higher risk per kilometre of road).
373 Although mortality rates in this area are likely to be relatively small due to low road density,
374 this region has high biodiversity and our analyses suggest road infrastructure development
375 could have severe impacts on many species. Considering the existing road network, as
376 expected, we found higher total risk in areas with higher road density. However, median risk
377 per species was not always high in areas, like Southern Brazil, with many threatened species
378 and high road densities, perhaps reflecting former population depression due to road mortality
379 (Teixeira, Kindel, Hartz, Mitchell, & Fahrig, 2017). Worryingly, our results suggest that more

380 than 8 million individual birds (nearly 180,000 from species threatened by extinction) and
381 more than 2 million mammals (over 72,000 from threatened species) may be killed each year
382 in existing Brazilian roads. These high values are predicted despite the fact that Brazil has a
383 relatively high number of roadless areas (Ibisch, Hoffmann, Kreft, Pe'er, Kati, Biber-
384 Freudenberger, ..., & Selva, 2016). Furthermore, our rates may be underestimated because we
385 do not consider unpaved roads. We also do not account for other indirect road impacts, such
386 as changes in spatial distribution due to road avoidance (Torres, Jaeger & Alonso, 2016),
387 which can reduce roadkill but may in turn impact population viability in other ways. Future
388 road development is also likely to result in increased risk, particularly in areas we identified
389 as sensitive (with intrinsically vulnerable species), like the Amazon. These results provide a
390 first overview of risk revealing potentially vulnerable species and areas. However, localized
391 and refined spatial predictions (accounting for unpaved roads and traffic levels) would be
392 useful to further describe areas in which road development is likely to have widespread
393 impacts on the local fauna, as well as areas in which mitigation measured would be most
394 valuable.

395 While our analyses offer useful insights, there are also limitations of the available data.
396 First, missing trait data is a common problem in comparative studies (González-Suárez et al.,
397 2012). Data imputation methods may be helpful but some limitations (e.g. handling variable
398 correlation) need consideration (Penone, Davidson, Shoemaker, Marco, Rondinini,
399 Brooks, ..., Costa, 2014). Also imputation of large proportions of the dataset incorporate
400 uncertainty in results, this can be quantified as done here, but results should still be interpreted
401 with caution. In addition, to missing trait data, empirical estimates of road mortality were also
402 not available for all species or areas. Instead, these data reflect a non-random subset of species
403 and locations, associated to biases in research effort and methodological issues. In fact, these
404 biases may explain the relatively abrupt geographic changes in our spatial predictions,
405 particularly for birds. Variation in detectability during surveys is a recurrent problem in road
406 surveys. Carcasses from small species may disappear from roads in less than 24 hours
407 (Teixeira et al., 2013). Carcasses in hot, humid areas, and those with high traffic levels may
408 also disappear faster. We applied corrections to the observed road mortality rates, but our
409 results were qualitatively the same when using uncorrected rates (Appendix 1) contrary to
410 what Santos et al. (2011) found in their study. The criteria we adopted to only include studies
411 with a 7-day minimum survey interval may have contributed to reduce differences; intervals

412 of one week or shorter have been found to significantly reduce bias for medium- and large-
413 sized birds and mammals (Bager & Rosa, 2011). Ultimately, data limitations and biases can
414 only be effectively addressed with additional research efforts. In the meantime, studies using
415 available data should consider uncertainty in results, explore correction methods, and interpret
416 findings with caution.

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

429

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619

620 **Data accessibility**

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

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

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

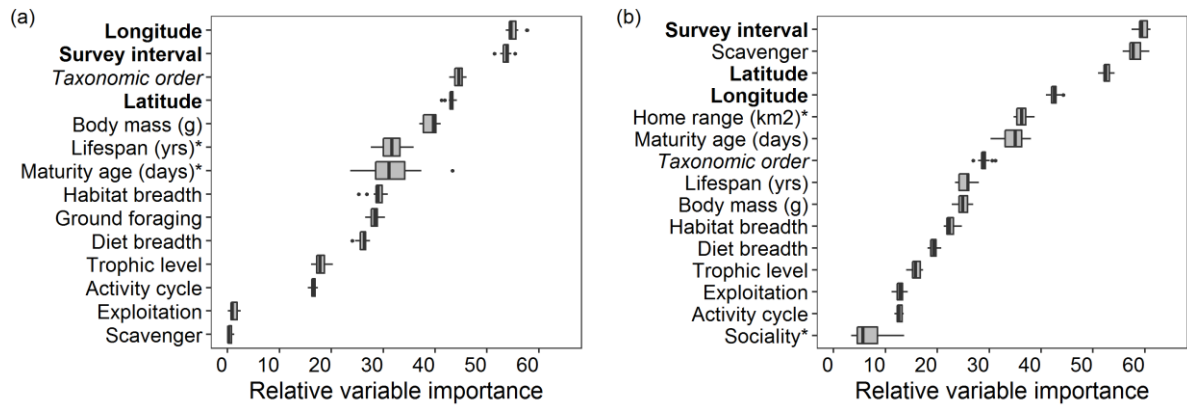
	Herbivores are more likely to utilize road verges, where vegetation can benefit from run-off, leading to higher roadkill rates.					
Habitat breadth	Total number of ecoregions within Brazil overlapping the current geographic range area of each species. Habitat specialists are likely to avoid novel environments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

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

Species with delayed maturation are more likely to prioritize survival, which can lead to greater perception of risk from roads and reduced roadkill rates.

