









Research article

Road mortality risk of a protected felid across fragmented and heterogeneous landscapes in Central Europe



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A B S T R A C T

Roads are a major driver of habitat fragmentation, creating mosaic-structured landscapes where some species can adapt, and others struggle to survive. In increasingly fragmented landscapes, highly mobile species, including mammalian carnivores, are frequently exposed to roads as they move between habitat patches to access resources such as shelter and prey. However, understanding the factors influencing carnivores' road mortality in human-modified landscapes remains limited, partly due to a lack of data at broad spatial scales. Yet, the European wildcat (*Felis silvestris*) serves as an ideal model species to examine carnivore-vehicle collision risk across diverse environmental conditions, as it occupies large home ranges in diverse habitats. We conducted the first national-scale assessment of wildcat-vehicle collisions, applying a use-availability framework to 827 recorded collisions across Germany. Our study reveals a complex interplay of factors influencing wildcat road mortality in heavily fragmented and heterogeneous landscapes. The highest collision risk occurred on roads with intermediate to high expected traffic volumes, posted speed, and widths. Collision risk was higher in favourable habitats characterised by minimal built-up areas and low road density. The risk peaked in areas with moderate to dense tree cover and increased with higher habitat diversity, corresponding to areas where both refuge and hunting grounds occur. Using our model, we mapped wildcat-vehicle collision risk across Germany's road network, validating that existing mitigation measures are well placed and highlighting road sections where further intervention is needed to support the persistence of wildcat populations.

1. Introduction

Humans have drastically changed ecosystems worldwide, resulting in enormous costs to biodiversity and ecosystem functioning (Pereira et al., 2010). One of the most critical forms of landscape modification is

the ever-growing global road network, which has exceeded 40 million km in recent decades and is expected to increase by at least 25 million km by 2050 (Dulac, 2013; Laurance et al., 2014). Roads exert cumulative impacts on landscapes and are a major driver of (i) habitat loss, through the conversion of natural land cover into roads and related

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land-use changes in surrounding areas, and (ii) habitat fragmentation, where natural habitat is divided into smaller, more isolated patches (Angelsen and Kaimowitz, 1999; Coffin, 2007; Haddad et al., 2015). This can result in mosaic-structured landscapes composed of natural, agricultural, and urban areas, dominated by edge habitats (Bischof et al., 2017; Saunders et al., 2002). Animals that are adapted to use a variety of habitats, including both closed and open vegetation, may exploit these heterogeneous landscapes (Blair, 2001; Sih et al., 2011) but could face increased exposure to roads, vehicular traffic, and associated mortality risk (Found and Boyce, 2011; Gunson et al., 2011; Malo et al., 2004).

Mammalian carnivores are particularly vulnerable to roads and related landscape changes (Ceia-Hasse et al., 2017; Grilo et al., 2015). Their high mobility increases the likelihood of road crossings, raising the risk (i.e. probability of occurrence) of vehicle collisions — a frequent cause of mortality for many carnivores (e.g. Ferreras et al., 1992; Snow et al., 2012; Taylor et al., 2002). Given carnivores' low reproductive rates, this can potentially lead to significant population declines (Fahrig and Rytwinski, 2009). For forest-dwelling carnivores, roads near or bisecting core habitats, such as closed-canopy forests or shrublands with minimal urban development, are especially risky (Garrote et al., 2018; Russo et al., 2020; Schmidt et al., 2020). Nonetheless, as landscape modification by humans continues to increase, some species have shown an ability to adapt to moderately fragmented landscapes (Basille et al., 2013; Tigas et al., 2002), provided that sufficiently heterogeneous habitats, offering both vegetation cover for shelter and open areas for hunting, remain (Fleschutz et al., 2016; Ruiz-Villar et al., 2023). Under these conditions, carnivores may be especially exposed to traffic and the risk of vehicle collisions as they move between habitat patches to access shelter and forage (Fleschutz et al., 2016; Kim et al., 2019; Tigas et al., 2002). Yet, the impact of habitat heterogeneity (represented by a mosaic of open and closed vegetation) on carnivore road mortality remains understudied. Moreover, limited data at broad spatial scales that comprise remote forests and fragmented, human-modified landscapes hinders comparisons of collision risk across diverse environments.

To address this gap, we analysed the spatial patterns of 827 wildlife-vehicle collisions involving the strictly protected European wildcat (*Felis silvestris*) (Bern Convention and the EU Habitats Directive) in the heavily fragmented and heterogeneous landscapes of Germany (Kramer-Schadt et al., 2004; Westekemper et al., 2021). Wildcats are threatened by habitat loss and fragmentation (Anile et al., 2019; Beugin et al., 2020; Gil-Sánchez et al., 2020), and roads have emerged as the main source of mortality and impediment to gene flow (Bastianelli et al., 2021; Klar et al., 2009; Westekemper et al., 2021). Wildcats maintain large home ranges (1–150 km²; Ruiz-Villar et al., 2023) across different habitats. Despite being dependent on forests and related vegetation cover (Anile et al., 2019; Jerosch et al., 2010; Klar et al., 2008), wildcats also use moderately fragmented and heterogeneous landscapes that provide shelter and high densities of their prey — rodents and rabbits (Klar et al., 2008; Monterroso et al., 2009; Portanier et al., 2022). These habitats include shrubland-pastureland ecotones (Lozano et al., 2003; Monterroso et al., 2009), forest edges (Jerosch et al., 2010; Klar et al., 2008) and low-intensity agricultural areas with structures such as hedgerows, shrubs, and small clusters of trees (Jerosch et al., 2017; Ruiz-Villar et al., 2023). Their habitat plasticity and high mobility make wildcats a perfect model species to explore variations of carnivore-vehicle collision risk across diverse environmental conditions. While factors increasing wildcat-vehicle collision risk have been identified on the local scale (Klar et al., 2009), a large-scale assessment that allows transferability of results to other regions or environmental contexts is still missing.

We analysed conditions at wildcat-vehicle collision locations with a use-availability design including variables describing roads (road category, width, and sinuosity) and surrounding landscape characteristics (land cover, road density, habitat heterogeneity, and topography). We anticipated that road properties would be the primary determinant of road crossing hazard (Visintin et al., 2016) and, thus, the risk of wildcat-vehicle collisions (*Hypothesis 1*). Specifically, wider roads with

moderate to high expected traffic volume and vehicle speed should increase the risk of wildcat mortality (*Prediction 1*). Furthermore, since favourable habitats in proximity to roads increase the likelihood of animals' presence and thus their exposure to roads (Grilo et al., 2009; Gunson et al., 2011; Visintin et al., 2016), we hypothesised that wildcats are at greater risk from roads in favourable habitats characterised by little urban development (*Hypothesis 2*). Specifically, we predicted higher collision risk on roads in remote areas characterised by low proportions of built-up areas (*Prediction 2*) and low road densities (*Prediction 3*). Finally, we hypothesised a higher risk on roads in mosaic landscapes with heterogeneous habitats offering closed vegetation for shelter and open areas for hunting (*Hypothesis 3*). We expected these landscapes to be characterised by moderate forest cover (*Prediction 4*) and high diversity of habitat types (*Prediction 5*) (Fig. 1).

