Wildlife-vehicle collisions simplify regional food webs

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Abstract

Roads and traffic stand as major threats to biodiversity, primarily due to roadkill, affecting the functioning of ecosystems and the provision of ecosystem services. Understanding how wildlife-vehicle collisions affects the dynamics of ecological interactions is essential to help manage human impacts on biodiversity, but such studies remain largely unexplored. We investigated the intricate relationship between roads, species vulnerability to roadkill, and the ensuing effects on food webs across Europe. Utilizing road density thresholds and trophic interaction data, we constructed regional food webs to assess the potential loss of trophic interactions due to roadkill. Our analysis, encompassing 551 species across three trophic levels, revealed spatially varied impacts, with areas surrounding major cities facing drastic trophic interaction losses exceeding 90%. Notably, 186 species faced significant risks of local extinction due to direct roadkill effects, while a similar number (190 species) encountered trophic interaction losses due to indirect effects (loss of prey or predator). Apex predators exhibited lower direct roadkill impacts while basal-level species are more exposed to direct effects, potentially triggering a cascade of interaction disruptions. Our findings underscore the necessity for tailored conservation measures to reduce roadkill risk, targeting different trophic levels, to preserve ecological network integrity amidst road development programs.

Introduction

Roads can play a vital role in human development by allowing access to important services, such as education and health care, further contributing to economic growth by enabling trade (Gachassin et al., 2010; Iimi et al., 2015; Sewell et al., 2019). However, roads and traffic stand as a major threat to biodiversity, leading to habitat fragmentation and degradation (Forman and Alexander, 1998; Maxwell et al., 2016; Van der Ree et al., 2015). Notably, the expansion of road networks and the associated increase in traffic drastically affects wildlife populations, primarily due to animal-vehicle collisions (Grilo et al., 2020; Morelli et al., 2020). In developed regions like Europe, where the density of roads rank among the highest globally, roads exert a considerable impact on wildlife. Recent estimates point to over 200 million individual birds and mammals being road-killed on European paved roads every year (Grilo et al., 2020).

Roadkill effects are likely to ripple through regional ecological communities when species' interactions are weakened or even lost following reductions in population abundance or local extinctions (Barrientos et al., 2020). A simplification of ecological network structure (Dunne et al., 2002; Mestre et al., 2022), such as food webs, can change fluxes of matter and energy (Barnes et al., 2018), affecting the functioning of ecosystems and ultimately disrupting the provision of ecosystem services (Barbosa et al., 2017; Dunne et al., 2002; Tylianakis et al., 2008). Ultimately, this simplification of trophic chains can lead to shifts in species distributions indirectly, when roadkill affect prey density or cause a relief of predator pressure (Leighton et al., 2023). Hence, understanding how roadkill affects the dynamics of ecological interactions, namely food webs, is essential to help manage human impacts on biodiversity. Yet, the study of road-induced wildlife mortality on ecological networks remains largely unexplored, probably due to the logistical and financial complexities associated with studying numerous regional food webs across varying road density scenarios.

Here, we build on the work of Grilo et al. (2020) to derive species-specific vulnerability to roadkill based on road density thresholds beyond which local populations may not persist. These authors used a generalized theoretical population model developed by Borda-de-Água et al. (2011) to calculate such thresholds for a collection of European birds and mammals. In parallel, we obtained information on trophic interactions from the TETRA-EU metaweb (Maiorano et al., 2020), which summarises the potential trophic interactions for tetrapod species across Europe. We categorised all focal species (birds and mammals common to the two databases) across Europe, into three trophic levels namely 'top-level', comprising species that solely prey on others; 'intermediate-level', encompassing species that both prey and are preyed upon; and 'basal-level', consisting of species that are exclusively preyed upon. We then built regional food webs, using the same 50x50 km grid (n=4,743 cells) provided by (Grilo et al., 2020), assuming that co-occurring species in each region interact with prey/predators following the metaweb interactions (see Methods).