Sociality	Binary descriptor to identify species in which individual spend most of their lives in a group. Defined as groups size=1 for solitary. Social species can benefit from collective vigilance and learning experienced that can reduce roadkill rates.	Jones et al., 2009	NA	NA	136	33
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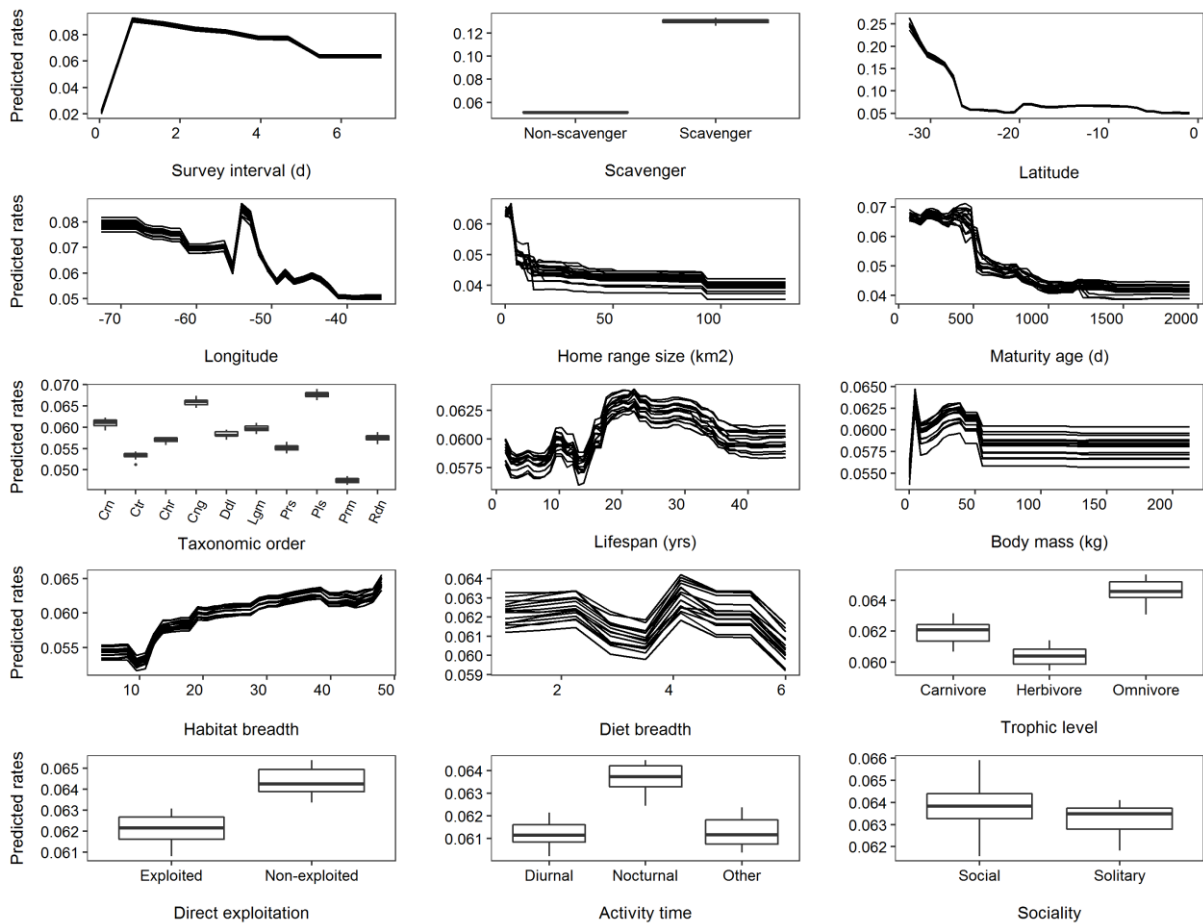
629 Figures and their legends



630

631 Figure 1. Relative importance of predictors associated with empirical road mortality based on
 632 random forest regression models for birds (a) and mammals (b). Boxplots show results for the
 633 15 imputed datasets for each taxonomic group. Study predictors (representing study site
 634 coordinates and survey sampling frequency) are in bold, taxonomic predictor (order) is in
 635 italics, traits with <50% empirical data are marked with an asterisk.

636

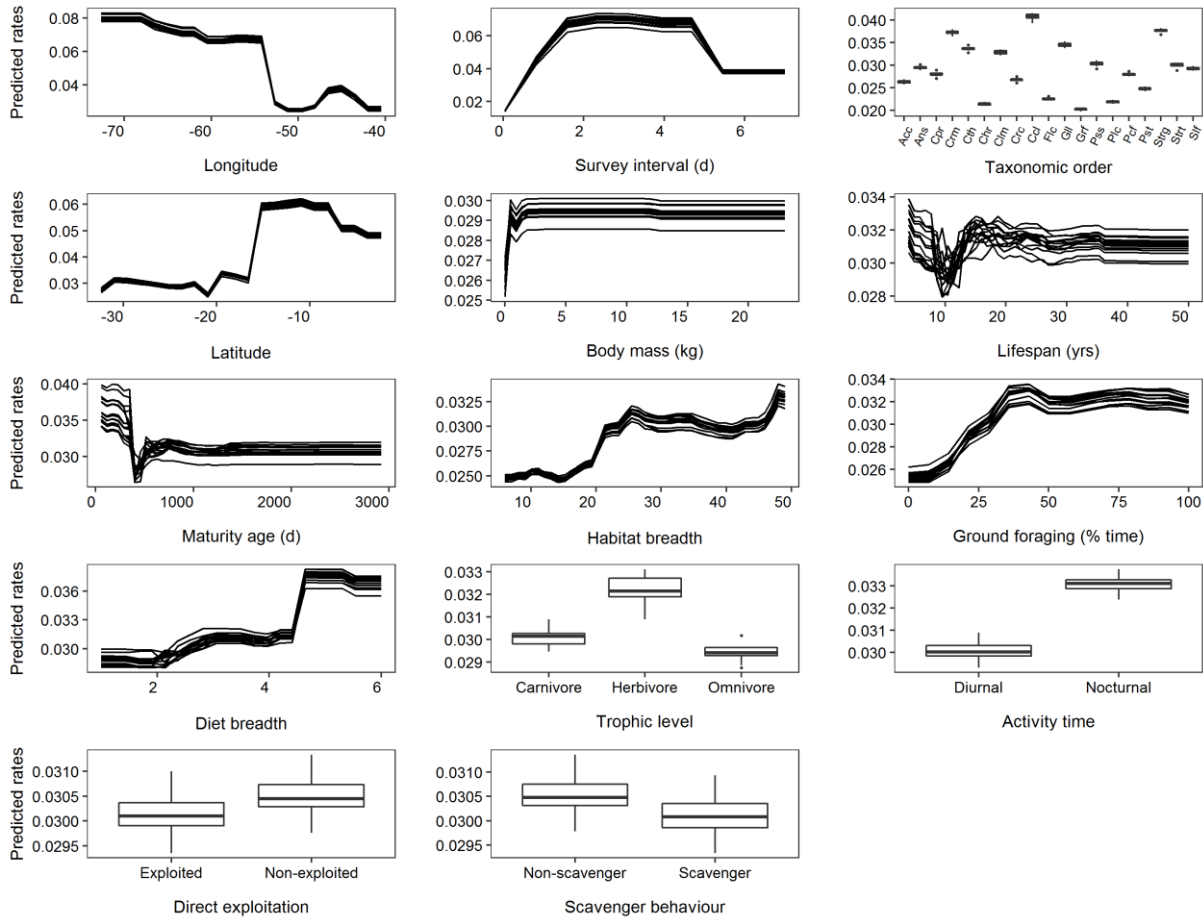


637

638 Figure 2. Partial dependence plots for all tested predictors on the predicted road mortality
 639 rates of Brazilian birds. Predictors are in descending variable importance order (see Fig. 1a).
 640 Showing results for the 15 imputed datasets. Note that y-scales differ among plots.

641 Taxonomic orders are abbreviated as follows: Acc (Accipitriformes), Ans (Anseriformes), Ccl
 642 (Cuculiformes), Chr (Charadriiformes), Clm (Columbiformes), Cpr (Caprimulgiformes), Crc
 643 (Coraciiformes), Crm (Cariamiformes), Cth (Cathartiformes), Flc (Falconiformes), Gll
 644 (Galliformes), Grf (Gruiformes), Pcf (Piciformes), Plc (Pelecaniformes), Pss (Passeriformes),
 645 Pst (Psittaciformes), Slf (Suliformes), Strg (Strigiformes), Strt (Struthioniformes).

646



647

648

649 Figure 3. Partial dependence plots for all tested predictors on the predicted road mortality

650 rates of Brazilian mammals. Predictors are in descending variable importance order (see Fig.

