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Rethinking road mitigation priorities through detection-informed interpretation of roadkill data and road crossability

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ABSTRACT

Roads play a critical role in biodiversity loss by reducing species survival and promoting habitat fragmentation. Most roadkill studies focus on single species or localized areas, using roadkill as a direct measure of risk, often overlooking or misinterpreting inherent biases (i.e. carcass-location, persistence and observation biases). In this study, we apply two concepts to better understand the relationship between wildlife-vehicle collisions and habitat connectivity. First, we interpret roadkill locations modelled using species distribution models as indicators of *roadkill detection*, rather than actual roadkill risk. Additionally, we introduce *road crossability*, a measure of habitat connectivity along roads, assessed using circuit theory. We adopt a multispecies approach, analyzing roadkill data from 15 forest mammals with different mobility across different landscapes (natural and anthropized) in northeastern Italy, to investigate the relationship between *roadkill detection* and *road crossability*. Our results show positive correlations between *roadkill detection* and *road crossability* for medium and high mobility species, particularly in anthropized landscape, while low mobility species exhibit a weaker correlation. Combining these metrics, we classified the regional road network into zones with different conservation and mitigation priorities: Priority Areas for Connectivity Improvement (PACoIs), Potential Areas for Roadkill Mitigation (PARoMs), and Potential Areas for Connectivity Preservation (PACoPs). Our study suggests that multispecie *roadkill detection* and *road crossability* assessment hold promise to facilitate more effective conservation strategies and mitigation measures to maintain habitat connectivity and reduce the impact of roads in different landscapes.

1. Introduction

Roads have numerous negative impacts on wildlife and habitats worldwide (Laurance et al., 2014; van der Ree et al., 2015), affecting biodiversity and ecosystems both directly and indirectly (Forman and Alexander, 1998). Roads are well known to cause direct mortality through vehicle collisions (hereafter roadkill, Ament et al., 2023) and significantly alter wildlife movements (Passoni et al., 2021), leading to modified behaviour patterns. In addition to these immediate impacts, roads contribute to habitat loss and fragmentation, which result in population declines, isolation, and a subsequent loss of genetic variability (Lesbarrères et al., 2006; Taylor and Goldingay, 2010). The effects of roads extend beyond individual species, as they fragment habitats, alter ecological connectivity and species interactions (Ament et al., 2023; Laurance et al., 2006). Ultimately, entire communities and ecosystems can be destabilized, leading to long-term ecological consequences.

Among the numerous adverse impacts of roads, wildlife roadkill is one of the most studied (Barrientos et al., 2021; D'Amico et al., 2018). Indeed, several studies have focused on both intrinsic (e.g. life-history traits) and extrinsic (e.g. road characteristics, habitat type) factors influencing roadkill (D'Amico et al., 2015; Visintin et al., 2016). For example, Cook and Blumstein (2013) found that vulnerability of mammals and birds to roadkill was influenced by their diet, with omnivorous

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mammals and herbivorous birds being more vulnerable. González-Suárez et al. (2018) identified body size, reproductive speed and ecological specialisation of the species as factors explaining the roadkill mortality of mammals and birds in Brazil. Among the extrinsic factors, previous studies analysed the relationships between roadkill and road characteristics and traffic volume (Jaeger and Fahrig, 2004; Trombulak and Frissell, 2000), as well as between habitat and landscape features (Fabrizio et al., 2019b; Grilo et al., 2011).

Despite the spatial distribution of roadkill is probably the most studied topic in road ecology (D'Amico et al., 2015; Kreling et al., 2019), the majority of the research has focused on single charismatic and/or threatened species, typically evaluated at local scales, with limited evidence on how wildlife populations are affected (Barrientos et al., 2021). Only recently, more complex multi-species analyses and landscape-scale projects have been carried out, highlighting in particular the critical relationship between habitat connectivity and the spatial distribution of roadkill (Ament et al., 2023). However, achieving a comprehensive understanding of roadkill patterns in relation to habitat connectivity remains challenging due to multitude of influencing factors and the intrinsic characteristics of individual species. Indeed, the scientific literature provides contrasting results. For example, the spatial distribution of supposed roadkill hotspots did not coincide with highly connected areas for felids in Brazil (Cerqueira et al., 2021), and in Canada the relationship between roadkill density and connectivity for moose (*Alces americanus*) was observed to be weak (Laliberté and St-Laurent, 2020). Boyle et al. (2017) found a discrete overlap for herpetofauna, but none at all for mammals. This can obviously vary depending on the species: for example Grilo et al. (2011) found higher mortality of stone marten (*Martes foina*) in well-connected areas, while Girardet et al. (2015) observed that landscape connectivity influenced roadkills for roe deer (*Capreolus capreolus*). These contrasting results may partly reflect the reliance of most studies on satellite-derived data (e.g. forest cover and land use) without validating whether these habitats are actually used by wildlife in their movements (e.g. using telemetry data). Moreover, areas with high connectivity may not coincide with roadkill locations if certain crossing points enable wildlife to traverse roads safely, thereby reducing the likelihood of collisions. Discrepancies of the results may also arise because the spatial distribution of detected roadkills is usually interpreted as a faithful representation of the wildlife-vehicle collisions occurred in a given area, whereas the recent literature showed that approximately one-third of roadkilled wildlife dies far from the road and consequently it's no available to be detected by traditional roadkill surveys (Román et al., 2024). Additionally, this source of error is spatially structured: for example crippling bias is more likely to occur on minor roads compared to highways (Román et al., 2024), as are other biases related to roadkill surveys, such as carcass-persistence bias and carcass-observation bias (Barrientos et al., 2021; Santos et al., 2011). This issue is especially relevant for opportunistic data (such as roadkill data from citizen science), in which not all the roads are surveyed with the same sampling effort (Vercayie and Herremans, 2015). Consequently, we propose that the amount of recorded roadkills in a given area should be interpreted as a *roadkill detection* (Table 1), rather than as a direct measure of roadkill risk. In our framework, *roadkill detection* reflects the spatial variation in the relative likelihood of detecting roadkills, under current data constraints. It does not quantify the actual risk of an animal being killed on the road but rather captures the relative environmental conditions under which roadkills are more likely to be observed and recorded (Table 1). By explicitly acknowledging these detection-related limitations, this metric helps to avoid misleading conclusions and can be used to deepen our understanding of how roadkill patterns relate to habitat connectivity, ultimately supporting road mitigation prioritization. *Roadkill detection* is especially useful in context where data are opportunistically collected and do not allow for formal correction of common roadkill data biases, such as carcass persistence, crippling bias and observation bias.