Using the combined information on road density thresholds and regional food webs, we investigated how food webs can be imperilled when considering the persistent negative influence of roadkill on species persistence. Specifically, we sought to evaluate the extent of potential interaction loss across Europe and trophic levels; and compare, for each species, the amount of distribution area that could be lost or degraded due to road density exceeding *i*) its specific vulnerability threshold (direct effect) and *ii*) that of the species that interact with it i.e., prey and/or predators (indirect effect). We expected higher loss of interactions and higher degradation of range area with increasing road density values. However, given the historical presence of roads in Europe and the higher vulnerability of apex predators to roadkill effects (Rytwinski and Fahrig, 2012), we predicted a higher direct effect for lower trophic levels, and a higher vulnerability of interactions at higher trophic levels due to indirect effects.

Methods

Species vulnerability to roads

Species vulnerability to roads was obtained from previous research on roadkill risk and population vulnerability for European wildlife, including information for 423 birds and 212 mammals (Grilo et al., 2020). A generalised theoretical population model was applied, which calculates species-specific vulnerability using road density thresholds beyond which local populations face the risk of extinction (Borda-de-Água et al., 2011). We used the estimated vulnerability to roadkill to predict potential points of trophic interaction disruption in the event of local species extinction or severe depletion caused by roadkill, using a grid of 50 x 50 km cells overlaid upon the European region.

Building local potential food webs and risk of interaction disruption

Using the same spatial grid as the road vulnerability information (50 x 50 km), we built local trophic structures. Our analysis was guided by the observed interactions outlined in the TETRA-EU metaweb (Maiorano et al., 2020). This metaweb is based on observed interactions obtained from the scientific literature and summarises the potential trophic interactions for tetrapod species (mammals, breeding birds, reptiles, and amphibians) across Europe and the Northern Mediterranean basin. If a trophic interaction between two species was documented in the metaweb, it was considered indicative of their potential interaction within the regional network (cell level).

We characterised the trophic level of each species in the metaweb resorting to a categorical classification, dividing species into top-level (those that only have prey species), intermediate level (those with predators and prey species), and basal species (those that only

have predators). We did this by resorting to the functions 'BasalNodes', 'IntermediateNodes', and 'TopLevelNodes' of the *cheddar* R package (Hudson et al., 2013).

We then used the estimated vulnerability to roadkill to predict potential points of trophic interaction disruption in the event of species extinction or severe depletion caused by roadkill. For each species, we assumed that grid cells exceeding their species-specific maximum road density threshold, i.e., beyond which long-term population persistence becomes improbable (Borda-de-Água et al., 2011), would exhibit an increased probability of losing trophic interactions associated with that species. Extinction simulation was conducted using the function 'RemoveNodes' of the *cheddar* R package (Hudson et al., 2013).

All the computations were conducted in R (R Core Team, 2021), using the R packages cheddar (for network analysis) (Hudson et al., 2013), igraph (for network analysis) (Csárdi et al., 2023), *taxize* (to combine both datasets, the vulnerability dataset and the metaweb) (Chamberlain and Szöcs, 2013), and terra (for R based spatial analysis and for creating the output shapefiles) (Hijmans, 2023). Images were produced in QGIS [44] and R (R Development Core Team, 2022). The dataset is available in Figshare. All code is available on GitHub.

Results

General patterns

Our pool consisted of 551 species obtained from the metaweb and from which a threshold of vulnerability to roadkill were available (see Methods). The pool comprised 12 top-level (2% of total species), 107 intermediate-level (20%), and 432 basal-level species (78%) (see Supplementary material S1 for species names). The three trophic levels currently exhibit varying distributions across Europe (Fig. 1A-C), notably with higher species richness in

regions characterised by lower road density (Fig. 1D), particularly top-level species. This pool of species assembled altogether a mean (±SD) of 2,057±819 predator-prey interactions per grid cell across Europe. A greater number of interactions were observed in mountainous regions like the Pyrenees, Alps, and Carpathians, alongside areas in eastern Europe, regions that exhibit lower road density (Fig. 1E).

