

## REVIEW

# Mammals with large home ranges, low reproductive rates and small body sizes are most vulnerable to roads: A meta-analysis

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## Abstract

1. In a previous meta-analysis, mammals with large home ranges, low reproductive rates and large body sizes were found to respond most negatively to roads. However, due to correlations among these traits, it is not known whether these responses were due to a subset or all three traits.
2. We conducted a multiple meta-regression of the effects of species traits on mammal responses to roads, using data from 92 studies, to determine whether an analysis with a larger sample size and controlling for correlations among traits will support the previous findings.
3. The results reinforce the findings that mammals with larger home ranges and lower reproductive rates respond more negatively to roads. Surprisingly, we found that when controlling for the effects of home range size and reproductive rate, larger mammals respond less negatively to roads than smaller mammals.
4. We speculate that the positive effect of body size is due to driver avoidance of collisions with larger mammals and/or differences in road attraction and car avoidance behaviours of larger versus smaller species that allow larger mammals to extract benefits of roads while avoiding oncoming vehicles
5. We also found high variability of individual responses to roads, above what could be explained by the species traits model, most likely due to site- and/or species-specific characteristics.
6. *Synthesis and applications.* Road mitigation for mammals should ideally be informed by site-level knowledge and generally involve prioritizing species with the combination of larger home ranges, lower reproductive rates and smaller body sizes. To protect these vulnerable mammals from roads, we should maintain low road densities and instal small-mesh mitigation fencing along roads. This differs from current road mitigation efforts which are typically targeted towards large mammals (e.g. large-mesh fencing along roads) and are often ineffective for smaller mammals.

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## KEYWORDS

connectivity, conservation, mitigation, population abundance, road ecology, roadkill, species traits, traffic, wildlife

## 1 | INTRODUCTION

Roads can reduce wildlife population abundance in three main ways: (1) increased mortality; (2) reduced habitat amount and quality; and/or (3) reduced connectivity (Rytwinski & Fahrig, 2015). Millions of vertebrates are killed on roads every day (Forman & Alexander, 1998), with vehicle collisions being responsible for about 5% of all deaths in terrestrial mammals worldwide (Hill et al., 2019). Moreover, the rates of mammals killed by vehicle collisions have increased over the last several decades (Hill et al., 2020) and are expected to continue to increase as road networks rapidly expand, particularly in tropical regions (González-Suárez et al., 2018; Laurance & Arrea, 2017). Habitat loss occurs directly from the habitat removed to build roads and/or indirectly through reduced habitat quality near roads (e.g. traffic noise, light, pollutants) (Forman et al., 2003). Reduced connectivity occurs when roads act as barriers to movement leading to inaccessibility of resources (e.g. mates, food) (Beckmann & Hilty, 2010).

Despite well-documented negative effects of roads on many wildlife populations, some species derive benefits from roads contributing to positive or neutral effects of roads on their population abundance (Fahrig & Rytwinski, 2009). Roads can provide benefits to these species in five main ways: (1) communication, (2) foraging, (3) movement, (4) refuge and (5) thermoregulation (Hill et al., 2021). While animals may derive positive effects from roads, roads may also act as ecological traps, where animals are attracted to roads for a benefit but may also be killed on the road (Coffin, 2007; Planillo et al., 2018).

Several species traits are hypothesized to be important predictors of species population responses to roads, mainly: (1) home range size, (2) reproductive rate and (3) body mass. Species with larger home ranges are hypothesized to be more negatively affected by roads because they more frequently encounter roads within a given landscape (Carr & Fahrig, 2001). Species with lower reproductive rates are hypothesized to be more negatively affected by roads because they are less capable of recovering from the loss of individuals caused by road mortality (Gibbs & Shriver, 2002). Larger species are hypothesized to be more negatively affected by roads because they generally have larger home ranges and lower reproductive rates (Fahrig & Rytwinski, 2009). Further, the negative effects of roads on larger predators are likely to lead to reduced predation of smaller species, causing an indirect lessening of negative road effects on smaller species (Rytwinski & Fahrig, 2007, 2013); although, this effect may be complicated by some mammals (e.g. wolves, pumas) that will predate on species larger than them, and by intraguild killing, for example, competition, aggression (Curveira-Santos et al., 2021).

These hypotheses were supported in a meta-analysis by Rytwinski and Fahrig (2012) where, using data for 84 mammal species from 34 studies, they found that mammal species with larger home ranges, lower reproductive rates and higher body masses, showed more

negative responses to roads. However, these traits were highly correlated and essentially indistinguishable in terms of model support.

It is not known whether all three of these traits are driving road responses in mammals or whether road responses are due to a subset of the traits. It is important to determine this because road mitigation strategies differ depending on which species trait is being targeted. For example, if mitigation is targeted towards species with larger home ranges that are impacted by frequent encounters with roads, then maintaining/reducing road density is an effective strategy (Rytwinski & Fahrig, 2015). If mitigation is targeted towards species with lower reproductive rates that are mainly impacted by roadkill, then fencing along roads is an effective strategy (Huijser et al., 2007; Rytwinski et al., 2016). If mitigation is targeted towards larger species, this will influence the characteristics of mitigation fencing (e.g. mesh size, height) (van der Ree et al., 2015). Therefore, knowledge of the relative effects of species traits on mammalian road responses would support decision making around whether and when to protect vulnerable mammals from road impacts.

Since Rytwinski and Fahrig (2012), the body of research about road effects has grown substantially (Bennett, 2017; Collinson et al., 2019; Pinto et al., 2020). Here, we conduct an updated meta-analysis to determine whether using a larger and more diverse evidence base, and controlling for correlations among traits using a multiple meta-regression, will support the findings of Rytwinski and Fahrig (2012).

## 2 | METHODS

We updated the literature search by Rytwinski and Fahrig (2012) with recent literature that quantified a relationship between roads and mammal population abundance (Section 2.1). After finding all relevant studies (Section 2.2), we extracted the information needed to calculate effect sizes (Section 2.3). We then adjusted sample sizes to allow for a comparable weighting of effect sizes in the meta-analysis (Section 2.3.1) and reduced multiple non-independent effect sizes from the same study (Section 2.3.2). We then collected information on species traits for all species for which a road effect could be calculated (Section 2.4). Finally, we conducted a meta-analysis with all effect sizes from this review combined with those from Rytwinski and Fahrig (2012) (Section 2.5). Our study did not require ethical approval.