Our aim is to contribute to the understanding of the relationship between *roadkill detection* and habitat connectivity using a multi-species approach across different landscapes, ultimately supporting more informed conservation planning and road management decisions. Specifically, we investigated *roadkill detection* in relation to habitat connectivity among species with different movement abilities across two contiguous landscapes types: one characterized by relatively intact, natural habitats (i.e. natural landscape), and the other by highly anthropized and fragmented areas (i.e. anthropized landscape). Here we implemented a novel concept: *road crossability*, intended as a specific measure of habitat connectivity across the whole road network of the study area (Table 1). Unlike the broader concept of habitat connectivity, *road crossability* is explicitly road-focused and represents the potential for wildlife to cross specific segments of the road network. It is derived from the assumption that some road segments, depending on adjacent habitats, may present more favourable conditions for crossing attempts. High *road crossability* values indicate that the surrounding habitats provides suitable conditions for potential movements across the road, regardless of whether crossings are successful or safe. By examining the relationship between *roadkill detection* and *road crossability*, we considered contrasting landscapes and a broad spectrum of species with different dispersal capabilities, ultimately contributing to the potential development of more effective conservation strategies to mitigate the impact of roads in different contexts. Indeed, we used these two concepts to propose zoning plans for the road network, identifying potential areas for mitigating road impacts and areas for maintaining connectivity. This approach allowed us to categorize the regional road network into distinct zones, each characterized by different levels of conservation, management and mitigation priorities. Specifically, we defined "Priority Areas for Connectivity Improvement" (PACoIs), zones of high *roadkill detection* and high *road crossability*, where mitigation measures such as wildlife crossings may be required to prevent roadkill and maintain connectivity. The PACoIs represent areas where higher numbers of roadkill could be observed and, at the same time, these areas may also have higher wildlife crossings due to high connectivity. Thus, they could represent location of higher roadkill risk but, without specifically designed and systematic field sampling to account for detection biases, it remains uncertain whether the observed patterns reflect actual roadkill mortality or are predominantly shaped by observation bias. We also

Table 1
Definition of terms used in this study, highlighting conceptual distinctions and relationships. The concepts of *roadkill detection* and *road crossability* are introduced in this study to distinguish the observed spatial patterns of roadkill and potential for road crossing from the broader concepts of *roadkill risk* and *habitat connectivity*.

Term	Definition
Roadkill risk	The probability of wildlife mortality occurring due to vehicle collisions, determined by species distribution, abundance, species traits, and both road/traffic and environmental characteristics. Estimating *roadkill risk* requires correcting for biases in roadkill data, such as carcass persistence, crippling bias and observation bias.
⇒ *Roadkill detection*	A modelled measure describing the spatial variation of detecting roadkills under current data constraints, including carcass-location bias, carcass persistence, and observation bias. It does not indicate the true probability of an animal being roadkilled, but rather it emphasizes how environmental and road features influence where roadkill is more likely to be recorded, given existing detection limitations. *Roadkill detection* is related to *roadkill risk*, but it represents a measure that reflects observed patterns without bias adjustment.
Habitat connectivity	A broader ecological concept that refers to the ease with which animals can move across landscapes between habitat patches, regardless of roads.
⇒ *Road crossability*	The potential of a road segment to be crossed by different groups of species, based on habitat continuity and local road features. High crossability indicates that the surrounding habitat is likely to facilitate crossing attempts but does not imply successful or safe crossings.

defined "Potential Areas for Roadkill Mitigation" (PARoM), which are zones of high *roadkill detection* but low *road crossability*. These zones could have high numbers of roadkill or higher *roadkill detection*, but are unlikely to be frequently crossed, suggesting that other factors influencing roadkill patterns should be considered. Finally, we defined the zones of low *roadkill detection* and high *road crossability* as "Potential Areas for Connectivity Preservation" (PACoP), since these areas could be roads with high wildlife crossings but with characteristics that favour safe crossing or that favour carcass-location bias. The road network zoning approach based on the assessment of *roadkill detection* and *road crossability* provides an initial assessment that can guide mitigation and conservation actions to address road impacts.

2. Materials and methods

2.1. Study area

The study was conducted in Friuli Venezia Giulia region in northeastern Italy, covering 7908 km^2 (Fig. 1). Characterized by a complex geology, an altitudinal range from 0 to 2780 m a.s.l., the study area support high biodiversity, including over 90 mammals (Loy et al., 2019). According to European Environment Agency (EEA, 2024), the region encompasses two biogeographical regions: the alpine and the continental (Fig. 1), covering 47 % and 53 % of the area respectively. The alpine (hereinafter 'natural landscape') is characterized by predominantly natural habitats, with only 6.4 % of the area being affected by human activities (i.e. farming, urbanisation). This region is largely composed of extensive montane mixed forests, featuring species such as *Fagus sylvatica*, *Picea abies*, and *Abies alba* (FVG, 2013). In contrast, the continental region (hereinafter 'anthropized landscape') is dominated by densely populated urban areas and agriculture (75.2 % in total; Appendix A, Table S1). However, in the southeastern area, the broadleaved deciduous woods and Mediterranean scrub of the karstic landscape, with species like *Fraxinus ornus*, *Ostrya carpinifolia*, and *Quercus pubescens,* offer more semi-natural conditions. The road network of the study area covers 13,392 km, mostly located in the lowland (10,994 km in anthropized landscape and 2398 km in natural landscape). Of this network, 86 % are local roads, 5 % regional roads, 4 % national roads and 5 % of highways (Fig. 1).

2.2. Roadkill and species mobility group classification

Roadkill data were recorded from November 2019 to January 2023 and were obtained via the InfoFaunaFVG data repository, created for the monitoring, rescue and veterinary care of debilitated and/or dead wildlife species in the study area (Tomè et al., 2023). All data were opportunistically collected and verified to ensure accurate species identification and determination of the cause of injury or death. From