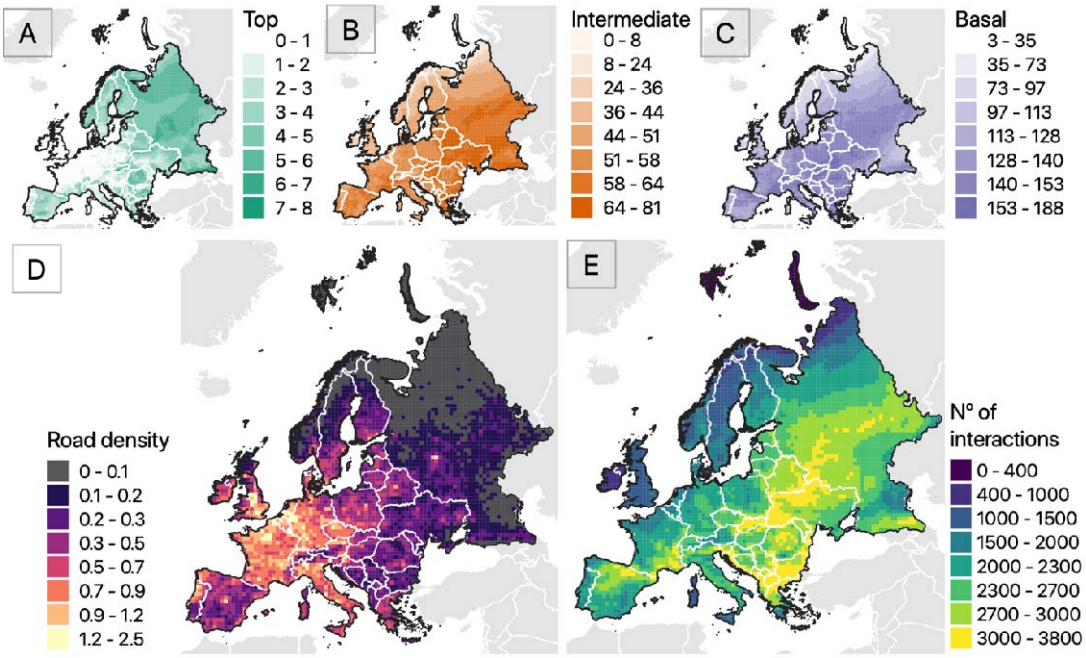

Figure 1 - Richness of top, intermediate and basal level species (A-C), number of interactions (D), and road density in km/km^2 (E), across Europe. All maps use a grid cell resolution of 50x50 km. White lines depict country borders.

Trophic interaction loss

On average, 4.5% (±9.4) of interactions in our regional food webs face potential loss due to roadkill i.e., when road density surpasses the species-specific vulnerability threshold of either the prey or predator engaged in the interaction. Yet, the impact of roadkill on food webs varied spatially, being particularly intense in areas surrounding large European cities, where road density can reach 2.5 km/km² (see Fig. 1D), causing the loss of >90% of potential interactions (Fig. 2A). The loss of interactions in the local food webs seems to have a strong

relationship with road density, reaching a 30% loss when road density approaches 1 km/km² (Fig. 2B).