### 2.1 | Search strategy

We conducted a comprehensive literature review to find relevant peer-reviewed journal articles and grey literature (reports, conference proceedings, theses) that quantified a relationship between roads and mammal population abundance published

between 2012 and 2020. We conducted searches in Web of Science Core Collections [WoSCC], ProQuest Dissertation & Theses Global, Scopus, Google Scholar and Google. We used a mammal-specific search string and a separate general (non-specific to mammals) search string to capture relevant information contained in studies on multiple taxa. The mammal-specific search string (in WoSCC format using the topic field) was as follows: ((road\* OR highway\$ OR traffic OR motorway\$ OR freeway\$) AND (mammal\$) AND (abundance\$ OR densit\* OR "population size" OR "population-level" OR presence OR distribution)). The general search string was as follows: ((road\* OR highway\$ OR traffic OR motorway\$ OR freeway\$) AND (wildlife OR animal\$ OR fauna) AND (abundance\$ OR densit\* OR "population size" OR "population-level" OR presence OR distribution)). Databases were also searched using Spanish and Portuguese search terms (Appendix S1). For Google Scholar and Google, we used simplified versions of the above database strings. See Appendix S1 for full details of the search strategy. We identified and removed duplicates across all sources. The bibliographies of review studies found during the search were manually searched for any additional literature.

## 2.2 | Screening and study selection

We screened studies (i.e. individual records returned by the search) in two stages: (1) title and abstract and (2) full text. A consistency check was done at the title and abstract stage (Appendix S1).

We screened studies according to the following inclusion criteria, structured using population, exposure, comparator and outcome key elements (Collaboration for Environmental Evidence, 2022).

### 2.2.1 | Population

We included studies with information on mammal species, at any life stage, that were terrestrial for at least part of their life cycle, in any habitat type or region/country, excluding captive and domestic mammals.

### 2.2.2 | Exposure

We included studies that investigated the effects of roads on species abundance (defined below), including any road-related impact (e.g. road/traffic density, distance to road, traffic noise) and any road type (gravel, paved, etc.). We excluded studies on linear infrastructure other than roads (e.g. railroads) and studies of road mitigation measures (e.g. road fencing, ecopassages).

### 2.2.3 | Outcome

We included studies that reported at least one quantitative direct effect of roads on population abundance. 'Abundance' included

(relative) population size or density and species presence or absence (as an index of high or low abundance). We excluded multispecies responses (e.g. species richness). We also excluded other non-abundance responses such as road mortality, reproduction, movement or genetic responses.

### 2.2.4 | Study class

We included empirical experimental or observational studies. We excluded computer simulation studies unless the study also contained empirical data. We also excluded reviews and conference proceedings.

Additionally, we included only English, Spanish and Portuguese language studies. A list of studies excluded at the full-text screening stage, with reasons, is available from the Dryad Digital Repository (Patterson et al., 2025).

## 2.3 | Data extraction and effect-size calculations

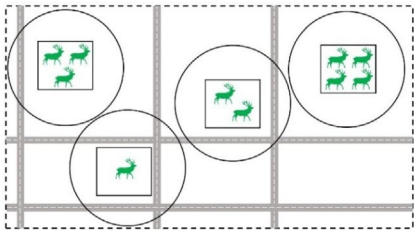
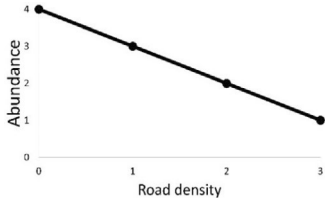
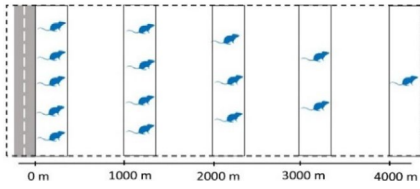
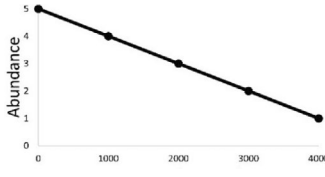
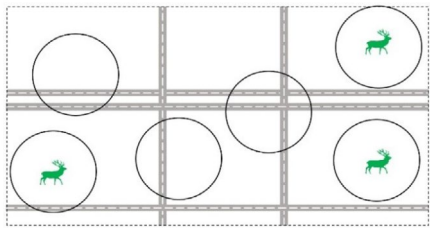
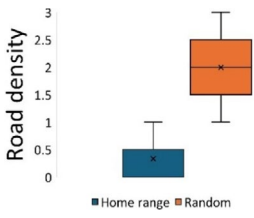
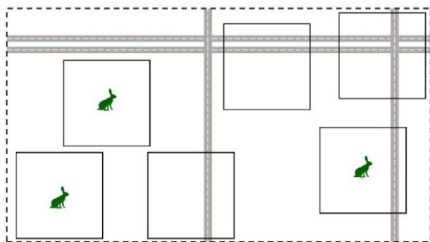
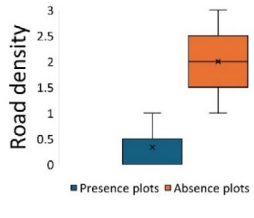
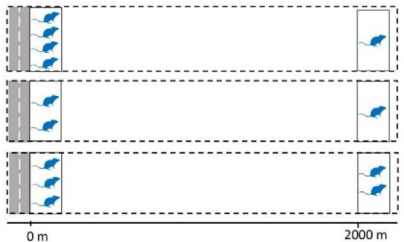
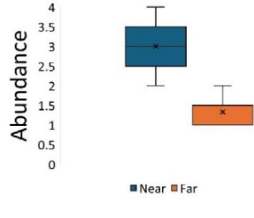
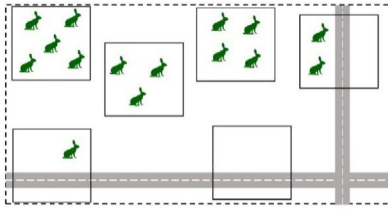
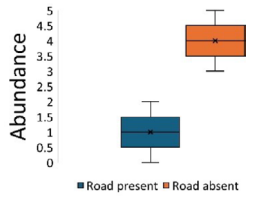
Following the full-text screening, all retained studies underwent data extraction. Where studies contained overlapping data, only the most complete version was included during data extraction. Therefore, 'studies' hereafter were independent evaluations of a road impact on mammal population abundance.