2. Materials and methods

2.1. Wildcat-vehicle collision data

In this study, we used data from 859 wildcat carcasses found along roads between 1998 and 2023 in seven German federal states (Lower Saxony, Saxony-Anhalt, North Rhine-Westphalia, Thuringia, Hesse, Rhineland-Palatinate, and Baden-Württemberg (Fig. 2; Appendix, Fig. A1). Species identification of carcasses was based on genetic ('C1'; n = 820, 95.46 %) or morphological and phenotypical ('C2'; n = 39, 4.54 %) evidence after the SCALP criteria (Gerngross et al., 2023). We only included data from carcasses found within 50 m of the nearest road, which could be accurately linked to the specific road where the accident occurred. The carcass collection date was also recorded, along with the animal's sex and age class (juvenile: 0–12 months; subadults: 12–24 months; adults: >24 months), when these could be estimated from the carcass.

2.2. Spatial predictors

To describe the characteristics of the roads and their surrounding landscapes that could affect the likelihood of wildcat-vehicle collisions, we created spatial raster layers for each 'predictor' across Germany, with a grid size of 100 × 100 m (i.e. the spatial accuracy of the carcass data and the lowest available spatial resolution of the predictor variables; Table 1). We masked all predictors to the road network (rasterised at 100m resolution) since vehicle collisions must occur on roads, and we standardised all non-categorical predictors to aid in model fitting and interpretation.

2.2.1. Road properties

Road width, traffic volume, and vehicle speed could influence the risk of wildcat-vehicle collisions (*Hypothesis 1*; *P1*). Road category serves as a proxy for traffic volume, which is often unavailable at large spatial scales (Cerqueira et al., 2021; Märtz et al., 2024; Pinto et al., 2018). We used four road categories assigned according to German administrative responsibility, as well as average daily traffic volume (ADT) and speed limits (Table 1). In detail, we considered, from the highest to the lowest traffic volume: Motorways (ADT: ~64,000, recommended speed: 130 km/h), Federal roads (ADT: ~14,500, posted speed: 100 km/h), State roads (ADT: ~5000, posted speed: 100 km/h), County roads (ADT: ~2500, posted speed: 100 km/h). For each raster grid cell intersected by the road network, we extracted the road category with the highest traffic volume. Furthermore, road width can provide additional insights, as it varies within the same road category (Appendix, Fig. A2). We extracted the maximum road width (width of the road paved area) in each raster grid cell. Finally, since curvier roads may decrease drivers' ability to detect animals crossing the road and thus increase collision risk (Grilo et al., 2009), we extracted the maximum curvature and the least efficient (i.e. least straight) road section in each raster grid cell to control for road sinuosity (Table 1).

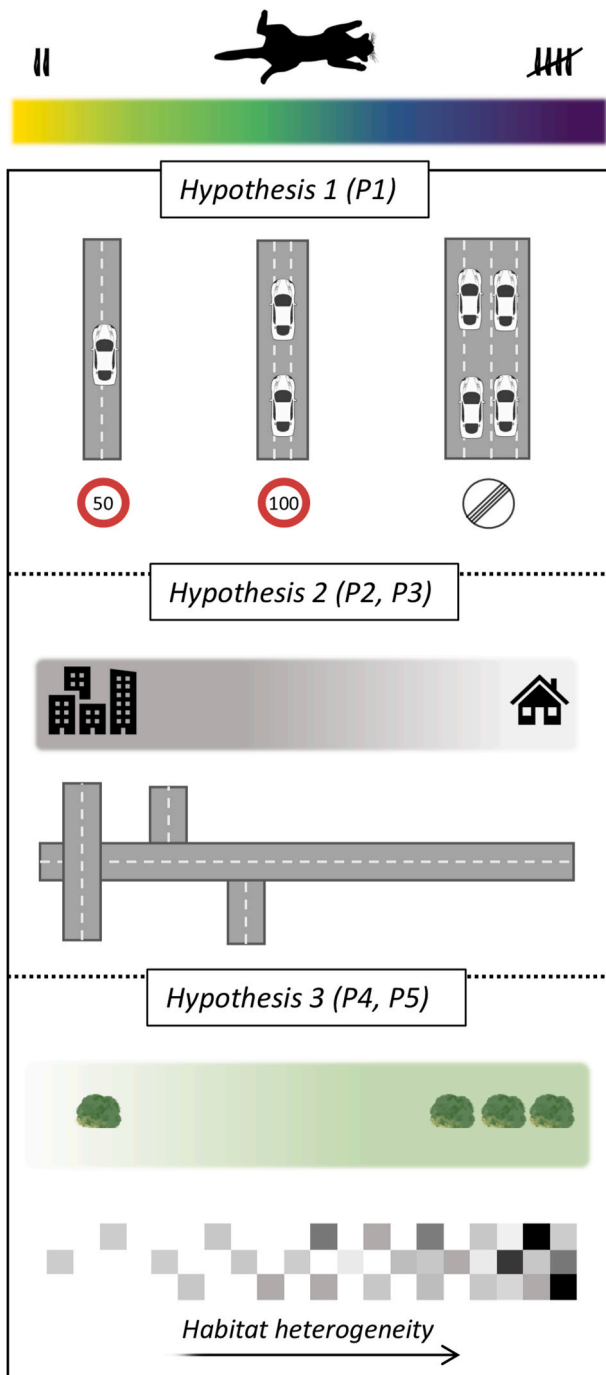


Fig. 1. Graphical representation of our hypotheses and related predictions indicating that the risk of wildcat-vehicle collisions is influenced by road properties (*Hypothesis 1*) and the surrounding landscape characteristics, including urban development (*Hypothesis 2*) and habitat heterogeneity (*Hypothesis 3*). Specifically, wildcat-vehicle collisions are more likely to occur: (*P1*) on wider roads with moderate to high expected traffic volume and vehicle speed; (*P2*) on roads in remote areas with low proportions of built-up areas (*P3*) and low road densities; (*P4*) on roads in areas with moderate forest cover and (*P5*) high diversity of habitat types.

2.2.2. Landscape characteristics

Landscape characteristics might influence the occurrence of wildcat-vehicle collisions differently, depending on the spatial scale at which they are considered. To account for these differences, for each raster grid cell intersected by the road network, we calculated landscape characteristics within two moving windows: 300×300 m, and 1000×1000 m

(Chyn et al., 2021; Märtz et al., 2024) (Table 1). The 300 m moving window describes the habitat adjacent to the road and the collision location. However, this scale also aligns with the resolution of the data and spatial predictors, while including enough pixels to accurately quantify land cover patterns (Blackburn et al., 2021). The 1000 m moving window is based on the smallest wildcat home range observed across Europe (Ruiz-Villar et al., 2023) and describes the broader landscape surrounding the road and the collision location, encompassing the features within a wildcat's home range.

We collected several predictors to explore our hypotheses regarding the surrounding landscape (Table 1; Appendix, Table A1). First, to explore the impact of urban development on the occurrence of wildcat-vehicle collisions (*Hypothesis 2*; *P2*, *P3*), we included the proportion of built-up areas and the density of all road categories (km/km^2). Second, to represent habitat heterogeneity, which may influence wildcat-vehicle collisions (*Hypothesis 3*; *P4*, *P5*), we included tree cover density and habitat diversity. Tree cover density ranges from 0 % (open areas) to 100 % (dense tree cover), with intermediate values indicating mosaic landscapes that blend open and wooded areas. We estimated habitat diversity as the Shannon diversity index of four ecologically relevant habitat types for wildcats: high-impact agriculture, low-impact agriculture, shrub and herbaceous vegetation, and forest (Bastianelli et al., 2021; Ruiz-Villar et al., 2023). Higher values indicate greater diversity of open and closed habitats suitable for wildcats.

