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Geography of roadkills within the Tropical Andes Biodiversity Hotspot: Poorly known vertebrates are part of the toll

Pablo Medrano-Vizcaíno^{1,2}  | Santiago Espinosa^{1,3} 

¹Facultad de Ciencias Exactas y Naturales,
Pontificia Universidad Católica del
Ecuador, Quito, Ecuador

²School of Biological Sciences, University
of Reading, Reading, UK

³Facultad de Ciencias, Universidad
Autónoma de San Luis Potosí, San Luis
Potosí, México

Correspondence

Pablo Medrano-Vizcaíno, School of
Biological Sciences, University of Reading,
Whiteknights, PO Box 217, Reading,
Berkshire, RG6 6AH, UK.
Email: p.medranovizcaino@pgr.reading.
ac.uk

Santiago Espinosa, Facultad de Ciencias,
Universidad Autónoma de San Luis Potosí,
Av. Chapultepec 1570, CP 78295, San Luis
Potosí, SLP, México.
Email: santiagoea@gmail.com

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Abstract

We explore the effect of roads in animal mortality within the Biodiversity Hotspot with the highest number of endemic species of vertebrates on Earth, the Tropical Andes. Our objectives were to know which species are killed on roads in this particularly biodiversity-rich area and how landscape composition and configuration influences roadkills. We systematically looked for roadkills along roads that border three protected areas in the Ecuadorian Andes. To evaluate our hypotheses, we used correlation, logistic regression, and GIS analyses. We surveyed a total of 7128 km and observed a roadkill rate of 6.24 (95% CI = 5.35–7.14) individuals per 100 km/day. Roadkills included poorly known endemic and endangered vertebrates; among them, one undescribed snake species of the genus *Atractus*. Most roadkills were by pastures, the dominant vegetation by roads in our study area. Roadkills were more likely to occur near bridges and were more frequent at greater distances from natural vegetation, towns, and rivers. We conclude that pastures and bridges may be functioning as ecological traps for small and poorly known vertebrates. Mitigation measures could include increasing road permeability to wildlife by constructing culverts in critical points where mortality is high, and the adaptation of areas beneath bridges for them to function effectively as wildlife underpasses. These measures should be complemented with fences to exclude vertebrates from roads in areas near wildlife passages and along pastures. We encourage the development of similar studies in biodiversity-rich areas to inform mitigation measures that can be adapted to local conditions.

Abstract in Spanish is available with online material.

KEY WORDS

Atractus, ecological trap, Ecuador, endangered species, Gymnophiona, protected areas, road ecology, wildlife mortality

1 | INTRODUCTION

There are over 40,000,000 km of paved roadway lanes in the world (Dulac, 2013). Many of those roads dissect natural habitats where they cause multiple and detrimental ecological effects. For example, roads are catalysts of habitat loss and fragmentation, facilitate the

introduction of invasive species, can interfere with local hydrological cycles, are associated with pollution of water sources and soil, among other effects (Coffin, 2007; Forman et al. 2003). Wildlife can be heavily affected by the presence of roads, which may hinder animal dispersal and be an important source of wildlife mortality due to vehicle collisions (Ament et al. 2008; Forman et al. 2003).

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As an example of the global effect of roads in animal mortality, it is estimated that every year 194 million birds and 29 million mammals are killed on European roads (Grilo et al. 2020), 80 million birds in the roads of the United States (Erickson et al., 2005), while eight million birds and two million mammals are killed on Brazilian roads (González-Suárez et al. 2018). Therefore, it is suspected that collisions with vehicles could have negative consequences in the genetic diversity of wildlife populations in natural areas dissected by roads (Jackson & Fahrig, 2011). This can be a particularly important threat for endangered species with small populations numbers; for example, between 2015 and 2016, 79 percent of the mortality of the Florida panther (*Felis concolor coryi*) was caused by vehicle collisions (FWC, 2016).

The composition of animal roadkills varies considerably across studies and regions. For example, in Goiás-Brazil, mammals represent 74.21 percent of roadkilled wildlife (Silveira-Miranda et al. 2017); in Costa Rica, amphibians accounted for 93.5 percent of roadkill events (Arévalo et al. 2017); and in Tanzania, birds accounted for 50 percent of roadkilled animals (Kioko et al. 2015). This variation likely responds to intrinsic differences in animal communities, landscape composition and configuration, and road characteristics (Ciochetti et al. 2017; Clevenger et al. 2003; Medinas et al. 2013), which will be unique for each study site. However, the relationship between landscape composition and roadkill rates still needs to be explored, particularly in tropical regions.

In this study, we analyze the relationships between different landscape attributes along a road network that dissects three protected areas in the Biodiversity Hotspot with the highest number of endemic species of vertebrates, the Tropical Andes (Myers et al. 2000). Understanding the effect of anthropogenic disturbances, such as roadkills, in megadiverse areas is critical because a large number of organisms, including endemic species, could be affected by such environmental impacts. The specific objectives of our research were as follows: (1) to determine the frequency and species composition of wildlife roadkills; (2) to explore how different landscape attributes are related to roadkills; and (3) to evaluate the relationship of vehicular traffic with roadkills.

