

Landscape and road features linked to wildlife mortality in the Amazon

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Landscape and road features linked to wildlife mortality in the Amazon

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Abstract

Roads impact wildlife around the world; however, dedicated studies are lacking in many biodiverse areas such as the Amazon. Identifying which species are more often hit by vehicles and which landscape and road-related features promote roadkill is essential to guide future development and ensure adequate mitigation actions. For six months, we monitored 240 km of roads in the Ecuadorian Amazon and recorded 1125 dead vertebrates (149 species). Reptiles were the most observed Class with 380 individuals (56 species), followed by amphibians with 278 individuals (11 species), birds with 259 individuals (62 species), and mammals with 208 individuals (20 species). We used Random Forest models to explore the role of various land cover types and road sinuosity on the observed mortality. Additionally, we created heatmaps to visualize the road segments where roadkills were more frequent. For all vertebrates, mortality was more likely in straight road sections near rivers. The effects of other variables were taxa-specific. Amphibian mortality was more likely near bare soil or forest, birds and mammals died more often near herbaceous-shrubby vegetation, and reptile mortality occurred more often in areas with high cover of agriculture. Road segments with high mortality (i.e., roadkill hotspots) varied across taxa. These hotspots identify areas where further research into mitigation is needed to assess road impacts and prevent collisions. Among records, we found rare and threatened species, for which road mortality could be a significant threat. Roadkill surveys not only aid in quantifying threats and informing future planning but can also provide insight into local biodiversity.

Keywords Ecuador · Hotspots · Tropical Andes · Neotropics · Roadkill · Road ecology

Communicated by Kwek Yan Chong.

Extended author information available on the last page of the article

Introduction

Roads are an important source of mortality for wildlife around the world (Kioko et al. 2015; Grilo et al. 2020; Medrano-Vizcaíno et al. 2022); however, some regions with high biodiversity and expanding road networks are understudied (Silva et al. 2021). For example, the Amazon is the most biodiverse wilderness area in the world (Sangermano et al. 2012) but is threatened by growing human activities such as hunting, urbanization, agriculture, and roads (Viteri-Salazar and Toledo 2020). In this region, inhabited by many species vulnerable to road mortality (Medrano-Vizcaíno et al. 2023b), the addition of over 12,000 km of new roads planned for the next five years (Vilela et al. 2020) may increase the risk of local extinction of several animal populations (Grilo et al. 2021) and could lead to the disappearance of many undescribed species (Funk et al. 2012).

Lack of local and regional information limits our understanding of how wildlife populations are affected by infrastructure and can hinder the sustainable development of new roads and effective mitigation plans. For example, in Ecuador the impacts of roads have been assessed in only 2.7% of primary and secondary roads yet nearly 12% of wild species have been identified as susceptible to road mortality (Medrano-Vizcaíno et al. 2023a). Conducting local studies is essential to better understand how species' traits and their habitat preferences, the natural and anthropogenic features of the landscape, the configuration of roads, and driver behaviours influence the incidence of road mortality and therefore guide future work and mitigation measures (Van Der Ree et al. 2015). For example, generalist and short-lived birds and mammals with faster reproductive rates and higher population densities have been found to be more vulnerable to road mortality in Latin America, but the distribution of these species varies regionally (Medrano-Vizcaíno et al. 2022). Road mortality has also been linked to neighboring habitat with distinct effects across vertebrate groups. For example, higher mortality occurs nearer water bodies for amphibians (Coelho et al. 2012), nearer shrubs for birds (Carvalho et al. 2014), nearer forests for mammals (Freitas et al. 2015), and nearer grassland for reptiles (Braz and Rodrigues 2016). Finally, the size and configuration of the road can also influence how animals use it (Mulero-Pázmány et al. 2022) and their risk of collision leading to mortality (Ciocheti et al. 2017).