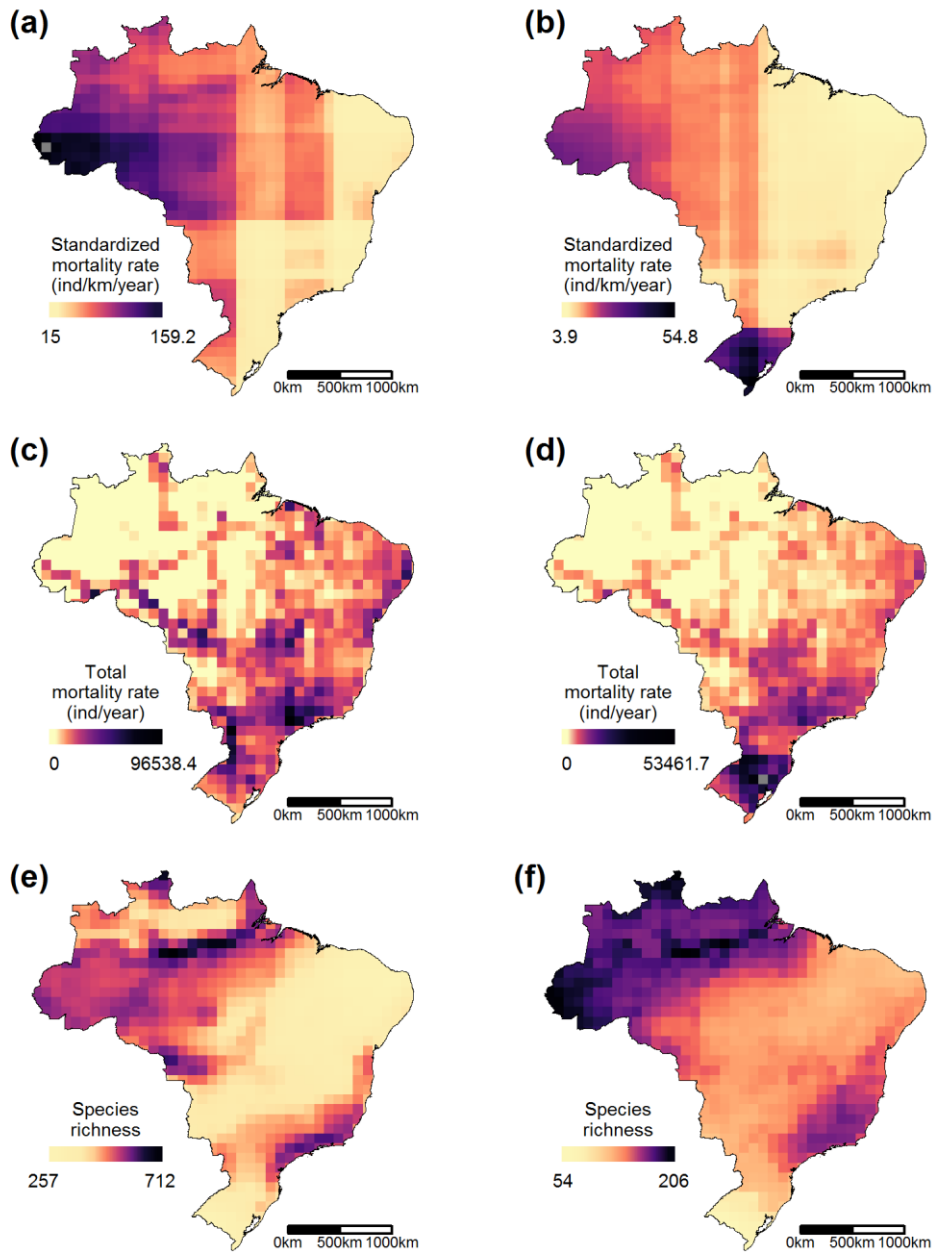
651 1b). Showing results for the 15 imputed datasets. Note that y-scales differ among plots.

652 Taxonomic orders are abbreviated as follows: Crn (Carnivora), Ctr (Cetartiodactyla), Chr

653 (Chiroptera), Cng (Cingulata), Ddl (Didelphimorphia), Lgm (Lagomorpha), Prs

654 (Perissodactyla), Pls (Pilosa), Prm (Primates), Rdn (Rodentia).

655



656

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

660

661 **Supplementary information** for González-Suárez, M; Zanchetta Ferreira, F; Grilo, C.
 662 Spatial and species-level predictions of road mortality risk using trait data. *Global Ecology*
 663 *and Biogeography*
 664 [Appendices S1-S3]

665

666 **Appendix S1. Correction of mortality rates**

667

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

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

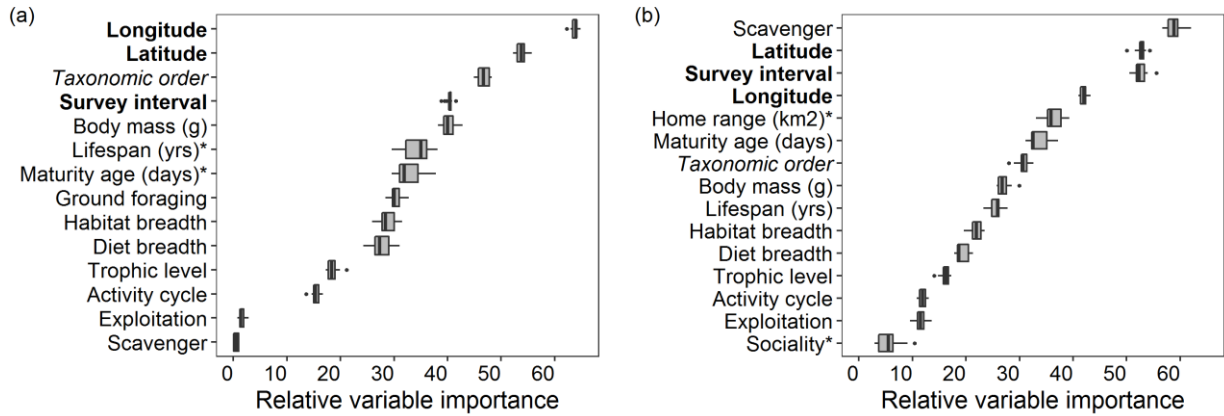
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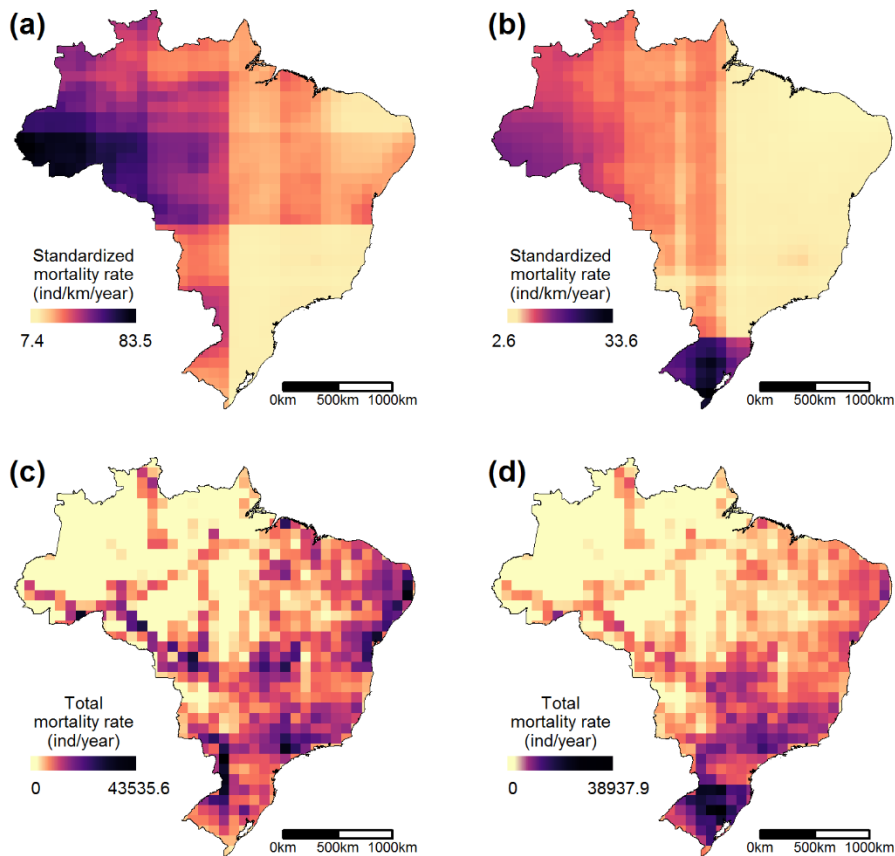
678 **Appendix S2. Results based on uncorrected road mortality rates**