Furthermore, we included additional predictors as control variables to account for other ecologically relevant habitats and topographical variation (Table 1). We calculated the proportion of each habitat type that was used for the Shannon diversity index (except for forest, which was already represented by tree cover density). We included forest edge density (km/km^2) and small woody features (%), which represent favourable habitats providing wildcats with abundant prey species and shelter structures (Jerosch et al., 2010; Klar et al., 2008; Ruiz-Villar et al., 2023). These habitats could also have a guiding function, potentially leading wildcats and other carnivores toward roads (Červinka et al., 2015; Jerosch et al., 2018). Finally, since landscape topography can affect animals' movement and visibility, drivers' visibility, and vehicle speed, we included the terrain ruggedness index. Zero indicates flat areas, and higher values indicate more complex and heterogeneous topographies.

2.3. Use-availability analysis

Since wildlife-vehicle collision locations are 'presence-only' data, we used Maximum Entropy Modelling to create spatially explicit predictions of their occurrence (Chyn et al., 2021; Märtz et al., 2024; Merow et al., 2013). To only include areas where wildcats are physically present and could potentially cross the roads, we created a bias grid using a two-dimensional kernel density estimate based on the coordinates of the presence locations and masked it to the road network (Syfert et al., 2013). We then generated background locations on this road network, with the probability of being sampled according to the bias grid, thus biased towards areas with a higher density of presence locations (Dudík et al., 2005; Elith et al., 2011; Phillips et al., 2009). We conducted a sensitivity pre-analysis to determine the optimal number of background locations (Valavi et al., 2022). Based on the results (Appendix, Fig. A3), we sampled 50,000 background locations, with at most one background location per raster grid cell. The presence data were also filtered to retain a single wildcat-vehicle collision per raster grid cell, resulting in 827 presence locations used for modelling.

We trained our model with all predictors using five-fold spatially blocked cross-validation to reduce spatial dependencies between training and testing data (Roberts et al., 2017) (Appendix, Fig. A4). To reduce collinearity and model complexity, we removed variables with a Spearman's correlation value greater than $|0.7|$, using the area under the receiver operating characteristic curve (AUC; Hanley and McNeil, 1982) to compare the simplified models and keep the variable leading to

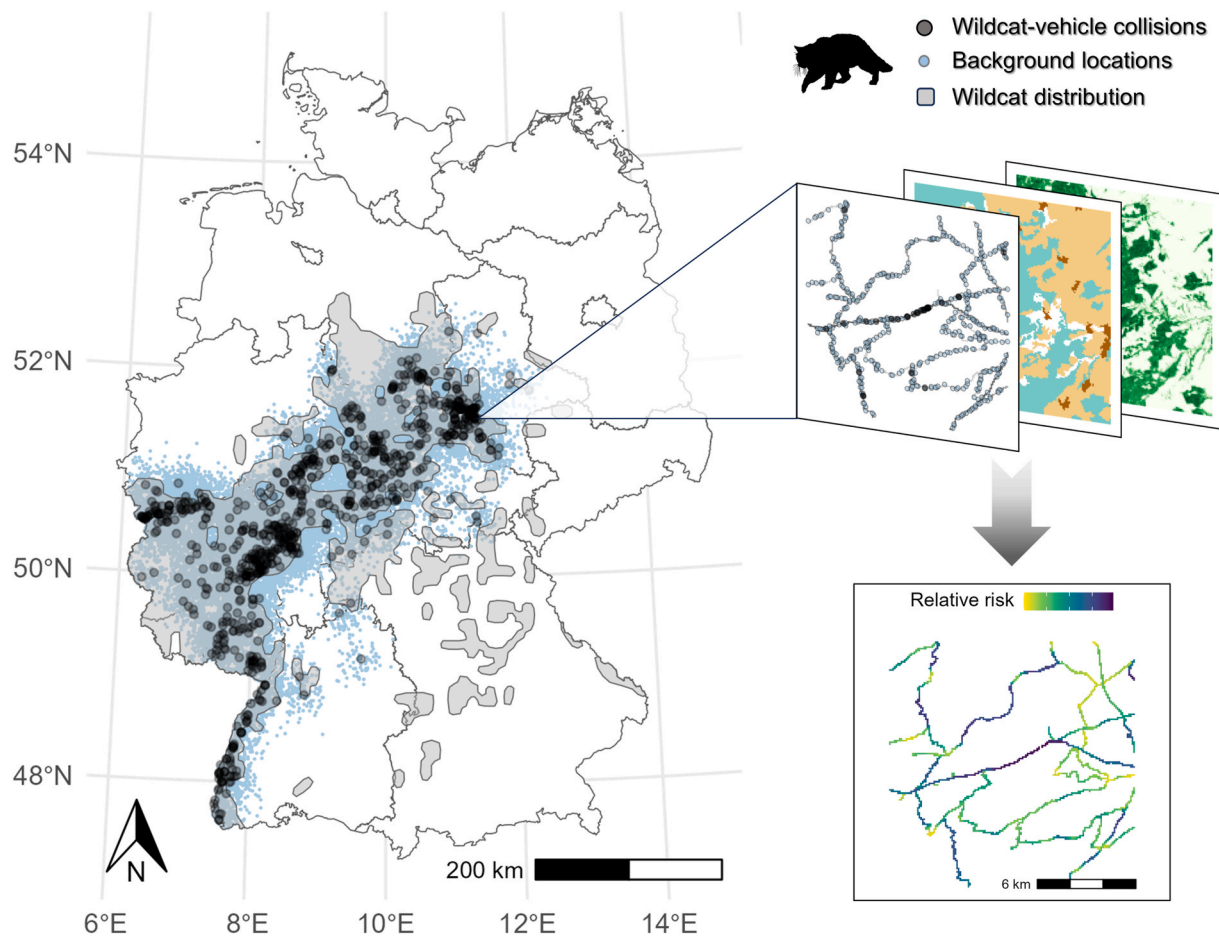


Fig. 2. Wildcat-vehicle collision locations (dark grey dots) collected across Germany and visualisation of the methodology. Light grey areas represent the distribution of wildcats in Germany according to the IUCN Red List of Threatened Species (Gerngross et al., 2022). Blue dots represent the 50,000 background locations sampled randomly using a bias grid based on the presence data. The top-right insets show the presence and background locations plotted over the road category, land cover, and tree cover density layers within a restricted area. The bottom-right inset shows the predicted wildcat-vehicle collision risk in the same restricted area, with a raster grid size of 100×100 m masked to the road network.

a better-performing model (Vignali et al., 2020) (see correlation table in Appendix, Table A2). We optimised the amount of regularisation (i.e. model complexity), testing values from 0.2 to 5.0, and the feature class combinations (i.e. the functional forms of environmental variables), testing for linear, quadratic, and product terms, with a genetic algorithm implementation (Merow et al., 2013; Vignali et al., 2020). Finally, we reduced the simplified and optimised models, excluding variables with a permutation importance lower than 2 %, but only if the model performance remained constant. The permutation importance measures the decrease in model performance, according to the AUC, when each predictor is randomly permuted.