2 | METHODS

2.1 | Study area

Our research was located within the Tropical Andes Biodiversity Hotspot in Ecuador (Myers et al. 2000) and between three adjacent protected areas: Antisana Ecological Reserve (120,000 ha), Sumaco-Napo-Galeras National Park (205,751 ha), and Cayambe-Coca National Park (404,103 ha) (Figure 1). We studied three 33-km segments of two-lane paved roads that run between these three protected areas and link the town of Baeza with the towns of Papallacta, El Chaco, and Cosanga (Figure 1). Road segment Baeza-Papallacta was within an altitude of 1827–2995 m, segment Baeza-El Chaco was within 1476–1914 m, and segment Baeza-Cosanga was within

1805–2285 m. All road segments had two lanes, and speed limits varied from 20 to 90 km/h (Figure S1). The natural vegetation of the study area corresponds to evergreen low mountain forest at lower elevations (1300–2000 m) and cloud forest at higher elevations (2000–2900 m) (Valencia et al. 1999). Agricultural lands exist along road margins and are dominated by pasturelands for cattle ranching. Based on the climatic stations closer to our study area, Papallacta (3150 m) and Sardines (1615 m), annual rainfall ranges between 1189 mm and 3180 mm, and average annual temperature fluctuates between 10.17 and 19.5°C, respectively.

2.2 | Survey of roadkills

We surveyed roads weekly, in periods of two or three consecutive days between March and August 2014. During each survey day, we looked for roadkills by driving each segment in both directions at an average speed of 40 km/h. All three road segments were monitored during each survey day between 0800 h and 1700 h by a same observer (PMV) who was accompanied by a driver. Each roadkill was photographed, identified to the lowest possible taxonomic level, and georeferenced with a GPS unit (Garmin GPSmap 76 Cx). Also, when species identification in the field was not possible (e.g., some reptiles and amphibians), carcasses were taken to the Museum of Zoology at Pontificia Universidad Católica del Ecuador (QCAZ) to obtain feedback from group specialists. We removed the carcasses from the road after their identification to avoid double counting in consecutive days.

2.3 | Effects of landscape attributes on roadkills

Based on results from previous studies in temperate regions (e.g. Clevenger et al., 2003; Medinas et al., 2013), and given the differences in vertebrates' biological traits (Rytwinski & Fahrig, 2012), we hypothesized that the importance of landscape attributes that predict roadkills will vary across taxa. To test this hypothesis, we developed a set of logistic regression models for each taxon. We confronted roadkill UTM coordinates with an equal number of random UTM coordinates along road segments that represented places where roadkills were not observed. Both, roadkill and random points were associated with five landscape attributes that could explain roadkills, which included Euclidean distances to: (1) the nearest river, (2) the nearest remnant of natural vegetation, (3) the nearest bridge (i.e., intersections between ravines or rivers and roads), and (4) the nearest town. The fifth landscape attribute was the percentage of forest cover inside a buffer of 100 m distance from each roadkill or random point. Distance to remnant vegetation and percentage of forest were calculated based on the shapefile of ecosystems of Ecuador (MAE, 2013); the rest of the variables were calculated using shapefiles from the Instituto Geográfico Militar del Ecuador (IGM). All these covariates were scaled from 0 to 1 with R package *scales* (Wickham & Seidel, 2020).