Furthermore, a single study could contain multiple 'datasets', that is, separate road impacts on mammal population abundance, such as when a study presented separate data/results for each of multiple species, road categories or study areas. Road categories were defined here as: (1) 4-lane or more, paved, divided highways, (2) 2-lane paved roads, (3) 1-lane paved roads or unpaved roads and (4) a combination of multiple road categories.

From each dataset, we extracted the information needed to calculate a Pearson correlation coefficient ( $r$ ) between a species response (e.g. abundance, occurrence) and a road predictor (e.g. road density, distance to road). The  $r$ -values were the 'effect sizes'. Where information needed to calculate an effect size was missing, we contacted the author(s) to request that information; if the information needed to calculate an effect size was still unavailable after contacting authors, the study was excluded. The information extracted to estimate the effect sizes depended on the study design and the information reported in the study. Commonly, primary studies evaluate road impacts by investigating the relationship between a continuous response (i.e. species abundance) and a continuous road predictor variable (e.g. road density, distance to road). Alternatively, road impact evaluations can consist of a comparison of mean abundances between an intervention and comparator group (e.g. mean abundance near versus far from roads). We divided studies into six categories based on the study design (Table 1).

Study designs that investigated the relationship between a continuous response and predictor variable included the following: (1) landscape or region and (2) distance from road (multiple distances).

TABLE 1 Study design category examples illustrating common sampling methods and results along with the adjusted sample size.

Study design	Description	Study/analysis results	Adjusted <i>n</i>
<p>Landscape or region</p> 	Species abundance surveyed in focal sampling areas with the road metric (e.g. road density) measured in buffers (based on the species home range size) surrounding the focal sampling areas		# of landscapes or regions e.g. 4
<p>Distance from road (multiple distances)</p> 	Species abundance surveyed at multiple distances from a road(s)		# of distance from road intervals that are spatially independent * # of roads e.g. 5
<p>Home range versus random</p> 	Comparison of a mean road metric (e.g. road density) in individuals' home ranges (typically determined by GPS-collared animals) to randomly selected non-home range areas of equal size		# of home ranges (individuals) + 1 (for all random/absence areas) e.g. 4
<p>Presence plot versus random</p> 	Comparison of a mean road metric (e.g. road density) in areas of an arbitrary size where a species is present to areas of equal size where a species is known or assumed to be absent		# of spatially independent presence plots + 1 (1 for all absence plots) e.g. 4
<p>Road near versus far</p> 	Comparison of mean species abundance surveyed near roads to mean abundance surveyed far from roads (e.g. forest interiors)		2 or 1 if the distances are not independent * # of roads e.g. 6
<p>Road present versus absent</p> 	Comparison of mean species abundance surveyed in areas of an arbitrary size containing a road to areas of equal size without a road		# of spatially independent sampling locations e.g. 6

Landscape or region studies surveyed species abundance in focal sampling areas with the road metric (e.g. road density) measured in buffers, based on the species home range size, surrounding the

focal sampling areas. Distance from road (multiple distances) studies surveyed species abundance at multiple distance intervals from the road(s). Results from these study designs were normally in the

form of the correlation coefficient ( $r$ ) relating species abundance to the road metric. It was also common for regression studies to report  $R^2$ , in which case we took the square root to obtain  $r$ . In other cases, we calculated  $r$  from data available in the paper/supplementary information, provided by authors or extracted from figures using WebPlotDigitizer 4.6. (Rohatgi 2022, unpublished internet freeware).

Study designs that contrasted the means of an intervention group to a comparator group included the following: (1) home range versus random, (2) presence plot versus random, (3) road near versus far and (4) road present versus absent. Home range versus random studies compared a mean road metric (e.g. road density) in individuals' known movement areas (e.g. determined by GPS-collared individuals) to random or absent areas of equal size. Presence plot versus random studies compared a mean road metric (e.g. road density) in areas of an arbitrary size centred over species presence locations to areas of equal size where a species is known or assumed to be absent. Road near versus far studies compared mean species abundance surveyed near roads to mean species abundance surveyed far from roads (e.g. forest interiors). Road present versus absent studies compared mean species abundance surveyed in areas of an arbitrary size containing a road to areas of equal size without a road. Results from these study designs were normally in the form of means and variances of the intervention and comparator groups. For these study designs, we calculated the effect sizes from the means, variances and sample sizes of the two groups using the following series of calculations (Borenstein et al., 2009).

We first calculated Cohen's  $d$ ,

$$d = \frac{\bar{X}_{G2} - \bar{X}_{G1}}{S_{\text{pooled}}}$$

where  $\bar{X}_{G1}$  was the mean of the comparator group and  $\bar{X}_{G2}$  was the mean of the intervention group.  $S_{\text{pooled}}$  was the pooled standard deviation of the two groups,

$$S_{\text{pooled}} = \sqrt{\frac{(n_{G2} - 1)s_{G2}^2 + (n_{G1} - 1)s_{G1}^2}{n_{G1} + n_{G2} - 2}}$$

where  $s$  = the standard deviation and  $n$  = the sample size for each group. Next, we multiplied  $d$  by  $J$ , a correction factor for small sample size,

$$J = \left[ 1 - \frac{3}{4N - 9} \right]$$

where  $N$  = total sample size. This converted Cohen's  $d$  to Hedges'  $g$ . We then transformed Hedges'  $g$  into  $r$ ,

$$r = \frac{g}{\sqrt{(g)^2 + \frac{1}{p(1-p)}}}$$

where  $p$  = the proportion of the total sample size in one of the two groups.

We transformed all correlation coefficients ( $r$ ) to Fisher's  $z$ ,  $z = \frac{1}{2} \ln \left[ \frac{1+r}{1-r} \right]$ , for its desirable statistical properties in meta-analyses (Koricheva et al., 2013).

