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Global exposure of carnivores to roads

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ABSTRACT

Aim Land-use change is a major threat to biodiversity globally. Roads cause direct mortality and limitation of individual movements, which may isolate populations and affect their viability in the long term. Here we provide the first comprehensive global assessment of the exposure of terrestrial mammalian carnivores to roads using an integrated modelling framework.

Location Global.

Methods We estimated critical road densities and critical patch sizes for each species based on a spatially explicit model and life-history traits. We calculated the distribution of landscape fragment sizes for each carnivore species by intersecting global road density with each species range. The proportion of a species' geographical range with fragments below the critical patch size is used as an index of the vulnerability to roads.

Results We found that the carnivores expected to be most exposed to roads belong to families Felidae, Ursidae, Mustelidae, Canidae and Procyonidae. Approximately one-third of the species most affected have not been identified by the IUCN as threatened by roads. Our model projects time to extinction that may be as low as one century for some species, such as the endangered Iberian lynx. Species are expected to be more exposed in areas with medium to high road density but, surprisingly, also in areas where road density is relatively low. Hotspots of the number of species locally endangered by roads occur in North America and Asia.

Main conclusions Our results suggest the need to reassess the status and threats of those species that have not been previously recognized as strongly affected by roads. Our framework can be applied at different spatial scales, to assess the effects of the development of the road network and inform prioritization schemes for road building, and to identify areas for conservation, and species requiring particular mitigation and restoration measures.

Keywords

Biodiversity conservation, carnivores, dispersal, global assessment, mortality, population viability, road impact.

INTRODUCTION

Land-use change is one of the major drivers of biodiversity loss (Pereira *et al.*, 2012). Biodiversity is projected to continue to decline despite society's increasing efforts to decelerate this trend (Tittensor *et al.*, 2014). The road infrastructure is a cause of mortality for many species and is also a major barrier to movement. Roads can subdivide populations and reduce population sizes,

thus affecting their viability (van der Ree *et al.*, 2015). The current and the projected expansion of the road network pose threats that should be evaluated across scales in order to minimize their negative effects (Laurance *et al.*, 2014) and to ensure the long-term viability of populations. The effect of roads on animal populations has been addressed by various studies at local and regional scales, focusing on components such as behavioural and

physiological responses to roads (Grilo *et al.*, 2012; Navarro-Castilla *et al.*, 2014), the effect of road noise and pollution (Hopkins *et al.*, 2013; McClure *et al.*, 2013) and projections of population declines and loss of genetic diversity (for a review see Balkenhol & Waits, 2009; Jackson & Fahrig, 2011). However, studies assessing the impact of roads on population persistence remain uncommon, and upscale, at best, to national levels, focusing on a limited number of species (Beaudry *et al.*, 2008; Borda-de-Água *et al.*, 2014). Assessments on larger scales up to global, and across species, have never been conducted (but see Torres *et al.*, 2016).

Here, we present a new spatially explicit modelling framework to assess the exposure of biodiversity to a major threat – the road infrastructure – and to map hotspots of road impact on biodiversity globally. We apply this framework to a particularly vulnerable group: terrestrial carnivore species. We carry out an assessment of which terrestrial carnivore species are more affected by roads at the global level, as well as where within their range they are most at risk. Mammalian carnivores usually have life-history traits that make them particularly vulnerable to the effects of human-induced environmental changes, such as relatively high mobility and low reproductive rates (Grilo *et al.*, 2015). Moreover, they are important for maintaining ecosystem function, structure and resilience (Ripple *et al.*, 2014).

We use a simple, spatially explicit reaction–diffusion demographic model describing population dynamics and the dispersal of individuals (Skellam, 1951; see also Cantrell & Cosner, 2003). Skellam's (1951) model can be used to simulate source–sink dynamics (Pulliam, 1988) of populations occupying several habitats within a landscape, where the population growth rate can be positive in favourable habitats (source habitats) or negative in unfavourable habitats (sink habitats) (Pereira & Borda-de-Água, 2013). It has been used to assess species vulnerability to land-use change (Pereira *et al.*, 2004; Pereira & Daily, 2006) and to develop metrics to analyse the impact of road networks on population persistence (Borda-de-Água *et al.*, 2011).

The analysis performed by Borda-de-Água *et al.* (2011) considered a population occupying a landscape composed of favourable habitat patches, where the population growth rate is positive, surrounded by roads, which are unfavourable habitat where the population growth rate is negative. The model predicts how road density and the size of favourable habitat patches that are delimited by roads determine population viability in landscapes fragmented by roads. In particular, it shows that the minimum patch size required for a population to persist increases with population mean dispersal distance, and decreases with intrinsic population growth

rate (Borda-de-Água *et al.*, 2011) (see model description in Methods).