679



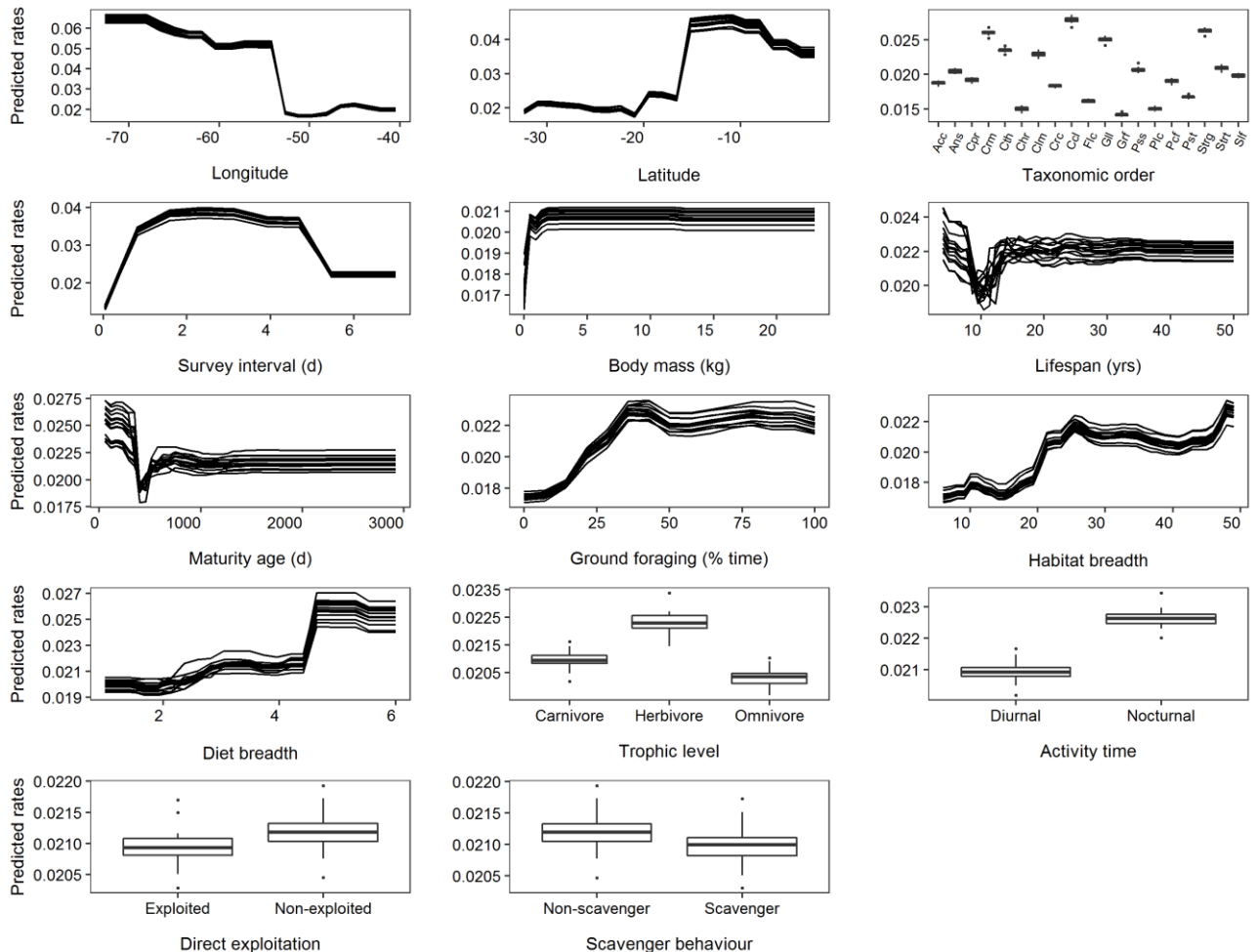
680

681 Figure S2.1. Relative importance of predictors associated with empirical uncorrected road
 682 mortality based on random forest regression models for bird (a) and mammal (b). Boxplots
 683 show results for the 15 imputed datasets for each taxonomic group. Study predictors
 684 (representing study site coordinates and survey sampling frequency) are in bold, taxonomic
 685 predictor (order) is in italics, traits with <50% empirical data are marked with an asterisk.
 686