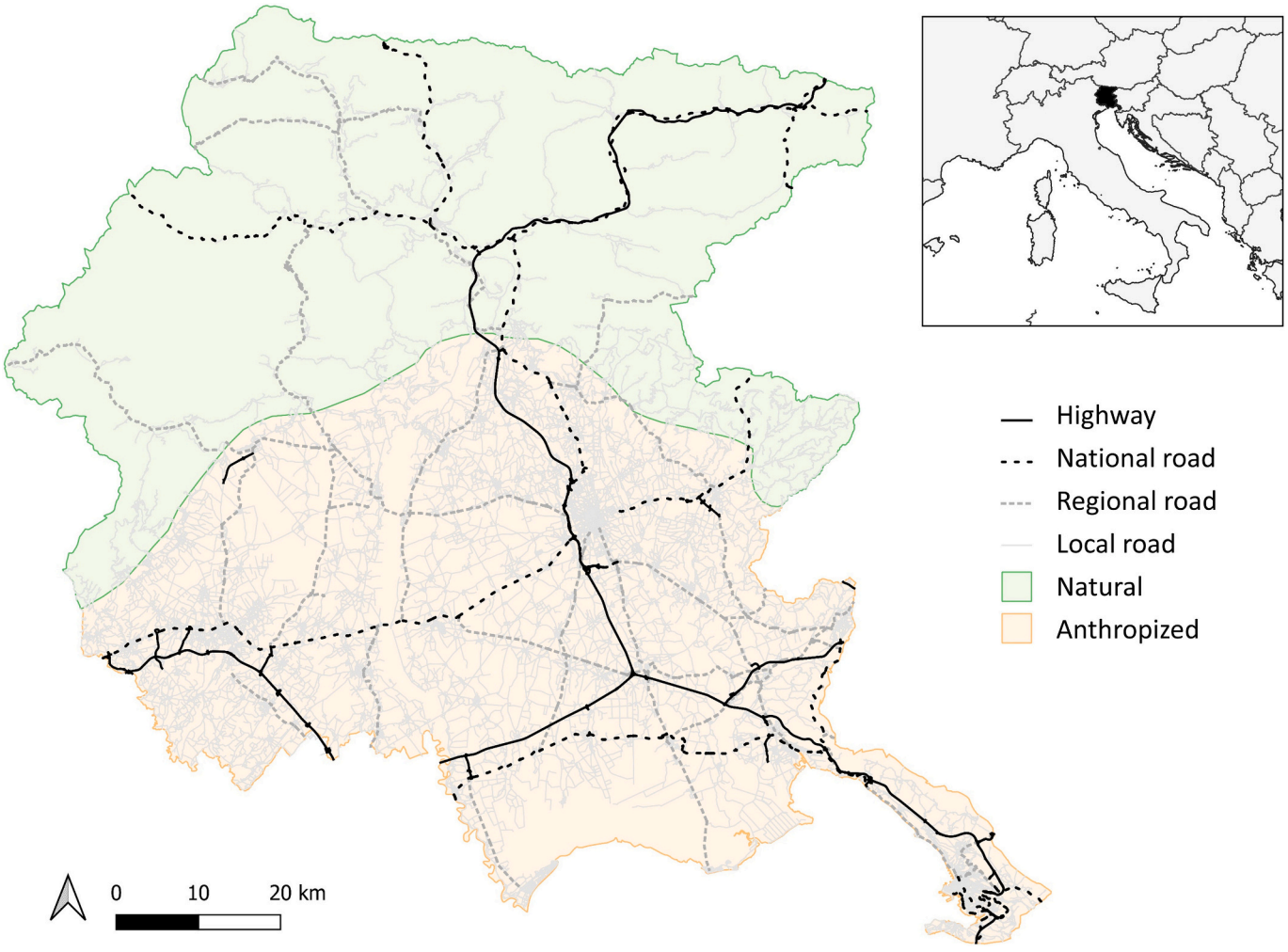

Fig. 1. The road network and landscape types of the study area are depicted, with the 'natural' landscape shown in green and the 'anthropized' in orange. These areas correspond to the alpine and continental biogeographical regions of Friuli Venezia Giulia in northeastern Italy. Shades of black and line types represent various road types, ranging from highways to local roads. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

this repository, we selected records of forest mammals injured or dead by vehicle identified at species level.

We divided forest mammals into three different groups according to their movement ability and body size (Kang et al., 2016). We calculated the median dispersal capacity for each species using allometric equations (Santini et al., 2013), utilizing body size and home range, obtained from the PanTHERIA database (Jones et al., 2009), as input data. Species with a median dispersal distance of less than 5 km were classified as low mobility, those with a median dispersal distance between 5 and 11 km were classified as medium mobility, and those with a median dispersal distance greater than 11 km were classified as high mobility (Appendix A, Table S2).

2.3. Roadkill detection models

We modelled *roadkill detection* along the road network separately for each species mobility group using the maximum entropy algorithm (*MaxEnt*; Elith et al., 2006; Phillips et al., 2006) with the "*ENMeval*" v.2.0.4 R v.4.3.1 (R Core Team, 2023) package (Kass et al., 2021). This method outperformed other presence-only models (Valavi et al., 2022) and it has been previously used to predict road mortality in other studies (e.g., Cerqueira et al., 2021; Fabrizio et al., 2019b). To avoid spatial autocorrelation issues and prior to model fitting, we thinned the roadkill data based on home range information using the "*spThin*" v.0.2.0 R package (Aiello-Lammens et al., 2015). This process involves two steps: (i) species-specific thinning, where roadkill data were filtered for each species based on its specific home range; (ii) group-specific thinning, where roadkill data were filtered using the mean weighted home range of each species' mobility group. The home range of each species was obtained from the PanTHERIA database (Jones et al., 2009) and the mean home range was calculated as the average of the species-specific home range values weighted by the species-specific number of roadkill (Appendix A, Table S2).

In the models, we included predictors likely to influence *roadkill detection* (Clevenger et al., 2003; D'Amico et al., 2015), including i) elevation; ii) Euclidean distance from urban areas, forests, cultivated areas (derived from Corine Land Cover 2018; CLC: https://land.copernicus.eu/en/products/corine-land-cover/clc2018); iii) Euclidean distance to the nearest water bodies, and protected areas (data from IRDAT FVG: https://irdat.regione.fvg.it/consultatore-dati-ambientali-territoriali). All spatial analyses were conducted in QGIS v.3.28.4. We also included the density of highways and national, regional and local roads as predictors in our models (data from IRDAT FVG: https://irdat.regione.fvg.it/consultatore-dati-ambientali-territoriali), which were calculated using moving windows equal in size to the weighted mean home range of each species mobility group (Fabrizio et al., 2019b). All predictors were calculated with a resolution of 30 m, 60 m and 120 m for the low, medium and high mobility groups to match the subsequent connectivity analyses. To avoid multicollinearity among predictors we removed those with Variance Inflation Factor > 3 (Zuur et al., 2010). Given the possibility that the non-random distribution of our data could lead to biased predictions from *MaxEnt* models (Kramer-Schadt et al., 2013), we created bias maps for each species group by constructing Gaussian kernel density maps of their roadkill (Worton, 1995). We subsequently overlaid to these bias maps 10,000 background points (Fourcade et al., 2014) constrained within a buffer around the road network of 220 m (for low), 660 m (for medium) and 2400 m (for high) radius matching the weighted mean home range size for each species mobility group (Fabrizio et al., 2019b).