Using the best-performing model, we estimated the probability of a wildcat-vehicle collision occurrence on the complementary log-log scale ranging between 0 and 1, in each 100×100 m pixel of the raster grid covering the road network in Germany. In recent decades, wildcat-proof fences and crossing structures have been installed to reduce wildcat road mortality in Germany (Brieger and Strein, 2024; Klar et al., 2009). We compiled georeferenced data from road authorities, covering 167 km of motorways, 29 km of federal roads, and 4 km of state roads equipped with wildcat-proof fences. These data do not comprehensively cover all existing fence locations. Because the data available were spatially scattered across our large study area, they could not be incorporated into the model. Moreover, we do not know the installation timing of most structures, precluding the application of a before-after-control-impact (BACI) design (Underwood, 1992). However, to evaluate whether existing mitigation measures targeted roads with high wildcat-vehicle

collision risk, we calculated the average collision risk predicted by our model for road sections equipped with wildcat-proof fences. A high predicted risk would suggest that mitigation measures are located appropriately where wildcats would face increased collision risk, given road and environmental conditions.

We evaluated the model's predictive performance with AUC, which evaluates the model's ability to discriminate between presence and background locations, ranging from 0, indicating an inverse model, to 1, indicating a perfect model (Syfert et al., 2013). We also calculated the correlation value (COR), which is the Pearson correlation between the predicted risk of wildcat-vehicle collisions and the presence and background locations (Syfert et al., 2013). Since the COR value might be sensitive to miscalibration, we used the presence-only calibration (POC) to evaluate the extent to which the predicted risk of wildcat-vehicle collisions was related to the actual presence locations in the data (Phillips and Elith, 2010). As a presence-only evaluator (i.e. based solely on presence data), we calculated the continuous Boyce index (CBI), ranging from -1 , indicating an inverse model, to 1, indicating a perfect model (Hirzel et al., 2006). In our case, the CBI assesses whether areas predicted as higher risk are more frequently associated with observed wildcat-vehicle collisions than expected by chance. We evaluated the model using: (i) the internal withheld testing data in each spatially blocked cross-validation fold, and (ii) semi-independent wildcat-vehicle collisions data (i.e. not used to fit the model, but with most occurrences within the modelled regions) available in the global roadkill dataset (Grilo et al., 2025). Finally, since our model was required to make

Table 1
Spatial predictors used for the analysis. All predictors covered the whole of Germany with a grid size of 100 × 100 m masked to the road network. ‘ADT’ refers to the Average Daily Traffic Volume [vehicles/day] for each road category. ‘w/300m’ and ‘w/1000m’ indicate the 300m and 1000m moving windows.

Predictor category		Predictor	Data source	Temporal extent	Original resolution	Range	Description	
Road properties	Hypothesis 1 (P1)	Road category	ATKIS (2018)	2018	25 m (vector)	Category: Motorways, Federal roads, State roads, County roads	Road type as a proxy of ADT and posted speed: Motorways (ADT: ~64,000, recommended speed: 130 km/h); Federal roads (ADT: ~14,500, posted speed: 100 km/h); State roads (ADT: ~5000, posted speed: 100 km/h); County roads (ADT: ~2500, posted speed: 100 km/h).	
	Control for road sinuosity	Road width [m]				2.5–30 m	Width of the road paved area rounded to the nearest 0.5 m.	
		Road curvature				0–1	Relative angle between consecutive points sampled at 25 m distance.	
Landscape characteristics ^a	Hypothesis 2 (P2)	Built-up areas	Copernicus Land Monitoring Service (2020)	2017–2018	100 m (raster)	w/300m: 0–1 w/1000m: 0–1	Proportion of land occupied by anthropogenic infrastructures (excluding roads) within 300m and 1000m moving windows.	
	Hypothesis 2 (P3)	Road density [km/km ²]	ATKIS (2018)	2018	25 m (vector)	w/300m: 0.2–19.4; w/1000m: 0.1–6.8	Length of all road categories within each raster grid cell, averaged within 300m and 1000m moving windows.	
	Hypothesis 3 (P4)	Tree cover density [%]	Copernicus Land Monitoring Service (2020)	2018 (March–October)	100 m (aggregation of 10 m raster)	w/300m: 0–97; w/1000m: 0–94	Mean forest cover percentage within 300m and 1000m moving windows.	
	Hypothesis 3 (P5)	Habitat diversity	Copernicus Land Monitoring Service (2020)	2017–2018	100 m (raster)	w/300m: 0–1.4; w/1000m: 0–1.4	Richness of four habitat types calculated as the Shannon diversity index within 300m and 1000m moving windows.	
	Control for other ecologically relevant habitats and topography	High-impact agriculture			2017–2019	100 m (raster)	w/300m: 0–1 w/1000m: 0–1	Proportion of land occupied by intensive agriculture (Ruiz-Villar et al., 2023) within 300m and 1000m moving windows.
		Low-impact agriculture			2017–2020	100 m (raster)	w/300m: 0–1 w/1000m: 0–1	Proportion of land occupied by extensive agriculture (Ruiz-Villar et al., 2023) within 300m and 1000m moving windows.
		Shrub and herbaceous vegetation			2017–2022	100 m (raster)	w/300m: 0–1; w/1000m: 0–0.9	Proportion of land occupied by shrub and herbaceous vegetation associations within 300m and 1000m moving windows.
	Forest edge density [km/km ²]			2017–2018	100 m (vector)	w/300m: 0–8.8; w/1000m: 0–5.6	Length of all forest types’ linear boundaries within each raster grid cell, averaged within 300m and 1000m moving windows.	
	Small woody features [%]	Copernicus Land Monitoring Service (2023)	2017–2019	100 m (aggregation of 5 m raster)	w/300m: 0–77.4; w/1000m: 0–58.4	Mean percentage of patchy or linear structures of woody vegetation (e.g. hedgerows, shrubs, and small clusters of trees) within 300m and 1000m moving windows.		
	Terrain Ruggedness Index	Copernicus Digital Elevation Model (2019)	2011–2015	25 m (raster)	w/300m: 0–16.9; w/1000m: 0.1–14.2	Mean of the absolute differences between the elevation value of a raster grid cell and its 8 surrounding cells (Wilson et al., 2007), averaged within 300m and 1000m moving windows.		

^a Predictors based on the Copernicus Land Monitoring Service (updated in six-year cycles) were created with the 2018 inventory because 74 % of our carcass data was collected between 2013 and 2020, making it the most appropriate layer available.

predictions for areas not included in the training data, we quantified the degree of extrapolation using multivariate environmental similarity surfaces (MESS), which measure the similarity between new environments and those in the training sample (Elith et al., 2010).

We performed all data preparation and analyses using R version 4.3.2 (R Core Team, 2023). For the preparation of presence and background locations, and spatial predictors, we used the R packages ‘dplyr’ (Wickham et al., 2023), ‘sf’ (Pebesma, 2018), ‘terra’ (Hijmans, 2023), ‘fasterize’ (Ross, 2023), ‘spatstat’ (Baddeley et al., 2015), and ‘MASS’ (Venables and Ripley, 2002). For the training, optimisation, and evaluation of the models, we used the R package ‘SDMtune’ (Vignali et al., 2020), ‘blockCV’ (Valavi et al., 2019), ‘predicts’ (Hijmans, 2025), and ‘ecospat’ (Broennimann et al., 2025). We used the R package ‘ggplot2’ (Wickham, 2016), ‘ggspatial’ (Dunnington, 2023), and ‘giscoR’ (Hernangómez, 2024) to visualise results.