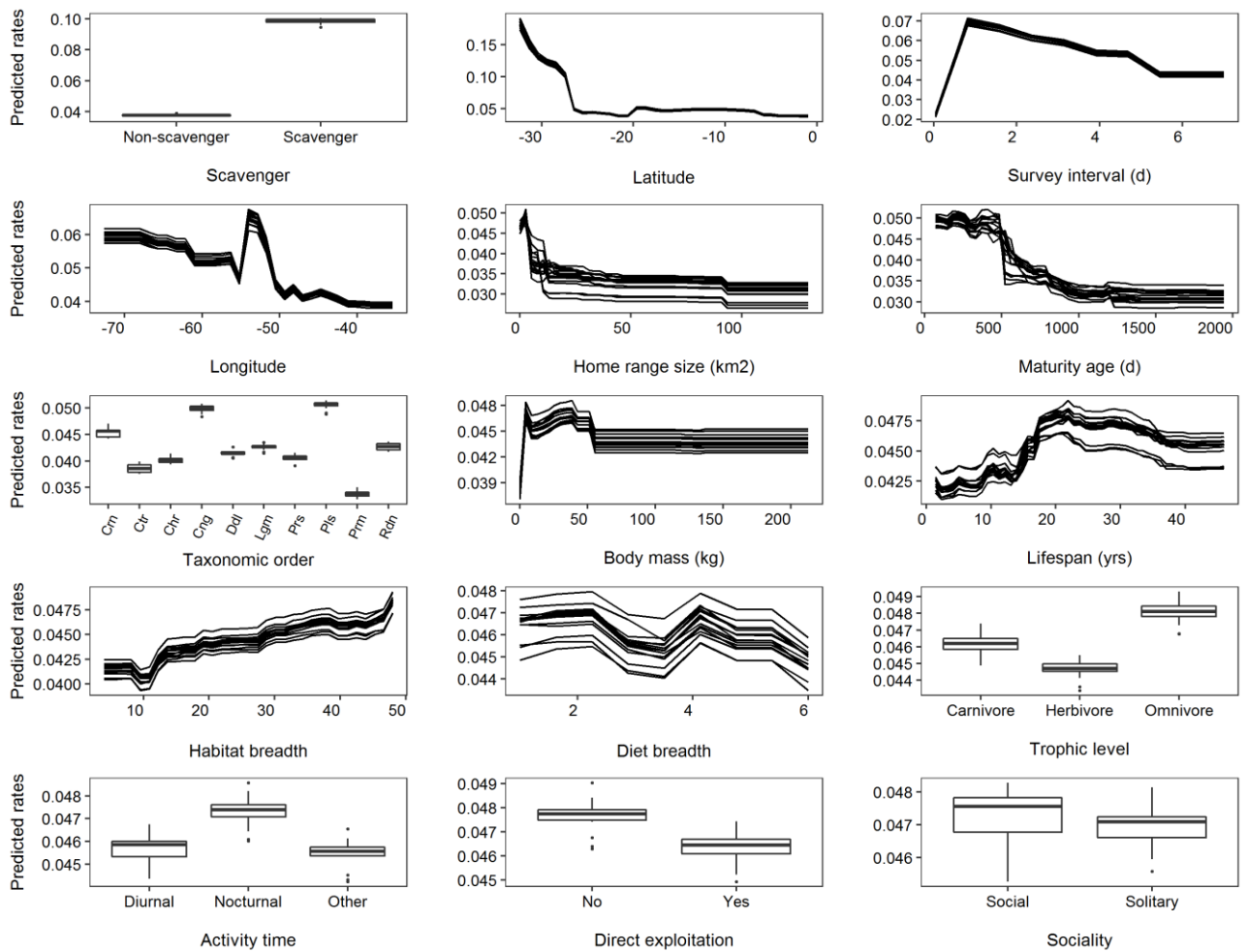
687

688 Figure S2.2. Predicted standardized road mortality rates (in ind/km/year) for birds (a) and
 689 mammals (b) in Brazil. Total road mortality rates based on existing paved roads (ind/year) for
 690 birds (c) and mammals (d). Values based on models fitted for uncorrected road-kill rates.
 691



692
 693 Figure S2.3. Partial dependence plots for all tested predictors on the predicted uncorrected
 694 road mortality rates of Brazilian birds. Rates are in ind/km/year. Predictors are in descending
 695 variable importance order (Fig. S2.1). Showing results for the 15 imputed datasets. Note that
 696 y-scales differ among plots. Taxonomic orders are abbreviated as follows: Acc
 697 (Accipitriformes), Ans (Anseriformes), Ccl (Cuculiformes), Chr (Charadriiformes), Clm
 698 (Columbiformes), Cpr (Caprimulgiformes), Crc (Coraciiformes), Crm (Cariamiformes), Cth
 699 (Cathartiformes), Flc (Falconiformes), Gll (Galliformes), Grf (Gruiformes), Pcf (Piciformes),
 700 Plc (Pelecaniformes), Pss (Passeriformes), Pst (Psittaciformes), Slf (Suliformes), Strg
 701 (Strigiformes), Strt (Struthioniformes).

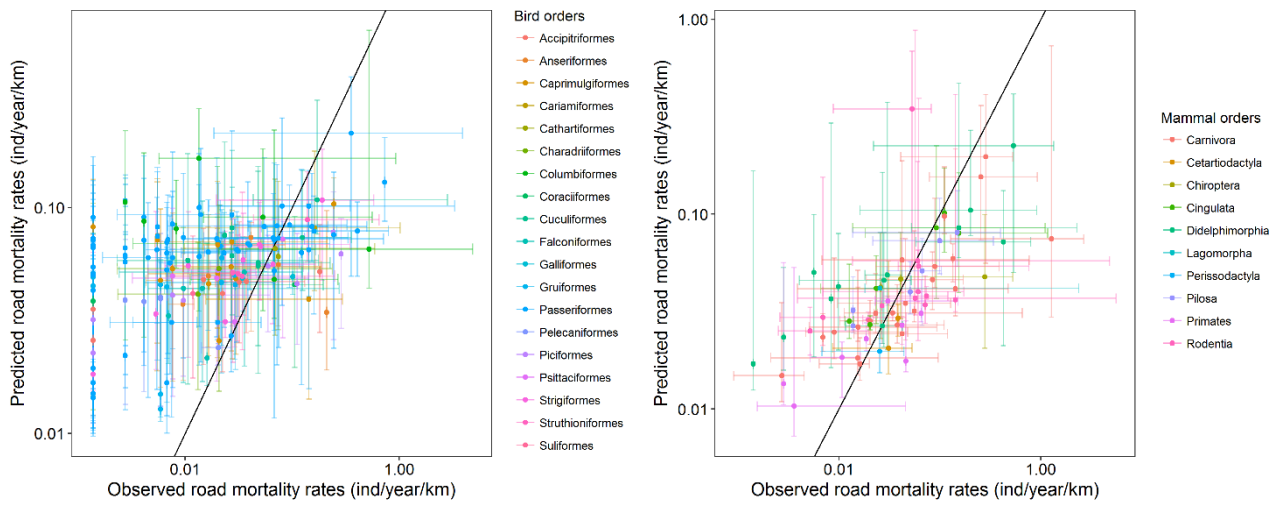
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703

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

710



712

713 Figure S2.5. Predicted and observed uncorrected road mortality rates for 170 species of birds

714 and 74 mammals. Symbol is the median value from all surveys for empirical data and across

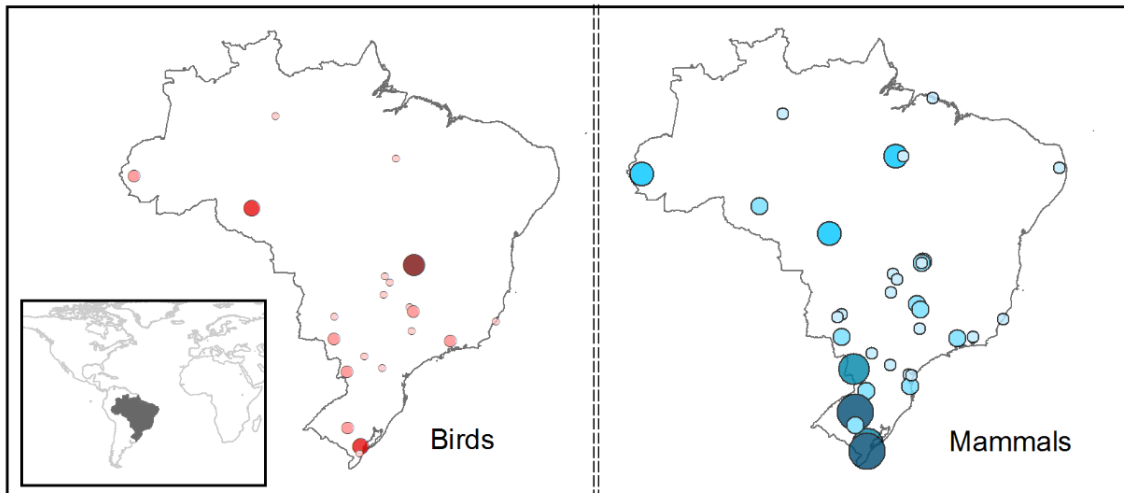
715 all predicted locations –grid cells, for predicted rates. Error bars represent the minimum and

716 maximum range in observed and predicted values. Diagonal line indicates the 1:1

717 relationship.