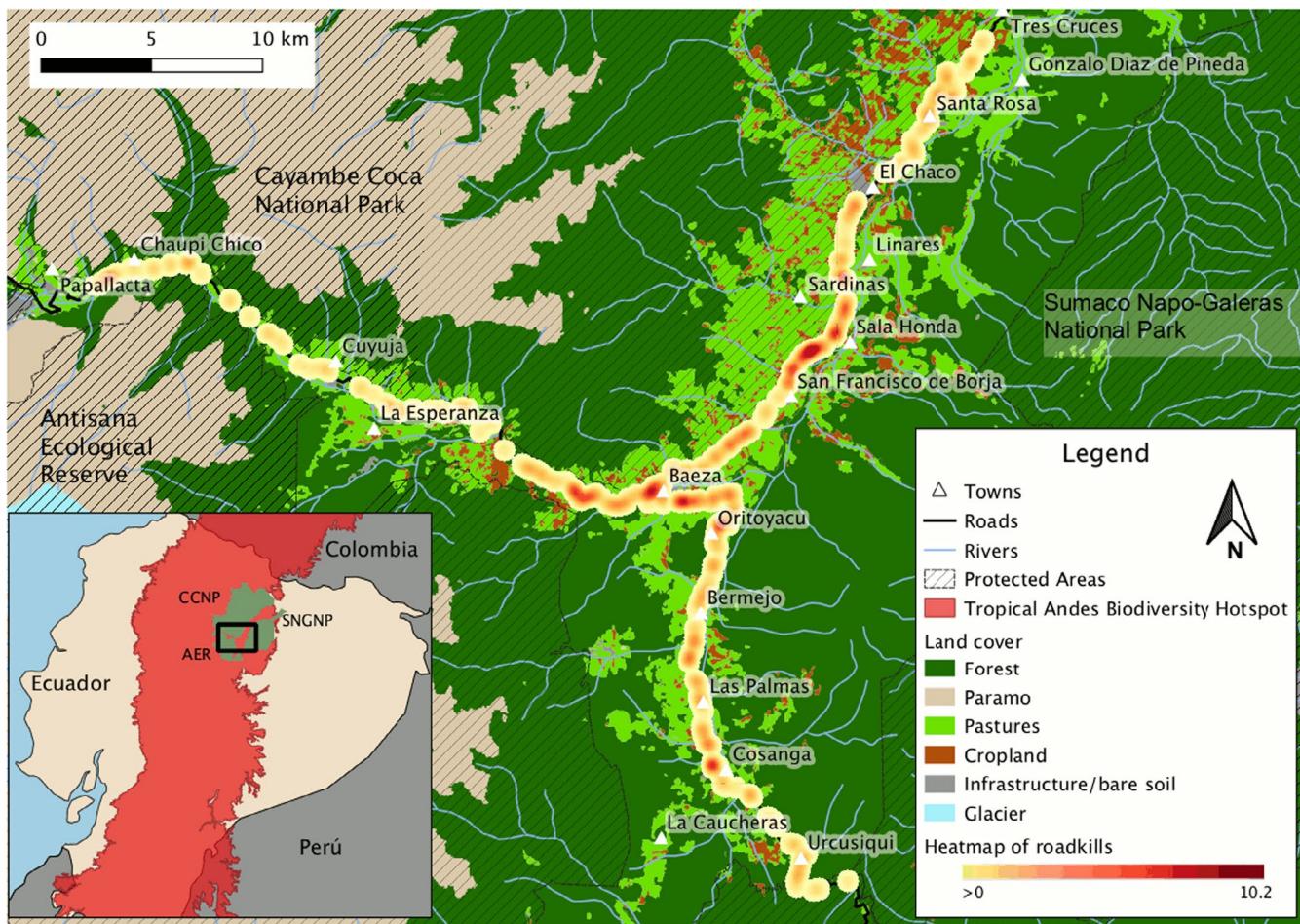


FIGURE 1 Study area within the Tropical Andes Biodiversity Hotspot in Ecuador. Scale bar of heatmap represents density of roadkills in a 50×50 m pixel during the study

The rationale and hypotheses behind our predictor variables were as follow: (1) Rivers are associated with water availability; if a river is close to a road, we could expect wildlife to approach to this resource and therefore be more exposed to vehicle collisions. This should be particularly true for those organisms more dependent on water and with low capability to avoid vehicles, such as amphibians (Rytwinski & Fahrig, 2012; Seo et al. 2013). (2) Distance to nearest remnant of natural vegetation can be used as a measure of landscape fragmentation near roads (Turner et al. 2001). In a fragmented landscape, animals with large spatial requirements and highly mobile should be more vulnerable to roadkills (Rytwinski & Fahrig, 2012), and therefore, a higher isolation from natural vegetation (i.e., larger distance to forest patch) should be associated with higher animal mortality on roads. (3) Bridges that are crossing above ravines or rivers could function as wildlife underpasses (Clevenger et al. 2003), and therefore, distance to this infrastructure should be positively associated with roadkills. (4) Distance to nearest town should be associated with traffic, with a higher vehicle frequency near towns; we could expect to find that wildlife is at higher risk of being roadkilled in areas where vehicle frequency is higher (Lodé, 2000; Orlowski & Nowak, 2006). (5) We expected roadkills to be more frequent along road sections that cross forest cover, which has been observed in

previous studies (e.g. Malo et al. 2004; Sillero et al. 2019). Before model implementation, we evaluated multicollinearity between our covariates with the variance inflation factor (VIF), which was estimated with the function `vif` in R package `car` (Fox & Weisberg, 2019).

We analyzed vertebrate classes (i.e., amphibians, reptiles, birds, and mammals) separately. For mammals we used two datasets, one with all species but opossum (*Didelphis pernigra*) and another only for opossum, which was the most roadkilled species in our study. For each vertebrate group, we developed 32 logistic regressions with function `glm` from R package `olsrr` (Hebbali, 2020); models included the null model and all the possible combinations of our five predictive variables. We used the corrected Akaike information criterion (AICc) to select best fit model (Burnham & Anderson, 2002), which was calculated with `dredge` function of R package `MuMIn` (Barton, 2020). When more than one model was competitive (i.e., $\Delta \text{AICc} \leq 2$), we performed model averaging with function `model.avg` from `MuMIn` package to estimate full model averaged coefficients of parameters. We also calculated the cumulative Akaike's information criterion weights of model parameters with the function `importance` from the same package to identify the most important variables for each taxonomic group. When there is uncertainty to choose a best-fit model (i.e., several models with $\Delta \text{AICc} \leq 2$), some uninformative parameters

may be present, and therefore, calculating the weight of each covariate across all the models is a useful method to identify the most important variables within the models (Arnold, 2010; Burnham & Anderson, 2002). Additionally, for each taxonomic group, the performance of models with the lowest AICc was evaluated by measuring the area under a receiver operating characteristic (ROC) curve with *roc* function of R package *pROC* (Robin et al. 2011). Additionally, to describe the relationship between the amount of roadkills and the surrounding land cover, for each roadkill we registered the landscape category along both sides of the road (i.e., pastures, towns, forest, shrubs, and crops) and quantified the frequency of roadkills of each vertebrate group within every combination of land cover category.

Finally, to visualize roadkill hot spots we used heatmaps (i.e., visual representation to depict areas with high point density) with kernel density estimation in a geographic information system (Quantum GIS v.3.12). To model kernel shape, we used a quartic interpolation function and a search radius of 500 m; we chose a spatial resolution of 50 × 50 m pixel size for the output. We developed heatmaps for all combined data and separately for amphibians, reptiles, birds, and mammals excluding opossums and opossums.