MaxEnt models were trained and tuned using the ENMevaluate function in the "*ENMeval*" v.2.0.4 R package (Kass et al., 2021) with the maxent.jar algorithm ("*dismo*" v.1.3–14 R package; Hijmans et al., 2020). We chose the 'block' method for data partitioning because it is particularly useful to generalize the models beyond the specific environmental conditions present in the training data, thus evaluating transferability to new conditions (Kass et al., 2021). We used the linear and quadratic feature combinations to ensure more ecologically realistic response curves (Bateman et al., 2016) and we tested regularization multipliers between 0.5 and 2, with 0.5 steps, resulting in a total of 12 models (Kass et al., 2021). The model with the lowest Akaike Information Criterion corrected for small sample size (AICc) was selected (Anderson and Burnham, 2002). We used the area under the receiver operating characteristic curve (AUC; Boyce et al., 2002), the difference between calibration and evaluation AUCs (AUCdiff; Warren and Seifert, 2011), the Boyce index (CBI; Hirzel et al., 2006), and the omission rate at 10th percentile to assess models performance.

2.4. Road crossability modelling

We applied circuit theory to model forest habitat connectivity in the study area and consequently *road crossability* along the road network (McRae et al., 2008) using the "*Circuitscape*" package in Julia v.1.8.0 (Hall et al., 2021). In "*Circuitscape*", the landscape is represented as a conductive surface where low resistances denote ease of movement and high resistances indicate barriers (McRae et al., 2009). Focal nodes represent locations from and to which movement flow is to be modelled (McRae et al., 2009). Applying circuit theory, areas with higher current density represent greater animal movement, i.e. wildlife corridors (Wade et al., 2015). The critical step in movement flow modelling is the definition of resistance surfaces, which can be parameterised by several approaches (Dutta et al., 2022). Considering that the multispecies focus of our research required the representation of different landscape permeabilities for distinct species, we chose the alternative approach proposed by de Sousa Miranda et al. (2021) to design the resistance surface. This implied the development of a set of resistance surfaces where possible combinations of resistance values were given for each land cover class. According to ecologically meaningful classes for our species, we reclassified the CLC by merging classes with similar environmental characteristics in order to obtain five classes: forested areas, urban areas, agricultural areas, heterogeneous and non-forested natural areas (see Appendix A, Table S1 for more details). Heterogeneous areas included diverse land covers like cultivation with significant areas of natural vegetation and agroforestry, while non-forested natural areas covered natural features without trees, such as grassland and pastures. We used the reclassified map of land cover as the basis for designing the set of resistance surfaces. As in de Sousa Miranda et al. (2021) and Bowman et al. (2020), we considered the resistance values ranging from 1 (no resistance) to 100 (maximum resistance) to animal movement. For all the resistance surfaces, we assigned the lowest resistance to forest class, as we have considered mammals with high forest habitat suitability, and the highest resistance to urban areas. For the three remaining land cover classes, we assigned three resistance values, i.e. high (90), medium (50) and low (10), taking into account the different levels of resistance for each class (de Sousa Miranda et al., 2021). Altogether, we defined 27 distinct resistance surfaces based on all possible combinations of the resistance values.

Our multi-species approach required us to consider not only the different levels of landscape permeability to species movement, but also the different grains of resistance surface (pixel resolution). The grain should match the perceptual grain of the species, depending on the specific type of connectivity being modelled, and should be selected based on the species characteristics such as organism size, dispersal and movement type (Wade et al., 2015). Since we included species with different characteristics, we selected three different spatial resolutions of the resistance surfaces. Based on the movement capacity of the species, we chose a pixel size of 30 m for species with low dispersal ability, 60 m for species with medium dispersal ability and 120 m for species with high dispersal ability (Wade et al., 2015). This resulted in a total of 81 resistance surfaces (i.e. 27 resistance surfaces for each spatial resolution).

For each of the resistance surfaces, we run a model setting the 8-cell neighbourhood rule and the pairwise modelling mode (McRae et al.,

2013). We randomly placed 50 focal nodes in a 30 km buffer around the study area, corresponding to approximately 20 % of the maximum length in our study area, to remove the effects of high current densities near the node placement (Koen et al., 2014). Each model returned a cumulative current density map. We then summed these to obtain a final consensus map for each resolution, thus obtaining a 30 m pixel map, a 60 m pixel map and a 120 m pixel map (de Sousa Miranda et al., 2021).

2.5. Roadkill detection and road crossability relationship

To assess the correlation between *roadkill detection* and *road crossability* we used the Sperman's correlation coefficient (ρ; Zar, 2005). Specifically, we calculated ρ by considering the pixel values of *roadkill detection* and *road crossability* for the whole road network and separately for the natural and the anthropized landscapes, to test whether the correlation between *roadkill detection* and *road crossability* differs between areas with different environmental conditions. Before estimating the correlation, we recalculated both *roadkill detection* and *road crossability* using moving windows with a size equal to the weighted mean home range for each species mobility group. In this way, we accounted for the effects of the surrounding environments within the species' home range. To consider only the relationship along the road, we then clipped both *roadkill detection* and *road crossability* layers for each group using a buffer around the road network of 30 m, 60 m and 120 m for low, medium and high mobility.

Finally, we categorised both *roadkill detection* and *road crossability* maps into terciles, thus dividing their values into low, medium and high (Medrano-Vizcaíno et al., 2023). Nine joint categories were obtained and mapped using bivariate choropleth maps in QGIS v.3.28.4. In this way, we identified and mapped the PACoIS (both *roadkill detection* and *road crossability* high), PARoMs (high *roadkill detection* and low *road crossability*) and PACoPs (low *roadkill detection* and high *road crossability*). This procedure was repeated for the entire study area and separately for the natural and anthropized landscapes. Then, for each of the nine categories, we calculated the density of roadkill and the percentage of the road network included in each category.

3. Results

From November 2019 to January 2023, 4882 roadkill (involving dead or injured animals) of 15 mammals were recorded across the road network in our study area (Appendix A, Table S2). Species characteristics vary widely, from the body size and home range of the edible dormouse (*Glis glis*) (0.13 kg and 0.001 km^2) to those of the Eurasian wolf (*Canis lupus*) (31.76 kg and 159.860 km^2; Appendix A, Table S2). The low mobility group included a total of 81 roadkill of five species: *Glis glis*, *Sciurus vulgaris*, *Erinaceus europeaeus*, *Mustela nivalis* and *Mustela putorius* (Appendix A, Table S2). The medium mobility group included a total of 3961 roadkill of seven species: *Meles meles*, *Felis silvestris*, *Martes martes*, *Martes foina*, *Capreolus capreolus*, *Canis aureus* and *Vulpes vulpes* (Appendix A, Table S2). The high mobility group included 840 roadkill of three different species: *Sus scrofa*, *Cervus elaphus* and *Canis lupus* (Appendix A, Table S2). The most common species recorded was roe deer *Capreolus capreolus*, followed by red fox *Vulpes vulpes*, European badger *Meles meles*, wild boar *Sus scrofa* and red deer *Cervus elaphus*. The low mobility group had a weighted mean home range of 0.12 km^2, the medium mobility group 1.38 km^2 and the high mobility group 18.18 km^2.