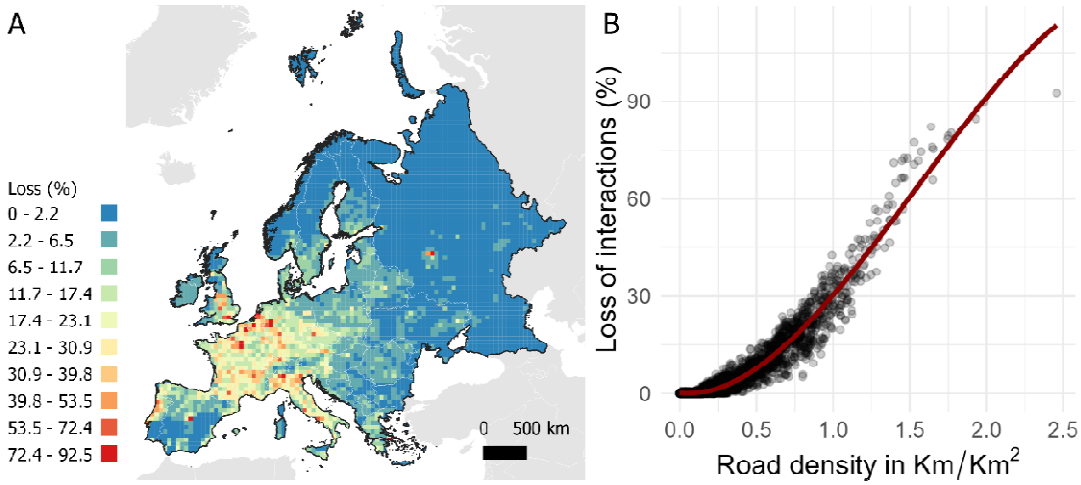

Figure 2 - A) Expected loss of interactions due to roadkill; B) Relation between road density and interaction loss due to roadkill (red line depicts the model fit using polynomial spline with the formula '*y ~ bs(x, df=3)*').

Effects within species range

Among the species examined, 186 (34% of the total) had over 10% of their range with road density surpassing their vulnerability threshold, putting them at significant risk of local extinction due to roadkill (direct effects). These include one top-level, 38 intermediate and 147 basal species (Fig. 3). Noteworthy, the apex predator booted eagle (*Hieraaetus pennatus*) may disappear from 16% of its current range (n=171 grid cells; see Supplementary material S1); the intermediate-level species garden dormouse (*Eliomys quercinus*) might experience a substantial loss or degradation within 43% of its range; and 14 basal-level species may experience losses over 73% of their range. The full range of both mole rats (*Spalax graecus* and *S. zemni*) have road densities surpassing their vulnerability threshold, facing potential local extinctions across its entire territory. This could in turn lead to the loss of 100% of interactions involving predators preying upon these species.

On the other hand, 190 species (34% of the total), including 10 top-level, 81 intermediate-level, and 99 basal-level species, exhibit more than 10% of their range at risk of losing trophic interactions due to indirect effects (Fig. 3). Two top-level species, wolf (*Canis lupus*) and golden eagle (*Aquila chrysaetos*), may experience interaction losses with prey in over half their territory**;** the intermediate-level barn owl (*T. alba*) may see prey losses in over 80% of its range; and the basal-level broom hare (*Lepus castroviejoi*) may experience a predatory release in 91% of its range (Fig. 3). Altogether, these findings strongly imply that the area affected by the detrimental impacts of roadkill extends far beyond what meets the eye. For example, top-level species currently face minor risk of being depleted due to roadkill. But they may suffer from indirect effects of their range area (i.e., at least one prey goes extinct due to roadkill) (Fig. 3).