2.4 | Influence of vehicular traffic on wildlife roadkills

We hypothesized that vehicle frequency will be positively associated with roadkill rates. We used Pearson correlation to test for an association between roadkills and daily vehicle frequency. For this purpose, we used three datasets: (1) a dataset with all carcasses of wildlife, (2) a sub-dataset excluding the first day of survey, which removed carcasses older than 24 h, and (3) a sub-dataset that excluded carcasses estimated to be older than 48 h. To estimate age of carcasses, we trained ourselves by spending the first 10 days of the study marking roadkills and revisiting carcasses daily to evaluate their degree of decomposition. Finally, we estimated vehicle frequency by counting the number of vehicles that passed for 15 minutes before and after the survey of roadkills in each road segment.

3 | RESULTS

3.1 | Wildlife mortality on roads

We surveyed each 33-km road segment during 72 non-consecutive days with a total survey effort of 7128 km. We found 445 dead animals—domestic animals are excluded from our results—with an average daily roadkill rate of 6.24 (95% CI = 5.35–7.14) individuals per 100 km. Roadkills included at least 44 vertebrate species (i.e., it was not possible to identify all carcasses to species level). The majority of roadkills corresponded to mammals with 207 (46.31% of all roadkills) individuals of at least 15 species (Table 1); the most frequent roadkill was opossum *Didelphis pernigra* (n = 153; Table 1). The second most roadkilled vertebrate group was birds with 107 (23.94%) individuals

of at least 16 species. Reptiles were represented by 88 (19.69%) individuals of at least 10 species of snakes; it was notable the presence of an undescribed snake species of the genus *Atractus* (Figure S2; Torres-Carvajal pers. comm.). Finally, we found 43 (9.62%) roadkilled amphibians of at least 3 species; a total of 34 individuals belonged to caecilians (Gymnophiona). The highest number of roadkills was at the road of Baeza–El Chaco (n = 193); followed by Baeza–Cosanga (n = 149) and Baeza–Papallacta (n = 103).

3.2 | Effects of landscape attributes and vehicular traffic on roadkills

The landscape surrounding our studied roads was heterogeneous; approximately 23 km of roads were adjacent to forested areas and the remaining 76 km were next to human-modified land cover types dominated by pastures for cattle ranching, but also including crops, shrubs, and urban areas. For all taxa, most roadkills (40%, n = 180) were in sites where pastures occupied both sides of roads or in sites where road margins were covered by a combination of pastures and forest (20%, n = 92) (Figure 2).

We did not find collinearity among the predictive variables for any group of vertebrates (i.e., all the VIF values were lower than 10). The highest VIF values corresponded to two variables for amphibians: distance to the nearest bridge (5.54) and distance to the nearest river (5.71) (Table S1).

Covariates of models that predicted roadkills varied between vertebrate classes. For amphibians, the best-fit model included distance to the nearest river and distance to the nearest bridge; one more model, which included percentage of forest cover, appeared to be competitive for this group (i.e., Δ AICc ≤ 2, Table S2). Roadkills of amphibians were positively associated with distance from rivers and negatively associated with distance from bridges (Table 2). Distance to rivers and bridges had a moderate collinearity; however, removing any of them resulted in worse model performance; without distance to rivers, the area under the ROC curve (AUC) was 47.1%, while, without distance to bridges, AUC was 75.3%. Modeling with both variables resulted in an AUC of 85.29% (Figure S3).

For reptiles, we did not find a clear best model; however, the model with the lowest AICc included distance to the nearest bridge, distance to the nearest remnant vegetation, distance to the nearest river, and percentage of forest cover, and although other four models were competitive (Table S2), distances to remnant vegetation and rivers were the most important covariates for this taxonomic group (Table S3). Distance to the nearest river and distance to the nearest remnant vegetation were positively associated with roadkills (Table 2). The AUC for the model with the lowest AICc was 71.14% (Figure S3).

For birds, the only competitive model included distance to the nearest bridge, distance to the nearest remnant vegetation, distance to the nearest river, distance to the nearest town, and percentage of forest cover (Table S2). Roadkills of birds were negatively associated with distance to bridges and percentage of remnant vegetation,

TABLE 1 Wildlife roadkills in a site within the Tropical Andes Biodiversity Hotspot in northern Ecuador

	N	% of roadkills
Amphibians		
<i>Caecilia</i> sp.	34	7.61
<i>Rhinella marina</i>	7	1.57
<i>Pristimantis</i> sp.	1	0.22
<i>Unidentified anuran</i>	1	0.22
Total amphibians	43	9.62
Reptiles		
<i>Atractus</i> sp.	29	6.49
<i>Dipsas</i> sp.	14	3.13
<i>Atractus snethlageae</i>	5	1.12
<i>Clelia</i> sp.	5	1.12
<i>Dipsas peruviana</i>	5	1.12
<i>Chironius monticola</i>	3	0.67
<i>Chironius</i> sp.	3	0.67
<i>Atractus duboisi</i>	2	0.45
<i>Dipsas gracilis</i>	1	0.22
<i>Micrurus</i> sp.	1	0.22
<i>Unidentified squamata</i>	20	4.47
Total reptiles	88	19.69
Birds		
<i>Notiochelidon cyanoleuca</i>	10	2.24
<i>Zonotrichia capensis</i>	10	2.24
<i>Cyanocorax yncas</i>	9	2.01
<i>Crotophaga ani</i>	4	0.89
<i>Psarocolius angustifrons</i>	4	0.89
<i>Troglodytes aedon</i>	4	0.89
<i>Ammodramus aurifrons</i>	2	0.45
<i>Platycichla leucops</i>	2	0.45
<i>Ammodramus</i> sp.	1	0.22
<i>Cacicus</i> sp.	1	0.22
<i>Diglossa albilateralis</i>	1	0.22
<i>Dryocopus lineatus</i>	1	0.22
<i>Penelope montagnii</i>	1	0.22
<i>Pipraeidea melanonota</i>	1	0.22
<i>Porphyrrula</i> sp.	1	0.22
<i>Synallaxis</i> sp.	1	0.22
<i>Unidentified passerine</i>	30	6.71
<i>Unidentified bird</i>	20	4.47
<i>Unidentified apodiforme</i>	2	0.45
<i>Unidentified falconiforme</i>	2	0.45
Total Birds	107	23.94
Mammals		
<i>Didelphis pernigra</i>	153	34.23
<i>Notosciurus granatensis</i>	6	1.34