Model performance values of the best fitting models for *roadkill detection* ranged from 0.63 to 0.70 AUC testing and 0.49 to 0.80 CBI (Table 2). The differences between training and testing AUCs (AUCdiff) were low for all species groups, ranging from 0.08 to 0.12, indicating limited overfitting problems, and the 10th percentile omission rates ranged from 0.13 to 0.20, indicating good prediction accuracy (Scridel et al., 2021; Table 2).

For the low mobility group, the variables that contributed more to the final model were the distance from cultivated and urban areas (quadratic relationship), as well as the density of national roads (quadratic) and highways (negative) (Appendix A, Fig. S1 and S2, Table S3). The *roadkill detection* for the medium mobility group was mostly affected by density of local roads (negative), the distance from cultivated (positive) and forested areas (negative), and the density of national roads (positive) (Appendix A, Fig. S3 and S4, Table S4). The best model for the high mobility group showed that *roadkill detection* increased at lower altitudes, near forested areas and at greater distances from cultivated areas (Appendix A, Fig. S5 and S6, Table S5). The outputs of the *MaxEnt* models indicated high *roadkill detection* for all mobility groups located in the natural landscape (Fig. 2). In contrast, in the anthropized landscape, medium and high mobility groups showed a higher *roadkill detection* near natural and forested areas, especially in the south-eastern region (karst), while for the low mobility group higher *roadkill detection* is predicted near urban areas (Fig. 2). The *Circuitscape* outputs showed significantly higher cumulative current in the northern part of the study area (natural landscape) and in the south-east region (karst), while current values decreased towards the south-west (Fig. 2).

We found notable differences in the correlations between *roadkill detection* and *road crossability* across species mobility groups and landscapes (Table 3). In the entire study area, our results showed no correlation for low mobility group ($\rho = -0.06$), and a positive correlation for medium ($\rho = 0.53$) and high mobility groups ($\rho = 0.73$; Table 3). We also found notable differences in the correlations between *road crossability* and *roadkill detection* between the natural and anthropized landscapes. Indeed, positive correlations were found in the anthropized landscape, similar to those found for the whole study area, with higher coefficient values associated with species movement ability (Table 3). Conversely, in the natural landscape, where *roadkill detection* and *road crossability* were generally higher, correlations were weaker or absent compared to those in the anthropized landscape (Table 3).

The bivariate choropleth map (Fig. 3) determined the location of the PACoIs, PARoMs and PACoPs (Fig. 4) for each species mobility group and landscape. The maps of the low mobility group showed less overlap of the PACoIs compared to those of the medium and high mobility group (Figs. 3 and 4; Appendix A, Tables S6, S7 and S8). This difference was more pronounced in the anthropized landscape, where the percentage of the road network classified as high *road crossability* and high *roadkill detection* was 8.86 % for the low mobility group, 16.04 % and 21.93 % for medium and high mobility group (Appendix A, Table S8). In the natural landscape, only areas with high *roadkill detection*, i.e. PARoMs, contained higher roadkill densities (Appendix A, Table S7). In contrast, in the anthropized landscape, higher roadkill densities were found in areas with both high *roadkill detection* and *road crossability*, i.e. PACoIs, and in areas with high *roadkill detection* only, i.e. PARoMs (Figs. 3 and 4,

Table 2
Sample sizes ("thinned roadkill") used in the *roadkill detection* analyses, alongside the MaxEnt best-performing model settings and performance metrics for each species mobility group. "FC" denotes the feature classes: "Linear" (L), "Quadratic" (Q), and the hybrid (LQ) model; "RM" refers to the Regularization Multiplier; "AUC" stands for the Area Under the Curve; and "CBI" denotes the Continuous Boyce Index. "OM-10" represents the 10th percentile threshold omission rates.

Species mobility group	Thinned roadkill	FC	RM	AUC training	AUC testing	AUC diff	CBI training	CBI testing	OM-10
Low	79	LQ	0.5	0.782	0.698	0.085	0.945	0.698	0.204
Medium	2656	Q	0.5	0.655	0.632	0.098	0.995	0.802	0.133
High	164	LQ	1	0.678	0.644	0.125	0.960	0.489	0.165