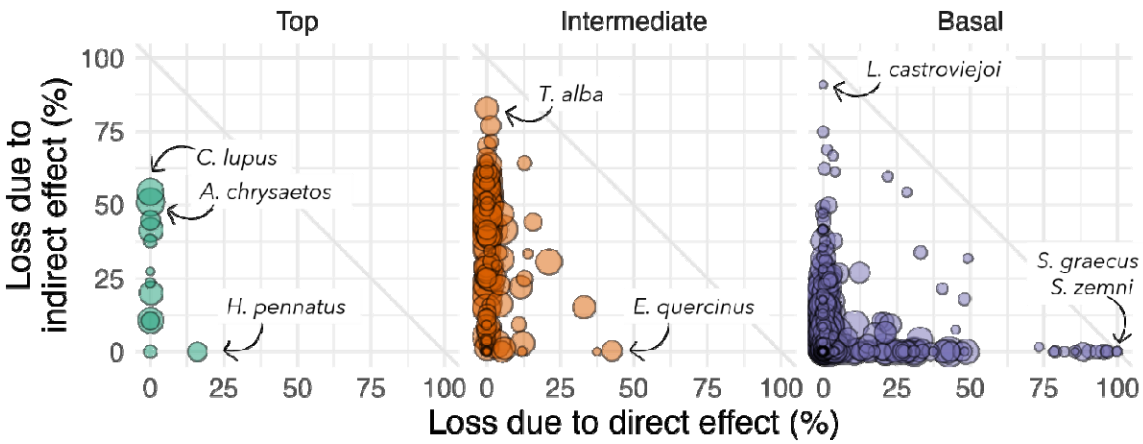

Figure 3 – Range area with potential trophic interaction losses due to direct and indirect effects of roadkill, by trophic level (top, intermediate and basal). The circle radius is proportional to the range of the species. Grey diagonal line represents 100% of range areas affected by combination of direct and indirect effects. Highlighted species are mentioned in the text.

Discussion

Roadkill is expected to have a direct impact on species persistence (Borda-de-Água et al., 2011; Grilo et al., 2020), although such effect has been shown only to a handful of species (Ascensão and Desbiez, 2022; Barrientos et al., 2021). Yet, beyond population level effects,

its repercussions are likely to exert more profound consequences on ecological networks. Our findings indicate that roadkill may significantly reduce the number of trophic interactions, both due to the direct depletion of populations, but also because of indirect effects on food chains, namely the elimination of predators or prey. Furthermore, this loss of interactions occurs differently across space, with a greater incidence near large cities, but also in large regions of Central Europe, Italy and the north of the Iberian Peninsula. Such imbalanced losses may have far-reaching implications for regional food webs, which could ultimately culminate in local extinctions, disturbing ecosystem functioning, and disrupting the delivery of essential ecosystem services.

Overall, top and intermediate species seem to follow a pattern dominated by loss of interactions due to indirect effects of roadkill, with intermediate species having higher range losses than top-level species. Apart from the booted eagle, which presently inhabits an extensive region marked by road densities exceeding its estimated vulnerability threshold, other top-level species like the golden eagle (*Aquila chrysaetos*), brown bear (*Ursus arctos*), or European lynx (*Lynx lynx*), face minimal risk of being depleted due to direct roadkill impact, as their ranges have low road densities. This implies that roadkill may not directly impact the persistence of the majority of apex predators, which is not surprising given that such top-level species are already restricted to habitats with relatively lower human impact and activity, and consequently with low road density areas (Bleyhl et al., 2021; Cretois et al., 2021). Conversely, basal species seems to be highly impacted by direct effects, therefore facing local extinction risk and potentially eliminating the interactions with their predators. Yet, several basal species may also benefit from a release of the predator interactions in their range areas.

We acknowledge that there are limitations in our study: although the metaweb approach offers valuable insights into species ecological associations, it overlooks the spatial

and ecological context of these interactions (Chamberlain et al., 2014; Liu and Gaines, 2022). The distribution and strength of species interactions may differ across different populations and habitats due to environmental conditions and the presence of other species. However, due to the lack of fine grain information on species interactions and intraspecific variability, our approach offers the best available solution to address these gaps of knowledge. On the other hand, undocumented interactions are not accounted in the metaweb, and consequently in our framework. Nonetheless, to our knowledge, this database stands as the most comprehensive resource regarding trophic interactions in Europe. Our use of a large-scale approach, characterised by low spatial resolution and extensive coverage, is likely to minimise biases but restricts its applicability at finer resolutions.

Our findings indicate that the impacts of roads hold profound implications for ecosystem conservation. Roads are likely preventing or hampering the spread of apex predators through direct roadkill (Maxwell et al., 2016; Ripple et al., 2014). The negative correlation between its distribution and road density reflects this restrictive relationship. However, while roadkill may be exerting a lower role in directly depleting top-level species, roads are likely to be constraining the functional connectivity among their populations. For example, a major threat to the Iberian and European lynxes' dispersers is roadkill (Kramer Schadt et al., 2004; Philips, 2020). On the other hand, the loss of prey due to roadkill may contribute to the failure of top-level species to persist throughout dispersal areas. Numerous basal species appear to encompass a significant portion of their ranges with high roadkill risk. Consequently, roads might be more noticeably depleting prey species, while generating less visible effects by limiting the presence of predators through disrupted interactions.

