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RESEARCH ARTICLE

# Roadkill patterns in Latin American birds and mammals

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## Abstract

**Aim:** Roads are a major threat for wildlife, degrading habitat and causing mortality via wildlife–vehicle collisions. In Latin America, the conjunction of high biodiversity and a rapidly expanding road network is reason for concern. We introduce an approach that combines species traits and habitat preferences to describe vulnerability and map areas of high roadkill risk. Thus, we present the first assessment of roadkill impacts for Latin American birds and mammals.

**Location:** Latin America.

**Time period:** 1994–2020.

**Major taxa studied:** Birds and mammals.

**Methods:** We compiled data from 85 roadkill surveys from Latin America that provided 1,691 roadkill rate estimates for 346 bird and 159 mammalian species, from which 520 rates from 249 birds and 457 rates from 103 mammals were used for analyses. We applied random forest models to predict observed roadkill rates considering species traits, habitat preferences and the geographical coordinates of each study to control for local and regional variation. Fitted models were used to predict spatial risks on Latin American roads for roadkilled birds and mammals across their areas of habitat.

**Results:** We found higher roadkill rates for larger birds and medium-sized mammals with faster reproduction (more clutches/litters per year and early maturity ages), higher population densities and wider use of habitats that included anthropized areas. In mammals, scavengers and those with diets based on invertebrates showed higher rates. Spatial predictions revealed higher rates on roads across Central America, northern Andean regions, eastern Brazil, Uruguay, central and eastern Argentina and southern Chile.

**Main conclusions:** This first comprehensive assessment for Latin America explores various drivers of roadkill risk for birds and mammals and identifies species and areas where existing roads can impact wildlife. Trait-based models fine-tuned with realistic spatial information that accounts for habitat suitability provide a valuable tool for the assessment of human impacts, including roads and traffic.

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body mass, Central America, diet, longevity, maturity age, Neotropics, random forest, road ecology, South America, traits

## 1 | INTRODUCTION

Transportation is key for many human activities, including commerce, tourism and education, which are essential for social and economic development (Forman et al., 2003). Unfortunately, this dependence on roads and vehicles can cause environmental destruction (Van Der Ree et al., 2015). Wildlife–vehicle collisions (hereafter roadkill) were found to be the second highest source of anthropogenic mortality for large and medium-sized mammals in North America, only surpassed by hunting (Collins & Kays, 2011). Road infrastructure can disrupt movement (Bischof et al., 2017; Cayuela et al., 2019; Chen & Koprowski, 2016) and prevent gene flow, leading to fragmentation and isolation of populations, loss of genetic diversity, and even genetic differentiation of populations (Clark et al., 2010; Jackson & Fahrig, 2011; Lesbarrères et al., 2006).

Latin America is a highly biodiverse region that includes seven global biodiversity hotspots (the Tropical Andes, Mesoamerica, Caribbean, Brazil's Atlantic Forest, Choco/Darien/Western Ecuador, Brazil's Cerrado and Central Chile) with very high concentrations of endemic vertebrates (Myers et al., 2000). This region currently has almost 3.5 million km of roads and is expected to have the highest rate of new road development globally in the near future (Meijer et al., 2018). For example, plans include construction and expansion of 12,000 km of roads in the Amazon Basin in the next 5 years (Vilela et al., 2020), which could lead to increased roadkill rates and affect local populations. The combination of high biodiversity and expanding infrastructure makes it urgent to assess how roads affect Latin American wildlife to facilitate sustainable development and effective mitigation.

Different habitat types and configurations have been shown to influence the risk of wildlife–vehicle collision. For example, amphibians are frequently roadkilled near forests (Braz & Rodrigues, 2016), birds are more affected in roads bordering pasturelands and fragmented forests (Medrano-Vizcaíno & Espinosa, 2021), some species of mammals, such as *Cerdocyon thous* and *Lepus europaeus*, are more vulnerable near water bodies (Freitas et al., 2015), and mortality of snakes is higher near pasturelands (Quintero-Ángel et al., 2012). Although habitat composition and configuration are important, they do not seem to explain wildlife mortality patterns fully. Species that use similar habitats can have different roadkill rates. For example, the crab-eating fox (*Cerdocyon thous*) and the white-eared opossum (*Didelphis albiventris*) are both habitat generalists that tolerate humanized areas (Cantor et al., 2010; De Barros Ferraz et al., 2010) but are affected very differently by roads: in a study conducted in Misiones-Argentina, the white-eared opossum made up 38.8% of total roadkills, whereas *Cerdocyon thous* represented only 3.3% (Bauni et al., 2017). Although variation in local abundance or density can explain, in part, the differences in roadkill rates (Caceres, 2011; Delgado-V, 2007; Medrano-Vizcaíno, 2015), rare species can also suffer high mortality. The western mountain coati (*Nasuella olivacea*), an elusive carnivore whose ecology is scarcely known (Medrano-Vizcaíno & Gutiérrez-Salazar, 2020), was the second most roadkilled species in Envigado-Colombia (Delgado-V, 2007).

Diet, life history and morphology have been shown to influence roadkill risk in some regions of Latin America (Caceres, 2011; González-Suárez et al., 2018). Large body size, ground-foraging behaviour and a wider dietary breadth have been associated with roadkill risk in Brazilian birds (González-Suárez et al., 2018), whereas mammals at higher risks were those with diurnal habits, intermediate body masses, slow movements, smaller home ranges and scavenging behaviour (Caceres, 2011; González-Suárez et al., 2018). These types of trait-based predictive models can offer initial assessment tools to identify vulnerable species and areas. A few previous studies have adopted this approach at local (Leonan et al., 2018; Rincón-Aranguri et al., 2019) and national (González-Suárez et al., 2018) scales within Latin America, but local inferences might not be applicable to all regions and diverse wildlife communities in the Neotropics. Here, we present the first continental-scale assessment of roadkill risk for Latin American birds and mammals.

We compiled a comprehensive database of roadkill rates for >500 species of birds and mammals across Latin America and the Caribbean and applied machine learning methods to develop predictive models of roadkill vulnerability. Predictors included diet, life history and morphological traits that we hypothesized a priori could influence roadkill rates (Table 1). Going a step beyond previous work, we refined spatial predictions using habitat preferences to provide a more realistic assessment of roadkill risk. Our analyses identify generalized traits that make Latin American birds and mammals more vulnerable to roadkill and offer a continental risk assessment that reveals both vulnerable species and areas where road mortality rates might be particularly high.

## 2 | METHODS

We searched peer-reviewed publications and grey literature (e.g., academic theses and dissertations) to locate systematic roadkill surveys published before July 2020 using the keywords "roadkill", "wildlife vehicle collision", "road mortality" "road ecology", "birds roadkills", "mammals roadkills" plus the name of each country in Latin America. We also searched for these terms in Spanish and Portuguese to identify additional sources in those languages. From each identified study reporting roadkill data, we collected, for each species, the number of individual carcasses found as roadkill, descriptors of the survey design (time between surveys, total sampling period from first to last survey and length of road surveyed) and the geographical coordinates of the study area (central point). We used the IUCN nomenclature and synonyms to standardize all species names after correcting identified spelling mistakes. We assumed correct taxonomic identification of roadkill individuals from each study.