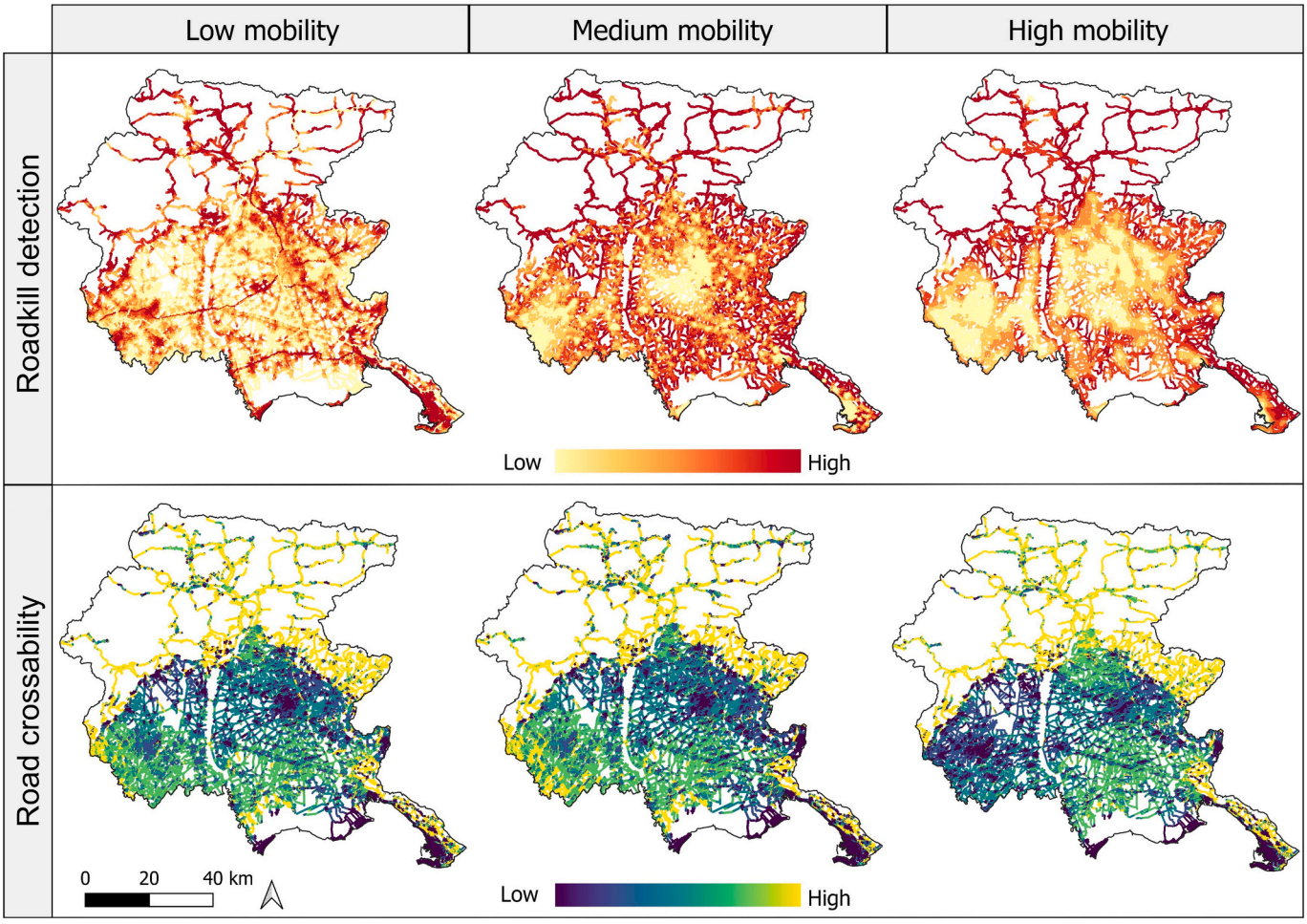

Fig. 2. *Roadkill detection* and *road crossability* recalculated using moving windows equal in size to the weighted mean home range of low, medium and high species mobility groups along the road network of the study area.

Table 3
Results of the Spearman (ρ) correlations between *roadkill detection* and *road crossability*, recalculated using moving windows equal to the weighted mean home range for the study area and the two landscapes for each mobility species group.

Species mobility group	Study area	Natural landscape	Anthropized landscape
Low	−0.058	−0.165	−0.266
Medium	0.527	0.229	0.374
High	0.726	0.100	0.602

Appendix A, Table S8). The PACoIs of the low mobility group were more limited and scattered than those of the medium and high mobility groups, which are particularly concentrated in the south-east and north of the anthropized landscape, corresponding to the presence of more natural areas (e.g. karst, Fig. 4). Similarly, PARoMs are dispersed for low mobility group and concentrated in the central-east of the anthropized landscape for medium and high mobility groups. On the other hand, PACoPs are widespread for the low mobility group and more restricted for the high mobility group (Fig. 4).

4. Discussion

By applying the concepts of *roadkill detection* and *road crossability*, our study offers an alternative perspective on the relationship between road mortality and habitat connectivity. We use them as tools within a broader framework for prioritising roads for connectivity conservation (PACoPs), and road impact mitigation (PARoMs and PACoIs). Our findings demonstrate the complexity of the relationship between *roadkill detection* and *road crossability*, highlighting the variability among species with different movement abilities and across distinct landscapes. Indeed, our results revealed a positive correlation between *roadkill detection* and *road crossability* for medium and high mobility species groups, whereas no correlation was observed for low mobility species. Furthermore, a clear distinction emerged between the two landscapes we considered, the natural and anthropized landscape. Correlation patterns within the anthropized landscape resembled those of the entire study area, where the degree of overlap between wildlife corridors crossing roads and areas of high *roadkill detection* decreased with increasing species mobility. In contrast, in the natural landscape, correlations were weaker or absent for all the species groups, suggesting region-specific factors influencing wildlife mortality and movement.

Species with different movement abilities respond differently to the presence of roads due to their distinct ecological and behavioural traits (Rytwinski and Fahrig, 2012). High and medium mobility species tend to cover larger areas, making them more susceptible to encountering roads (González-Suárez et al., 2018), and therefore have higher *roadkill detection* in areas where the movement is facilitated, i.e. with high *road crossability*. This may explain the relationship found for these species' groups, which have a higher overlap of high *roadkill detection* areas with high *road crossability* areas. Conversely, low mobility species have smaller home ranges and fewer dispersal movements, limiting their exposure to roads (Rytwinski and Fahrig, 2012). This limited movement