### 2.3.1 | Calculating effect-size weights

To perform the meta-analysis (Section 2.5 below), we needed to weight the effect sizes to account for differences among datasets in sampling error. Effect sizes are typically weighted according to some measure of reliability, for instance, sample size, such that datasets with larger sample sizes have greater weight. However, in the case of this review, estimating comparable sample sizes is challenging because studies with different study designs report qualitatively different measures of sample size (e.g. number of individuals, sampling locations, GPS points). Therefore, we estimated adjusted sample sizes such that they were comparable across studies. We did this by attributing one data point to each individual or spatially independent sampling location based on home range size. Once we determined the adjusted sample size for each effect size, we converted it to an inverse variance weight  $w$ , where  $w = n - 3$  (Lipsey & Wilson, 2001). This effectively removes effect sizes with  $n < 4$ .

Adjusted sample sizes were estimated as follows for each study design category (Section 2.3 above) (Table 1). For landscape or region studies, the adjusted sample size was the number of landscapes or regions. For distance from road (multiple distances), the adjusted sample size was the number of spatially independent distances from road multiplied by the number of roads sampled. For home range versus random studies, the adjusted sample size was the number of home ranges (individuals) + 1 (representing all random/absent areas). For presence plot versus random studies, the adjusted sample size was the number of spatially independent presence plots + 1 (representing all random/absence plots). For road near versus far studies, the adjusted sample size was 2 for near versus far, or 1 if the near and far distances were not spatially independent, multiplied by the number of roads sampled. For road present versus absent studies, the adjusted sample size was the number of spatially independent sampling locations.

For all study designs except landscape or region and home range versus random studies, when the distance between sampling locations was unknown, we set the adjusted sample size to the minimum ( $n = 4$ ) for inclusion in the meta-analysis (25.1% of effect sizes). We also set the adjusted sample size to 4 when  $>4$  individuals traveled together in  $\leq 4$  group(s) of individuals (0.3% of effect sizes).

We did not conduct a formal risk of bias assessment because we independently evaluated each effect size and adjusted the sample sizes accordingly.

### 2.3.2 | Reducing multiple non-independent effect sizes within studies

The extraction procedure (Section 2.3 above) eliminated redundant studies containing the same data. However, within a

given retained study, there could be multiple datasets which, in some cases, were not independent. We reduced multiple non-independent effect size estimates from the same study in one of two ways.

#### *Selection of one effect size*

When a single study presented data/results using different study designs for the same species but in multiple years or habitat types, we selected the effect size from the year or habitat with the largest (adjusted) sample size. When a single study presented data/results at multiple spatial scales for the same species, we selected the largest effect size regardless of the direction of the effect, assuming that this scale was closest to the relevant scale for the species. When a single study reported data/results for multiple road effect measures within a single study design (e.g. separate results were reported for mean road density and mean distance to road), we selected the road effect with the largest effect size regardless of the direction of the effect, on the assumption that this road effect was the most relevant exposure. When a single study presented data/results where the effect size could be extracted as a study design involving either a relationship between a continuous response and a continuous predictor or contrasting group means, we selected the study design involving a relationship between continuous variables. This maximized the adjusted sample size because each sampling location was included in the adjusted sample size. However, if there were more than 10% absences, we selected the study design contrasting group means for the effect size.

#### *Aggregation of effect sizes*

The second approach to reducing multiple non-independent effect size estimates from the same study was to average effect sizes. We averaged effect sizes across years when a study presented separate data/results for each of multiple years, on the same species using the same study design and in the same location. We also averaged effect sizes across sampling methods when a study presented separate data/results for multiple sampling methods (e.g. camera traps and sign surveys) for the same species and same locations. Additionally, we averaged effect sizes when a study presented separate data/results within a single road category. For example, if a study reported separate results for unpaved roads and 1-lane paved roads, which were both considered road category 3, we averaged the effect sizes. In each case, we calculated the arithmetic mean of the effect sizes across different comparisons within a study (equation 24.1 in Borenstein et al., 2009). We calculated the variance using the methods of Borenstein et al. (2009). Since the correlations between effect sizes were unknown, we conservatively assumed a correlation coefficient of  $r = 1$ . This overestimated variance, resulting in an increased likelihood of finding that the effect size is not significantly different from zero. However, as we had to compute a mean effect size in only 10.5% of cases, this assumption was unlikely to have a large impact on the results.

## 2.4 | Species traits data

We collected species traits information using the database PanTHERIA (Jones et al., 2009), with taxonomy from Wilson and Reeder (2005), and filled in missing information with other sources as needed (Appendix S2). We collected all available information, considering all regions, from non-captive populations on: (1) home range, (2) reproductive rate and (3) body mass. Home range (km<sup>2</sup>) was the median area within which daily movements of individuals of both sexes occur. Reproductive rate was the median number of offspring per litter per female multiplied by the median number of litters per female per year. Body mass (g) was the median body mass of adult individuals of both sexes.

## 2.5 | Meta-analyses

We combined the effect sizes from this review with those in Rytwinski and Fahrig (2012) to include all available effect sizes to the end of 2020. We conducted all analyses in R version 4.2.1 (R Core Team, 2022) using the 'metafor' package (version 3.4-0) (Viechtbauer, 2010). We conducted all meta-analyses using the `rma.mv` function, specifying Study ID as a random factor in each model to account for multiple effect sizes from the same study (e.g. multiple species). We used the restricted maximum-likelihood estimator to compute weighted summary effect sizes and the maximum-likelihood estimator to evaluate model fit of mixed-effects models.

We began by conducting a global meta-analysis of the summary effect of road impacts on mammal population abundance. The summary effect size was considered significantly different from zero when the 95% confidence interval (CI) did not overlap with zero. We calculated heterogeneity in effect sizes using the  $Q$  statistic, which we tested against a chi-square ( $\chi^2$ ) distribution to determine if the total variation in observed effect sizes was significantly greater than expected due to sampling error alone. We explored publication bias using a funnel plot.

We then tested the predictions of the effect of species traits on population responses to roads, that is, the interaction effects of the species traits on the road effect. We first removed effect sizes for species with missing species traits information. See Appendix S3 for an alternative analysis where missing species traits values were estimated instead of removing the effect sizes for these species. We  $\log_e$  transformed the species traits to remove skewness (Appendix S4). We conducted pairwise correlations among species traits to assess independence. We then performed individual meta-regressions for the effect of each species trait on the road effect, and then, a multiple meta-regression of the effects of all traits contained in a single model. The results are interpreted according to the direction of each species trait on the road effect. For instance, a negative effect indicates that species with larger values of the species trait respond more negatively to roads. Total heterogeneity ( $Q$ ) was separated into the heterogeneity explained by the model ( $Q_M$ ) and heterogeneity not explained

by the model ( $Q_E$ ), that is,  $Q = Q_M + Q_E$ , and tested against a  $\chi^2$  distribution to determine statistical significance. We evaluated model fit based on the finite sample size corrected Akaike Information Criterion values.