**TABLE 1** Variables used as predictors of roadkill rates

| Type of variable | Variable | Description | Hypotheses | Birds | | Mammals | |
|---|---|---|---|---|---|---|---|
| | | | | $N_T$ | $N_M$ | $N_T$ | $N_M$ |
| Geographical | Latitude and longitude | Geographical coordinates of the centroid of every study analysed | Roadkill rates can vary across areas owing to local factors, including traffic patterns, road and landscape features that could be captured broadly by coordinates | 346 (100%) | 249 (100%) | 159 (100%) | 103 (100%) |
| Morphological | Body mass | Median adult body mass (in kilograms) | Large sized species are more visible to drivers, which decreases their probability of being hit by vehicles | 346 (100%) | 249 (100%) | 159 (100%) | 103 (100%) |
| Life history | Age at maturity | Median age (in days) when individuals reach sexual maturity | Species with lower ages at maturity generally have higher local population abundances, which, in turn, can result in higher roadkill rates | 89 (25.7%) | 51 (20.5%) | 110 (69.2%) | 75 (72.8%) |
| | Litter/clutch size | Median number of offspring in each reproductive event | Species with larger litter sizes generally have higher local population abundances, which, in turn, can result in higher roadkill rates | 330 (95.3%) | 236 (94.8%) | 146 (91.8%) | 93 (90.3%) |
| | Litters/clutches per year | Median number of reproductive events per year | Species that have more litters per year generally have higher local population abundances, which, in turn, can result in higher roadkill rates | 109 (31.5%) | 68 (27.3%) | 111 (69.8%) | 71 (68.9%) |
| | Longevity | Median life span (in years) | Long-lived species have more opportunities to acquire experience and learn to cope with novel habitats, such as roads, which could result in lower roadkill rates | 119 (34.3%) | 76 (30.5%) | 133 (83.6%) | 92 (89.3%) |
| | Group size | Median size of social groups | More individuals can be roadkilled in a single collision if animals cross roads in groups. Given that group crossings are more likely to occur in social species, these species could have higher roadkill rates | 232 (67.0%) | 164 (65.9%) | 85 (53.5%) | 64 (62.1%) |
| | Home range | Median home range (in square kilometres) | Species with larger home ranges are more likely to encounter and cross roads, increasing their probabilities of being roadkilled | 37 (10.7%) | 27* (10.8%) | 99 (62.3%) | 73 (70.9%) |
| | Activity | Categorical descriptors of the main time of daily activity: Diurnal or nocturnal | Driver visibility is reduced at night; therefore, collisions might be more common during that period, resulting in higher rates for nocturnal animals | 326 (94.2%) | 232 (93.2%) | 159 (100%) | 103 (100%) |

(Continues)

TABLE 1 (Continued)

| Type of variable | Variable | Description | Hypotheses | Birds | | Mammals | |
|---|---|---|---|---|---|---|---|
| | | | | $N_T$ | $N_M$ | $N_T$ | $N_M$ |
| | Population density | Median number of individuals per square kilometre | Higher population densities (local abundance) can increase roadkill because more individuals might be found near and on roads | 103 (29.8%) | 61 (24.5%) | 61 (38.3%) | 44 (42.7%) |
| Diet | Invertebrate diet (%) | Percentage of diet based on invertebrates | Invertebrates might be attracted to resources near roads, such as verges, in turn attracting animals with an invertebrate-based diet and increasing their exposure to roadkill | 343 (99.1%) | 246 (98.8%) | 157 (98.7%) | 102 (99.0%) |
| | Ectotherm vertebrate diet (%) | Percentage of diet based on ectotherm vertebrates | Ectotherm species can use roads for thermoregulation, which can attract their predators and increase their roadkill rates | 343 (99.1%) | 246 (98.8%) | 157 (98.7%) | 102 (99.0%) |
| | Scavenger diet (%) | Percentage of diet based on scavenging | Scavenger species can be attracted to roads to feed on dead animals, increasing their roadkill rates | 343 (99.1%) | 246 (98.8%) | 157 (98.7%) | 102 (99.0%) |
| | Seed diet (%) | Percentage of diet based on seeds | Road verges can provide food sources for seed-eaters and attract them to roads, increasing their roadkill rates | 343 (99.1%) | 246 (98.8%) | Not assessed | Not assessed |
| | Plant diet (%) | Percentage of diet based on plants | Road verges can provide food sources for herbivores and attract them to roads, increasing their roadkill rates | 343 (99.1%) | 246 (98.8%) | 157 (98.7%) | 102 (99.0%) |
| | Dietary breadth | Number of different categories consumed (out of 10 possible diet categories) | Species with a generalist diet can be attracted to diverse resources, such as road verge vegetation, prey feeding on verges and carrion, thus increasing their roadkill rates | 343 (99.1%) | 246 (98.8%) | 157 (98.7%) | 102 (99.0%) |

TABLE 1 (Continued)

| Type of variable | Variable | Description | Hypotheses | Birds | | Mammals | |
|---|---|---|---|---|---|---|---|
| | | | | $N_T$ | $N_M$ | $N_T$ | $N_M$ |
| Habitat | Artificial | Whether the species occur in artificial habitats (1 = yes, 0 = no) | Roads are very common in artificial habitats, hence species that use this habitat will be more exposed to roads | 346 (100%) | 249 (100%) | 158 (99.4%) | 103 (100%) |
| | Cropland | Whether the species occur in cropland habitats (1 = yes, 0 = no) | Roads are relatively common near croplands, and some species might be attracted to the resources in crops, hence species that use this habitat will be more exposed to roads | 346 (100%) | 249 (100%) | 158 (99.4%) | 104 (100%) |
| | Grassland | Whether the species occur in grassland habitats (1 = yes, 0 = no) | Roads can be relatively common near grasslands (particularly those in flat areas, which are more suitable for infrastructure), hence species that use this habitat will be more exposed to roads | 346 (100%) | 249 (100%) | 158 (99.4%) | 104 (100%) |
| | Forest | Whether the species occur in forest habitats (1 = yes, 0 = no) | Species that prefer forests are more likely to be specialists and avoid novel and altered areas, decreasing their roadkill rates | 346 (100%) | 249 (100%) | 158 (99.4%) | 104 (100%) |
| | Sparse vegetation | Whether the species occur in sparse vegetation habitats (1 = yes, 0 = no) | Areas with sparse vegetation can be associated with unproductive regions (with few animals) where roadkill rates will be lower | 346 (100%) | 249 (100%) | 158 (99.4%) | 104 (100%) |
| | Water bodies | Whether the species uses aquatic habitats (1 = yes, 0 = no) | Species that use water bodies might be less likely to cross roads (unsuitable habitat), resulting in lower roadkill rates. An alternative hypothesis is that species using water bodies might need to move if sources dry up and could cross roads while dispersing, increasing their roadkill risk | 346 (100%) | 249 (100%) | 158 (99.4%) | 104 (100%) |
| | Habitat breadth | Number of habitat types where a species occurs, from 10 possible types | Habitat generalists can occupy altered areas, including roads or places near roads, leading to higher roadkill rates | 346 (100%) | 249 (100%) | 158 (99.4%) | 104 (100%) |

*Notes*: We report the number of species with available data and, in parentheses, the percentage from the total ($N_T$) of 346 birds and 159 mammals for which roadkill estimates were available and for the subset ($N_M$) of 249 birds and 103 mammals from more comprehensive studies used to fit the model. Missing trait data were imputed before analyses (see Methods). We also present a priori hypotheses for how each variable could influence roadkill rates. *Variables not included in the analysis.

Roadkill rates per species and study were calculated as the total number of carcasses found divided by the length of the road surveyed (in kilometres) and the study duration (in days). This daily rate was then converted to the number of individuals per kilometre per year (multiplying by 365), assuming a constant roadkill rate across the year. Given that detectability and survey intervals can influence the number of carcasses detected as roadkill, we adjusted these values with correction factors proposed by Santos et al. (2011), which estimate the timings of persistence of carcasses on roads among taxonomic groups. Then, roadkill rates were multiplied by correction factors based primarily on body size categories and survey intervals (a full list of correction factors is given in Supporting Information Appendix S1).