This work is the first where a mechanistic population model has been combined with life-history data, biogeographical data and land-use data to produce a global assessment of population viability for a complete taxonomic group. Despite not taking into account other factors that influence how populations are affected by roads, such as the behaviour of animals towards roads, the type of road or traffic intensity, or indirect mortality caused by resource inaccessibility and population subdivision (Jaeger & Fahrig, 2004; Jaeger *et al.*, 2005), our work opens the way for similar global mechanistic assessments of other threats. Our framework can be applied at different spatial scales, promoting quantitative-based assessments directing road development (or avoidance) and reducing conflicts with biodiversity conservation.

METHODS

For each species analysed, we determined its intrinsic vulnerability to roads by computing two metrics: (1) the maximum road density above which populations are expected to go locally extinct (D_{\max}) and (2) the minimum size of favourable habitat patches that are delimited by roads, below which populations are expected to go locally extinct (A_{\min}) (Borda-de-Água *et al.*, 2011). We computed these metrics using species-specific empirical data on life-history traits (see details below; a list of the data sources is found in the Appendix). We then calculated the observed road density (D_{obs}), and the sizes of the patches delimited by roads (A_{obs}), that exist within each species' range, to compare with the critical values of road density and of patch size, respectively. We applied this approach to 232 terrestrial carnivore species for which an IUCN range map is available (IUCN, 2015), but excluded those species that can disperse through water (Tables S1 & S2 in the Supporting Information).

Critical values of D_{\max} and of A_{\min}

The expressions for D_{\max} and A_{\min} were derived by Borda-de-Água *et al.* (2011) considering a population in a landscape composed of patches surrounded by roads. The patches consist of favourable habitat where the population growth rate is positive and equal to the intrinsic population growth rate (r_1), and the roads consist of unfavourable habitats where the growth rate is negative (r_0). The dispersal distance of individuals is modelled by its dispersal variance (σ^2). The dynamics are given by (Skellam, 1951; Borda-de-Água *et al.*, 2011):

$$\frac{dN(x, y, t)}{dt} = \begin{cases} \frac{\sigma^2}{2} \nabla^2 N(x, y, t) + r_1 N(x, y, t) \left(1 - \frac{N(x, y, t)}{K}\right) & \text{if } (x, y) \notin \text{road} \\ \frac{\sigma^2}{2} \nabla^2 N(x, y, t) + r_0 N(x, y, t) & \text{if } (x, y) \in \text{road} \end{cases},$$

where $N(x, y, t)$ is the population density at location (x, y) at time t , K is the carrying capacity and ∇^2 is $d^2/dx^2 + d^2/dy^2$. The first term on the right-hand side of the equation (top and bottom branches) describes the changes in population density in space and time on the basis of the dispersal distance, which is assumed to follow a Gaussian distribution. The second term describes logistic growth outside roads (top branch) and the population decay (since r_0 is assumed to be negative) on roads (bottom branch) (Borda-de-Água *et al.*, 2011). While r_0 mathematically is the population growth rate on roads, here it is a measure of the loss of individuals from the population (i.e. roads behave as a sink habitat), representing the instantaneous mortality rate when an animal crosses a road.

Maximum road density and minimum patch size

The expressions for the maximum road density above which populations cannot persist (D_{\max}) and for the minimum patch size below which populations cannot persist (A_{\min}) were obtained by solving the equation above for simplified situations, providing easy rules of thumb to estimate population viability in landscapes fragmented by roads. See Borda-de-Água *et al.* (2011) and its corresponding Supporting Information for the details on the derivation of D_{\max} and of A_{\min} . D_{\max} was derived assuming very large dispersal ($\sigma^2 \rightarrow \infty$) and large carrying capacity ($K \rightarrow \infty$, so the term $1 - N(x, y, t)/K$ in the top branch of the equation above is not considered), and ignoring the spatial location of the roads and considering road density only:

$$D_{\max} = r_1 / (r_1 + |r_0|),$$

where r_1 is the growth rate of the population and r_0 is mortality on roads. In Borda-de-Água *et al.* (2011) the maximum road density was computed as a ratio of two areas, and is therefore a dimensionless quantity. Here we divided D_{\max} by 0.01 to compare it with the road density that is observed within each species' range (considering a constant road width of 0.01 km; D_{obs} in km km^{-2} ; see below).

The expression for the minimum patch size below which populations go extinct (A_{\min}) was derived assuming infinite carrying capacity ($K \rightarrow \infty$), and that individuals always die when crossing a road ($r_0 \rightarrow -\infty$), considering the location of the roads explicitly and assuming their configuration to be that of a square grid (Borda-de-Água *et al.*, 2011):

$$A_{\min} = \pi^2 (\sigma^2 / r_1),$$

where σ^2 is dispersal variance and r_1 is the growth rate of the population.