### 3 | RESULTS

#### 3.1 | Review statistics

We found 58 studies from 31 countries published from 2012 to 2020 that met the selection criteria (Appendix S5), from which we extracted 267 road effects for 160 mammal species. When combined with the 34 studies published prior to 2012 from Rytwinski and Fahrig (2012), the total was 394 road effects for 210 mammal species from 92 studies in 34 countries. Most studies (45/92; Appendix S6) and datasets (161/394) were from North America, while African studies included the largest proportion of species (108/209) (Figure 1).

We collected complete species traits information for 169 out of the 210 species included in the meta-analysis. There were high correlations among species traits (Appendix S7). The untransformed distribution of each species trait was right-skewed, that is, most datasets were for species with small home ranges, low reproductive rates and low body masses; however, the log transformations removed this skew.

Data used to conduct the meta-analysis are available from the Dryad Digital Repository (Patterson et al., 2025). A list of the studies included in the meta-analysis is provided in Appendix S8.

#### 3.2 | Global meta-analysis

Roads had an overall significant negative effect on mammal population abundance ( $ESr = -0.116$ , 95% CI:  $-0.213$ ,  $-0.018$ ), with statistically significant heterogeneity among effect sizes ( $Q = 1708.07$ ,  $p < 0.0001$ ,  $n = 394$ ). The funnel plot indicated no obvious publication bias (Appendix S9).

#### 3.3 | Species traits analysis

In univariate models, we found the following: (i) species with larger home ranges responded significantly more negatively to roads; (ii) species with higher reproductive rates responded significantly less negatively to roads; and (iii) no detectable effect of body mass on the effect of roads (Figure 2a; Appendix S10). In the multiple meta-regression model containing all three species traits, home range remained negative and significant, reproductive rate remained positive but was no longer statistically significant, while body mass became positive and significant (Figures 2b and 3), that is, larger species responded less negatively to roads. Thus, the largest and unexpected difference between results for the single-variable meta-regressions and the multiple meta-regression was the appearance of a less negative road impact on larger mammal species. The most parsimonious model was the one that contained all three species traits (Appendix S10). Although the model explained significant variation in mammal population responses to roads ( $Q_M = 26.19$ ,  $p \leq 0.0001$ ), there was a large amount of unexplained variation leftover in the model ( $Q_E = 1348.80$ ).

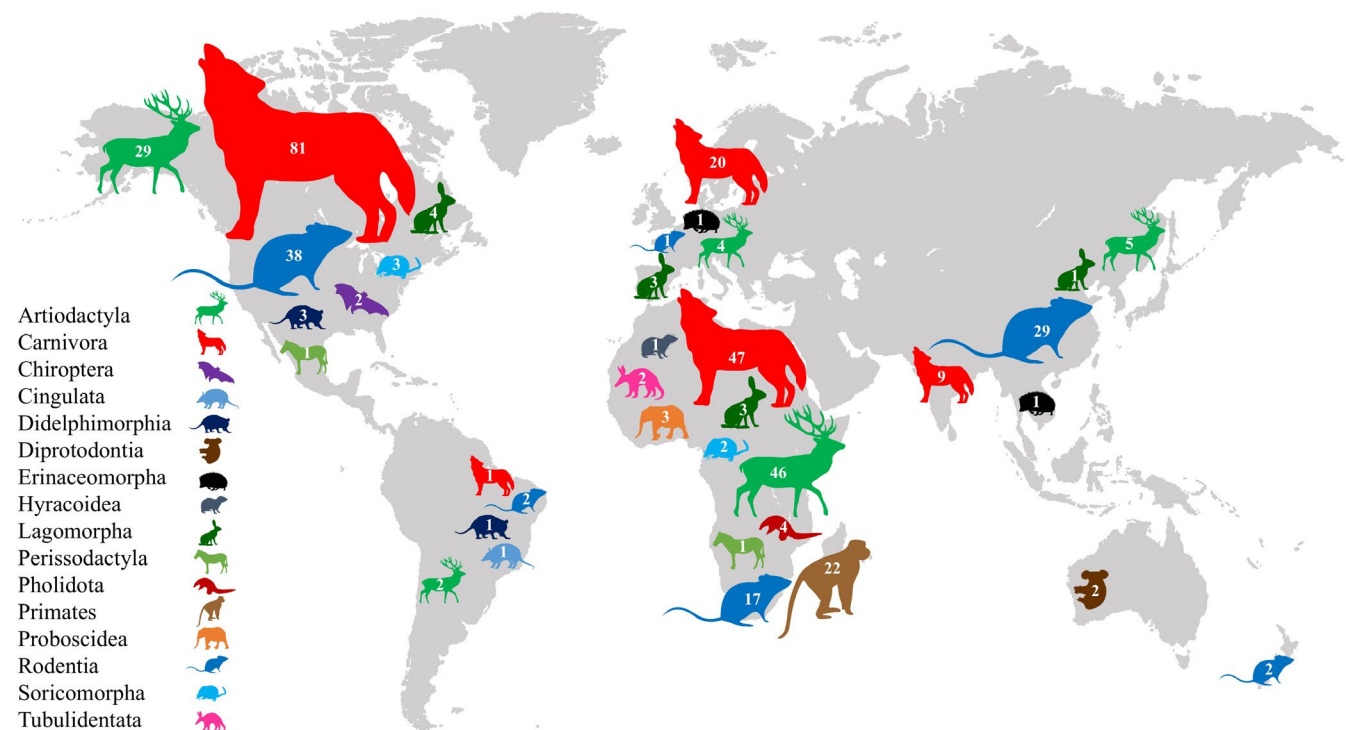
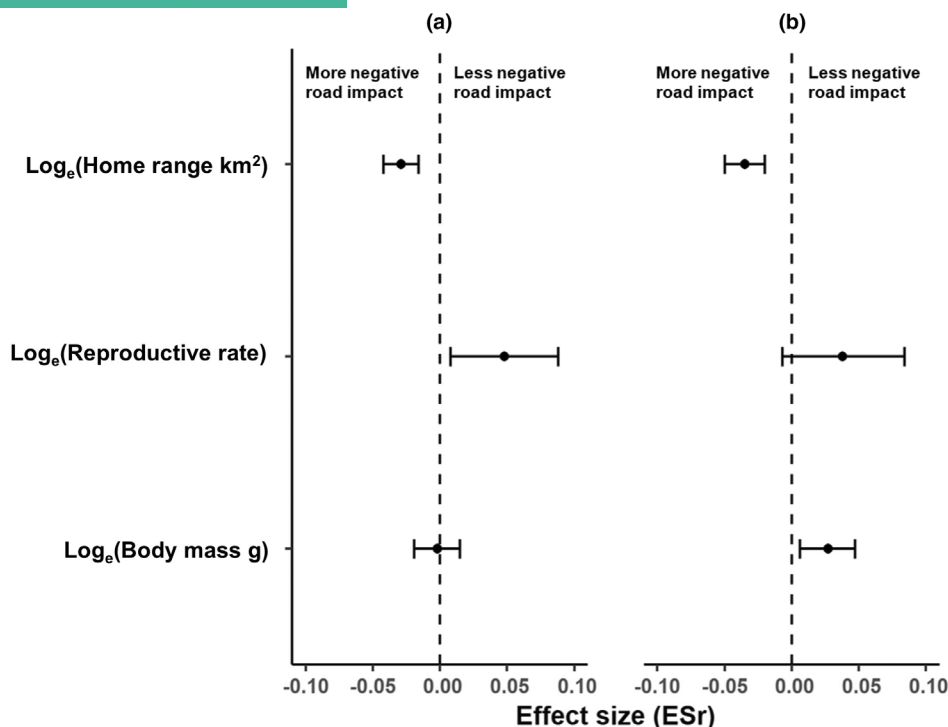