We also compiled species-level data for 22 variables that describe diet, life history, morphological traits and habitat preferences in birds and mammals (Table 1). The list of variables was initially the same for both groups, but home range was removed for birds owing to low data availability, and seed diet was excluded for mammals owing to low variability in the studied species, which made this variable uninformative. Trait data were collected from multiple published databases, books and published papers referenced in the Appendix (all trait and roadkill data are available in a public repository: https://figshare.com/s/6e48c050e84ee1ba6a12).

## 2.1 | Vulnerability to roadkill

Trait data are often not available for all species, but given that traits are generally correlated, imputation can be a useful method for handling missing values (Johnson et al., 2021). Before predicting roadkill rates, we imputed missing trait values using the default settings of the function "missForest" (maxiter = 10, ntree = 100) from the R package "missForest" (Stekhoven, 2013). This approach uses random forests iteratively to predict one trait using data from all other traits and has been shown to work well with multivariate data, outperforming other methods, such as *k*-nearest neighbours imputation or multivariate imputation (Stekhoven & Bühlmann, 2012). To account for uncertainty in imputed values, we generated and analysed 15 imputed datasets for birds and 15 for mammals. In addition, we fitted models excluding variables for which empirical data were available for <40% of species to ensure that results were not affected by heavily imputed variables. Previous studies found imputation of trait data to be reliable with ≤60% of missing values (Penone et al., 2014). Imputation was done using data for all species recorded as roadkill, but to fit the model predicting roadkill rates we consider that studies had been conducted using a diversity of sampling methods and covered different survey areas and periods. To reduce some of the variability in estimated rates attributable to methodological differences, we then fitted models using only studies with a minimum duration of 3 months, a minimum road length surveyed of 5 km, and a maximum survey interval of 7 days.

Following González-Suárez et al. (2018), we used machine learning random forest regression, which can capture nonlinear relationships and interactions among predictions, to predict roadkill rates. This effective tool for prediction assembles multiple regression trees, with each constructed from a bootstrap sample of the original dataset. Approximately two-thirds of the samples form a bootstrap sample, while the other third is left out [out of bag samples (OOB samples); Breiman, 2001]. We trained models using all roadkill rates that met the methodological criteria described above because we considered that splitting the data to create a single test dataset could bias our taxonomically and spatially structured data. As a result, model fit might be overestimated.

Random forests were generated based on 2,000 regression trees using the function "randomForest" from the R package "randomForest" (Liaw & Wiener, 2002). We fitted separate models for birds and mammals because different relationships could exist for each class. These models included all trait variables and the taxonomic order of each species to account for evolutionary relatedness and similarities across taxa not reflected in the tested traits. The models also included as predictors the latitude and longitude of the central road point of the survey area of each study to account broadly for spatial variability and local factors affecting roadkill estimates.

Model performance was reported using the total variance explained, which is calculated as 1 − MSE/Variance_y, where mean square error (MSE) is the sum of squared residuals of the OOB sample/OOB sample size, and Variance_y is the variance in predicted values (Acharjee et al., 2011). We used permutation feature importance to evaluate how well different features (variables) predicted roadkill. The variable importance was calculated for each feature as the difference in MSE between 2,000 regression trees fitted with the original data and 2,000 trees fitted after the permutation of values in that variable. The average of these differences was divided by their standard deviation and reported as variable importance (we report 15 importance estimates for each variable obtained from the analyses of the 15 imputed datasets). Permutation of important variables results in lower variance explained (poorer model performance), whereas permutation of less important variables does not greatly reduce the variance explained. Owing to the stochastic nature of random forest, negative variable importance values can occur by chance, when permuting an uninformative variable, which results in slightly lower MSE than with the original data. These can be considered as effectively zero importance.

We also generated dependence plots using the function "partial" from the R package "pdp" (Greenwell, 2017). These are informative graphics to understand the relationship between the predicted response and predictor variables. These plots represented the prediction of roadkill rates for a given variable obtained by marginalizing the machine learning model output over the distribution of all other features, hence the function depends only on the focal variables with interactions with other variables included.

## 2.2 | Predicting spatial roadkill risks

We predicted roadkill rates for all Latin American birds and mammals reported as roadkill at least once in the compiled systematic surveys.

We defined current distribution areas for each species using IUCN maps (IUCN, 2021), considering only those polygons with certainty of presence (i.e., possible extant, possible extinct and extinct categories were removed). Additionally, for bird ranges for which migration classifiers are included, we selected breeding, no breeding and passage, removing those classed as vagrant. Given that distribution areas can include unsuitable habitat, the use of area of habitat has been recommended to provide a better representation of the true area used by the species (Brooks et al., 2019). Therefore, to reduce overestimation of risk by including areas where a species is unlikely to occur, we defined area of habitat by selecting only areas of the distribution range that matched the preferred habitats of each species. Habitats were delimited geographically using high-resolution (30 arc-sec$^2$, *c.* 1 km$^2$) land-cover datasets of 1998–2012 (Latham et al., 2014).

We then defined a 1° × 1° grid of Latin America and generated a list of species present in each grid cell, considering as present all whose area of habitat overlapped to any extent with the cell. Each grid was then considered as a potential study site, with location defined by the geographical coordinates of the centroid of the cell. Using the fitted random forest models, we then predicted roadkill rates for the species in each grid cell given trait values, taxonomy and the centroid coordinates of the cell. We used median rates per species and cell calculated from the 15 imputed datasets. For each grid cell, we then calculated the total roadkill rates per cell for birds and mammals by adding roadkill rates for all species in each class in that cell. Considering the length of all primary and secondary roads (Meijer et al., 2018) within each grid cell, we finally calculated the total predicted number of birds and mammals roadkilled per year in each cell by multiplying the total roadkill rate by the existing kilometres of road in each species habitat.

## 3 | RESULTS

### 3.1 | Roadkilled birds and mammals in Latin America

The full compiled roadkill dataset included 1,691 roadkill rate estimates, representing 346 bird species and 159 mammal species and 85 studies from 12 Latin American countries (Argentina, Brazil, Chile, Colombia, Costa Rica, Ecuador, Guatemala, Panama, Paraguay, Peru, Mexico and Venezuela). Most of the birds reported as roadkill are classified as Least Concern (LC) by the IUCN Red List (IUCN, 2021), with seven in higher risk categories, including three listed as Near Threatened (NT): yellow-faced Amazon parrot (*Alipiopsitta xanthops*), greater rhea (*Rhea Americana*) and eastern meadowlark (*Sturnella magna*); three as Vulnerable (VU): black-masked finch (*Coryphaspiza melanotis*), sharp-tailed tyrant (*Culicivora caudacuta*) and channel-billed toucan (*Ramphastos vitellinus*); and one as Endangered (EN): violet-throated metaltail (*Metallura baroni*).

The top roadkilled birds (those with the highest corrected rates; Table 2) are all listed as Least Concern and included the long-tailed mockingbird (*Mimus longicaudatus*; median roadkill rate across studies: 1.56 individuals/km/year), the social flycatcher (*Myiozetetes similis*; median rate .98 individuals/km/year) and the groove-billed ani (*Crotophaga sulcirostris*; median rate .97 individuals/km/year). Among threatened birds, the violet-throated metaltail, listed as Endangered, had a roadkill rate of .26 individuals/km/year, which is relatively high considering that its distribution is restricted to the south of Ecuador, where only a few occurrences have been reported (13 records; Tinoco et al., 2009). Although potentially worrying, this roadkill rate was estimated from a single study with only two roadkilled individuals (Aguilar et al., 2019); mortality might be less frequent in other areas of the species distribution. Relatively high rates of .15 individuals/km/year were also reported for the eastern meadowlark, which is listed as Near Threatened.