Population parameters: growth rates and dispersal

To compute D_{\max} and A_{\min} we first estimated the parameters of the model (r_1 , r_0 and σ^2) for each species. We computed the intrinsic population growth rate, r_1 , using a simplified version of the Euler equation following the approach by

Pereira & Daily (2006), and assuming: (1) a constant mortality rate, μ ; (2) zero fecundity before the breeding age, β ; (3) fecundity equals the number of female offspring (50% of the litter size), b , at regular birth intervals after the breeding age; and (4) birth pulse intervals are spaced by the mean interval between litters, Δ . The implicit equation for r_1 is then:

$$b \times \int_0^\infty \sum_{y=0}^\infty \delta(x-y\Delta-\beta) e^{-(r_1+\mu)x} dx = 1,$$

where $\delta(x)$ is the birth pulse function, which has a value of $1/T$ for x between 0 and T and 0 elsewhere. This equation can be solved numerically to determine r_1 .

We estimated the rate of population decay on roads, r_0 , as:

$$r_0 = -\mu \times 10^3 \text{ year}^{-1},$$

where μ is the annual natural mortality rate (see below). We assume a 1000 times higher mortality rate (and zero birth rate) on roads than the natural mortality rate. For example, for a species with natural mortality rate of 0.5 year^{-1} , this corresponds to a mortality rate per crossing of 500 year^{-1} on roads. We assessed the robustness of this assumption by comparing the results with $r_0 = -\mu \times 10^2$, and with $r_0 = -\mu \times 10^4$ (Table S3). Our estimates of D_{\max} are consistent with previous maximum road density estimates (e.g. Anderson *et al.*, 2011).

Dispersal variance (σ^2) was computed assuming Gaussian dispersal as:

$$\sigma^2 = (\sigma_m / 1.18)^2 \times \mu,$$

where σ_m is the dispersal median and μ is the annual mortality rate, which converts the dispersal median from $\text{km}^2 \text{ generation}^{-1}$ to $\text{km}^2 \text{ year}^{-1}$ (Pereira & Daily, 2006).

We computed these parameters (r_1 , r_0 and σ^2) for each species using species-specific life-history data (Tables S1 & S2). We computed mortality rate (μ) as the inverse of mean life span, and the dispersal median (σ_m) from home range (HR) data as $\sigma_m = 7\sqrt{\text{HR}}$ (Bowman *et al.*, 2002). Since not all data were available for all species, we established allometric relationships (Table S4) based on the available data, and then used these relationships to estimate the missing life-history values. When data for body mass and litter size were lacking for a given species we used the mean of the genus, or the mean of the corresponding family (Pereira & Daily, 2006). The percentage of missing life-history values ranged from 12.9% (for body mass) to 92.7% (for mortality rate).

Observed values of road density (D_{obs}) and of patch size (A_{obs})

After computing the critical values of road density and patch size, we assessed what is observed within each species range with respect to roads. We did this by intersecting each species range map from the IUCN (IUCN, 2015) with the road