TABLE 1 (Continued)

	N	% of roadkills
<i>Conepatus semistriatus</i>	4	0.89
<i>Mustela frenata</i>	3	0.67
<i>Herpailurus yagouaroundi</i>	2	0.45
<i>Marmosops</i> sp.	2	0.45
<i>Rhinophylla</i> sp.	2	0.45
<i>Anoura</i> sp.	1	0.22
<i>Coendou quichua</i>	1	0.22
<i>Dasyprocta fuliginosa</i>	1	0.22
<i>Leopardus tigrinus</i>	1	0.22
<i>Metachirus nudicaudatus</i>	1	0.22
<i>Microsciurus flaviventer</i>	1	0.22
<i>Potos flavus</i>	1	0.22
<i>Sylvilagus brasiliensis</i>	1	0.22
Unidentified rodent	15	3.36
Unidentified bat	7	1.57
Unidentified mammal	5	1.12
Total mammals	207	46.31
Total	445	

Domestic or invasive (e.g., brown rat *Rattus norvegicus* and house mouse *Mus musculus*) species are not reported

and positively associated with the rest of the variables (Table 2). The AUC for this model was 76.32% (Figure S3).

For mammals, the model with the lowest AICc included distance to the nearest bridge, distance to the nearest remnant vegetation, and percentage of forest cover (Table 2). Other ten models were also competitive (i.e., Δ AICc ≤ 2 ; Table S2); however, we identified that distances to bridges and remnant vegetation were the most important covariates to predict roadkills for mammals (Table S3). Distance to remnant vegetation was positively associated with roadkills, while distance to the nearest bridge was negatively associated (Table 2). The AUC for the model with the lowest AICc was 65.5% (Figure S3).

The model with the lowest AICc for opossums included four covariates: distance to the nearest bridge, distance to the nearest remnant vegetation, distance to the nearest river, and distance to the nearest town. Other eight models were competitive (Table S2); however, we found that distance to bridges was the most important covariate (Table S3), which was negatively associated with roadkills (Table 2). The AUC for the model with the lowest AICc was 63.4% (Figure S3).

The heatmap from all roadkills shows that wildlife was killed along all the road; however, roadkill hot spots frequently occurred near towns (Figure 1). This pattern is clearer in the case of amphibians where hot spots appear near the towns of Baeza, Oritoyacu, and Consanga (Figure S4). Also, we observed that for amphibians and reptiles, roadkills were concentrated at lower altitudes of our study site, with no roadkills above 1900 or 2300 m for these two groups, respectively (Figure S4).

(Continues)