The top roadkilled mammals are listed as Least Concern (Table 2), but 23 species have higher IUCN risk status. Fourteen species are listed as Near Threatened; eight as Vulnerable: brown howler monkey (*Alouatta guariba*), greater naked-tailed armadillo (*Cabassous tatouay*), bristle-spined rat (*Chaetomys subspinosus*), northern tiger cat (*Leopardus tigrinus*), Brazilian dwarf brocket (*Mazama nana*), giant anteater (*Myrmecophaga tridactyla*), giant armadillo (*Priodontes maximus*) and lowland tapir (*Tapirus terrestris*); and one as Endangered: tapeti (*Sylvilagus brasiliensis*). In addition, two roadkilled mammals are listed as Data Deficient: Azara's agouti (*Dasyprocta azarae*) and red brocket (*Mazama americana*).

The Andean white-eared opossum (*Didelphis pernigra*; LC) had the highest reported rate (4.68 individuals/km/year), followed by the Sechuran fox (*Lycalopex sechurae*; NT) with a rate of 3.44 individuals/km/year, and the common opossum (*Didelphis marsupialis*; LC) with a median rate of 1.45 individuals/km/year. Although rates for the common opossum are lower, this species has been reported as roadkilled in 17 studies from six countries (Brazil, Colombia, Ecuador, Mexico, Panama and Peru), whereas the Andean white-eared opossum and the Sechuran fox were reported in only one study in Ecuador and Peru, respectively.

### 3.2 | Vulnerability to roadkill

Thirty-five of the compiled studies did not meet our methodological criteria (see Methods), hence models were fitted using 50 studies conducted in nine countries (Argentina, Brazil, Chile, Colombia, Ecuador, Guatemala, Mexico, Panama and Peru), which provided 520 roadkill rate estimates for 249 bird species and 457 roadkill rates for 103 mammals. Random forest models explained on average (across models fitted for the 15 imputed datasets) 57.3% of the observed variance in bird roadkill rates (*SD* across the 15 datasets; .002), and 47.7% for mammals (*SD* across the 15 datasets; .002). The latitude and longitude (location) of the study were the most important variables for both taxonomic groups (Figure 1). These were expected a priori to be important because they are the only variables that could explain observed within-species variability in rates. In addition, several traits were also identified as relevant predictors in each taxonomic group (Figure 1). Among birds, larger species

**TABLE 2** Top 10 roadkilled birds and mammals in Latin America, in descending order

| Class | Order | Scientific name | IUCN status | Number of studies | Roadkill rate (individuals/km/year) |
|---|---|---|---|---|---|
| Aves | Passeriformes | *Mimus longicaudatus* | LC | 1 | 1.561 |
| | Passeriformes | *Myiozetetes similis* | LC | 2 | .979 |
| | Cuculiformes | *Crotophaga sulcirostris* | LC | 2 | .971 |
| | Pelecaniformes | *Bubulcus ibis* | LC | 2 | .929 |
| | Caprimulgiformes | *Amazilia tzacatl* | LC | 1 | .908 |
| | Accipitriformes | *Rostrhamus sociabilis* | LC | 1 | .888 |
| | Passeriformes | *Geospizopsis unicolor* | LC | 1 | .785 |
| | Passeriformes | *Platyrinchus cancrominus* | LC | 1 | .762 |
| | Falconiformes | *Caracara cheriway* | LC | 1 | .760 |
| | Passeriformes | *Ochthornis littoralis* | LC | 1 | .730 |
| Mammalia | Didelphimorphia | *Didelphis pernigra* | LC | 1 | 4.681 |
| | Carnivora | *Lycalopex sechurae* | NT | 1 | 3.436 |
| | Didelphimorphia | *Didelphis marsupialis* | LC | 16 | 1.453 |
| | Pilosa | *Choloepus hoffmanni* | LC | 3 | .859 |
| | Rodentia | *Galea flavidens* | LC | 1 | .706 |
| | Rodentia | *Oligoryzomys flavescens* | LC | 1 | .652 |
| | Pilosa | *Tamandua mexicana* | LC | 5 | .594 |
| | Carnivora | *Conepatus chinga* | LC | 5 | .532 |
| | Carnivora | *Lycalopex gymnocercus* | LC | 3 | .355 |
| | Pilosa | *Bradypus variegatus* | LC | 2 | .312 |

*Notes*: We report species name, IUCN Red List status (LC = least concern; NT = near threatened), the number of studies in which that species was reported as roadkill and the estimated roadkill rate (when data were available for more than one study, we calculated a median rate across studies using corrected values). The number of studies and observed rates are reported considering those studies that met the methodological criteria (minimum duration of 3 months, a minimum road length surveyed of 5 km, and a maximum survey interval of 7 days) that we consider to provide more reliable estimates.

(>2.5 kg) with a higher population density had higher roadkill rates, as did those with a shorter lifspan, <5 years; age at sexual maturity <500 days; and at least two clutches per year (Figure 2). More generalist birds, with wider habitat breadths (occupying more than five different habitats) and that regularly use artificial habitat, croplands, grasslands and water bodies, also had higher roadkill rates (Figure 2). Among mammals, species with adult body mass between 2 and 35 kg, faster life histories (life spans <10 years; age at maturity <500 days), higher population density, scavenger and invertebrate diets, smaller home ranges (<10 km) and generalist habits (habitat breadth more than five categories) had higher mortality rates (Figure 3). Cuculiformes birds and Pilosa mammals were the taxonomic orders with the highest roadkill rates.

Models that excluded trait variables with <40% of empirical values (more imputed values; clutches per year, longevity, maturity age and population density for birds) produced qualitatively similar results, suggesting that including highly imputed variables did not influence our inferences (Supporting Information Appendix S2).

### 3.3 | Roadkill risk maps

Our analyses predict that 12,431,670 birds and 5,136,373 mammals can be killed on Latin American primary and secondary roads each year. These high numbers are likely to underestimate total mortality, because we calculated risk cautiously, only for species reported in systematic studies included in our database (i.e., species known to be susceptible to roadkill). However, it is likely that many other Latin American birds and mammals are susceptible to collisions (particularly those in regions where no road surveys have been conducted). Moreover, our calculations did not consider tertiary, illegal and unofficial roads, which could increase these numbers dramatically.

