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Research Article

Green City and connected habitats? Assessing the impact of urbanization on mammal diversity

Marius Huber[1,2], **Ilse Storch**[1], **Geva Peerenboom**[1] **and Marufa Sultana**[1,2]

[1]Chair of Wildlife Ecology and Management, University of Freiburg, Freiburg, Germany
[2]Institute for Technology Assessment and Systems Analysis (ITAS), Karlsruhe Institute for Technology (KIT), Karlsruhe, Germany

Correspondence: Marius Huber (mariushuber123@gmail.com)

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As urban expansion fragments natural habitats, there is a growing concern to improve green patch connectivity for biodiversity within cities globally. Focusing on Freiburg, Germany, one of the greenest cities in Europe, we investigated how patch connectivity is shaping mammal occurrences and species-specific consequences in urban areas. We particularly aimed to gain insight into patch connectivity's effect on species richness of medium- to large-sized urban mammals. For this, we analyzed mammal occurrence data collected using motion-triggered camera traps. We assessed the patch connectivity's effect, as well as urbanization, vegetation, and fragmentation proxies, on the species-specific occurrence probability and on the total species richness of urban medium- to large-sized mammals by multi-model inference. We found that higher impervious surface proportion significantly decreases the occurrence probability of the European badger *Meles meles*, roe deer *Capreolus capreolus*, red fox *Vulpes vulpes*, and the overall measured medium- to large-sized urban mammal species richness. Our analysis shows less influence of patch connectivity on species-specific occurrences and highlights a negative influence of urbanization on total mammal species richness. More empirical studies connecting multi-city comparisons are necessary to reveal commonalities/variations in understanding how mammals respond to patch connectivity across urban environments globally.

Keywords: Freiburg im Breisgau, least-cost distance, patch connectivity, species richness, urban wildlife, wild mammals

Introduction

Over half of the world's population lives in urban areas, which is predicted to become 68% by 2050 (UN DESA 2018). This trend drives urban landscape expansion, converting natural habitats into built environments, leading to habitat fragmentation and loss of connectivity (Angel et al. 2011, UN DESA 2018). There is, thus, a growing interest in incorporating different green infrastructure features like parks, street trees,

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gardens and other vegetation patches for greater habitat connectivity in cities globally (Lepczyk et al. 2017). Green infrastructure is defined as 'the network of open space, woodlands, wildlife habitat, parks and other natural areas' (McMahon and Benedict 2000, p. 4). Research on green infrastructure indicates to opportunities with enhanced socioecological benefits (e.g. human-nature connectedness) in urban areas (Benton-Short and Keeley 2017). However, there is a lack of consistent knowledge about how patch connectivity shapes biodiversity, particularly wildlife species, in such green cities (Rands et al. 2010, LaPoint et al. 2015). This research gap is particularly relevant for mammals as they are often studied concerning their urban habitat selection (Moesch et al. 2024), whereas understanding of species specific connectivity in cities remains limited (Gelmi-Candusso et al. 2025).

Urban areas are usually composed of different land uses and habitat intactness, ranging from large green patches/nature reserves to small, isolated patches with scattered trees, which may benefit different mammals in various ways. In general, wildlife species diversity increases as green patch size increases, following the species–area relationship theory (Ferenc et al. 2014, Leveau et al. 2019). For example, while red fox *Vulpes vulpes* occurrence typically declines with increasing proportions of developed area, foxes respond positively to increasing urban intensity if the proportion of green space is > 20% of total land use (Fidino et al. 2021). A network of green patches in the surroundings improves biodiversity in an urban neighborhood (Sultana et al. 2022). These competing trends led to the SLOSS – a single large or several small – theory (Fahrig et al. 2022), which suggests that small green patches can act as stepping stones and provide corridors for animal movement that can be a valuable resource in urban areas (Soanes et al. 2019).

Occurrence and movement of mammal species across urban areas also depend on their behavioral flexibility to different land use factors (Lowry et al. 2013, Ritzel and Gallo 2020). In general, there are species which are sensitive to habitat conversion and are often the first to disappear in developed areas (i.e. urban avoiders). Urban adapters can establish themselves within both natural and urban landscapes, while urban exploiters demonstrate the behavioral flexibility to thrive on anthropogenic resources and are frequently found to be more abundant in urban environments than in other habitats (Blair 2001, Fischer et al. 2015). For example, the abundance of European rabbits *Oryctolagus cuniculus* is increasing in urban areas (Ziege et al. 2020), and stone martens *Martes foina* and red foxes can persist remarkably well in urban areas compared to rural areas (Rodewald and Gehrt 2014, Peerenboom et al. 2020). These species-specific consequences can be different between cities across regions.