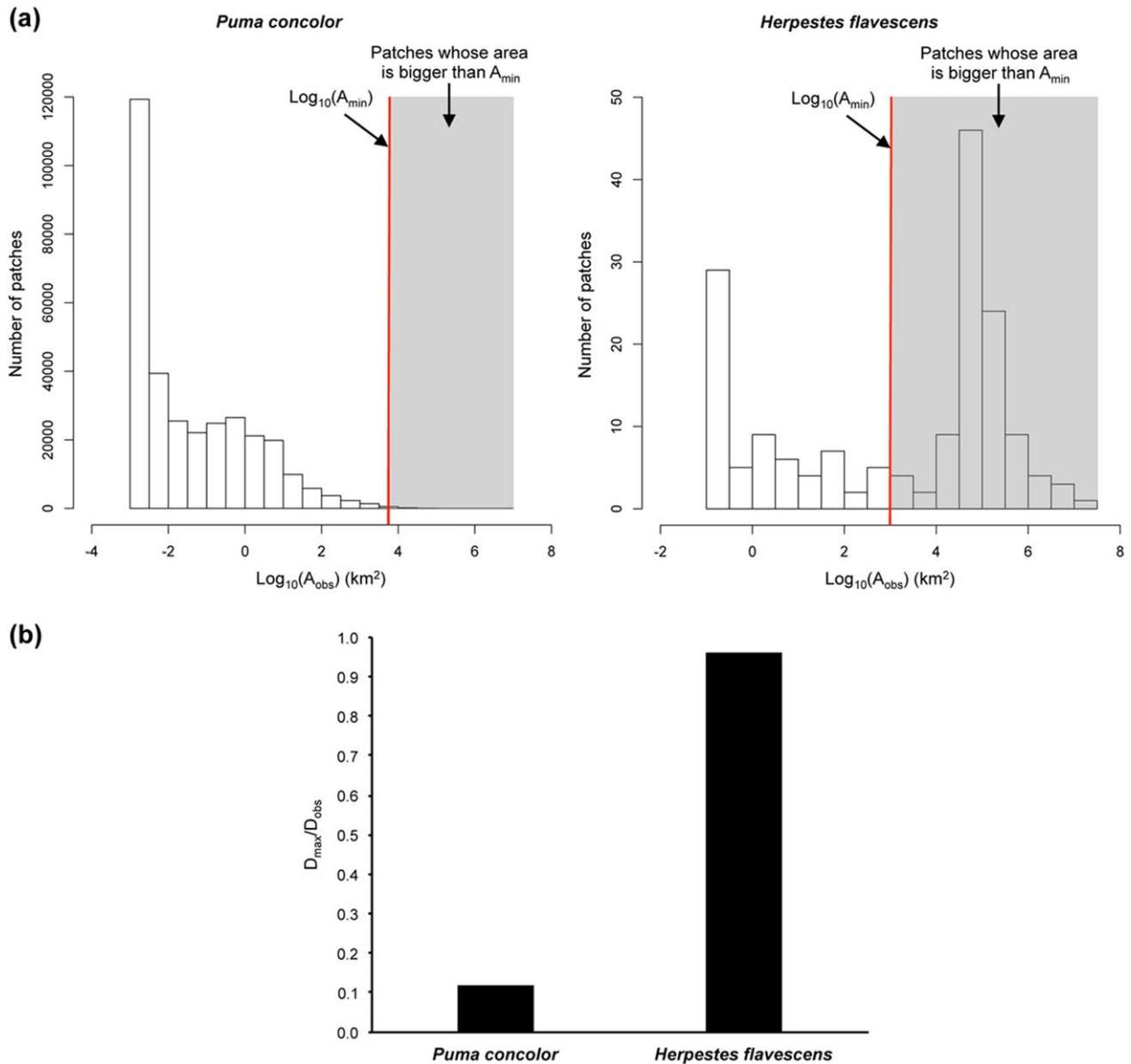


Figure 1 Observed and critical values of patch size and of road density for two species: frequency of observed patch sizes (A_{obs}) and the relation with minimum patch size (A_{min}) (a), and the ratio of theoretical maximum road density to observed road density ($D_{\text{max}}/D_{\text{obs}}$) (b). The puma (*Puma concolor* (Linnaeus, 1771)) is among the 5% of species with lower $P[A_{\text{obs}} > A_{\text{min}}]$ and the 5% of species with smaller $D_{\text{max}}/D_{\text{obs}}$. In contrast, the black slender mongoose (*Herpestes flavescens* Bocage, 1889) has high $P[A_{\text{obs}} > A_{\text{min}}]$ and high $D_{\text{max}}/D_{\text{obs}}$. Fewer patches larger than A_{min} (areas shaded in grey in (a)), or with a small value of $D_{\text{max}}/D_{\text{obs}}$ (in (b)), reveal a highly vulnerable species.

network from Open Street Map (OSM) (Geofabrik, 2015), using QGIS v.2.2.0 (QGIS Development Team, 2014). The road categories included from the OSM data were: ‘motorway’, ‘trunk’, ‘primary’, ‘secondary’, ‘tertiary’, ‘minor’, ‘road’ and ‘unclassified’.

We then computed the observed road density (D_{obs}) as the ratio of the road length that exists within the species range to the species range area. We also computed the area of each patch that is delimited by roads (observed patch sizes, A_{obs}), existing within each species range. This differs from the effective mesh size metric proposed by Jaeger (2000), which

combines the areas of all patches within the region investigated, as well as its total area, into one metric of landscape fragmentation; in our model each A_{obs} is simply the area of one patch (see below for the use of A_{obs} in ranking species exposure to the road network).

Species exposure to the road network

We ranked the species with regard to their exposure to the extant road network by computing for each species: (1) the ratio of the maximum road density to the observed road

Table 1 Species most exposed to roads.