Here we present an assessment of mortality among terrestrial vertebrates on roads in the Ecuadorian Amazon. First, we describe the species found as roadkill and calculate standardized roadkill rates to allow comparison with data from other studies and areas. Second, we evaluated the role of distance and coverage of different land covers and road configuration on roadkill incidence and identified hotspots of mortality. We hypothesized that different land covers would influence roadkill events differently due to species differences in habitat preferences and resources requirements. In particular, we predicted a high incidence of roadkill in areas with greater availability of and proximity to natural land types (forest and herbaceous-shrubby vegetation) where the vertebrates are more abundant (Carrete et al. 2009). We also predicted more roadkill of species that use human-dominated ecosystems near agriculture and urban areas where more road traffic would occur (Weisbrod et al. 2003). In addition, because rivers provide water resources and individuals may approach them regularly (Seo et al. 2013; Medrano-Vizcaíno 2018), we expected higher mortality near rivers. We also predicted more roadkill in straighter roads particularly for species that do not show behavioural avoidance towards traffic (e.g., herpetofauna, Jacobson et al. 2016). Speed limits in Ecuador are 90–100 km/h for straight roads, and 60 km/h for curves (ANT

2021), therefore, vehicles generally travel faster on straight (less sinuous) roads, which may increase roadkill likelihood (Tejera et al. 2018). On the other hand, sinuosity affects visibility which decreases the ability of drivers to prevent collision on the roads and therefore we may find more roadkills in sinuous road sections. To test these predictions, we collected roadkill data over a period of six months along 240 km of roads in the Napo province of Ecuador, an area of high endemism within the Amazon (Ribas et al. 2022) where previous research along 99 km of these roads revealed that rare, threatened and undescribed species were susceptible to road mortality, (Medrano-Vizcaíno and Espinosa 2021), suggesting that further research efforts were necessary.

Methods

Roadkill surveys

Our work covered almost the entire network of primary and secondary roads in the province of Napo-Ecuador. These roads link main towns in the region and are near four protected areas: Antisana Ecological Reserve, Sumaco-Napo-Galeras National Park, Cayambe-Coca National Park, and Colonso Chalupas Biological Reserve, where the dominant ecosystems are the evergreen high, mid-, and low montane and piemontane forests of the north of the eastern Andes mountain range (MAE 2013). The sampled areas covered an altitudinal range between 300 and 3000 m a.s.l., with annual average temperatures ranging from 4.63 to 23.7 °C, and annual precipitation from 1100 to 3400 mm (GADPN 2018; FONAG-EPMAPS 2021). All roads are paved with most of them having two lanes with similar widths and are mainly surrounded by agricultural land and forest.

From the 19th September 2020 to 23rd March 2021, two people conducted roadkill surveys four to five days per week between 08:00 and 17:00 from a car driving at an average speed of 40 km/h (total: 100 survey days). One observer (always PMV), supported by a designated driver (DBZ), scanned the road (and road shoulders when visible) to locate carcasses on the pavement (i.e., roadkills). The total study area covered 240 km of primary (roads connecting main cities) and secondary (roads connecting urban/rural areas to primary roads) paved roads, where speed limits vary between 20 and 90 km/h. For the full sampling period, we generally monitored half of the study area every three days. Therefore, our monitoring regimen included two consecutive days of sampling followed by a non-sampling day dedicated to data processing. When a carcass was detected, the vehicle stopped on the side of the road on a safe area. Both observers wore high-visibility vests for safety. All carcasses were photographed onsite and georeferenced with a GPS unit (Garmin Etrex 22X). Then carcasses were either collected or removed from the pavement to avoid double counting. We aimed to identify all carcasses to species but in some cases, the specimen was too deteriorated or differed from recognized species (potentially undescribed fauna). Taxonomic identification was based on observer knowledge and specialized guides (e.g. Ridgely and Greenfield 2006; Tirira 2017; Valencia et al. 2016; Wallach et al. 2014). In some cases, further taxonomic evaluation was done in the laboratory at Universidad Regional Amazónica IKIAM.

Land cover and road configuration

We used available land cover data (Ministerio del Ambiente del Ecuador 2018) in QGIS software v.3.18.2-Zürich (<https://qgis.org/en/site/>) to calculate proximity and percentage of six different land cover types (agricultural lands, bare soil, herbaceous-shrubby vegetation, human settlements, forest, rivers) for each roadkill record and control sites. For the control sites, we generated multiple sets of random points and selected points that were at least 200 m from a recorded roadkill and at least 50 m from another control site. This was done to allow discrimination between roadkill and control sites and to reduce spatial correlation among control sites, while still ensuring a sufficient large control sample. The same number of control sites as road kill records were generated this way. We estimated Euclidean distances to the nearest feature (e.g., closest distance to a river) for all land covers and percentages of the dominant land covers (forest and agriculture, which provide resources such as food and refuge) at two buffer scales to assess the effect of resource availability at smaller (100 m) and larger (500 m) scales.