3. Results

Wildcat-vehicle collisions mostly involved males and peaked twice during the year: once from January to April, aligning with the mating season, and again from September to November, during the weaning season, when a notably high number of juvenile wildcats were involved in collisions (Fig. 3). Of 859 wildcat-vehicle collisions, 114 occurred on

motorways (0.013 collisions/km of road within the range of presence data), 309 on federal roads (0.017 collisions/km), 341 on state roads (0.009 collisions/km) and 95 on county roads (0.003 collisions/km) (Appendix, Table A3).

The model that best predicted wildcat-vehicle collisions included the following predictors, ranked from the highest to the lowest contribution, based on permutation importance (Appendix Fig. A5): proportion of built-up areas (moving window w/300m) (permutation importance = 37.7 ± 2.3 standard deviation (SD)), road category (20.6 ± 1.6 SD), tree cover density (w/300m) (19.3 ± 2.3 SD), habitat diversity (w/1000m) (6.9 ± 1.9 SD), road width (5.5 ± 2.1 SD), terrain ruggedness (w/300m) (5.3 ± 1.2 SD), proportion of low-impact agriculture (w/1000m) (2.3 ± 1 SD), road density (w/1000m) (1.4 ± 1 SD) and small woody features (w/300m) (0.8 ± 0.3 SD). All continuous predictors had linear effects, except for tree cover, habitat diversity, and road width, which showed quadratic responses. In detail, the marginal effects of the best-performing model (Fig. 4) showed that the risk of wildcat-vehicle collisions was highest on federal roads (>0.75), followed by motorways and state roads ($0.5-0.75$), and it was lowest on county roads (<0.5). The collision risk increased with increasing road widths until reaching a plateau, with no collisions recorded on roads 21.5 m wide or wider. Collision risk decreased continuously with increasing proportion of built-up areas and road

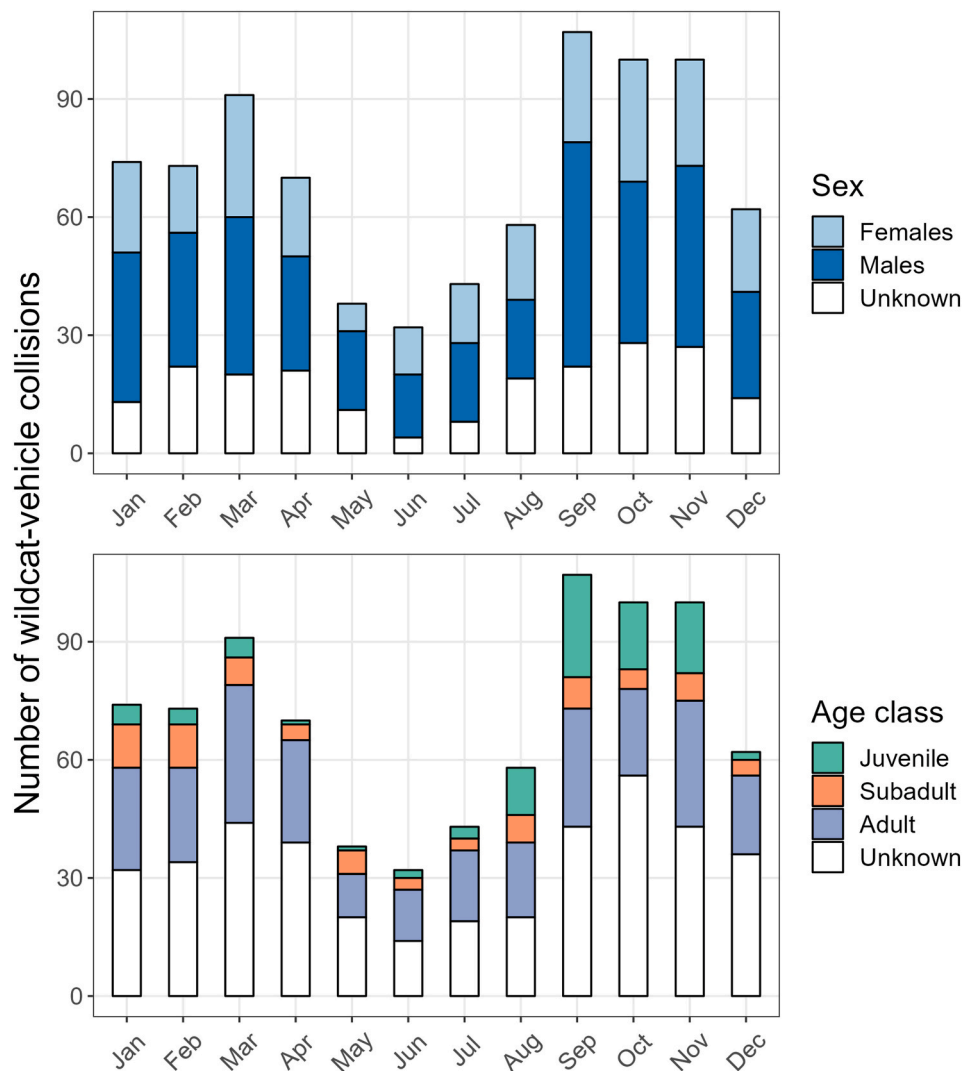


Fig. 3. Distribution of the sex and age classes of road-killed wildcats throughout the year. “Unknown” indicates that either sex or age class could not be estimated from the carcass.