Common name	Species	Family	Smaller D_{\max}/D_{obs}	Smaller $P[A_{\text{obs}} > A_{\min}]$	Percentage of range affected	Threatened by roads IUCN	Red List status
Iberian lynx	<i>Lynx pardinus</i>	Feli	+	+	100	+	EN
Japanese badger	<i>Meles anakuma</i>	Must	+	+	100		LC
Japanese marten	<i>Martes melampus</i>	Must	+	+	100		LC
Bobcat	<i>Lynx rufus</i>	Feli		+	93	+	LC
Stone marten	<i>Martes foina</i>	Must	+	+	90		LC
Sloth bear	<i>Melursus ursinus</i>	Ursi	+		89	+	VU
Nilgiri marten	<i>Martes gwatkinsii</i>	Must	+	+	86	+	VU
Asiatic black bear	<i>Ursus thibetanus</i>	Ursi	+		86	+	VU
Puma	<i>Puma concolor</i>	Feli	+	+	69	+	LC
American black bear	<i>Ursus americanus</i>	Ursi	+	+	68	+	LC
Darwin's fox	<i>Pseudalopex fulvipes</i>	Cani		+	67		CR
Brown bear	<i>Ursus arctos</i>	Ursi	+		65	+	LC
Jaguarundi	<i>Herpailurus yagouaroundi</i>	Feli		+	60	+	LC
Leopard	<i>Panthera pardus</i>	Feli		+	59	+	NT
Pygmy racoon	<i>Procyon pygmaeus</i>	Procy		+	50	+	CR
Coyote	<i>Canis latrans</i>	Cani	+		48		LC
Jaguar	<i>Panthera onca</i>	Feli	+		38	+	NT

These are the species within the 5% lowest values of D_{\max}/D_{obs} or within the 5% lowest values of $P[A_{\text{obs}} > A_{\min}]$. We indicate the percentage of 100 km \times 100 km grid cells where each species is present having $D_{\text{obs}} > D_{\max}$ or at least one patch with A_{obs} smaller than A_{\min} , whether the species is identified by the IUCN as being threatened by roads, and the species' IUCN Red List status: CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern. Family names are truncated to the first four letters: Cani, Canidae; Feli, Felidae; Must, Mustelidae; Proc, Procyonidae; Ursi, Ursidae.

density (D_{\max}/D_{obs}), and (2) the proportion of patches delimited by roads observed within the species range with area (A_{obs}) larger than the minimum patch size (A_{\min}), $P[A_{\text{obs}} > A_{\min}]$ (Fig. 1). Then for each of these quantities, we selected the species within the lower fifth percentile as the species that are expected to be more exposed to roads. In this way, those species that are expected to be most exposed to roads are the ones with a lower D_{\max}/D_{obs} and/or the ones with a smaller $P[A_{\text{obs}} > A_{\min}]$.

For each species in the lower fifth percentile we also mapped where it is expected to be more exposed to roads within its range. We did so using 100 km \times 100 km grid cells and identifying in which cells D_{obs} is higher than D_{\max} , or there is at least one patch with A_{obs} smaller than A_{\min} for population persistence. This is a conservative estimate, because it does not imply that a species is more exposed to roads in all the area of a grid cell, but only in parts of that grid cell (where $A_{\text{obs}} < A_{\min}$).

Time to extinction

Borda-de-Água *et al.* (2011) also derived an expression for computing the time to extinction of a population in a patch with area smaller than the minimum patch size (A_{\min}). Using this expression, we determined the time to extinction (T_{ext}) for the species within the lower fifth percentile of $P[A_{\text{obs}} > A_{\min}]$ for which there is at least one patch with A_{obs} smaller than A_{\min} in all the grid cells where those species are present, as follows (Borda-de-Água *et al.*, 2011):

$$T_{\text{ext}} = \frac{1}{\left(\frac{\sigma^2 \pi^2}{A_{\text{obs}}}\right) - r_1}$$

Time to extinction here is the time that it takes for the species to disappear from 90% of the area where A_{obs} is smaller than A_{\min} , and A_{obs} is the area of the largest patch smaller than A_{\min} within that area.

RESULTS

Using the fifth percentile criterion, we identified 17 species as those most exposed to roads. They belong to the families Felidae (six species, corresponding to 17% of the species analysed in this family), Ursidae (four species, 57%), Mustelidae (four species, 9%), Canidae (two species, 6%) and Procyonidae (one species, 7%) (Table 1). The percentage of the range where each species is expected to be affected varies from 38% to 100% (Table 1). These are the parts of the range where each species is projected to disappear or have low abundance. The Iberian lynx (*Lynx pardinus* (Temminck, 1827)), an endangered species endemic to the Iberian Peninsula, is estimated to go extinct from 90% of the area where A_{obs} is smaller than A_{\min} in 114 years.