We also evaluated how road configuration influenced roadkill, using road data from the Instituto Geográfico Militar (2017). For this, we calculated a sinuosity score for each roadkill and control site considering a section of 100 m of road. We also tested 200 m, but sinuosity at 100 m showed higher importance for the models. The roadkill site was located in the center of each section as we did not know the travelling direction of the vehicle that caused the collision and therefore had to consider sinuosity in both directions. We then calculated the score as the actual length of the road divided by the Euclidian distance between the two ends. A straight road had a sinuosity score of 1. Other road features such as road width and number of lanes were not evaluated because surveyed roads were mostly identical.

Data analyses

First, we calculated the total number of roadkills per taxonomic class and for all identified species and estimated standardized roadkill rates per species (ind./km/year) calculated as: (total number of detected carcasses/240 km of road surveyed/185 days of survey period) *365 days. Here, the survey period corresponds to the number of days between the first and the last sampling day. During surveys we detected and recorded animals that could have died during non-survey days, thus the mortality detected is considered to reflect the mortality over the entire duration of the survey period rather than only the survey days. We applied a machine learning classification method, Random Forest, to identify features differentiating roadkill sites from control sites. This method ensembles multiple classification trees from a bootstrap sample of the original data, and shows higher classification accuracy than other methods such as logistic regression and linear discriminant analysis (Cutler et al. 2007).

We created Random Forest models based on 1500 classification trees using the R package “randomForest” and applying the function “randomForest” (Liaw and Wiener 2002). We fitted a general model including data from all vertebrates. Additionally, we fitted Class-specific models (i.e., amphibians, reptiles, birds, and mammals), and a model for Caecilians (amphibians) and Amphisbaenians (reptiles) as a group of fossorial species due to a previously known high prevalence of road mortality in this area (see Filius et al. 2020; Medrano-Vizcaino and Espinosa 2021). In addition, for any group in which any single spe-

cies or related species were dominant (> 50% of the data within a taxonomic class), we also completed two additional analyses: (1) for the dominant taxa and (2) for all others in the taxonomic class. Models included 11 variables as predictors (proximity for each of the six land covers, percentage cover at 100 and 500 m for forest and agricultural land, and road sinuosity). We determined variable importance considering two measures: mean decrease in accuracy and mean decrease in gini index; means were calculated across all fitted trees. Mean in decrease accuracy, measured by the out-of-bag error rate, is calculated as the loss of accuracy in the model when a variable (i.e., feature) is removed, while the mean decrease gini measures the impurity of nodes in split based on a feature. We used the functions “important_variables” and “plot_multi_way_importance” from the R package “randomForestExplainer” (Paluszynska et al. 2020) to calculate and plot these metrics. Additionally, we generated dependence plots to represent the probability of roadkill according to changes in the value of each predictor using the function “partial” from the R package “pdp” (Greenwell 2017). This function allows visualization of the relationship between the response variable and a given feature including the interaction with the rest of features in the model. Model performance was evaluated using the area under the ROC curve (AUC) with the function “roc” from the R package pROC (Robin et al. 2011).

In addition, we created heatmaps of roadkill based on kernel estimation density using QGIS software v.3.18.2-Zürich (<https://qgis.org/en/site/>) to visualize the areas where roadkills were more frequent for all vertebrates and for each taxonomic class. These hotspots are areas where research and/or mitigation actions may be important. The analysis was done across the road network at three buffer distances: 100, 500, and 2000 m. By testing different scales, we distinguish very local and more general hotspots which may require different mitigation measures or actions. Finally, we classified the heatmap data using a discrete interpolation into three classes of equal intervals, where values in the top tercile were identified as roadkill hotspots.

Results

Wildlife mortality

We found 1125 wildlife vertebrate carcasses representing at least 149 species (308 carcasses could not be identified to species level mainly because of their poor state) (Table S1). Reptiles were the most common with 380 individuals from 56 species (89.74% of individuals and 91.5% of species were snakes), followed by amphibians with 278 individuals (11 species), birds with 259 individuals (62 species), and mammals with 208 individuals (20 species). The most roadkilled species was the cane toad *Rhinella marina* (208 carcasses: 1.71 ind./km/year), followed by the Andean opossum *Didelphis pernigra* (87 roadkills: 0.715 ind./km/year), the common opossum *Didelphis marsupialis* (48 individuals: 0.385 ind./km/year), and the klebba's snail-eater *Dipsas klebbai* (47 individuals: 0.386 ind./km/year). The smooth-billed ani *Crotophaga ani* (23 individuals: 0.189 ind./km/year) was the most common roadkilled bird. We found numerous carcasses from fossorial organisms including Caecilians (40 individuals: 0.239 ind./km/year) and the speckled worm lizard *Amphisbaena bassleri* (29 individuals: 0.238 ind./km/year) (Fig. S1).