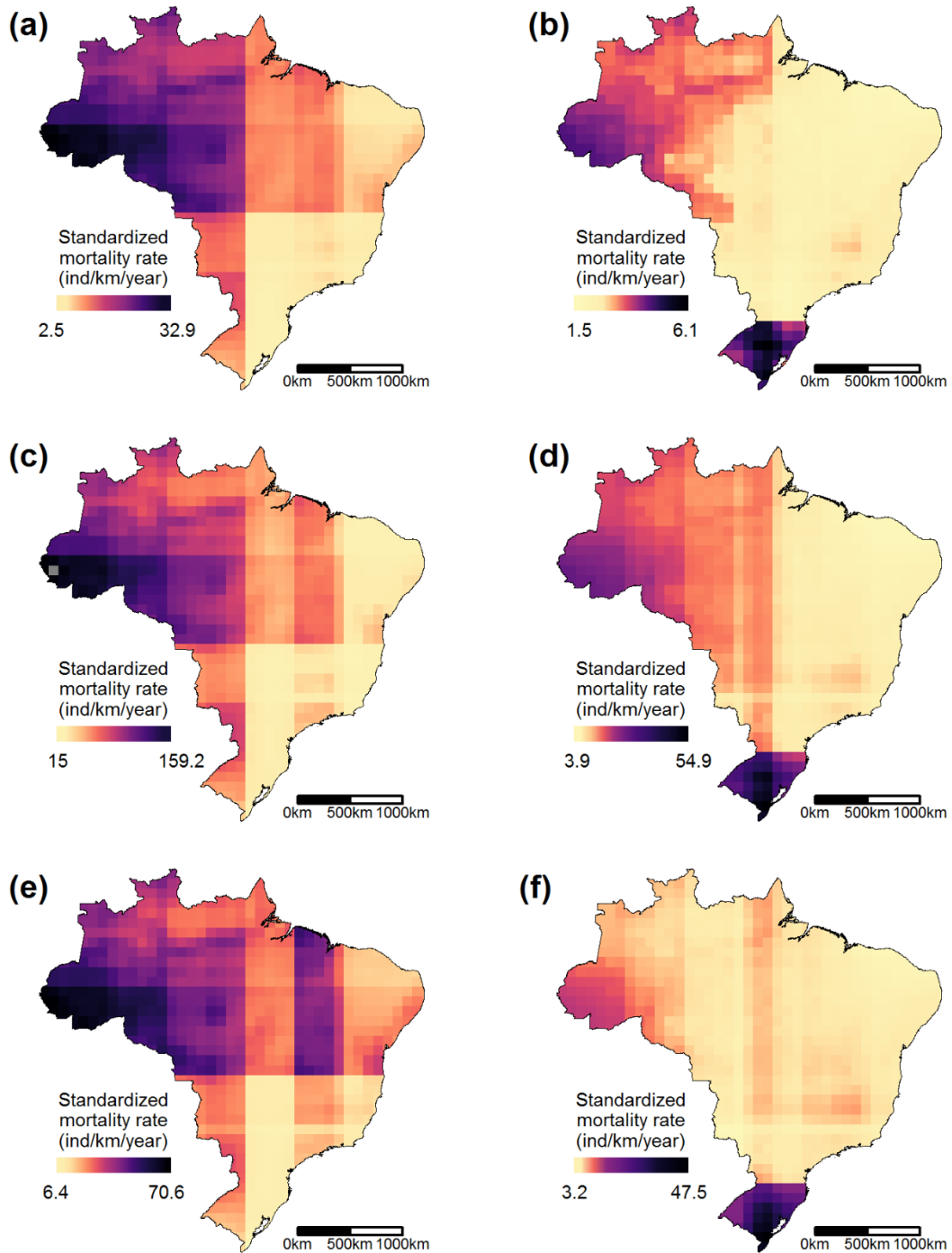
718 **Appendix 3. Additional results with corrected road mortality rates**