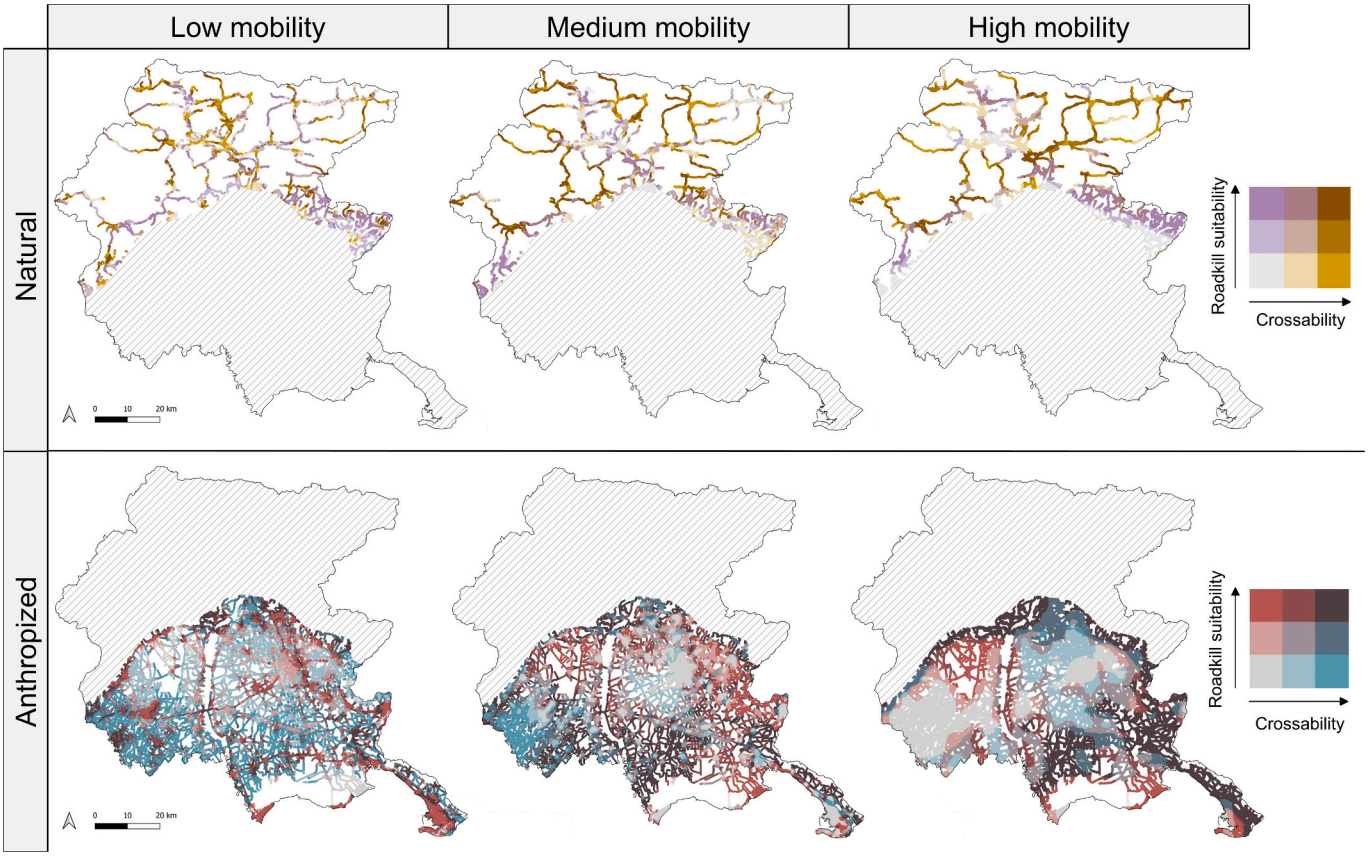

Fig. 3. Bivariate choropleth maps highlighting the nine categories based on terciles values for *roadkill detection* and *road crossability*. Class values were calculated using moving windows according to the weighted mean home range. The terciles were calculated separately for the two landscape type (natural and anthropized) and for each species mobility group (low, medium and high).

range and the weak correlation found between *road crossability* and *roadkill detection* suggest that interactions with roads are less frequent and the roadkill pattern is more dependent on local habitat characteristics rather than wider landscape connectivity. Furthermore, studies have demonstrated the barrier effect of roads on mammals (Rytwinski and Fahrig, 2015), affecting species with varying mobility (Chen and Koprowski, 2019; Grilo et al., 2018). Chen and Koprowski (2019) found that the barrier effects of roads decrease as species' body size, and consequently movement abilities, increase. Medium-sized carnivores and large ungulates can easily cross minor roads but tend to avoid high-traffic roads (Underhill and Angold, 2000), whereas narrow, low-traffic roads may inhibit small mammals' movement (Galantinho et al., 2022). Though with species-specific variations, large mammals are generally less susceptible to roads' barrier effect than small mammals, as even narrow roads can significantly reduce their crossing. The barrier effect may also explain the low correlation found between *road crossability* and *roadkill detection* for the low mobility species group: although our modelling identified wildlife corridors for low mobility species, some of these corridors crossing roads could not be effectively used because of the barrier effect.

Another interesting result was the landscape-level difference in the relationships between *road crossability* and *roadkill detection*. Both factors varied greatly between natural and anthropized landscape, with generally higher *crossability* and *roadkill detection* in the natural (Fig. 2). However, for medium and high mobility species, correlations were weaker or absent compared to the anthropized landscape, suggesting that in fragmented areas, connectivity may play a more important role in shaping roadkill patterns. This can be attributed to the natural landscape's higher permeability and more extensive forested areas, which facilitate multiple movement pathways for wildlife (Pither et al., 2023). Consequently, the dispersed movements in this landscape could reduce the likelihood of wildlife being channelled into specific road crossings where there would be higher likelihood of roadkill. *Circuitscape* models are also designed to highlight movement bottlenecks where high current densities are more concentrated due to high resistance in the surrounding areas (McRae et al., 2008). These movement bottlenecks are particularly evident in the anthropized landscape, where high fragmentation of forested areas force wildlife to move more frequently through human-altered environments (Hilty et al., 2019). As animals move between isolated forest habitat patches using well-defined and concentrated movement corridors, they frequently encounter roads, increasing the likelihood of roadkill. Considering this, the positive correlation observed for medium and high mobile species could be attributed to increased movement along these corridors, increasing their exposure to specific road crossing points with higher *roadkill detection*.

Our multi-species approach was similarly used in both connectivity (de Sousa Miranda et al., 2021) and roadkill (Kang et al., 2016) studies. One of the main advantages of this approach is its ability to create general models that can be applied to a wide range of species, facilitating more comprehensive conservation strategies, but it has inherent limitations. The *Circuitscape* and *Maxent* models used may suffer from reduced accuracy when different species are grouped together, potentially lacking the precision of species-specific models. This could lead to less accurate predictions for individual species, as the unique ecological and behavioural characteristics of each species may not be fully captured. Therefore, the inclusion of species-specific analysis in future studies could help refine predictions, enhancing the applicability of results to species-level conservation planning and management. Despite this, our results are coherent with those from species-specific studies. For example, in our same study area the habitat connectivity and