Although most species found in this study (93.4%) are listed as Least Concern according to the IUCN red list (IUCN 2022), we recorded carcasses from two species catalogued as Vulnerable: the bailey's blind snake *Trilepida anthracina* (one roadkill) and the giant armadillo *Priodontes maximus* (one roadkill); one catalogued as Near Threatened: the grey ground snake *Atractus occipitoalbus* (one roadkill); two listed as Data Deficient: the touzet's ground snake *Atractus touzeti* (two roadkills), and the Andean cottontail *Sylvilagus andinus* (one roadkill), and three not yet evaluated: *Dipsas klebbai* (47 roadkills), the giant Ecuadorian toad *Rhaebo ecuadorensis* (two roadkills), and the white-striped eyed lizard *Cercosaura oshaughnessyi* (one roadkill).

How land cover and road configuration influence roadkill

The general (i.e., all vertebrates) and class-specific models revealed consistency regarding some factors that explain road mortality but also considerable variation among groups (Figs. 1 and 2). In all models, roadkill sites were more likely to be in straight roads (lower sinuosity) and nearer rivers than control sites. In general, distances to land cover were more important than percentages of cover to explain roadkill. While not always found to be very important variables, agriculture and forest covers at 500 m were more important than at 100 m. (Fig. 1).

Class-specific models revealed that amphibians were more likely to be roadkilled on straight roads located near rivers, bare soil or forest, and at intermediate distances from herbaceous-shrubby vegetation (Figs. 1 and 2). Reptile mortality was higher on straight roads away from herbaceous-shrubby vegetation, near rivers, and with a higher agriculture cover. Roadkilled birds were more often found across straight roads near herbaceous-

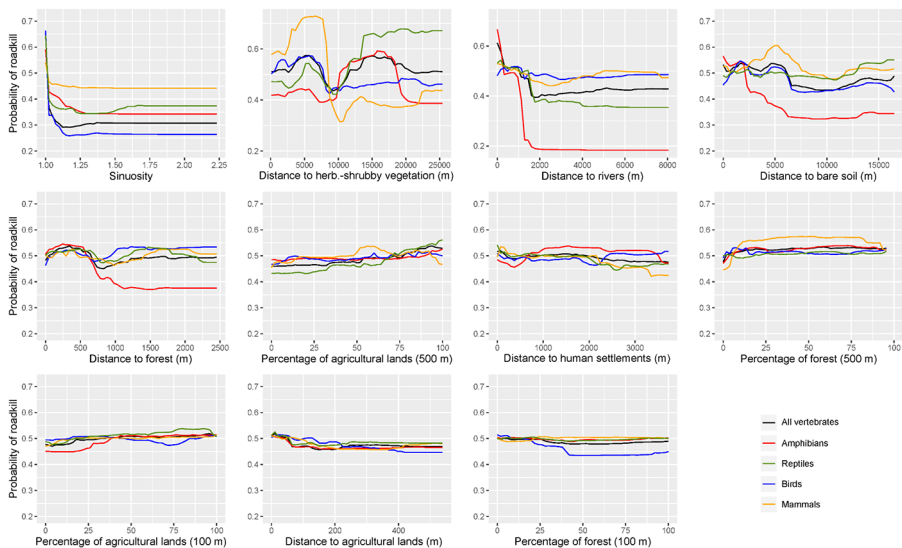


Fig. 1 Dependence plots showing how land cover and road configuration influence probability of vertebrate roadkill in the Napo region of Ecuador. Plots are shown in descending order of variable importance for models fitted for all vertebrates and the separate taxonomic classes. Probability of roadkill (y axis) ranges from 0 (lowest probability) to 1 (highest probability)