FIGURE 1 Map of the number datasets (represented by the relative size of icons) included in the meta-analysis presented by taxonomic order for each continent.



**FIGURE 2** Weighted-mean effect sizes ( $ES_r$ ) from (a) univariate and (b) multiple (containing all three species traits) meta-regressions testing the influence of species traits on variation among mammal population responses to roads ( $n = 342$  effect sizes). All species traits were  $\log_e$  transformed. A positive effect size indicates that species with larger values of the species trait respond less negatively to roads. A negative effect size indicates that species with larger values of the species trait respond more negatively to roads. Error bars indicate 95% confidence intervals.

### 3.4 | Post hoc analyses

We carried out post hoc analyses to explore possible explanations for the large amount of variation leftover in the model (Appendix S11). First, we explored whether mammal population responses to roads differed in tropical compared to temperate regions; we did not detect a significant difference among temperate and tropical regions in their average road effects ( $Q_M = 0.31$ ,  $p = 0.575$ ). Second, we explored whether there was a difference in average road effects among trophic groups (i.e. herbivores, omnivores, carnivores); we did not detect a significant difference ( $Q_M = 1.48$ ,  $p = 0.476$ ).

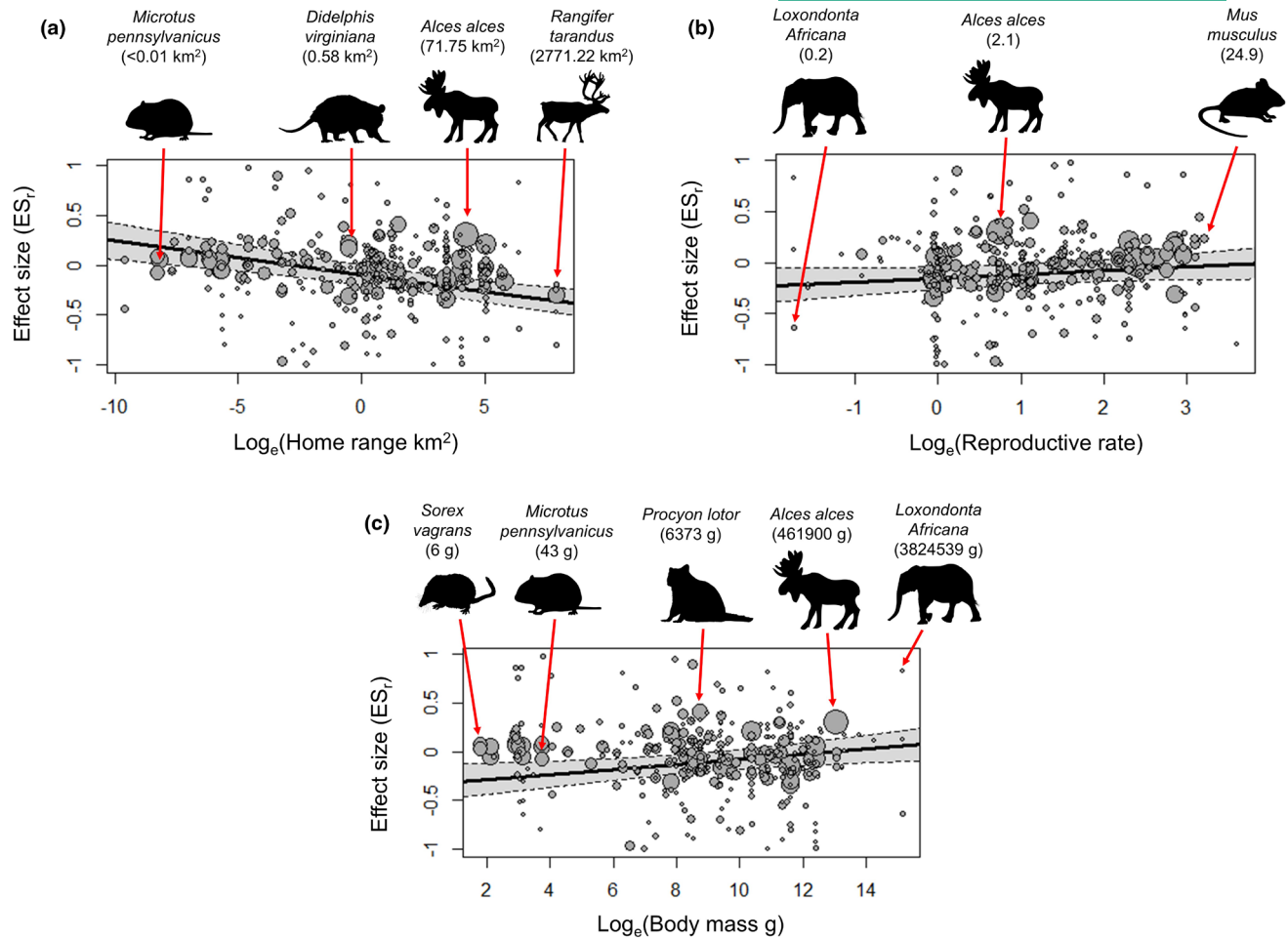
## 4 | DISCUSSION

The results support the predicted negative effect of home range size and positive effect of reproductive rate on mammal population responses to roads. We expected these results because species with larger home ranges interact with roads more frequently and species with lower reproductive rates are less capable of recovering from the loss of individuals due to road mortality. These results reinforce the findings of the meta-analysis by Rytwinski and Fahrig (2012) and the empirical study by Rytwinski and Fahrig (2011). That the significant positive effect of reproductive rate in the univariate meta-regression model became smaller and non-significant in

the multiple meta-regression indicates that some of the variation explained by reproductive rate may in fact be due to its correlation to the other species traits.

The most unexpected and most interesting result of this study is that larger species overall showed a significantly lower negative road impact than smaller species. Previous studies have found the opposite (Rytwinski & Fahrig, 2011, 2012), and we expected the opposite because larger mammals generally have larger home ranges and lower reproductive rates than smaller mammals. In addition, negative effects of roads on larger predators are thought to result in neutral or positive effects of roads on their smaller prey species (Rytwinski & Fahrig, 2007, 2013). That we found the effect of body mass only in the multiple meta-regression containing all three traits indicates that by accounting for the variation explained by home range and reproductive rate, a positive effect of body mass is revealed. It is important to note that, as the smallest mammals generally have small home ranges and high reproductive rates, the most negative responses to roads were observed for medium-sized species that had larger home ranges and lower reproductive rates (Figure 3a,c). The wolverine (*Gulo gulo*) is an example of a species with a combination of a larger home range (343.27 km<sup>2</sup>), lower reproductive rate (1.42) and smaller body mass (12,792.49 g) that was found to have strong negative responses to roads in this meta-analysis.

There are several possible explanations for the reduced negative road impact with increasing body mass. First, studies on