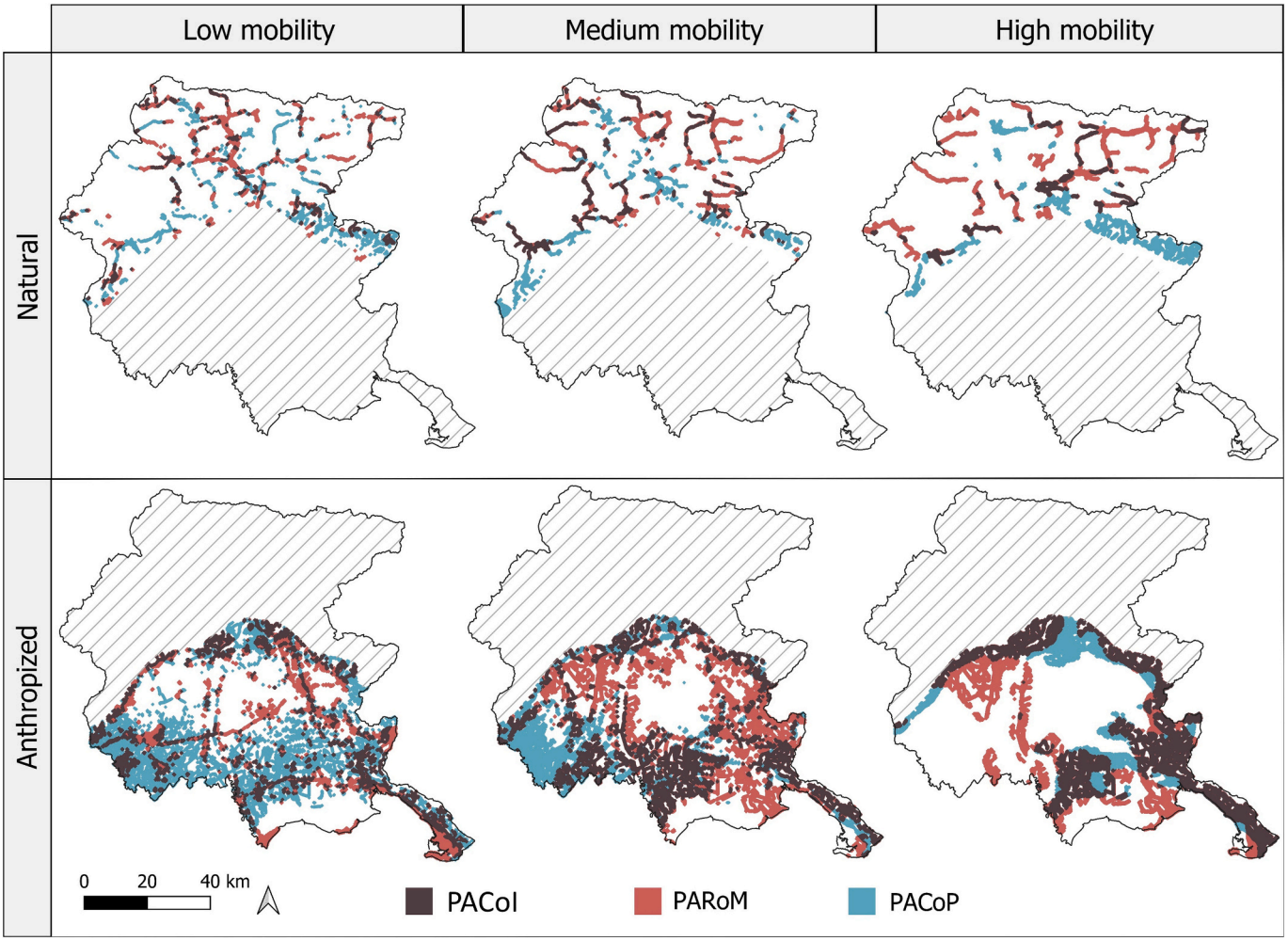

Fig. 4. Spatial distribution of the Priority Areas for Connectivity Improvement (PACoI), Potential Areas for Roadkill Mitigation (PARoM) and Potential Areas for Connectivity Preservation (PACoP) across the two landscape types (natural and anthropized) and for low, medium and high species mobility groups.

roadkill models highlight similar results for golden jackal, one of our medium mobility species (Frangini et al., 2022; Torretta et al., 2020). Mayer et al. (2021) found that more vehicle collisions of red deer occurred in areas with high forest cover as found for the high mobility species in our study, while the occurrence of roadkilled hedgehogs was positively associated with cultivated areas, as for the low mobility species (Canova and Balestrieri, 2019). Similar to findings from other studies, we observed that road type, used as a proxy for traffic volume and speed, plays a significant role in explaining roadkill patterns (e.g., D'Amico et al., 2015; Trombulak and Frissell, 2000). In particular, regional roads, which represent an intermediate infrastructure in our study area and are characterized by intermediate traffic volumes and permitted vehicle speeds, emerged as important predictors of roadkill distribution. This was particularly the case for the European badger (Fabrizio et al., 2019a) and the European polecat (Russo et al., 2020), which is consistent with our models for medium and low mobility species, respectively.

Recent attention to biases in roadkill data is increasingly highlighting their importance and potentially revolutionising road ecology studies (Barrientos et al., 2021, 2018; Román et al., 2024). Indeed, roadkill data, especially those collected opportunistically, are often subject to biases such as carcass-location, persistence and observation bias, which can distort the interpretation of roadkill risk and distribution. By redefining roadkill locations as a measure of detection rather than actual risk, our approach provides a more nuanced understanding and, while acknowledging the limitation, presents a more realistic interpretation of what roadkill locations mean. We emphasise the need for future research to explicitly incorporate bias correction methods into spatially explicit modelling frameworks, which will be essential to improve the reliability of roadkill data interpretation and advance road management and impact mitigation. One well-established approach that can explicitly account for detectability is the occupancy modelling framework (MacKenzie et al., 2002). Occupancy models allow for the estimation of the true probability that a site is occupied by a species while simultaneously correcting for the probability of detecting the species if it is present, i.e. detection probability. It is important to note that our use of the term *roadkill detection* differs fundamentally from detection probability in occupancy models: while detection probability is an explicit statistical parameter estimated from replicated surveys (MacKenzie et al., 2002), *roadkill detection* in our study is a measure derived from presence-only roadkill records, reflecting spatial variation in the condition under which roadkills are likely to be observed. Occupancy models hold great potential for roadkill research, as they provide a rigorous means of disentangling true roadkill risk from roadkill data biases. However, they require a structured and often intensive sampling design, including repeated surveys of the same segment of roads within defined sampling periods. This make their application challenging for many roadkill databases, particularly at large spatial scales, where data are frequently collected opportunistically, as in our study, or originate from citizen science projects, which often violate the assumptions of occupancy models and lack the necessary replication for their implementation. Our study highlights the importance of carefully considering

the limitations and potential biases of roadkill data when interpreting model outputs. In particular, we support a more cautious use of the term roadkill risk in studies where data bias corrections are not possible, as model outputs may not always reflect true risk patterns.

By using *roadkill detection* combined with the concept of *road crossability*, we provided a first assessment of road impacts and zoned the road network based on the potential conservation and/or management measures required. This assessment could guide conservation and mitigation efforts by identifying different areas that require further investigation to accurately place mitigation measures. The PACoIs could represent true roadkill hotspots, as many animals could be roadkilled or more detected and *road crossability* is potentially high. In these areas, once the roadkill hotspot has been confirmed by further analysis, mitigation measures will be required to prevent roadkill and maintain connectivity, such as wildlife crossings. Once confirmed by further analysis, the PARoMs may represent roads with high mortality due to some road characteristics that increase the risk to be roadkilled that should be removed as a mitigation measure. Finally, the PACoPs should be further investigated to understand whether these areas actually have few roadkill or whether they are areas particularly suited to roadkill data bias. If roadkill numbers are indeed low, the factors influencing them (e.g. low traffic) should be preserved to maintain connectivity.

Our zoning approach included the complex and varied relationships between species groups and different landscape types, but the method can be reproduced and adapted to other species or taxa and different environmental conditions, providing a versatile tool for guiding road impact mitigation and conservation planning.

CRediT authorship contribution statement

Federica Fonda: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marcello D'Amico:** Writing – review & editing, Supervision, Conceptualization. **Francesco Petruzzellis:** Writing – review & editing, Methodology. **Davide Scridel:** Writing – review & editing, Methodology. **Stefano Pesaro:** Writing – review & editing, Data curation. **Paolo Tomè:** Writing – review & editing, Data curation. **Giovanni Bacaro:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111619.

Data availability

Roadkill data are available in the "InfoFaunaFVG monitoring and surveillance network" dataset in the Global Biodiversity Information Facility (GBIF) platform. InfoFaunaFVG monitoring and surveillance network.

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