Areas with higher mortality rates were mainly located across all Central America, northern Venezuela, northern and western Colombia, Ecuador, western Perú, southern Chile, central and eastern Argentina, Uruguay and eastern Brazil. Generally, areas with high road densities resulted in high estimates of mortality per year (Figure 4a,b); however, some areas with a high road density, such

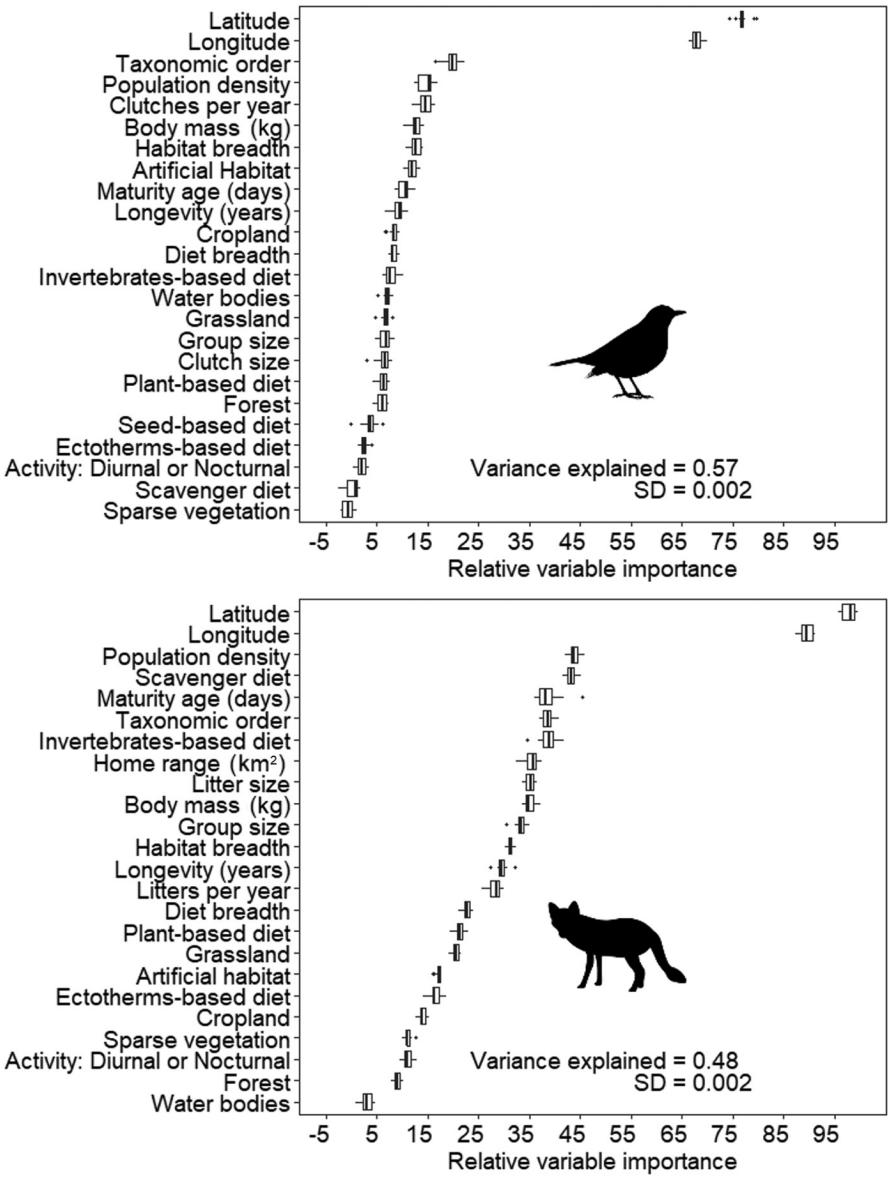


**FIGURE 1** Relative importance of variables considered in random forest regression models to predict bird and mammal roadkill rates. Boxplots show results for models fitted to each of the 15 imputed datasets (trait data were not available for all species, and missing values were imputed 15 times to capture uncertainty). We also report the total variance explained, reported as the median and standard deviation calculated from the 15 models fitted for different imputed datasets.

as the Caribbean region, Paraguay and western Brazil (border with Bolivia), showed low roadkill rates. High roadkill rates were not the direct result of higher richness of species known to be roadkilled (those in our dataset). Some areas with high richness, such as northern Bolivia, southern Brazil and the south-east of Paraguay, did not show high estimates. On the contrary, some high-risk areas in Central America, north-east and south-east Ecuador, central and eastern Argentina and Uruguay have relatively low richness (Figure 5).

## 4 | DISCUSSION

Our compilation revealed a diversity of birds and mammals killed on Latin American roads owing to collision with vehicles. Although most of these species are common and non-threatened, there are some taxa of conservation concern reported as roadkill that should be considered for future research and targeted mitigation. Observed roadkill rates were associated with several life-history traits, ecological traits, morphological traits and habitat preferences. In particular, we found higher roadkill rates in larger birds and medium-sized mammals; likewise, shorter life expectancies, wider habitat breadths and early maturity ages were related to higher mortality for birds and mammals. Our predictive maps revealed areas of high mortality in Central America, the Northern Andean region (Venezuela, Colombia, Ecuador and Peru), southern Chile, central and eastern Argentina, Uruguay and eastern Brazil.

### 4.1 | Vulnerability to roadkill

Body mass was one of the traits associated with road mortality of birds, with larger species (>2.5 kg) generally being more likely to die on roads. Bird body sizes mostly varied between 3 g and 5.7 kg (median weight: 55 g) in our dataset, with an extreme value of 23 kg for *Rhea americana*. In contrast, mammalian sizes in the roadkill dataset ranged from 5 g to 207 kg (median weight: 1.15 kg), and in this group