Among the species expected to be most exposed to roads, 71% (12 species) are also classified by the IUCN as threatened by roads (Table 1). However, we also identified species for which roads are not listed as a threat by the IUCN (IUCN, 2015), some of which are expected to be affected in more than 75% of their range. These include species that have been categorized as of Least

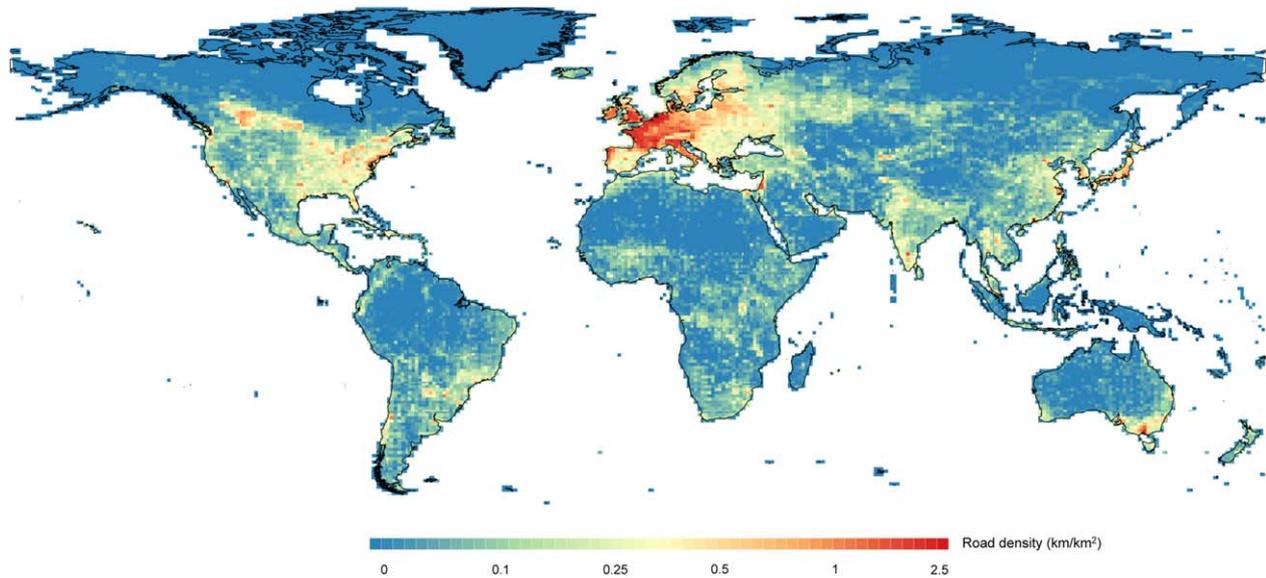


Figure 2 Road density (km km^{-2}) per $100 \text{ km} \times 100 \text{ km}$ grid cell. We intersected the global road network (Geofabrik, 2015) with the world map in $100 \text{ km} \times 100 \text{ km}$ grid cells and then summed the road length in each grid cell. The scale represents 50 road density classes obtained using the Jenks natural breaks optimization method (QGIS Development Team, 2014).

Concern by the IUCN, and for which we have identified another factor of threat: the stone marten (*Martes foina* (Erxleben, 1777)), which despite being widespread is vulnerable to traffic and is frequently road-killed (Grilo *et al.*, 2009), and the Japanese badger (*Meles anakuma* Temminck, 1844) and Japanese marten (*Martes melampus* (Wagner, 1840)), which both occur only in Japan and are estimated to disappear from 90% of the areas where A_{obs} is smaller than A_{min} in 9 and 17 years, respectively.

When using the lower 25th percentile as a criterion to select the species that are expected to be most exposed to roads, we captured 39 out of the 53 species (74%) that are listed by the IUCN as threatened by roads (among the 232 species analysed; Table S2). However, we also identify 50 more species – besides the species already identified at the lower fifth percentile (Table 1) – for which roads are not listed as a threat by the IUCN.

Species are clearly affected in regions with a medium to high road density, as in Europe (mean road density \pm SD $0.65 \pm 0.54 \text{ km km}^{-2}$), North America (eastern USA, mean \pm SD $0.49 \pm 0.24 \text{ km km}^{-2}$; south-central Canada, $0.48 \pm 0.31 \text{ km km}^{-2}$) and Japan (mean \pm SD $0.43 \pm 0.32 \text{ km km}^{-2}$), but also in regions with relatively low road density, such as Africa (mean \pm SD $0.04 \pm 0.07 \text{ km km}^{-2}$) (Figs 2 & 3). In Africa, only one of the fifth percentile-selected species occurs, but the leopard (*Panthera pardus* (Linnaeus, 1758)), having low D_{max} and large A_{min} (Table S2), shows a strong effect of roads throughout its range. The highest number of species affected by roads per $100 \text{ km} \times 100 \text{ km}$ grid cell is observed in North America (up to six species), followed by Asia (four species), South America (three species) and Europe (two species) (Fig. 3). We observe a similar pattern when we use the 25th percentile (Fig. S1).