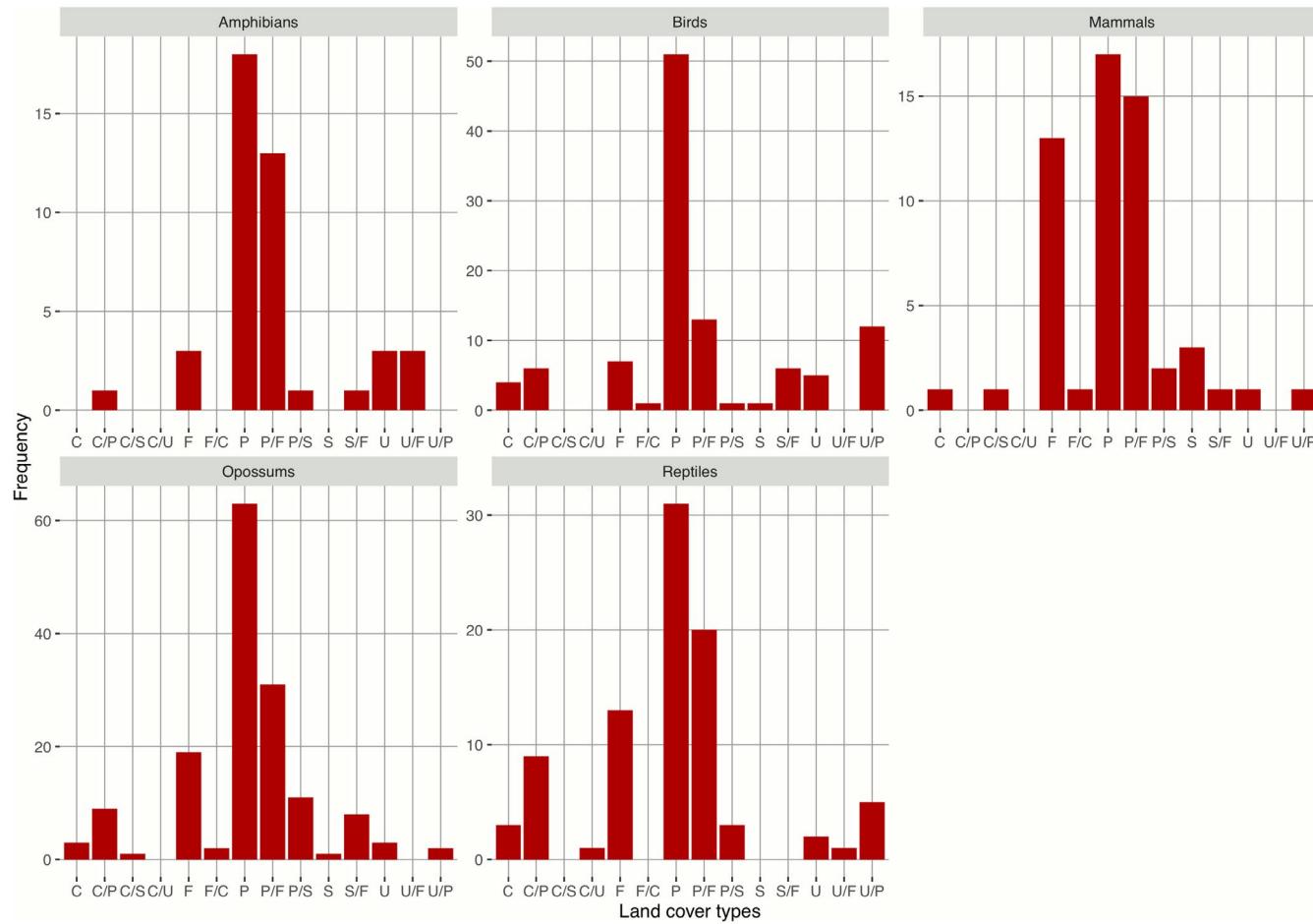


FIGURE 2 Roadkills grouped by land cover types along both sites of roads. Shrubs (S), Forest (F), Urban (U), Cropland (C), Pastures (P). A single land cover character on x-axis indicates the same land cover type at both sides of road. Mammal dataset excludes opossums which is depicted in a separate histogram

Correlation analysis between vehicular traffic and the complete dataset of roadkills presented a non-significant association ($r = -0.101$, $p = 0.137$, $n = 216$), and a similar result was obtained when excluding the first day of survey of each field trip ($r = -0.140$, $p = 0.088$, $n = 150$). However, correlation analysis using the sub-dataset with carcasses estimated to be less than 48 h old presented a weak but significant negative association with vehicular traffic ($r = -0.141$, $p = 0.038$, $n = 216$).

4 | DISCUSSION

4.1 | Wildlife mortality on roads

We found 445 roadkills which corresponded to 44 animal species. It was notable among roadkills the presence of an undescribed species of snake (*Atractus* sp.), which exemplifies the relevance of understanding the impact of roads on wildlife populations in a Biodiversity Hotspot. Three decades ago botanist Alwyn Gentry witnessed the rapid disappearance of endemic plant species caused by deforestation in another Biodiversity Hotspot in Ecuador, the Chocó Darién/

Western Ecuador (Dodson & Gentry, 1991). We believe roads, as deforestation, are a major threat that also could lead to rapid extinctions.

Populations of endemic wildlife with low dispersal capabilities might be particularly endangered by roadkills. It was striking the large number of fossorial species (i.e., organisms with low vagility) among roadkilled amphibians and reptiles. Roads represent an alarming threat for snakes and even a relatively small numbers of roadkills are enough to disproportionately increase the probability of extinction of populations (Row et al. 2007). A noteworthy situation was that similar to other studies (Filius et al. 2020; Quintero-Ángel et al., 2012), *Atractus* genus was highly impacted. Forty percent of reptiles belonged to this genus and included *Atractus duboisi*, an endangered and endemic species whose distribution is not much larger than our study area in the eastern Andes of Ecuador (Cisneros-Heredia & Bustamante, 2017). Snakes of the genus *Atractus* are primarily fossorial (Martins & Oliveira, 1993) and with a high rate of endemism. Of 29 species of *Atractus* snakes present in Ecuador, 15 are endemic and 13 are either data deficient or their conservation status has not been evaluated (Torres-Carvajal et al., 2019). Similarly, 34 of 43 amphibians were caecilians, also fossorial organisms and a

TABLE 2 Parameter estimates of best-fit (BF) or averaged models (AM) to predict wildlife roadkills.

Faunistic group	Explanatory variables	Estimate	SE	z value	p
Amphibians (AM)	I	-1.14	0.44	2.55	0.01
	DB	-11.08	3.62	3.02	0.00
	DR	9.97	2.48	3.96	0.00
	PF	-0.14	0.58	0.24	0.81
Reptiles (AM)	I	-0.71	0.31	2.29	0.02
	DB	-1.73	1.46	1.18	0.24
	DR	2.17	1.13	1.91	0.06
	DT	0.03	0.26	0.13	0.90
	DV	1.66	0.61	2.70	0.00
	PF	-0.48	0.58	0.83	0.41
Birds (BF)	I	-0.99	0.41	-2.42	0.01
	DB	-4.48	1.48	-3.04	0.00
	DR	2.52	1.10	2.29	0.02
	DT	1.33	0.64	2.07	0.04
	DV	3.45	0.91	3.77	0.00
	PF	-2.27	0.68	-3.36	0.00
Mammals (AM)	I	-0.03	0.39	0.09	0.93
	DB	-2.23	1.61	1.37	0.17
	DR	0.75	1.14	0.65	0.52
	DT	0.11	0.42	0.26	0.79
	DV	1.36	0.91	1.49	0.14
	PF	-0.54	0.67	0.80	0.42
Opossums (AM)	I	-0.00	0.34	0.00	0.99
	DB	-2.06	0.66	3.01	0.00
	DR	0.40	0.63	0.63	0.53
	DT	0.41	0.51	0.80	0.42
	DV	0.86	0.61	1.41	0.16
	PF	-0.07	0.22	0.31	0.76