**FIGURE 3** Multiple (containing all three species traits) meta-regression testing the influence of (a) home range (km<sup>2</sup>), (b) reproductive rate and (c) body mass (g) on variation among mammal population responses to roads ( $n=342$  effect sizes). The regression line in each plot reflects the relationship between the moderator and effect sizes, while the other moderators are held constant at their mean. A larger effect size means a less negative road effect. All species traits were  $\text{log}_e$  transformed. Adjusted sample sizes, that is weight of effect sizes in the multiple meta-regression, are represented by the size of dots.

smaller mammals may have evaluated more severe road exposures compared to studies on larger mammals due to differences in common study designs used. For example, it was common for studies on smaller mammals to use a near versus far study design, where the road exposure was typically a single two or four-lane paved road (road category 1 or 2). Instead, it was common for studies on larger mammals to use a home range versus random study design, where the road exposure was typically mixed roads (road category 4). However, this is unlikely to explain the body mass response because we found no significant effect of road category on average road effects when included in the multiple meta-regression (Appendix S12).

Second, it is possible that some studies included in this meta-analysis could have been from locations that already have fencing installed along the roads. In such cases, existing fences may have been effective at keeping larger mammals off the roads while being ineffective for smaller mammals. However, this is unlikely to explain the results of our meta-analysis because no studies mentioned the existence of fencing at their study location(s).

Third, larger mammals may be less likely to be hit by vehicles due to their being more visible to drivers (González-Suárez et al., 2018). Drivers are better able to detect larger hazards compared to smaller hazards (Asadamraji et al., 2018). Drivers also commonly take additional actions (e.g. braking, swerving, honking the horn) to avoid collisions with larger mammals due to the vehicle damage and personal safety risk that would result (Vanlaar et al., 2019). These driver reactions could explain the lower roadkill rates of larger mammals found in Grilo et al. (2020) and partly explain the peaked body-mass (~1000–3000 g) roadkill pattern for mammals found in several studies (Ford & Fahrig, 2007; González-Suárez et al., 2018; Medrano-Vizcaíno et al., 2022). However, the lower roadkill rates of larger mammals in these studies could also be explained by larger mammals generally having lower population densities compared to smaller mammals (Ford & Fahrig, 2007).

Fourth, larger mammals may be better able to avoid cars and/or may be more likely to obtain resources from roads, reducing their negative effects. Population abundance can increase with roads for species that can extract a benefit from them such as

scavenging roadkill (i.e. road attraction) while moving out of the path of oncoming vehicles (Fahrig & Rytwinski, 2009; Jacobson et al., 2016; Jaeger et al., 2005). While quantitative studies on behavioural responses to roads and vehicles are lacking, anecdotal evidence of road attraction and car avoidance behaviours is common, particularly for larger mammals such as black bears (*Ursus americanus*) (Jaeger et al., 2005; Rytwinski & Fahrig, 2015). Wolves (*Canis lupus*) have also been found to preferentially travel along roads but only at night, indicating road attraction behaviour to extract the benefit of increased travel speed along roads, and car avoidance behaviour as this travel only occurs at times with reduced traffic (Zimmermann et al., 2014). We expect that these behavioural responses to roads and vehicles are more common for larger mammals because they generally have higher cognitive ability than smaller mammals (Benson-Amram et al., 2016; Burger et al., 2019). Therefore, we speculate that the lower negative road impact on larger mammals than smaller mammals is due to driver avoidance of collisions with larger mammals and/or larger mammals' road attraction and car avoidance behaviours.