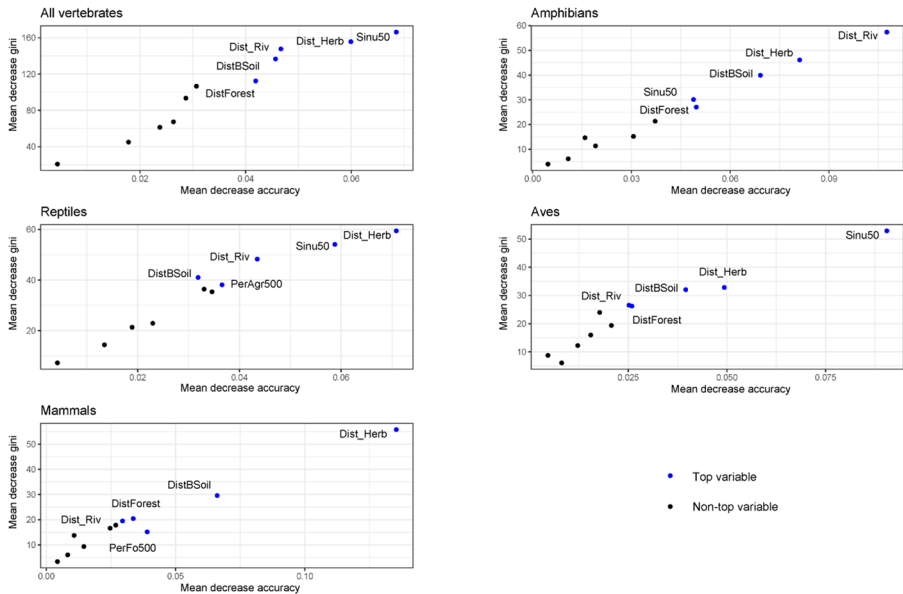


Fig. 2 Variable importance from Random Forest models evaluating the effect of land cover and road configuration on vertebrate roadkill in the Napo region of Ecuador. Results are presented for models fitted for all vertebrates combined and for each taxonomic group. Variable importance is based on mean gini decrease and mean accuracy decrease. Labels indicate the five most important variables in blue dots (higher accuracy and gini decrease values). Sinu50=sinuosity (50 m), Dist_Herb=distance to herbaceous-shrubby vegetation, Dist_Riv=distance to rivers, DistForest=distance to forest, DistBsoil=Distance to bare soil, PerAgr500=Percentage of agricultural lands (500 m buffer), PerFo500=Percentage of forest (500 m buffer)

shrubby vegetation, with less clear effects for other variables. Mammals were more likely to die from collisions on straight roads at low to intermediate distances from herbaceous-shrubby vegetation.

For amphibians we also separately analysed data from the common cane toad (very common species) and other taxa. Distance to river was the most important variable in both models, and cane toads were more likely to be found as roadkill away from herbaceous-shrubby vegetation (Figs. S2, S3). Because of the high abundance of opossums (*Didelphis pernigra* and *Didelphis marsupialis*) also mammals, we also analysed these and all others separately; relevant factors were largely consistent in both models (Figs. S2, S4).

Fossorial species that included caecilians and amphisbaenians were more likely road-killed on straight roads located near herbaceous-shrubby vegetation, and rivers. Additionally, the probability of mortality was higher on roads near and with high cover of agriculture and forest (Figs. S2, S5).

We note that some relationships were non-linear. For example, dependence plots for amphibians showed a hump-shaped relationship with distance to herbaceous-shrubby vegetation and for mammals both distance to bare soil and herbaceous-shrubby vegetation. (Fig. 1). Finally, all models had a good performance (AUC values ranging from 0.78 to 0.97) (Fig. S6).

Roadkill hotspots

We identified several roadkill hotspots for all vertebrates particularly located around urban areas in Sala honda, Baeza, Oritoyacu, Puerto Napo, El Ansu, Santa Rosa and Buena Esperanza (Fig. 3). At the lowest scale these areas had more than 3.7 detected carcasses in 100 m buffer areas, with the larger scale reflecting over 25 vertebrates killed in the 2 km buffer over a 6-month period (~ 1 vertebrate killed per week). Some of these areas were also detected as hotspots when analysing data for each taxonomic class separately, but also new tax-specific hotspots were detected. For amphibians (excluding *R. marina*), hotspots were near Oritoyacu, Urcusiqui, and Sarayacu towns ≥ 1.92 roadkills at 100 m buffer, ≥ 2.81 roadkills at 500 m buffer, and ≥ 4.45 roadkills at 2 km buffer. Fig. S7). Hotspots for *R. marina* were distinct and found at low altitude (between 373 and 569 m a.s.l.) near Puerto Napo, Sindy, Pucaurcu, Buena Esperanza, and Santa Rosa towns (≥ 2.37 roadkills at 100 m buffer, ≥ 5.58 roadkills at 500 m buffer, and ≥ 10.24 roadkills at 2 km buffer. Fig. S8). We identified three reptile hotspots near Sala honda, Baeza, and Santa Rosa (≥ 3.21 roadkills at 100 m buffer, ≥ 7.46 roadkills at 500 m buffer, and ≥ 12 roadkills at 2 km buffer. Fig. S9). There were four hotspots of bird roadkill, one near San Francisco de Borja and Baeza and the other three near Las Cavernas, Calmituyacu, El Ansu, Buena Esperanza, and Santa Rosa (≥ 2.23 roadkills at 100 m buffer, ≥ 2.83 roadkills at 500 m buffer, and ≥ 6.38 roadkills at 2 km buffer. Fig. S10). We found one hotspot of mammal roadkill (excluding opossums) near Baeza (≥ 1.29 roadkills at 100 m buffer, ≥ 1.81 roadkills at 500 m buffer, and ≥ 4.19 roadkills at 2 km buffer) which was near one of the four hotspots identified for opossums (the other three hotspots for opossums were near Sardinas, Sala honda, Oritoyacu, and Cuyuja. Figs. S11 and S12).