Model covariates: I = intercept, DB = distance to bridge, DR = distance to river, DV = distance to remnant of natural vegetation, DT = distance to towns, PF = percentage of forest cover; β parameter estimate; standard error; z value; and p-value.

widely understudied group. There are 24 known species of caecilians in Ecuador and 10 of those are endemic; however, 19 species lack information or their conservation status has not been evaluated (Ron et al., 2019). Another study in the Tropical Andes also reported a high number of fossorial species being affected by roads (Filius et al., 2020); therefore, these findings support the need to conduct similar studies in other tropical Biodiversity Hotspots where the populations of practically unknown species may be severely affected by mortality associated with road networks.

Among mammals, it was notable the presence of oncilla *Leopardus tigrinus* a species categorized as vulnerable in IUCN red list (Payán & de Oliveira, 2016). The oncilla is one of the most unknown felids in the Neotropics. For example, its geographical range is thought to cover Amazonia and Andean foothills (Payán & Oliveira, 2016); however,

this species has not been detected by extensive camera trap surveys in Ecuador's Amazonian areas that correspond to humid tropical forest beneath 400 m.a.s.l. (e.g. Espinosa et al. 2018; Mena et al. 2020). Given the poor knowledge available even for medium-sized and charismatic species such as oncilla, our study highlights the importance of studying the biology and ecology of threatened species to understand the impact roads might be having on their populations.

In contrast to oncilla, the highest numbers of roadkills among mammals corresponded to opossum (*D. pernigra*), which was by far the most roadkilled species in this study with a rate of 2 individuals killed per 100 km/day. Opossums seem to be some of the most roadkilled species in the Neotropics (Monge-Nájera, 2018), and likely this reflects its abundance in rural areas where agriculture along roads provide resources for these animals.

Our systematic survey allows the estimation of a yearly roadkill rate of 2279 (95% CI = 1951–2606) wild animals per 100 km of roads at this site in the Tropical Andes Biodiversity Hotspot. However, it is important to consider that this estimate should be a fraction of the true number of animals that die at these roads each year. The detectability of roadkills can be limited by several factors such as weather, vehicular traffic, animal size (e.g., small animals are more difficult to see), removal of carcasses by predators, or scavengers, and the fact that some carcasses can be on the vegetation along road margins and not be detected from a vehicle (Santos et al. 2011). Therefore, despite our systematic study, we can expect our results are underestimating the impact of roadkills on tropical vertebrate communities.

4.2 | Landscape components associated with wildlife mortality on roads

Roadkills for all taxa were more frequent in sites adjacent to pasturelands, which was expected given that pastures were the most dominant landcover along roads in our study area. In the case of reptiles, a similar pattern was observed in the Central Andes of Colombia, where the mortality of snakes was also related to pasturelands (Quintero-Ángel et al. 2012). The high number of snakes killed on roads by this vegetation type can be explained by the abundance of resources (e.g., rodents) that can be found in agricultural lands (Stenseth et al. 2003). Therefore, agricultural areas such as pasturelands, adjacent to natural areas, and crossed by roads can be functioning as ecological traps whose impact on wildlife populations will be positively related to road density.

For all vertebrate classes, distance to river had a positive association with roadkills. In other words, roadkills were more likely to occur further from rivers, which may be explained by higher movement rates of individuals looking for this important resource. This finding is the opposite of the pattern observed in South Korea, where amphibian roadkills were more frequent near water bodies (Seo et al. 2013). However, we also observed that for all vertebrate classes, including amphibians, roadkills were more likely to occur at closer distances to bridges, which are crossing rivers. This last finding was unexpected because we hypothesized that bridges would work as wildlife

passages; therefore, less roadkills would occur around these areas (Clevenger et al. 2003). Although this result seems to be counterintuitive, it is not. It has been observed that for wildlife passages to be effective, they need to be accompanied with fencing that excludes animals from roads (Cunnington et al. 2014; Rytwinski et al. 2016). Hence, in mountain areas in the humid tropics, such as in the Tropical Andes, where roads include numerous bridges, these infrastructures could be functioning as ecological traps if their surroundings are not adapted with fences to reduce animal mortality.

Distances to remnant vegetation appeared in best models for reptiles, birds, and mammals, and were positively associated with roadkills. That is, the further from natural vegetation patches, the more likely animals are more likely to be killed, which is consistent with our prediction that roadkills will be higher in fragmented habitats. Animals that have the capacity to cross roads in look for their resources will be more exposed to roadkills (Rytwinski, & Fahrig, 2012). As habitat fragmentation and road density increases, we can expect higher rates of animal mortality, which in biodiversity hotspots could catalyze species extinction.

For all taxa, percentage of forest cover had a negative association with roadkills, which was the opposite other studies (e.g. Malo et al. 2004; Sillero et al. 2019). These areas were expected to concentrate roadkills because they provide structural connectivity, and therefore, animals could use them to disperse and be more exposed to collisions with vehicles, as observed, for example, with birds and amphibians (Orlowski, 2008; Sillero et al., 2019). In our study, areas near roads are dominated by pastures for cattle and forest patches by roads are small. Therefore, these forest fragments are inhabited by small organisms that may find the resources they need within their patch, which reduces their exposure to vehicle collisions as they do not need to move across patches often.