DISCUSSION

We have assessed the impact of roads on terrestrial carnivore species at the global level, using a species-specific, spatially explicit approach – thereby identifying not only species that are expected to be most exposed to roads at the global level, but also where, within its range, each species is expected to be more affected.

Our approach has several limitations that need to be considered when interpreting the results of our analysis. The maximum road density (D_{max}) was derived assuming unlimited dispersal ability, and the minimum size of favourable habitat patches that are surrounded by roads (A_{min}) was derived assuming that individuals always die when crossing a road (see Methods and Borda-de-Água *et al.*, 2011). Such assumptions are simplifications of real ecological systems: these metrics may underestimate the maximum possible road density and overestimate the minimum possible patch size necessary for population persistence, and it is possible that even if $D_{\text{obs}} > D_{\text{max}}$ or when $A_{\text{obs}} < A_{\text{min}}$, populations persist (Borda-de-Água *et al.*, 2011). Moreover, the behaviour of individuals towards roads influences how roads affect species (Jaeger & Fahrig, 2004; Jaeger *et al.*, 2005). Many large predator species move along low-traffic roads (Forman & Alexander, 1998); for example, wolves can select low-use roads as travel routes (e.g. Whittington *et al.*, 2005). Also, road mortality may be compensated for by increased fecundity or survival (e.g. Seiler & Helldin, 2006).

For these reasons, it is not appropriate to use D_{max} or A_{min} as strict thresholds for population persistence. Instead, we have ranked the species analysed in relation to one another to detect which species would be more exposed to roads than other species, and we have estimated in which

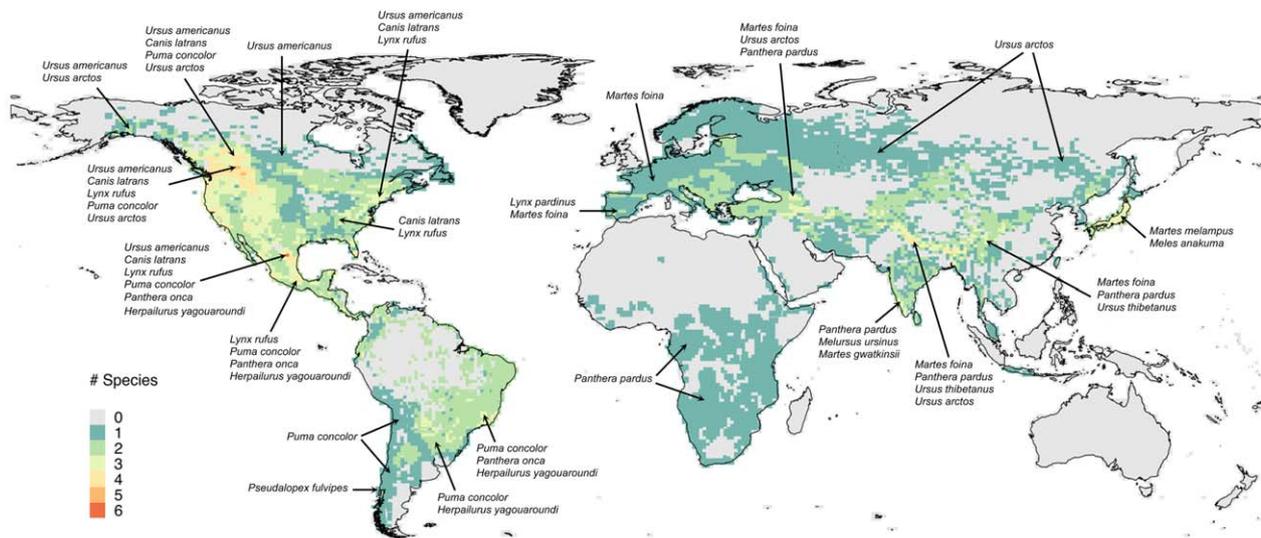


Figure 3 The number of species expected to be more exposed to the impact of roads per $100 \text{ km} \times 100 \text{ km}$ grid cell. The species mapped are within the lower fifth percentile of D_{\max}/D_{obs} or of $P[A_{\text{obs}} > A_{\min}]$. The scale represents the total number of species per grid cell for which D_{obs} is higher than D_{\max} , or A_{obs} is smaller than A_{\min} .

areas within its range a species would be more exposed to roads than in other areas of its range. We did so because even though populations may persist where $D_{\text{obs}} > D_{\max}$ or where $A_{\text{obs}} < A_{\min}$ they are expected to be more exposed to the impact of roads in those areas than in areas where $D_{\text{obs}} < D_{\max}$, or $A_{\text{obs}} > A_{\min}$, respectively.