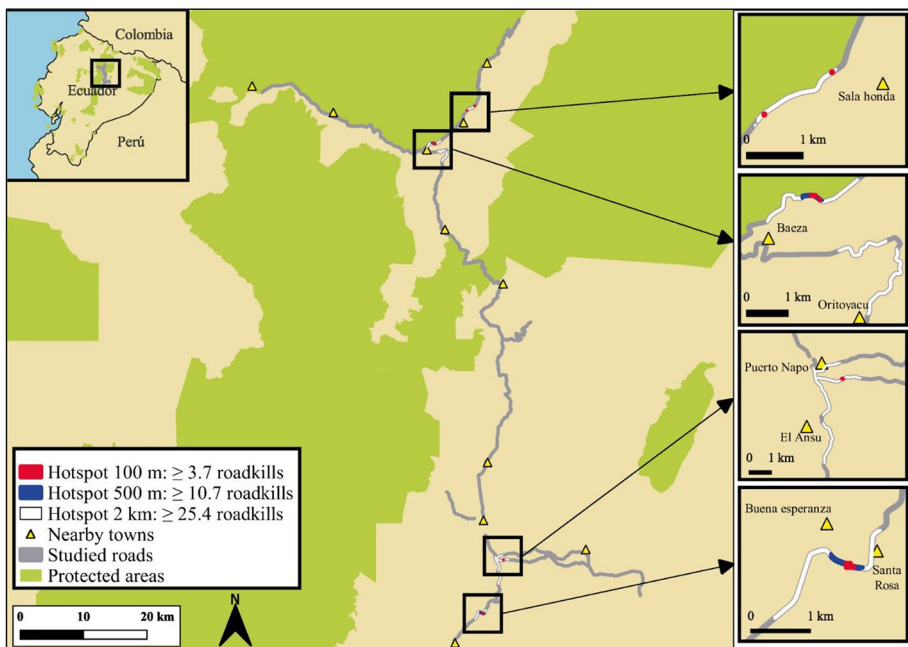


Fig. 3 Roadkill hotspots across the 240 km of our study area in Napo when data for all vertebrates were combined (amphibians, reptiles, birds, and mammals)

Discussion

Our study in the Ecuadorian Amazon revealed a great diversity of wild tetrapods being killed on roads (149 species from 1125 carcasses). This mortality followed some general spatial patterns for all vertebrates but also showed variation between classes and in some cases within classes. Roadkill occurred more often on straight roads (lower sinuosity) near rivers for all vertebrates. Distances to herbaceous-shrubby vegetation, forest, and bare soil were also important predictors but their association with mortality were taxa-dependent. We additionally identified several mortality hotspots with locations varying among taxa but largely located near urban areas.

Wildlife mortality

We estimate on average 9.25 vertebrates die per kilometre of road in this province each year. This mortality rate is higher than those reported by other studies in Latin America, such as in Rio de Janeiro-Brazil (0.5 ind./km/year) (Bueno et al. 2015), Goiás-Brazil (4.04 ind./km/year) (Braz and Rodrigues 2016), Panama (2.07 ind./km/year) (Gálvez 2021), the Gulf of Mexico (3.93 ind./km/year) (Canales-Delgadillo et al. 2021), Limon-Costa Rica (3.27 ind./km/year) (Artavia et al. 2015), Magdalena-Colombia (6.31 ind./km/year) (Adárraga-Caballero and Gutiérrez-Moreno 2019), Andean Yungas-Argentina (1.06 ind./km/year) (Cuyckens et al. 2016), but lower than in Upper Paraná Atlantic forest-Argentina (13.12 ind./km/year) (Bauni et al. 2017). These differences likely result from variation in wildlife abundance and composition, and in configuration and composition of landscapes among study areas.