719

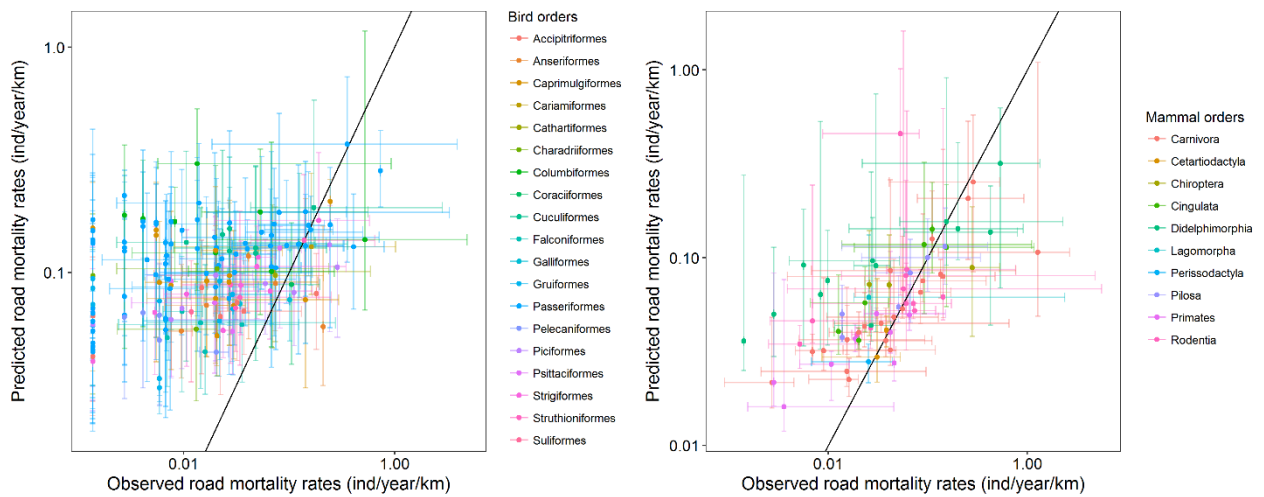


720

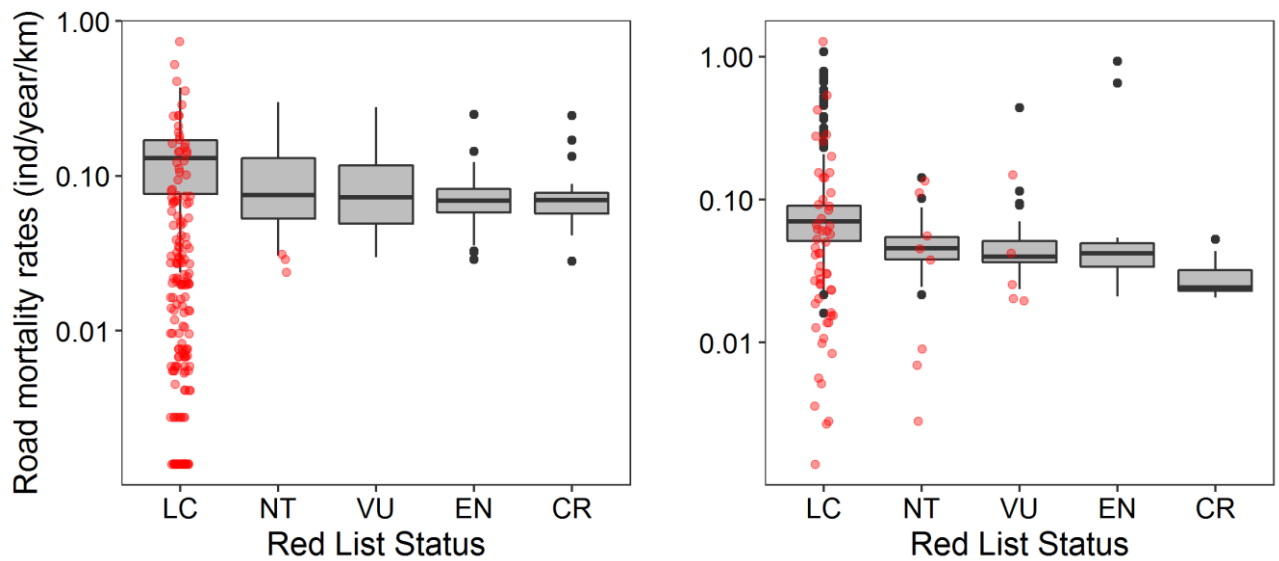
721 Figure S3.1. Location of the surveyed roads in Brazil represented in the 41 studies with road
722 mortality data for birds and mammals (note that some studies provided mortality rates for
723 both groups). The size of the symbols represent the median road mortality rates for each
724 taxonomic group.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



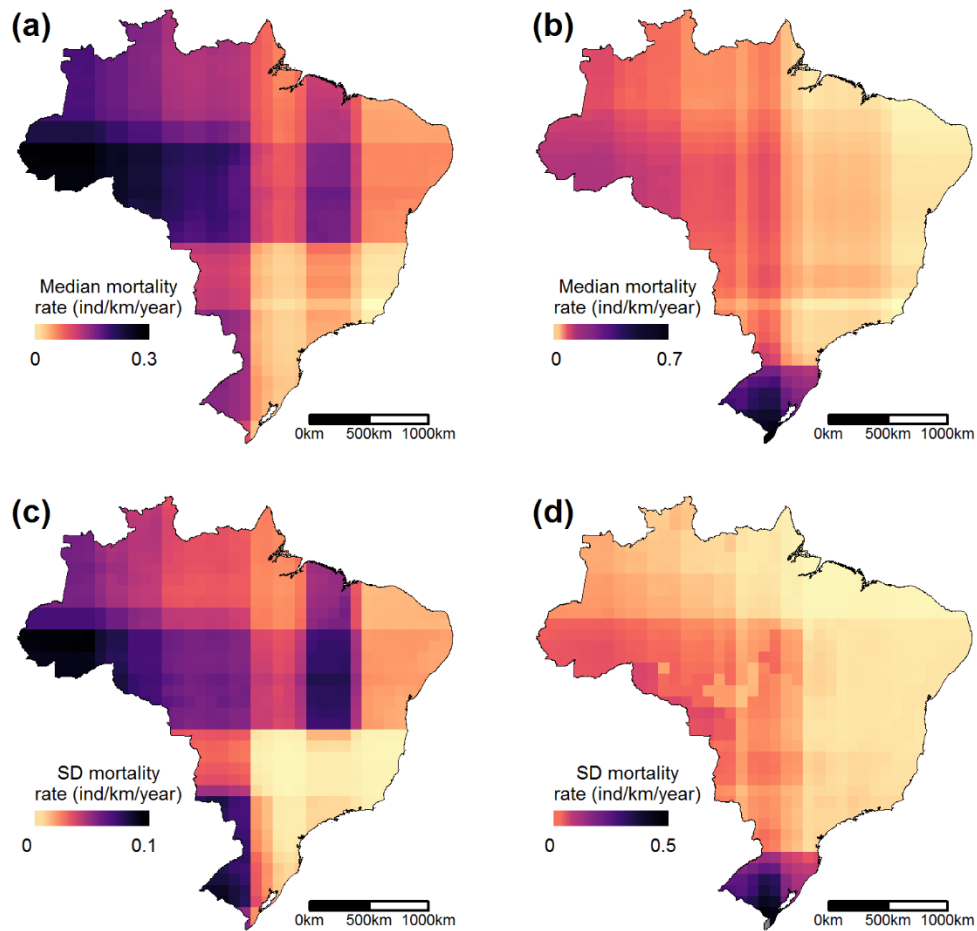
726
 727 Figure S3.2. Predicted standardized road mortality rates (in ind/km/year) in Brazil assuming
 728 the minimum observed survey interval [(a) birds, (b) mammals, both 0.0417 days between
 729 surveys], mean observed interval [(c) birds 3.40 days between surveys, (d) mammals 3.64
 730 days between surveys], and maximum observed interval [(e) birds, (f) mammals, both 7 days
 731 between surveys, which was the maximum interval we considered for our study).
 732



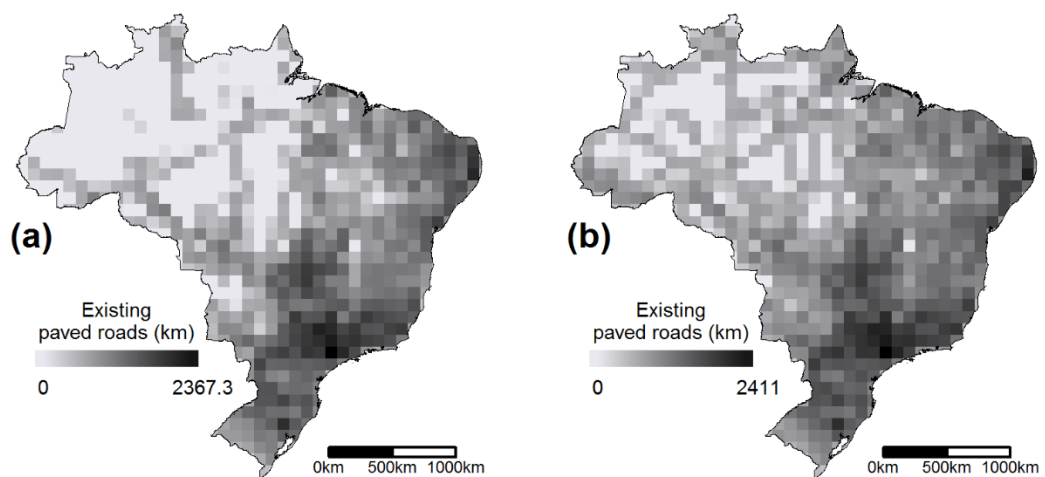
733
 734 Figure S3.3. Predicted and observed road mortality rates for 170 species of birds and 74
 735 mammals. Symbol is the median value from all surveys for empirical data and across all
 736 predicted locations –grid cells, for predicted rates. Error bars represent the minimum and
 737 maximum range in observed and predicted values. Diagonal line indicates the 1:1
 738 relationship.
 739



740
 741 Figure S3.4. Median predicted (grey boxplot) and observed (red symbols) road mortality rates
 742 for birds (left panel) and mammals (right panel) classified in the different IUCN Red List
 743 status categories.