We suggest that roads are contributing and probably accelerating the simplification and contraction of ecological networks (Felipe-Lucia et al., 2020; Heleno et al., 2020). With

the expected massive expansion of road networks, including the construction of 3–5 Mio km of new roads worldwide by 2050 (Meijer et al., 2018), these adverse impacts will likely extend to previously undisturbed ecosystems in developing regions, while exacerbating them in more developed countries. Therefore, immediate action is imperative to address the changes in ecosystems that may arise, namely to preserve food webs, as there is an imminent risk of pushing entire ecosystems beyond their safe limits (Steffen et al., 2015). This requires improving our understanding of the interconnections that occur between transport networks and higher levels of ecological organisation, such as ecological communities and their interactions.

This study carries significant implications for road planning and landscape management strategies, especially concerning protected areas and their connecting corridors. The focus for conserving top predators should revolve around establishing connectivity between high-quality habitat areas, strategically steering away from regions having high road density. For example, wolves and other large carnivores are known to avoid sources of human disturbance, including high road density areas (Bleyhl et al., 2021; Cretois et al., 2021; Rio-Maior et al., 2019). However, their conservation must include measures to prevent the depletion of prey due to roadkill, otherwise top-level species may struggle to persist in the areas they seek to colonize. On the other hand, the roadkill of intermediate and basal-level generalist species warrants a more cautious approach and study. These species have extensive environmental adaptability and a broad dietary spectrum, often having wide distributions throughout Europe. As a result, they interact with a disproportionately large set of coexisting species, playing a fundamental role in the formation of ecological communities and influencing the functioning of ecosystems (Gaston, 2010). As so, their disappearance, namely due to high roadkill rates, may cause substantial losses in predator-prey interactions.

However, the conservation of generalists, and particularly road mitigation targeting those species, is not always a priority.

Overall, road and landscape management should account for the preservation of conditions for species persistence and movement for the different trophic levels. This includes habitat restoration and reducing road fragmentation by implementing tailored measures that bolster the resilience of the different trophic levels within their habitats and road proximity, such as different typologies of road passages (Clevenger et al., 2001; Lesbarrères and Fahrig, 2012). Such targeted species-specific approaches of habitat restoration and functional connectivity could play a pivotal role in mitigating the detrimental impacts of road networks on wildlife and preserving ecological network integrity.

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Supplementary Information

TABLE S1 – Information on species' interaction characteristics.

Metadata of Table S1

Species	Focal species
TLevel	Trophic level
Nint_total	Total number of interactions with this species
Nint_pred	Nº of interactions as predator
Nint_prey	Nº of interactions as prey
Mean.int	Mean number of interactions per region
SD.int	Standard deviation of interactions per region
Nint.at.risk_Direct	Nº of total interactions at risk due to direct roadkill (direct effects)
Nint.at.risk_Direct_as.pred	Nº of interactions at risk due to direct roadkill (direct effects) as predator
Nint.at.risk_Direct_as.prey	Nº of interactions at risk due to direct roadkill (direct effects) as prey
Nint.at.risk_Indirect	Nº of total interactions at risk due to indirect effects
Nint.at.risk_Indirect_as.pred	Nº of interactions at risk due to indirect effects as predator
Nint.at.risk_Indirect_as.prey	Nº of interactions at risk due to indirect effects as prey
Range	Range area in nº of cells
Range_area_risk_Direct	Range area in nº of cells at risk due to direct roadkill
Range_area_risk_Indirect	Range area in nº of cells at risk due to indirect effects
Range_area_risk_Direct%	Range area in % of cells at risk due to direct roadkill
Range_area_risk_Indirect%	Range area in % of cells at risk due to indirect effects