Our estimate of road mortality is likely an underestimate because individuals may be hit by vehicles but die away from the road and not all carcasses are detected during road surveys (Ogletree and Mead 2020). Moreover, factors such as weather conditions, survey method and vehicle speed, and the destruction or removal of carcasses by predators, scavengers, and circulating vehicles influence detectability (Santos et al. 2011). However, while total mortality may be higher, our roadkill list included a great proportion of the species distributed in Napo province. The area hosts 85 amphibian, 48 reptile, 587 bird, and 134 mammal species (Calles López 2008). Roadkills encountered in our study covered 12.94% of these amphibian species, all reptile species, 10.56% of bird species, and 14.9% of mammal species known from this area. In fact, we found more reptile species among our roadkills than those previously described as present in Napo. Although it is evident that Napo roads are a relevant source of mortality for many vertebrates, the fact that we recorded more reptiles' species than those already reported in the literature reflects the great biological richness of this area where the description of new species and distribution ranges is frequent (e.g., Medrano-Vizcaino and Brito-Zapata 2021; Melo-Sampaio et al. 2021). At the same time, it reflects the major impact of roads on reptiles. This may relate to higher local abundance but also could reflect driver behaviour. Snakes (89.74% of roadkilled reptiles in our study) can be intentionally killed by drivers (de Resende Assis et al. 2020).

The mortality of threatened species was low, with single records for the giant armadillo and the bailey's blind snake, both catalogued as Vulnerable (IUCN 2022). However, *Atractus* spp. snakes were the most roadkilled genus of reptiles (Fig. S1). This is a poorly studied genus of neotropical herpetofauna (Cisneros-Heredia 2005), with 23% of the species distributed in Ecuador listed as threatened, and 47% as Data Deficient or remaining unassessed

(Torres-Carvajal et al. 2022). Additionally, caecilians, considered as the least known terrestrial vertebrates (Jared et al. 2019), with 56% of the species distributed in Ecuador classified as threatened, and 28% as Data Deficient or remaining unassessed (Ron et al. 2021), had the second highest mortality among amphibians. While detailed population assessments are needed to understand the impacts of road mortality, for threatened species even low roadkill rates can have major impacts on their populations (Grilo et al. 2021).

Road ecology studies not only provide information on wildlife mortality but can also expand our knowledge of local biodiversity. Records from our survey have already contributed to extend the geographic distribution ranges for six snake species rarely observed in the wild (*Anilius scytale*, *Drymarchon corais*, *Erythrolamprus breviceps*, *Micrurus lemniscatus*, *Oxyrhopus vanidicus*, *Trilepida anthracina*; Medrano-Vizcaino and Brito-Zapata 2021). Additionally, ongoing research can identify new species and extended geographic areas among roadkill specimens of caecilians and *Atractus* snakes, which are poorly-studied vertebrates with taxonomic uncertainties (Cisneros-Heredia 2005; Wilkinson 2012). A road-killed specimen collected in a previous study in this area (Medrano-Vizcaino and Espinosa 2021) was described as a new snake species by Melo-Sampaio et al. (2021).

Our study suggests that roads in Napo could be affecting the vertebrate community, including threatened, poorly studied, and even undescribed species. Research and conservation actions should focus on threatened and poorly-known species, but a special effort to quantify risk for snakes seems a priority as road mortality of even few individuals can lead to local extinctions (Row et al. 2007).

How land cover and road configuration influence roadkill

Road configuration was an important predictor in all cases and there was support for our hypothesis that vehicles travel faster on straight roads which may make drivers less able to detect and avoid collision on these areas leading to a higher wildlife mortality. This is also in line with previous research that found higher mortality from wildlife-vehicle collisions in roads with fewer turns (Pagany 2020). Our other hypothesis, that sinuous roads could prevent early detection and lead to higher mortality was not supported. Also as hypothesized, generally for all vertebrates roadkill occurred more often in areas closer to rivers (see also Bastos et al. 2019; Lala et al. 2021). The need for individuals to access this vital resource can increase local abundance near water sources leading to greater chances of mortality from vehicle collision (Newmark et al. 1996). Proximity to rivers was especially relevant for amphibians, which is not surprising given how many of these species breed and live in water (Ficetola and De Bernardi 2004). This association has been described in other studies in temperate regions (e.g., D'Amico et al. 2015; Seo et al. 2013), and some have recommended avoiding the construction of artificial water bodies near roads as it can particularly affect amphibian populations (Coelho et al. 2012). Additionally, the stronger importance of agriculture and forest covers at 500 m compared to 100 m in some groups may reflect increased local abundance in larger suitable habitat patches (of different covers depending on the species), and thus higher mortality (Figs. 1 and 2, S2, S3, S4, and S5).