Distances to nearest town appeared as covariates in best models of opossum and birds; these animals were more likely to die at greater distance from towns. It is possible that species dwelling near towns are more habituated to anthropogenic pressures, including learning to avoid collisions with vehicles, as reflected with some bird species (e.g. Brown & Brown, 2013; Mumme et al. 2000). However, there is also the possibility that near towns wildlife has been already depleted, and therefore, this pattern would reflect the numerical availability of vertebrates in areas near and far away from towns.

4.3 | Roadkills and traffic volume

Previous studies have found traffic volume can be related to animal mortality on roads (e.g. Lin, 2016; Tejera et al. 2018), although other studies using daily data on traffic have found that traffic is not an important variable to explain roadkills (e.g. Carvalho et al. 2017; Clevenger et al. 2003; Conard & Gipson, 2006). We found a weak negative association between roadkills and traffic, which is contrary to our initial hypothesis but not surprising given mixed results in literature regarding the direction of this association (e.g., see Lin, 2016;

Tejera et al. 2018). Likely, there is a threshold related to the effect of vehicle frequency on roadkills. For example, animal mortality can increase with traffic until a point when it is perceived as a threat and animals do not venture to cross a road. Also, other aspects related to traffic such as vehicle speed and car length could be determining the direction of this association.

4.4 | Mitigation of roadkills

Although landscape covariates varied in their importance for predicting roadkills of different taxa, our findings showed the direction of the association of landscape attributes that predicted roadkills were similar across vertebrate groups which could facilitate management. Among current management tools, wildlife crossings are one of the most effective measures and can be useful for a wide variety of animals, from insects to big carnivores, providing a safe place to maintain functional connectivity (Forman et al. 2003; Polak et al. 2014; Rytwinski et al. 2016). Although constructing wildlife passages is expensive, some existing infrastructure on roads, such as bridges and drainage culverts, can make roads more permeable to wildlife. However, for these structures to be effective, wildlife passages need to be used with barriers that exclude animals from roads; the combination of both methods reduces roadkills by 83% (Cunnington et al. 2014; Rytwinski et al. 2016). For example, Dodd et al. (2004) observed the use of culverts increased 10-fold after barriers that excluded wildlife were installed along a road in Florida. Also, culverts of relatively small diameter (e.g., diameter ≤ 50 cm) accompanied with fencing in critical road sections could effectively promote the movement of small organisms such as amphibians and small reptiles (Lesbarrères et al. 2004; Patrick et al. 2010; Wolitz et al. 2008), which seem to be the most threatened groups in this study. Given that roadkills were associated with pasturelands, the placement of these structures should include both natural and transformed habitats that can be functioning as ecological traps.

An alternative or complement to infrastructure creation or modification is the management of vegetation along roads to either limit or deter animal movement in high-risk areas, which, for example, has been used to reduce roadkills of ungulates (Rea, 2003; Tanner & Leroux, 2015). We observed that pastures used for cattle were associated with roadkills of all vertebrate classes. As pastures are generally associated with private lands, it could be requested to landowners to fence the margins of their properties that limit with roads. Ideally, this measure could be complemented with infrastructure to increase road permeability. However, we recognize that given the social and economic reality in most tropical areas, it is unlikely landowners will be able to assume the cost of fencing without financial support from governmental or non-governmental institutions.

Also, vegetation can be managed to facilitate road crossing through secure areas such as underneath bridges over gullies and ravines which can function as wildlife underpasses. In our study area, frequently areas under bridges had large amounts of litter and

garbage, and for this reason, a simple and low-cost management strategy could be educational campaigns to create public awareness on the importance of these sites and the creation of policies that deter people from using these sites as garbage deposits.

Animal detection systems, which are mechanisms that activate flashing lights to warn drivers when animals are near the road, have also proven to be effective in reducing roadkills (Rytwinski et al. 2016). However, it is suspected that these signals become less effective as drivers become used to them, and therefore, their use is recommended only during high-risk times (e.g., high vehicular traffic periods, identified periods of animal movement) and in certain places where high wildlife crossing rates are evidenced (Grace et al. 2017). Other mechanisms such as wildlife reflectors or warning signs are less effective in preventing roadkills because wildlife or drivers, respectively, become used to them (Rytwinski et al. 2016). The installation of speed reducers is another strategy to reduce roadkills; however, their effectiveness has not been evaluated and their installation in highly transited roads could cause problems with traffic.

Finally, it is important to notice that the composition of roadkills will vary across sites due to various aspects such as composition of animal communities and animal behavior (Jacobson et al. 2016), differences in landscape composition and configuration, characteristics of infrastructure itself such as type of construction of roads and drainages that can function as wildlife underpasses (Clevenger et al. 2001, 2003), climatic conditions (Garriga et al. 2017; Rosa & Bager, 2012), among others. For this reason, this kind of studies need to be replicated to develop informed management tools that respond to the particularities of different areas, especially those in biodiversity hotspots where high numbers of poorly known and unique species are being killed on roads.

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DATA AVAILABILITY STATEMENT

The data used in this study are openly available at the Dryad Digital Repository: <https://doi.org/10.5061/dryad.xwdbrv1cp> (Medrano-Vizcaíno & Espinosa, 2021).

ORCID

Pablo Medrano-Vizcaíno  <https://orcid.org/0000-0003-3122-048X>

Santiago Espinosa  <https://orcid.org/0000-0002-7416-7167>

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SUPPORTING INFORMATION

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

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