Another important finding of this meta-analysis was the high variability of individual responses to roads. Our post hoc analyses could not explain the large amount of variation left in our model. First, we explored whether there was a difference in average road effects among temperate and tropical regions because these regions can vary in several ways, including in their: (1) biodiversity; and (2) road infrastructure. While we did not detect a difference in average road effects among tropical and temperate regions, geographical effects may be important at a smaller scale. For instance, studies have shown that the geographical coordinates of study locations are an important predictor of roadkill rates at a continental or national scale (González-Suárez et al., 2018; Medrano-Vizcaino et al., 2022). Second, we explored whether there was a difference in average road effects among trophic groups (i.e. herbivores, omnivores, carnivores). Trophic groups can vary in their species traits. For example, in our meta-analysis, carnivores had narrower ranges of all three species traits in comparison to herbivores and omnivores. Trophic groups may also vary in their behavioral responses to roads. While we did not detect a difference in average road effects among trophic groups, it is possible that the variation left in our model could be explained by an underlying pattern or another untested variable. We speculate, however, that this variation is most likely due to site- and/or species-specific characteristics.

## 4.1 | Implications

Our findings suggest that mitigation efforts to protect vulnerable mammal populations from road impacts should involve maintaining low road densities and installing small-mesh fencing along roads. Maintaining low road densities (e.g. avoiding the construction of additional roads) protects species with larger home ranges because it reduces the frequency with which these species interact with roads (Rytwinski & Fahrig, 2015). Small-mesh fencing along roads

protects species with lower reproductive rates and species with smaller bodies because it keeps them off roads and, therefore, decreases their risk of road mortality (Rytwinski et al., 2016; van der Ree et al., 2015). These suggested road mitigation measures will require high upfront costs; however, the benefits are likely to exceed the costs over time (Huijser et al., 2009; Rytwinski et al., 2016).

The recommendation of using small-mesh fence to mitigate road impacts on smaller mammals differs from previous recommendations that mitigation should be targeted towards larger mammals (Rytwinski & Fahrig, 2011, 2012, 2013, 2015). In practice, mitigation is most often targeted towards larger mammals due to concerns about driver safety (Huijser et al., 2015). However, wildlife fencing targeted towards large mammals typically has large meshes that are not effective at preventing smaller mammals from moving onto roads (van der Ree et al., 2015). Fortunately, existing fences can be easily retrofitted to be effective for a wide range of body sizes by adding small mesh at the base (van der Ree et al., 2015).

Depending on the climbing or digging abilities of the target species, fences may require features to prevent crossing over or under (Huijser et al., 2015). To prevent animals from climbing over, fences can be designed with an overhanging lip or floppy top, or they can be made smooth (e.g. sheeting) to reduce climbing grip (Klar et al., 2009; Moseby & Read, 2006; van der Ree et al., 2015). To prevent animals from digging under, fences can be buried (Huijser et al., 2015). Fences need to be long enough to reduce the fence-end effect (Clevenger et al., 2001; Plante et al., 2019).

Our findings further suggest that mammal population responses to roads vary greatly due to site- and/or species-specific characteristics. This implies that road mitigation decisions would be best informed by the target site and/or species-specific information. For example, road mitigation decisions could consider pre-existing knowledge of local wildlife and/or involve conducting site-level Environmental Impact Assessments. Our species traits model, however, can be important for predicting mammal population responses to roads despite the differences in site- and/or species-specific characteristics. Our model should therefore be used to guide the general road mitigation plans and policies. In some cases (e.g. when there is pre-existing site-level knowledge), our model could also remove the need for costly site-level evaluations and instead direct more resources towards mitigation.

## 4.2 | Limitations

Our methods may have inherent biases. First, we assumed that all studies had similar errors in their estimates of abundance at all sampling locations. Second, we assumed that all sites had characteristics that represented similar amounts of confounding of the road effect. Third, we used median species trait values in this meta-analysis, which could have biased our results because many species are understudied, and species trait values can vary across individuals/regions.

## 5 | CONCLUSION

Our results imply that road mitigation for mammals should ideally be informed by site-level knowledge, but in general, mammal species with larger home ranges, lower reproductive rates and smaller body masses are most vulnerable to roads. These results strengthen support for the home range and reproductive rate hypotheses but are contrary to previous conclusions regarding body mass. We speculate that the positive effect of body mass is due to driver avoidance of collisions with larger species and/or differences in road attraction and car avoidance behaviours of larger versus smaller species that allow larger mammals to extract benefits of roads while avoiding oncoming vehicles. Based on our results, we can also infer that several mammal species whose responses to roads have not yet been studied are highly vulnerable to road effects. These include sables (*Martes zibellina*), meerkats (*Suricata suricatta*), jaguarundis (*Puma yagouaroundi*), patas monkeys (*Erythrocebus patas*), white-nosed saki (*Chiropotes albinasus*) and southern tamanduas (*Tamandua tetradactyla*). Road mitigation for these highly vulnerable mammals should involve maintaining low road densities and installing small-mesh fencing along roads.

### AUTHOR CONTRIBUTIONS

**Sean Patterson:** Conceptualization, methodology, data curation, formal analysis, investigation, visualization, writing—original draft, writing—review and editing. **Lenore Fahrig:** Conceptualization, methodology, supervision, visualization, writing—original draft, writing—review and editing. **Jochen A. G. Jaeger:** Conceptualization, methodology, writing—review and editing. **Oriana Meek-Sauriol:** Data curation, investigation, writing—review and editing. **Fernanda Z. Teixeira:** Conceptualization, methodology, writing—review and editing. **Aurora Torres:** Conceptualization, methodology, writing—review and editing. **Trina Rytwinski:** Conceptualization, methodology, data curation, formal analysis, investigation, supervision, visualization, writing—original draft, writing—review and editing.

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### CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

### DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1g1jwsv9v> (Patterson et al., 2025).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Search strategy and consistency checks.

**Appendix S2.** Species traits and reference information.

**Appendix S3.** Estimated missing traits analysis.

**Appendix S4.** Log transformations of species traits to remove skewness.

- Appendix S5.** Search results information.
- Appendix S6.** Country information.
- Appendix S7.** Correlations among species traits.
- Appendix S8.** List of studies included in the meta-analysis.
- Appendix S9.** Exploration of publication bias.
- Appendix S10.** Meta-regression models.
- Appendix S11.** Post-hoc analyses.
- Appendix S12.** Analysis of road category on species traits effects.

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