The effect of other land cover types was taxa-specific. Proximity to bare soil or forest predicted amphibian roadkill, potentially linked to higher abundance and movement within suitable habitats (forests) and to increased movement when crossing largely unsuitable areas to access other resources (bare soil). Bird and mammal mortality was greater

nearer herbaceous-shrubby vegetation (see also Ferreguetti et al. 2020; Plante et al. 2019). For birds, collision risk may increase with low or medium high vegetation as birds that fly from low vegetation to low vegetation likely stay closer to the ground and thus in the path of circulating vehicles increasing collision risk (Santos et al. 2016). Likewise, shrubs near roads are used as nestling sites for some birds, and as refuge and foraging sites for birds and mammals and this proximity could increase their risk of collision with vehicles on the road (Gunson et al. 2011; Bravo-Naranjo et al. 2019). Shrubby vegetation near road edges can also reduce visibility preventing drivers from noticing approaching birds or mammals in time to avoid collision and preventing animals from detecting travelling vehicles (Lala et al. 2021). Additionally, areas with herbaceous-shrubby vegetation may attract animals, leading to greater local abundance and movement and thus, higher roadkill. These effects would increase when vehicles travel faster (as expected on straight roads). Reptiles roadkill occurred more often close to human settlements and in areas of higher agricultural land cover, potentially because these areas often hosts high prey abundances (e.g. rodents, Stenseth et al. 2003). A higher mortality of fossorial species (caecilians and amphisbaenians) associated to herbaceous-shrubby vegetation, rivers, agricultural land and forest could be due to soils rich in organic matter across these land covers. These soils offer shelter, and harbor a great diversity of invertebrates, which can be attractive for these fossorial species whose diet is mainly composed by earthworms and insects (Jared et al. 2019; Amorim et al. 2019; Kouete and Blackburn 2020). In addition, soil compaction near roads could limit underground movements forcing fossorial animals to emerge to the surface, and consequently expose them to vehicular traffic (Maschio et al. 2016).

In some cases we observed non-linear relationships that may be caused by the combination of different mortality patterns among species (Plante et al. 2019). Analyses at the species-level could help disentangle these patterns but obtaining sufficient data can be challenging. Conducting surveys over longer periods and the use of data from citizen science projects may be helpful to improve our understanding on this matter.

Roadkill hotspots

Identified hotspots were generally in the vicinity of towns, likely due to increased traffic. When hotspots were defined for different classes (and even for different taxa within class) we found that locations were not consistent. This can reflect differences in animal behaviour, movement and abundance, as well as traffic patterns and driver behaviour, factors that can lead to different hotspots for various taxa (Teixeira et al. 2013; Silveira Miranda et al. 2020). Importantly, as roadkill survey always underestimate mortality (animals dying away from roads after collision, not being detected, etc.), we may have missed other mortality hotspots that may exist or affect particular taxa. From those areas identified in our study, two were consistent with hotspots identified in a study conducted in 2014 (see Medrano-Vizcaíno and Espinosa 2021). These areas were located near Baeza and Sala honda towns and could be potential sites for further research to assess how roadkill impacts long term population viability. Walking surveys (that can increase carcass detectability) may be useful in the identified hotspots to further understand mortality and risks to particular species which may need protection.

Conclusions

Our work reveals the influence of landscape and road features in wildlife mortality across the biodiverse Amazonian province of Napo and identified some taxonomic groups and areas that would benefit from additional attention and dedicated research to assess the impact of road mortality on their populations. We hope that this work can be useful to guide future research and conservation initiatives and allow local authorities to make evidence-based decisions for wildlife protection and sustainable roads.

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Authors' contributions PM-V, MG-S and CG conceived the ideas and designed methodology; PM-V and DB-Z collected the data; PM-V analysed the data; PM-V led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Availability Datasets that include distances to landscape features, percentage of cover, and road sinuosity are available on figshare: <https://doi.org/10.6084/m9.figshare.21181069.v1>.

Declarations

Competing interests The authors declare no competing interests.

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