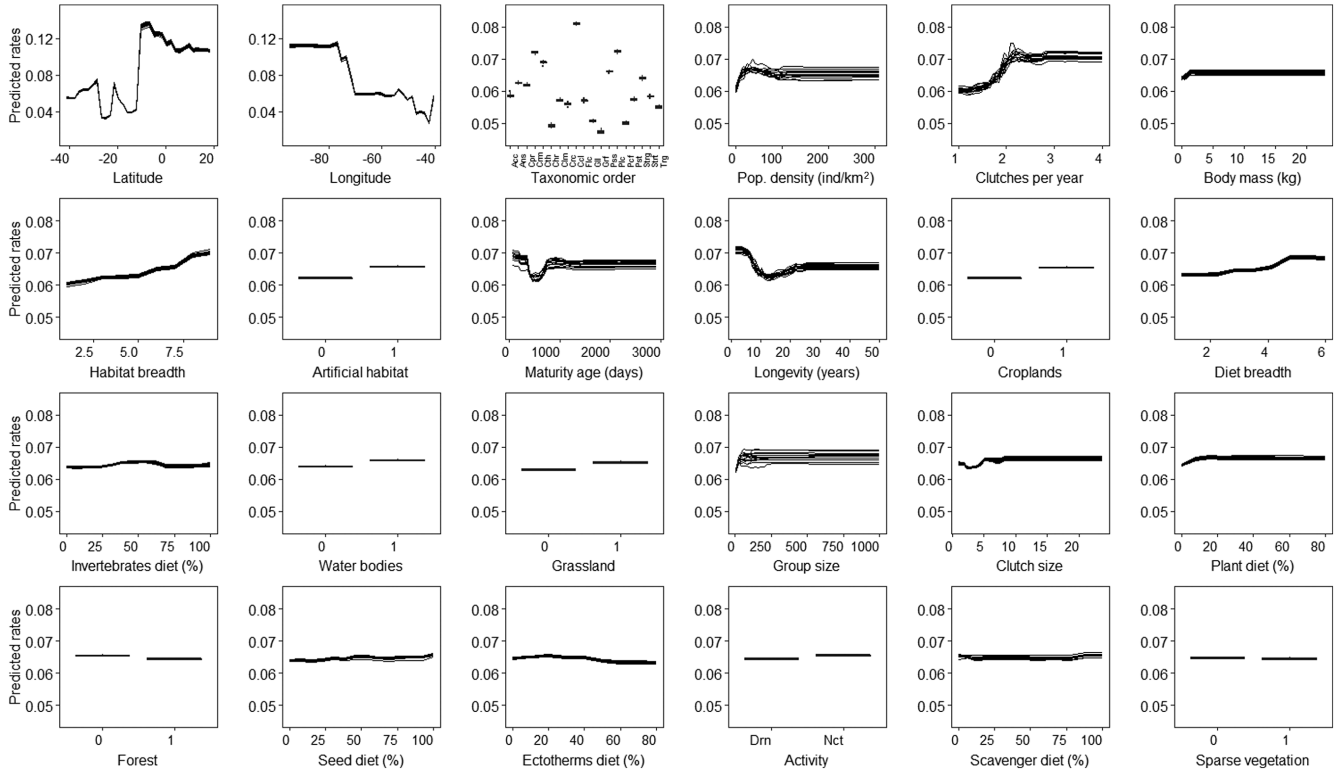


**FIGURE 2** Dependence plots showing changes in predicted roadkill rates for birds for each tested predictor variable. Predictors are shown in descending order of relative variable importance (Figure 1). Each panel shows results for the 15 models fitted for different imputed datasets (trait data were not available for all species, and missing values were imputed 15 times to capture uncertainty). For numerical predictors we show 15 lines and for categorical variables we show boxplots representing the distribution of predicted rates. For habitat preferences (artificial habitat, cropland, forest, grassland, sparse vegetation and water bodies), category 1 indicates species that uses that habitat, and category 0 indicates no use. Note that owing to a wider range of predicted values, the *y*-axis scale for latitude and longitude is different from the rest of the variables.

higher roadkill rates were associated with species of intermediate sizes (with a peak at *c*. 3 kg). This pattern of higher risk in medium-sized mammals is similar to that found in Brazil by González-Suárez et al. (2018) and might be explained, in part, by the ability of vehicle drivers to detect and avoid collisions with larger animals. In addition, lower rates for larger animals could be associated with lower population density or local abundances; indeed, larger mammals have been shown to avoid roads, leading to lower population densities near roads or areas with more roads (D'Amico et al., 2016; Rytwinski & Fahrig, 2012). Among Latin American mammals, large carnivores, such as the jaguar (*Panthera onca*), have much lower population densities near roads (Espinosa et al., 2018). Indeed, we found that bird and mammal species with higher species-level population densities (expected to be on average more locally abundant) were more likely to have high roadkill rates. We note that although estimates of local abundance (or density) were not available, it is likely that some of the within-species variation in roadkill rates reflects variation in local abundance.

We also found that long-lived animals are less likely to be roadkilled. As mentioned in our hypotheses, species with longer life spans could have more opportunity to learn new skills and acquire experience with new environments, such as roads, reducing their risks (Street et al., 2017). However, the relationship could also reflect variation in local abundance because longer life spans are associated with larger body size and slower reproductive rates, which can influence roadkill risk.

Generalists, those with wider diets and habitat breadths, were also more likely to have high roadkill rates. This is likely to reflect greater exposure to roads because generalists can be more likely to visit a variety of environments and be less reluctant to approach roads, and they take advantage of any food resource, such as rubbish thrown from vehicles, carcasses and species that use road verge vegetation. Generalist mammals have been found to use roads extensively in order to obtain food and move across habitats (Hill et al., 2021), and other studies found also that generalist/omnivorous mammals are more vulnerable to roadkill (Cook & Blumstein, 2013). Indeed, we found that mammals with a scavenger and invertebrate-based diet had higher roadkill rates. Scavengers can be directly attracted to roadkill on roads (Rød-Eriksen et al., 2020), increasing their exposure to circulating vehicles and their risk of collision. Insects can also be locally abundant on roads because they can be attracted to decomposing carcasses, verge vegetation resources and light sources near roads and, in turn, attract insectivores to roads.

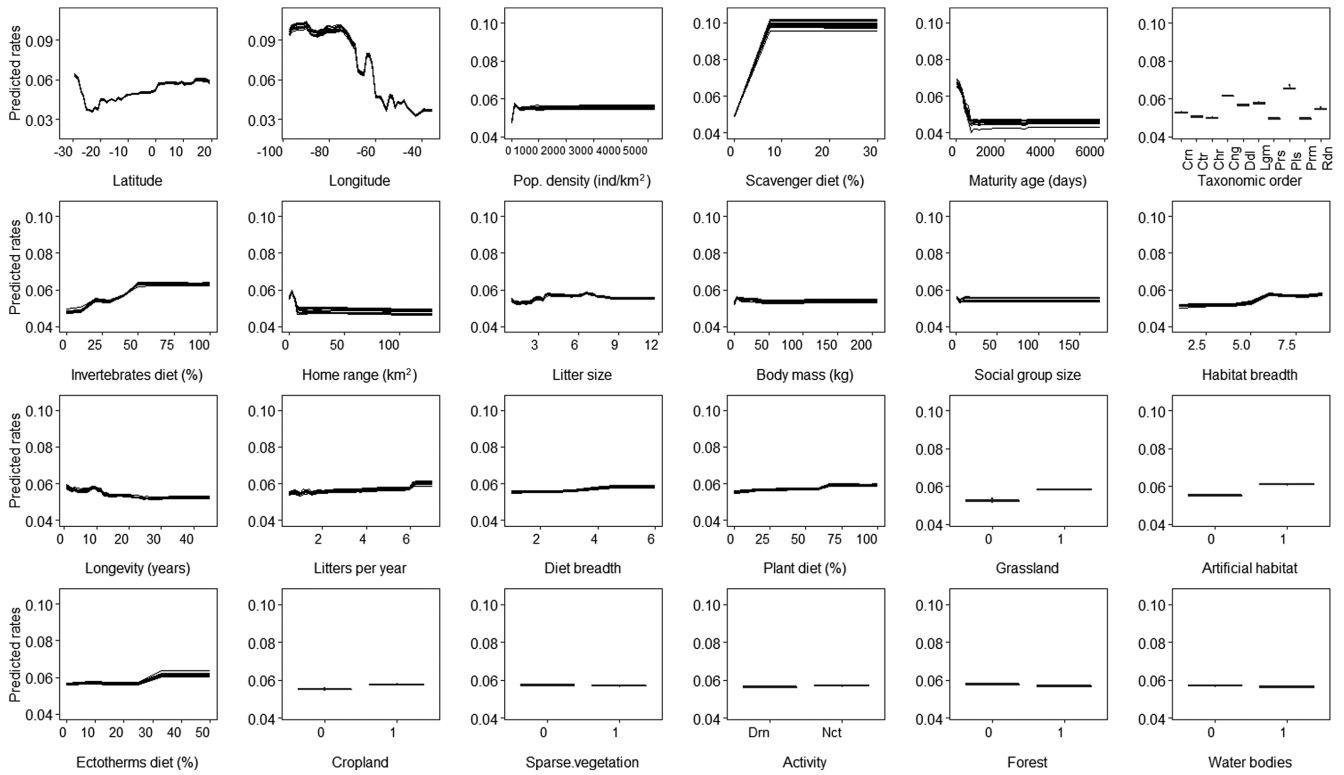


**FIGURE 3** Dependence plots showing changes in predicted roadkill rates for mammals for each tested predictor variable. Predictors are shown in descending order of relative variable importance (Figure 1). Each panel shows results for the 15 models fitted for different imputed datasets (trait data were not available for all species, and missing values were imputed 15 times to capture uncertainty). For numerical predictors we show 15 lines and for categorical variables we show boxplots representing the distribution of predicted rates. For habitat preferences (artificial habitat, cropland, forest, grassland, sparse vegetation and water bodies), category 1 indicates species that uses that habitat, and category 0 indicates no use. Note that owing to a wider range of predicted values, the *y*-axis scale for latitude and longitude is different from the rest of the variables.