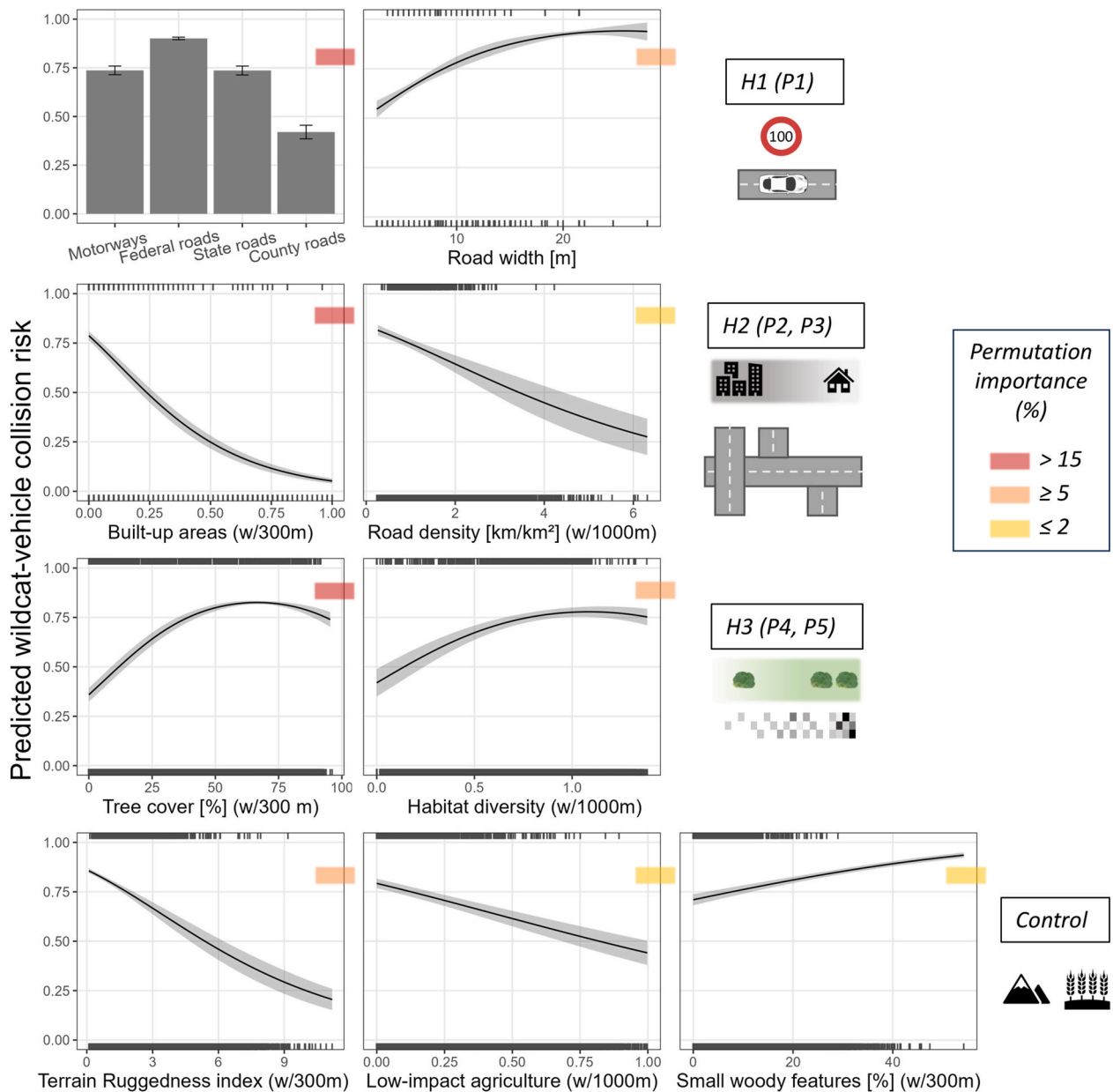


Fig. 4. Marginal response curves on the complementary log-log scale of the best-performing model. The y-axis represents the probability of occurrence of a wildcat-vehicle collision, and the x-axis represents the observed variable domain. Black rugs indicate the distribution of the presence (upper) and background (lower) locations. ‘w/300m’ and ‘w/1000m’ indicate the 300m and 1000m moving windows. Each plot row is linked to the corresponding hypothesis and predictions. The permutation importance of each variable is indicated by colour labels (red = high, orange = medium, yellow = low).

density, with only two recorded collisions at road densities exceeding 3 km/km². The risk was highest between 50 and 75 % tree cover, and it slightly decreased in higher tree cover densities. The risk increased with increasing habitat diversity until reaching a plateau. Finally, wildcat-vehicle collision risk decreased with terrain ruggedness and low-impact agriculture, and it increased with increasing small woody features.

The median predicted risk of wildcat-vehicle collisions (Fig. 5) was 0.3, representing approximately 50,000 km of roads within the range of our presence data. An estimated 25 % of roads (~25,000 km) had a predicted collision risk of 0.5 or higher, 10 % (~10,000 km) had a risk of 0.7 or higher, and 5 % (~5000 km) had a risk of 0.8 or higher. On road sections with wildcat-proof fences, our model predicted an average wildcat-vehicle collision risk of 0.78 ± 0.14 SD. Specifically, the predicted risk was 0.80 ± 0.09 SD on fenced motorways, 0.96 ± 0.05 SD on fenced federal roads, and 0.58 ± 0.13 SD on fenced state roads

(Appendix, Fig. A6).

The best-performing model provided moderate to good predictive performance calculated on the internal withheld testing data in each cross-validation fold (AUC = 0.79 ± 0.009 SD; COR = 0.14 ± 0.001 SD; CBI = 0.97 ± 0.022 SD) and on the semi-independent data (AUC = 0.71 ± 0.006 SD; COR = 0.07 ± 0.002 SD; CBI = 0.95 ± 0.021 SD). The POC curve deviated little from the expected line, with the predicted probability of presence being slightly underestimated after a risk of 0.8 (Appendix, Table A4, Fig. A7). The extent of extrapolation required for predictions in areas not included in the training data was limited, with novel environments mostly occurring in large cities and in alpine and coastal areas (Appendix, Fig. A8).