Despite its limitations, our framework provides a way to obtain a first approximation to pinpoint species that may be more exposed to the impact of roads, to identify the areas within a species range where it may be more exposed to roads and also to highlight regions that may have a higher number of species more exposed to roads.

Time to extinction should also be interpreted with caution given the assumptions made when deriving the expressions for A_{\min} and T_{ext} (see Methods and Borda-de-Água *et al.*, 2011) and the unknown effects of the behaviour of each species. While our approach allows us to estimate the time to extinction in those areas within a species' range where $A_{\text{obs}} < A_{\min}$, the assumption that animals always die when crossing a road is a simplification. Moreover, the impact of roads on population persistence, and therefore time to extinction, will also depend on their sensitivity to the effects of roads (including not only road mortality but also habitat loss, resource inaccessibility and population subdivision), on the type of behavioural response of the animals towards roads, on the types of roads, on traffic intensity (Jaeger *et al.*, 2005), on habitat affinities and on the variation of population density within species ranges (Grilo *et al.*, 2014). Because these factors were not explicitly taken into account in our analysis, T_{ext} should be considered as a first approximation.

We also grouped all roads together when computing D_{obs} , and we did not differentiate road mortality according to the type of road (e.g. Jaeger *et al.*, 2005; Grilo *et al.*, 2009)

because it would have been impractical in an analysis performed at the global scale and for such a large number of species. Assessments performed at smaller spatial scales, or for a smaller number of species, could include computing separate D_{\max} and separate D_{obs} for different road types.

Our results suggest the need to reassess the status and threats of those species that have not been previously recognized as exposed to roads. In such cases applying a modelling approach such as ours, which explicitly combines extrinsic factors of threat and intrinsic species traits, will allow us to move from a descriptive to a mechanistic, biologically sound evaluation of threats (Lee & Jetz, 2010; Dirzo *et al.*, 2014).

Our approach brings together process-based models that link species-specific life histories, population dynamics and dispersal with biogeographical and land-use data – in this case, the road infrastructure. However, as discussed above, other factors that we did not account for can influence how roads affect animals. In more localized studies it may be desirable to incorporate those issues in order to obtain a refined understanding of the impacts across species and regions, but for that it is necessary to deepen our knowledge on the impact of roads, and strengthen the link between empirical knowledge and models (e.g. using models to guide data collection, or collecting parameters that are implementable for models).

Our analysis differs from a simple spatial overlap between species ranges and road density. Despite its limitations, it provides a first quantitative approximation to assess whether the road density that is observed within a species' range may be beyond a threat threshold. By integrating species traits, this analysis also allowed us to detect species which, despite having relatively low road density within their range, are nevertheless estimated to be more exposed to roads than other species for which road density is relatively high within

their range. Such inferences would not have been possible using a simple spatial overlap analysis between species ranges and road density.

By pinpointing where species are expected to be affected by roads within their ranges, and which regions have more species vulnerable to roads, this type of spatial analysis can be used for identifying areas for conservation, for prioritizing regions where mitigation measures, such as passages or fences, should be implemented and for informing the development of schemes for road building (Laurance *et al.*, 2014). Moreover, this framework can also be applied at different spatial and temporal scales, for example for conservation or management purposes at the local scale, for environmental impact assessments or for projecting the effects of future large-scale road network developments, which can then feed, for example, World Bank projections or scenarios for global biodiversity change (Pereira *et al.*, 2010).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Figure S1 Number of species expected to be more exposed to the impact of roads per 100 km × 100 km grid cell, within the 25th percentile of D_{\max}/D_{obs} or of $P[A_{\text{obs}} > A_{\min}]$.

Table S1 Species analysed and life-history data.

Table S2 Parameters for the species analysed.

Table S3 D_{\max} and D_{\max}/D_{obs} computed using $r_0 = -\mu \times 10^2$, $r_0 = -\mu \times 10^3$ and $r_0 = -\mu \times 10^4$.

Table S4 Allometric relationships.

DATA ACCESSIBILITY

Species range maps are available at <http://www.iucnredlist.org/technical-documents/spatial-data>. Road network data are available at <http://download.geofabrik.de/>. Source references and data for life-history traits are presented in the Appendix and in the Supporting Information.

BIOSKETCH

Ana Ceia-Hasse is a PhD student working under the supervision of Henrique M. Pereira. Her work focuses on process-based models of the response of biodiversity to global environmental change. The research team seeks to understand the patterns and processes of global biodiversity change – namely the impact of roads on biodiversity – with the aim of informing environmental policies and ecosystem management.

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APPENDIX: DATA SOURCES FOR LIFE-HISTORY TRAITS USED IN THIS STUDY.

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