Faster reproductive rates, early maturity ages and more litters or clutches per year were related to higher roadkill mortality. These variables might be relevant owing to the association with variation in local abundance or density, because species with faster reproduction rates generally have higher local abundance. In addition, previous work found an association between seasonal roadkill patterns and mating periods (Ascensão et al., 2019; Canova & Balestrieri, 2019). Given that mating behaviour should be more frequent in species with more reproductive events per year, this can lead to more individuals of those species moving across areas looking for mates, and they are more likely to encounter roads.

Previous local studies found that open areas, such as grasslands and croplands, are associated with higher vertebrate roadkill rates (de Freitas et al., 2014; Medrano-Vizcaíno & Espinosa, 2021; Seo et al., 2013; Silva et al., 2019), which is supported by our large-scale results, particularly for birds. These habitat types might be working as ecological traps; for instance, croplands might offer a great quantity of food resources for certain species, which could die on roads when approaching these resources, whereas pasturelands might act as corridors to approach crops. Although the same relationship was found for mammals, habitat variables were not as important for predicting mammalian roadkill rates.

Although traits were relevant predictors, as expected, much of the variation in roadkill rates was explained by location. Strong geographical patterns are common in large-scale studies, reflecting environmental variation and within-species variability that cannot be captured by species-level trait data (as mentioned in our hypothesis). In our case, fitting simpler models that ignored location and its interaction with trait effects (models excluding latitude and longitude) resulted in lower variance explained: 3.04% for birds (*SD* across the 15 datasets: .004) and 24.9% for mammals (*SD* across the 15 datasets: .001) (Supporting Information Appendix S3). The particularly low value for birds might reflect distinct regional trait relationships, such that traits have different effects in different regions (such interactions would be captured in the complete regression trees). For example, two studies exploring how traits influence roadkill rates in European birds reported different patterns. Grilo et al. (2020) found that body mass and diet were among the most important traits for predicting bird roadkill rates when using regression trees that allowed for nonlinear relationships and interactions with geographical location. Meanwhile, Morelli et al. (2020) used linear regression models that did not account for location or tested nonlinearities and reported a weak association with body mass and no relationship with diet.

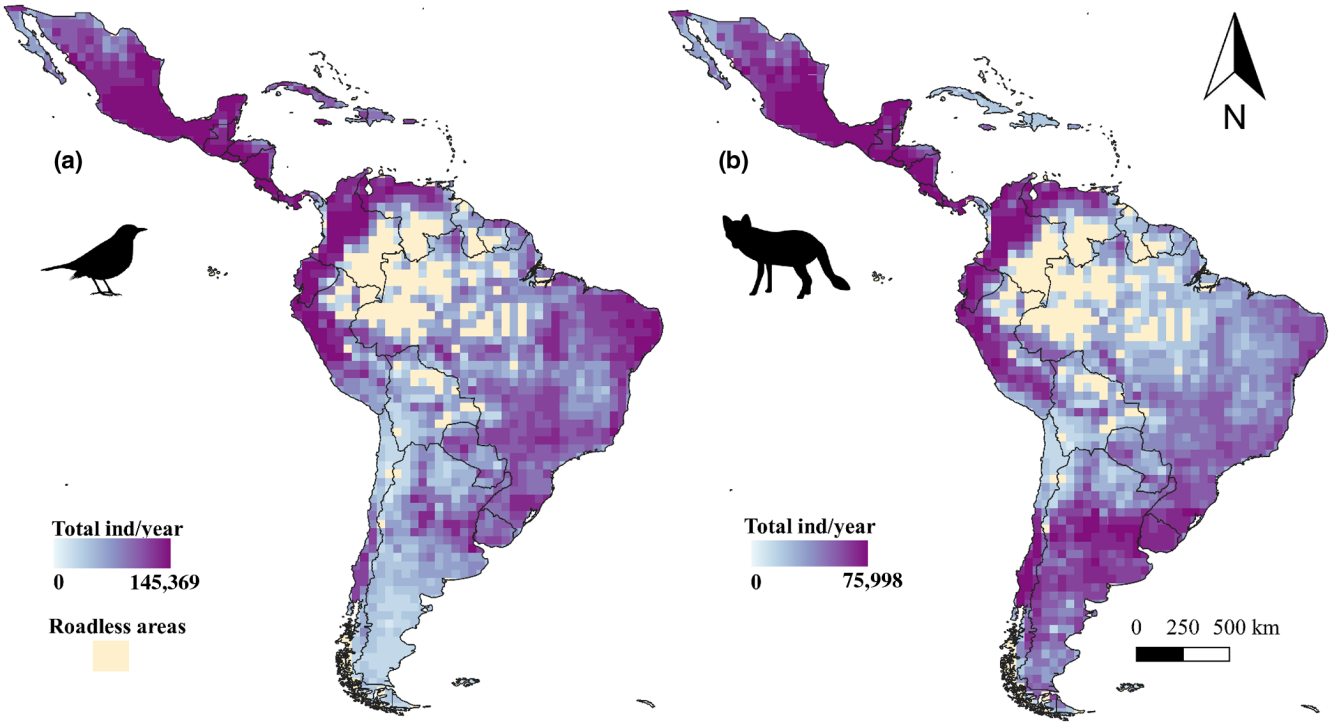


FIGURE 4 Predicted total number of (a) birds and (b) mammals to be roadkilled each year in Latin America and the Caribbean. Total numbers were calculated by multiplying roadkill rates [individuals (ind) per kilometre per year] predicted for each species and grid cell using random regression models and species traits and location data (for all variables, see Table 1) by the total length of existing main roads (in kilometres) in each grid cell. Grid cells with no predictions (cream colour) represent areas where roads are not present.

Alternatively, we might have missed important traits to explain roadkill rates in birds, such as mode of locomotion and movement patterns. Birds with a low-flight behaviour tend to be more roadkilled, which has been observed for owls (Kociolek et al., 2015), and more mobile birds were identified as generally more susceptible to negative effects of roads (Rytwinski & Fahrig, 2012). However, for most of our studied species those data were not available; for example, concerning mobility, we were able to collect home range data for only 10% of bird species. Finally, it is possible that traits are overall poorer predictors of road impacts in birds than in mammals. Future work considering additional taxonomic groups and comparing different areas will be useful to understand further how trait-based approaches can contribute to our understanding of road mortality patterns across different taxa.

## 4.2 | Roadkill risk maps

Our predictions offer a worrying picture, with potentially >12 million birds and >5 million mammals dying each year across main Latin American roads. Furthermore, these estimates reflect only those species with observed roadkill. The Latin America and Caribbean region is home to *c.* 4,613 bird species and *c.* 1,859 mammal species (IUCN, 2021), of which our dataset included 7.50% of birds and 8.55% of mammals. Even if some species show road-avoidance behaviour and are less likely to be roadkilled, road mortality risks for >90% of the avian and mammalian biodiversity are still unknown, and thus, the total number of roadkilled birds and mammals is likely to be much higher than what we estimate here.

Predicted risks from the existing road network are worrying. Unfortunately, Latin America is projected to have one of the highest rates of future road development in the world (Meijer et al., 2018), which is likely to cause even greater impacts on wildlife. For example, we were able to obtain data on planned roads for Ecuador (MTOP, 2016), a country with high predicted roadkill rates. Considering the existing network of 16,647.65 km of primary and secondary roads (Meijer et al., 2018), our model predicts 420,861 birds and 119,599 mammals roadkilled each year. Those numbers were predicted to increase by 9.3% (39,321 additional birds and 11,174 additional mammals) with the development of 1,555.4 km of new roads planned by 2030 (MTOP, 2016). As mentioned above, the real roadkill numbers are likely to be much higher because our dataset represents <20% of the avian and mammalian biodiversity of Ecuador.