4. Discussion

With a large dataset of wildcat-vehicle collisions, we provided a

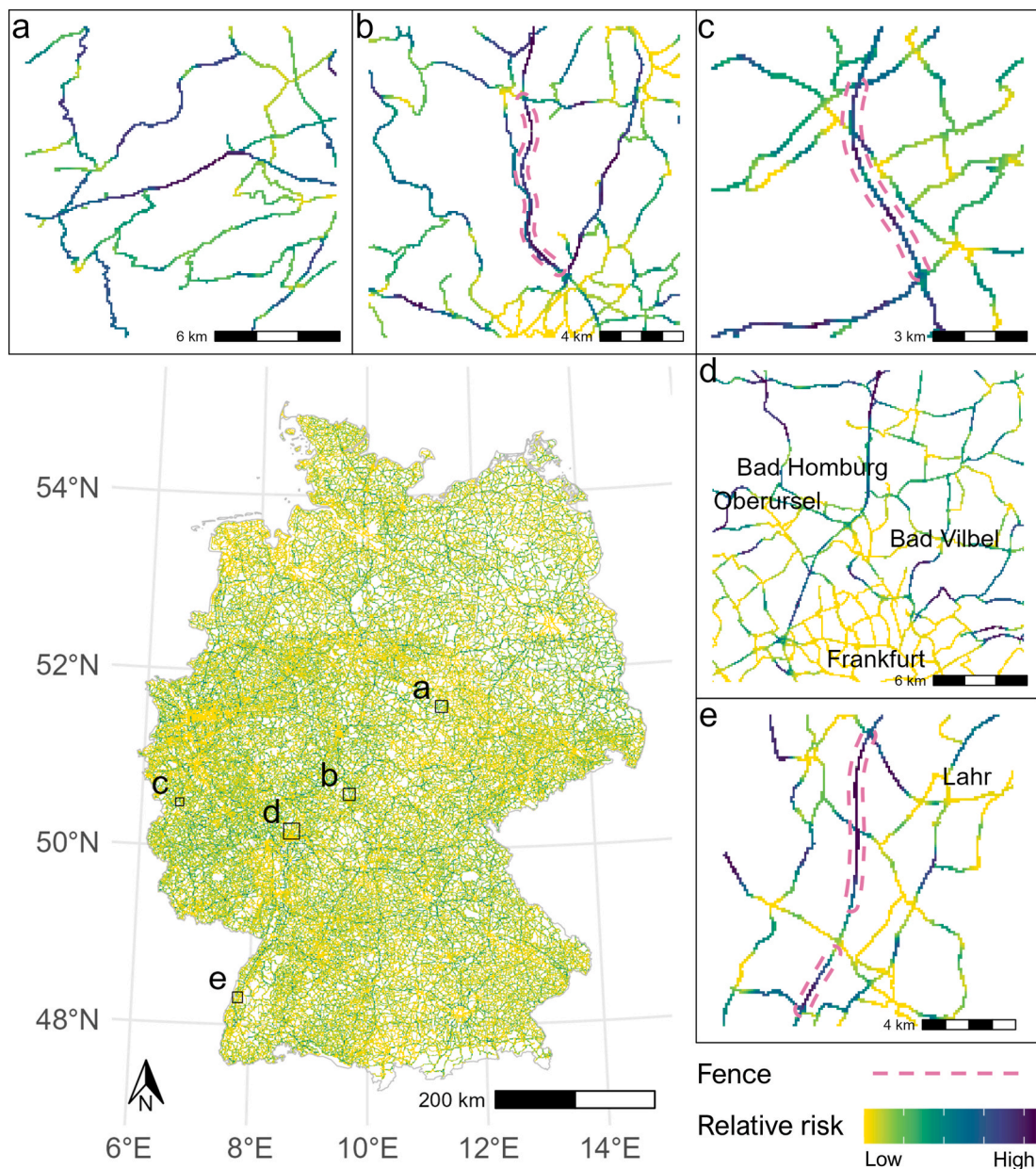


Fig. 5. Predicted risk of wildcat-vehicle collisions across the road network in Germany based on the best-performing model, with yellow indicating low risk and blue indicating high risk. Five insets show the predicted risk in zoomed-in areas: a) eastern Harz Mountains (Saxony-Anhalt); b) fenced A7 motorway north of Fulda (Hesse); c) fenced A1 motorway east of Hohes Venn-Eifel Nature Park (North Rhine-Westphalia); d) north of Frankfurt (Hesse); and e) fenced A5 motorway north of Freiburg (Baden-Württemberg). Pink dashed lines in the insets represent road sections with wildcat-proof fences. The predicted risk of wildcat-vehicle collisions across Germany is available as raster data (TIF) in the Mendeley Data repository.

comprehensive analysis of the factors influencing wildcat road mortality across heavily fragmented and heterogeneous landscapes. According to our expectations, we found that both road properties (determining the hazard of a road crossing) and landscape characteristics (determining the likelihood of wildcats' exposure to roads) influenced the risk of wildcat-vehicle collisions. For the first time, we identified road sections with a high risk of wildcat-vehicle collisions on a national scale, where conservation planners and wildlife managers should prioritise mitigation measures to reduce wildcat road mortality.

Consistent with our first prediction, when classifying German roads based on ADT and posted speed (motorways > federal roads > state roads > county roads), our results showed that the risk peaked at moderate to high vehicular traffic and posted speed. These findings align with previous studies showing major highways as substantial mortality risks for wildcats (Bastianelli et al., 2021; Klar et al., 2009) but also

highlight the role of minor roads, which are more abundant within their home ranges (Bastianelli et al., 2021) and limit gene flow between populations (Westekemper et al., 2021). The lower risk on motorways compared to federal roads aligns with previous findings on wildlife-vehicle collision risk that while roads with low traffic pose minimal threat, heavy traffic can deter animal crossings (Märtz et al., 2024; Russo et al., 2020; Seiler, 2005). The non-linear effect of road width observed in our model, where collision risk increases with road width up to a plateau, supports this interpretation. Similarly, leopard cat (*Prionailurus bengalensis*) collisions in Korea peak at moderate traffic and narrow roads, with no collisions on roads with eight or more lanes (Kim et al., 2019). However, other studies found a linear increase in mortality with road width, as wider roads increase animals' exposure to traffic during road crossings (Barthelmeß, 2014). Accordingly, roads with more lanes increase the mortality of bobcats (*Lynx rufus*) in Ohio (Bencin

et al., 2019) and five felid species in Brazil (Cerqueira et al., 2021). Whether through behavioural avoidance or increased mortality, wide roads pose a significant barrier to wildcats, hindering access to resources such as shelter, food, and mates, and potentially isolating populations.

In accordance with our second hypothesis, wildcat-vehicle collision risk decreased as urban development around roads increased. Specifically, the risk declined with a higher proportion of built-up areas. This is not surprising, as wildcats rarely use these areas (Klar et al., 2008; Oliveira et al., 2018), making collisions more likely on roads in less disturbed habitats. Consistent with our findings, urban development reduces the risk of wildlife-vehicle collisions in general (Gunson et al., 2011; Malo et al., 2004). High-risk road sections for bobcats in Ohio, ocelots in Texas, and leopard cats in the Republic of Korea mainly occurred in areas with minimal urban development (Bencin et al., 2019; Kim et al., 2019; Schmidt et al., 2020). Similarly, the risk of vehicle collision for red fox (*Vulpes vulpes*) and Eurasian badger (*Meles meles*) was lower near urban areas (Grilo et al., 2009). Furthermore, we found that the risk of collision declined with increasing road density, which could again be explained by wildcats' avoidance of such areas. However, it is also possible that wildcat populations in these areas declined due to historically high mortality (Zimmermann Teixeira et al., 2017). Although animals' avoidance of areas with high road densities may reduce the risk of collisions (Found and Boyce, 2011; Märtz et al., 2024; Schmidt et al., 2020), it also strengthens the barrier effect of roads, limiting gene flow between populations (Westekemper et al., 2021). Our model predicted the highest risk of wildcat-vehicle collisions at low road densities (<1 km/km²). Beyond this threshold, wildcats may struggle to survive, as they can only tolerate a limited number of major highways within their home ranges (Bastianelli et al., 2021; Klar et al., 2009). Notably, a 1 km/km² increase in road density within wildcat home ranges increased mortality risk ninefold (Bastianelli et al., 2021). Although the wildcat is a wide-ranging species that inhabits diverse habitats, urban development remains a significant long-term constraint on its population persistence.

The results were also consistent with our third hypothesis regarding the effect of habitat heterogeneity on wildcat-vehicle collision risk. The risk increased until reaching a plateau at moderate to high tree cover, with a slight decrease after 75 % tree cover. Our findings align with previous studies that report high felid-vehicle collision rates on roads bisecting suitable vegetation cover (Blackburn et al., 2021; Garrote et al., 2018; Schmidt et al., 2020). However, we found that the risk of collision increased with increasing habitat diversity until reaching a plateau, suggesting that for wildcats, the highest risk occurs on roads surrounded by a mix of forest cover and open areas. These mosaic-structured landscapes are highly suitable for wildcats, as they provide both shelter and high densities of rodents and rabbits (Jerosch et al., 2010; Klar et al., 2008; Lozano et al., 2003). When roads fragment these habitats, wildcats may need to cross them to reach resources in different patches, increasing the risk of vehicle collisions. Future studies should investigate this hypothesis using movement data to better understand the interplay of resource distribution and roads in shaping wildcat space use. A similar increase in vehicle collisions in areas where dense vegetation cover alternates with open areas has been observed in other carnivores (Červinka et al., 2015; Kim et al., 2019). However, to our knowledge, a direct link between habitat diversity and road mortality has only been documented in ungulates (Found and Boyce, 2011; Gunson et al., 2011; Malo et al., 2004). Efforts to reduce wildlife-vehicle collisions should also prioritise these areas to minimise collisions across a broader range of species and habitats.