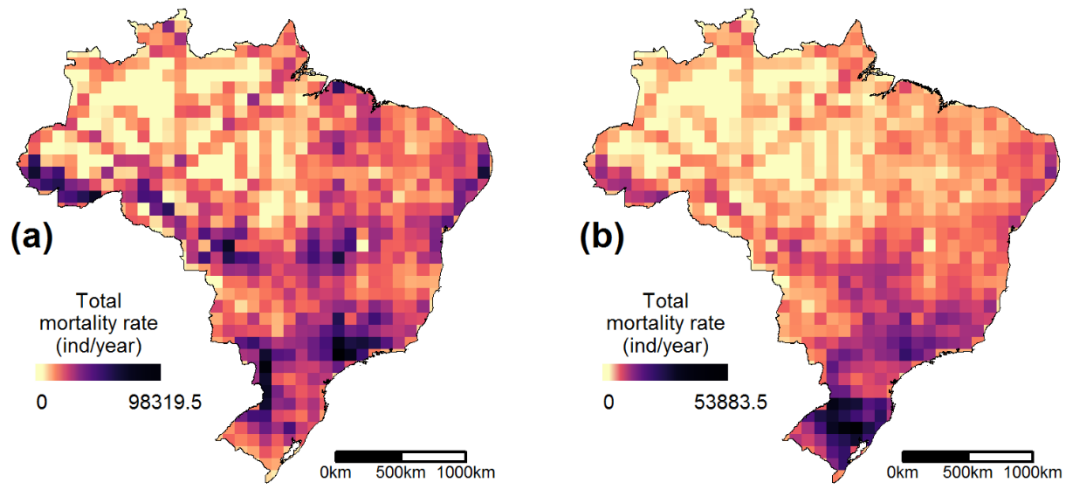


744
 745 Figure S3.5. Predicted standardized road mortality rates (in ind/km/year) for birds [(a) median
 746 rates, (c) standard deviation among species within each cell] and mammals [(a) median rates,
 747 (c) standard deviation among species within each cell] in Brazil.



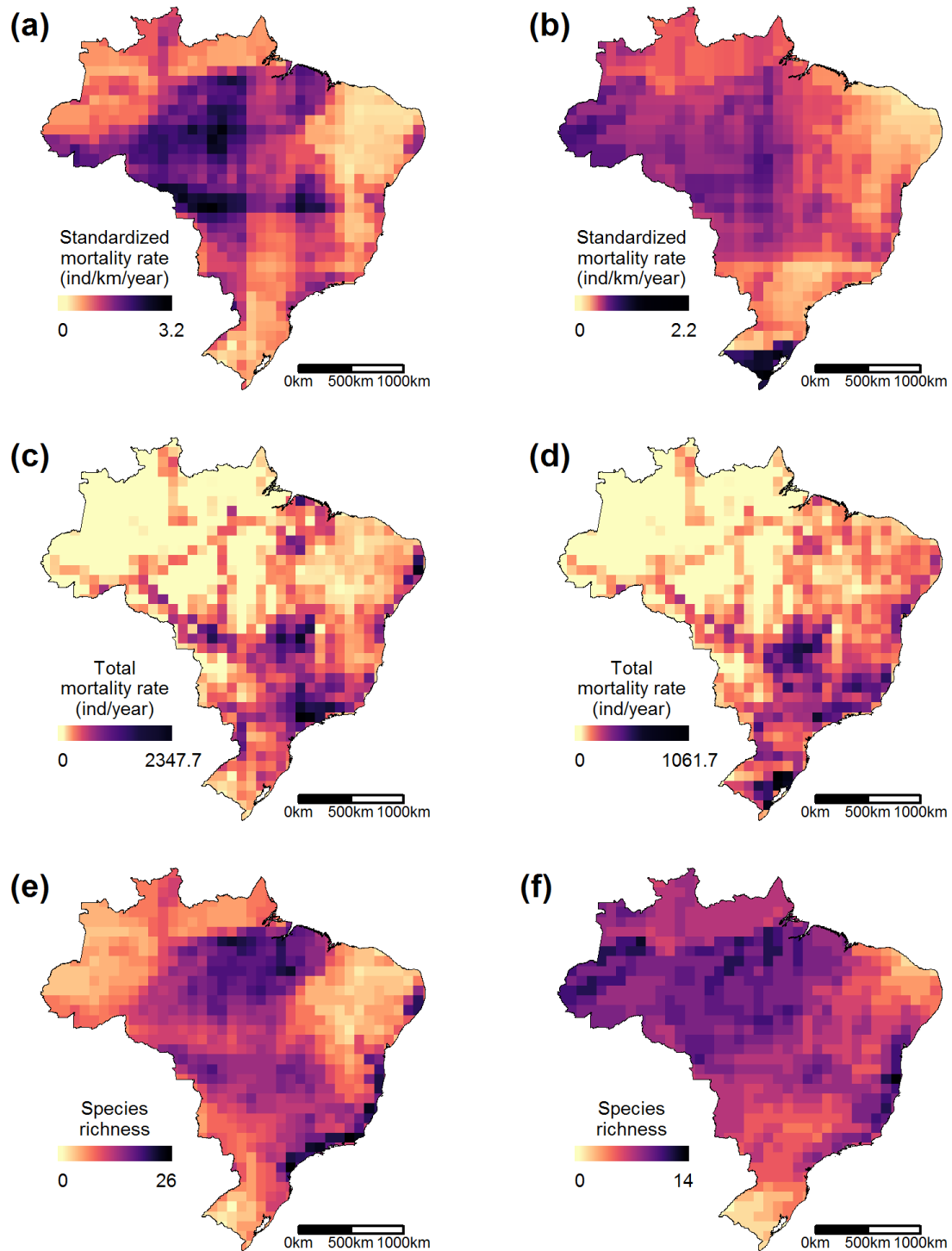
748

749 Figure 3.6. Road density map for Brazil reflecting current paved roads (panel a) and current
750 and planned paved roads (b). Road data from <https://www.openstreetmap.org>.
751



752
753 Figure S3.7. Predicted total road mortality rates (in ind/year) for birds (a) and mammals (b)
754 given the existing and planned paved road network in Brazil. Road data from
755 <https://www.openstreetmap.org>.

756
757
758



759

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

764