Our paper provides insights into how roadkill can impact wildlife in Latin America, but there are some limitations of the data used for analyses. For instance, we assumed that taxonomic identification of roadkill was correct, but it is possible that a few carcasses could have been misclassified. Although it is not possible for us to correct potential taxonomic misidentification, errors are likely to be rare

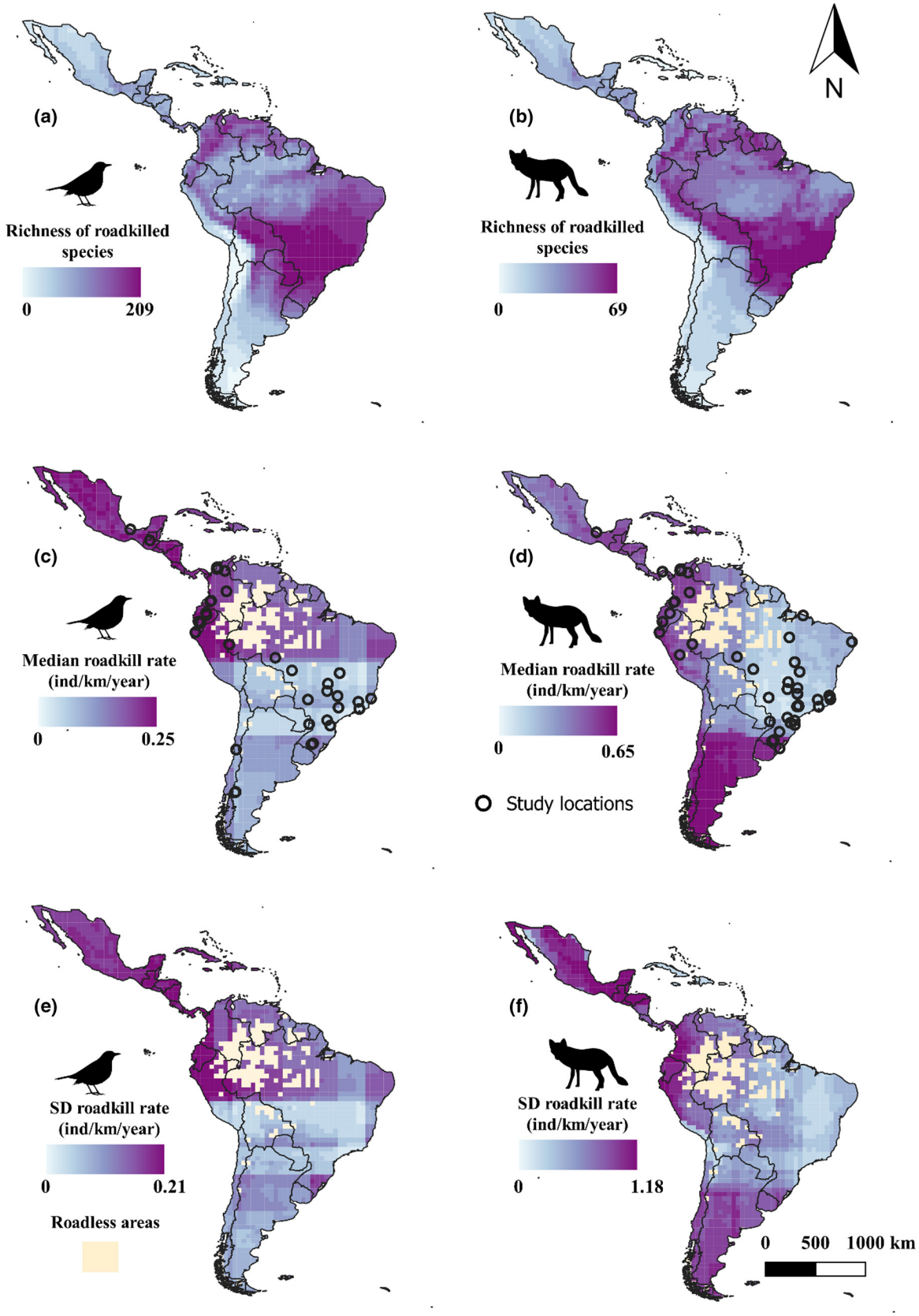


FIGURE 5 (a,b) Species richness of roadkilled (a) birds and (b) mammals. (c,d) Predicted median roadkill rates [individuals (ind) per kilometre per year] for (c) birds and (d) mammals obtained by averaging species estimates obtained for each species and grid cell using random regression models and species traits and location data (see Table 1 for all variables). (e,f) Standard deviation of the predicted rates values among species within each cell for (e) birds and (f) mammals. In panels c and d, we show the locations of the roadkill surveys used for analyses (those that met our methodological criteria). Note that in panels c–f, cream colour indicates areas without any roads.

because unrecognized carcasses are generally listed as unclassified. Taxonomic disagreements or new classifications could also affect the data. For example, the common tapeti (*Sylvilagus brasiliensis*) was considered until 2018 as a widely distributed species, but in 2019 it was separated into several species. The name *Sylvilagus brasiliensis* now refers to tapeti found only in Pernambuco-Brazil (Ruedas & Smith, 2019). Given that our data included studies conducted before 2019 when the taxon was re-evaluated, we compiled roadkill records that mention the common tapeti from 18 studies across five countries (Argentina, Brazil, Costa Rica, Ecuador and Mexico), none within the new restricted distribution. To map roadkill, we used current IUCN distribution data, which means that projected roadkill numbers for tapeti were limited to a small region, potentially underrepresenting the risk for other tapeti species. Although it is beyond of the scope of our study (and non-trivial) to reclassify records into new species, we expect these disparities to be minor and not to bias our results.

Our work contributes to highlight the value of combining models based on traits and habitat preferences to gain a better understanding and predict the threats and impacts from human activities. This approach can be applied widely to investigate other taxonomic groups and geographical areas. For instance, although very high roadkill rates for herpetofauna have been reported in several studies across the world, our understanding of which traits influence risk and the development of predictive models remain limited. Trait data can be useful, but readily available compiled sources remain relatively rare. Increased efforts to provide access to natural history description and standardized datasets will be very valuable to apply this approach and gain further insights into how roads impact wildlife. Additionally, systematic studies that report road impacts, including roadkill rates, in a clear, easy-to-use way are also essential (Silva et al., 2021). Some areas remain unstudied, but it is likely that some have been surveyed but the data remain unpublished or were presented only in monitoring reports that can be difficult to obtain and do not always report raw values (e.g., providing only summary values across taxonomic groups instead of detailed roadkill observations). Easier access to roadkill survey data is essential to build improved models that lead to better decisions for wildlife conservation.

In conclusion, this first continental-scale evaluation of roadkill risk for Latin American birds and mammals offers several useful outputs, identifying Latin American species and areas with higher road mortality. This approach, wherein trait-based models are fine-tuned with realistic spatial information (by considering habitat suitability of species), is a valuable tool for the evaluation of human impacts, including roads and traffic, and we hope that this will be used increasingly by ecologists and managers.

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## CONFLICT OF INTEREST

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

All data used for analyses including roadkill rates, and associated life-history, ecological, morphological traits and habitat preferences for birds and mammals from Latin America are available as appendices.

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## BIOSKETCH

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## SUPPORTING INFORMATION

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## APPENDIX

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