Major highways in Europe expanded from approximately 30,000 to 70,000 km between 1990 and 2020 (Ignatov, 2024), and both road networks and traffic volumes are expected to continue increasing alongside human population and economic growth. This expansion may increase the frequency of wildcat-vehicle collisions and further restrict gene flow among wildcat populations. Furthermore, increased habitat fragmentation from roads and other anthropogenic activities may

reduce the ecological separation between wildcats and domestic cats (*Felis catus*), thereby increasing the risk of hybridisation — a major threat to many wildcat populations (Beugin et al., 2020; Matias et al., 2022; Nussberger et al., 2018). Genetic integrity is, in fact, better maintained in continuous forested habitats with low anthropogenic disturbance, where higher wildcat densities provide sufficient mates within the wild population (Beugin et al., 2020; Matias et al., 2022). Furthermore, recent evidence suggests that introgression results from wildcat range expansion rather than domestic cat incursions into wildcat habitats (Nussberger et al., 2018). The ongoing expansion of wildcat populations, likely driven by adaptation to anthropogenic environments and successful conservation measures, is encouraging but warrants close monitoring of potential genetic introgression (Nieto-Blázquez et al., 2022; Nussberger et al., 2018) and rising human-caused mortality. Future research should integrate long-term population and genetic data to assess the lasting impacts of roads and human expansion on wildcat population dynamics and genetic integrity. In combination with movement data, these data could also clarify how genetic or individual behavioural differences influence the propensity to use fragmented landscapes and face associated risks.

4.1. Study limitations

Moderate to good predictive performance indicates that the model was reliable in predicting the occurrence of wildcat-vehicle collisions. Furthermore, the extent of extrapolation required for prediction across Germany was limited, suggesting that the model provides reliable predictions in most areas not included in the training data. The model was well calibrated up to a risk threshold of 0.8, beyond which the predicted probability of wildcat-vehicle collision occurrence was less certain and leaning towards an underestimation. This deviation can partly be explained by the rarity of landscape conditions associated with collision risks greater than 0.8. Another contributing factor is the sampling bias inherent in wildlife-vehicle collision data. Some collisions may go unreported due to carcasses being undetected or removed, or because of uneven collection efforts (Bíl et al., 2025; Jung et al., 2024; Santos et al., 2011). For example, collecting carcasses on motorways is more hazardous, which may lead to underreporting, and roads with heavy traffic can result in flattened, unrecognisable carcasses. Although the wildcat's small body size poses minimal traffic concerns, its charismatic appeal and legal protection generate public interest and facilitate the reporting of road-killed individuals. Additionally, the remaining reporting bias was partially addressed by sampling background locations with respect to the sampling effort (i.e. biased towards areas with a higher density of presence locations). Another limitation was the absence, at the spatial scale of our analysis, of data on the population abundance of wildcats and their prey, which are important predictors of wildcat occurrence and exposure to roads. This was partially addressed by including covariates representing favourable habitats for wildcats. Future studies could focus on developing large-scale wildcat habitat suitability models that integrate movement and occurrence data, providing a proxy for occurrence probability and serving as a foundational layer for further analyses. Despite these limitations, wildlife-vehicle collision data remain invaluable for identifying high-risk road sections on large scales (Bíl et al., 2019; Chyn et al., 2021; Visintin et al., 2016) and for guiding effective management strategies (Gunson and Teixeira, 2015), especially for rare and elusive species for which other data types are difficult to obtain (Russo et al., 2020).

4.2. Management implications

Using our model, we predicted wildcat-vehicle collision risk across Germany's road network, providing conservation planners with a tool to identify critical roads for wildcat mortality. Following a pilot study that reduced wildcat road mortality by 83 % (Klar et al., 2009), about 200 km of roads in Germany have already been equipped with wildcat-proof

fences and wildlife crossing structures. Our model predicted high risk on fenced roads, confirming that mitigation measures indeed targeted roads with conditions leading to high wildcat-vehicle collision risk. These fences are at least 1.8 m high and equipped with undermining and climbing protections to effectively prevent wildcats and other species capable of digging or climbing from entering the road (Brieger and Strein, 2024; Klar et al., 2009). To maintain landscape connectivity, they should be combined with under- or overpasses, such as open-span viaducts, which appear to be the preferred crossing structures for wildcats (Klar et al., 2009). Given the high costs associated with such measures (Brieger and Strein, 2024), future studies should identify wildcat movement corridors intersecting high-risk roads highlighted in our study to define priority areas (Cerqueira et al., 2021). Movement data would also help clarify whether low-collision areas function as safe crossing zones (i.e. cold spots) or as barriers to movement (Märtz et al., 2024). Furthermore, when the installation of fences and crossing structures is not feasible, mitigation on high-risk roads should focus on reducing vehicle speeds (e.g. through warning signs, speed bumps, and radar) during twilight and nighttime, when wildcats and other wildlife species are most active and likely to cross (Bastianelli et al., 2024; Brieger et al., 2022; Klar et al., 2009).

5. Conclusions

Our study highlights the complex interplay of factors influencing wildcat road mortality in human-modified landscapes. Roads intersecting areas with dense vegetation cover alternating with open areas are a significant source of mortality for wildcats. While mitigation measures typically focus on major roads, our results show that minor roads can also pose substantial risks. With roadless areas rapidly declining (Ibisch et al., 2016), measures to reduce road mortality and enhance habitat connectivity are essential for the long-term viability of highly mobile carnivore populations. Using this framework, we validated the placement of existing mitigation measures for wildcats and highlighted areas where further action is needed. With limited time and resources, prioritising conservation efforts for species that attract considerable public interest, like felids, can also yield benefits for less charismatic species (Macdonald et al., 2015). For instance, fencing designed for wildcats has also proven effective for other sympatric carnivores, including pine marten (*Martes martes*), badgers (*Meles meles*), and red foxes (*Vulpes vulpes*) (Brieger and Strein, 2024; Klar et al., 2009). This study represents the first national-scale assessment of wildcat road mortality and provides insights to guide targeted interventions aimed at reducing road mortality and enhancing the connectivity of wildcat populations and other co-occurring carnivores. Such research is particularly important for felids like the wildcat, which can adapt to increasingly fragmented landscapes but for which roads are, or may become, a major source of mortality and a barrier to movement. Roads and railways currently threaten 77 % of felid species, of which 47 % facing a high risk of extinction (i.e., classified as Vulnerable or Endangered) and 70 % experiencing population declines (IUCN, 2025). Similar large-scale risk assessments are urgently needed to support mitigation efforts for other felids inhabiting landscapes increasingly dominated by humans.

CRedit authorship contribution statement

Matteo Luca Bastianelli: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Johanna Heeres:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Malte Götz:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization. **Saskia Jerosch:** Investigation, Data curation, Conceptualization. **Olaf Simon:** Writing – review & editing, Investigation, Data curation. **Johannes Lang:** Writing – review & editing, Investigation, Data curation. **Teresa Nava:** Writing – review

& editing, Investigation, Data curation. **Sabrina Streif:** Investigation, Data curation. **Christine Thiel-Bender:** Investigation, Data curation. **Tomma Lilli Middelhoff:** Investigation, Data curation. **Ole Anders:** Investigation, Data curation. **Sönke Twietmeyer:** Writing – review & editing, Investigation, Data curation. **Francesca Cagnacci:** Resources, Project administration, Writing – review & editing. **Carsten F. Dormann:** Writing – review & editing, Validation, Supervision. **Simone Ciuti:** Writing – review & editing, Supervision. **Joe Premier:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Manisha Bhardwaj:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis, Conceptualization. **Marco Heurich:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, 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.jenvman.2025.128152>.

Data availability

The predicted probability of wildcat-vehicle collision occurrence across Germany is available as raster data, along with the R code used for data processing, analysis, and result visualisation, from the Mendeley Data repository: <https://data.mendeley.com/datasets/6t2jmvnhhk/1>. The raw data could not be shared because the species is protected.

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