Given the variability in species-specific consequences observed in cities, it is increasingly important to explore the role of connectivity on mammals' occurrences in urban areas (Ayram et al. 2016, Magle and Fidino 2018). Connectivity can be classified into two main types: 1) structural connectivity refers to the maintenance of physical interconnectedness among habitat areas (LaPoint et al. 2015), and 2) functional connectivity, which signifies the extent to which a landscape facilitates the movement and genetic exchange of species among patches (Ayram et al. 2016). Functional connectivity facilitates species navigation between habitat patches with minimal disruption, thereby supporting wildlife movement (Adriaensen et al. 2003, Ayram et al. 2016). Given the variation in species-specific responses to habitat fragmentation and matrix habitat quality, connectivity research emphasizes the need for species-specific investigation of landscape connectivity (Beier et al. 2009, Cushman and Landguth 2012) and how different matrix types facilitate or impede movement beyond just interpatch distance (Kupfer 2012).

In our study, we examine urban mammal occurrences along gradient of urbanization from forest to high urban areas and how they are shaped by structural patch connectivity in Freiburg im Breisgau, Germany. Focusing on medium- to large-sized mammals, we investigate how environmental factors influence species richness and species-specific occurrences through the two following research questions:

1) How does the proportion of different land use categories affect urban species richness and species-specific probability of occurrence of medium- to large-sized urban mammals?
2) How do fragmentation, structural patch connectivity, urbanization, and vegetation impact species richness and species-specific occurrences in an urban landscape?

We hypothesize that increasing impervious area will affect overall species richness negatively. However, species-specific consequence may vary. We assume that vegetated land use types, such as forests and urban green spaces, promote occurrences of urban avoiders. Additionally, we expect urban exploiter species to respond differently – their probability of occurrence increases with higher urbanization levels, whereas greater vegetation cover decreases it.

Furthermore, we hypothesize that increased patch connectivity will generally enhance species richness and species-specific occurrence. However, urban exploiters may constitute an exception to this pattern, as they could benefit from a more fragmented, spatially heterogeneous urban landscape.

Material and methods

Study area and site selection

Our study was conducted in the city of Freiburg im Breisgau, located in the south of Baden-Württemberg, Germany (47°59′45″N, 07°51′07″E). The city encompasses an area of approximately 15 300 ha – therefore it is categorized as a medium-sized city. Freiburg im Breisgau comprises 3464 ha of agriculture, 6533 ha of forest, and 670 ha of sports, leisure and recreational areas, including urban green spaces. The city's periphery is predominantly composed of forest and agricultural lands. The population of Freiburg im Breisgau is approximately 230 000 inhabitants (Amt für Bürgerservice und Informationsmanagement 2021), resulting in a population density of approximately 1500 inhabitants per km^2.

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Following the Urban Wildlife International Network (UWIN) study design, 19 motion-triggered trail cameras (hereafter camera traps) were placed in green spaces within and surrounding the city of Freiburg to conduct a comprehensive survey of wildlife occurrences (Fig. 1). For the grid cell approach, 1.5 × 1.5 km square grids were projected on the entire city area using the QGIS interface. For each grid cell, the level of imperviousness (i.e. the percentage of developed area) was extracted from the Global Man-made Impervious Surface Dataset from Landsat (Brown de Colstoun et al. 2017). This data was then used to interpret the urbanization gradient. Subsequently, potential camera locations (at least 1 km apart) were identified in the green spaces of the selected grid cells, representing different urban gradients. However, due to the presence of numerous restricted and private areas within the city, which were primarily attributable to varied land ownership patterns, it was not feasible to consider every location of interest. Consequently, only locations that had received approval from the relevant authorities, both private and public, were selected for the installation of cameras (Fig. 1).

Data collection and preparation

Species data were collected using camera traps (Bushnell Trophy Cam Essential E3 (119837); Lenexa, Kansas State, USA, 2016) during October 2021–July 2022, following four sampling seasons in accordance with the UWIN methodology (Urban Wildlife Information Network 2020). We set up camera traps in October for the first season, January for the second season, April for the third season, and July for the final season. The camera settings, the duration of the trapping period, and the recommended control after 14 trap nights were all in accordance with the UWIN study design (Urban Wildlife Information Network 2020). The quarterly data collection is suggested to account for the study organisms' seasonality in their activity. To minimize information loss, the capture number per sequence was set to two images in the camera settings. For the classification of the camera trap records, the TIMELAPSE2 picture classification software was used, following a template created specifically for the camera trap photo classification.

The response variables of the study were species richness and species-specific presence data in each camera location. The species-specific presence data comprised binary data on whether a species was photographed or not at each location (hereafter referred to as presence data or occurrence probability). The species richness was measured as the number of distinct species present in each location. The analysis included all mammal species with a body mass greater than or equal to that of a European hedgehog *Erinaceus europaeus* (hereafter hedgehog; Table 1). Because rare species add statistical noise to the modeling while providing little additional input for

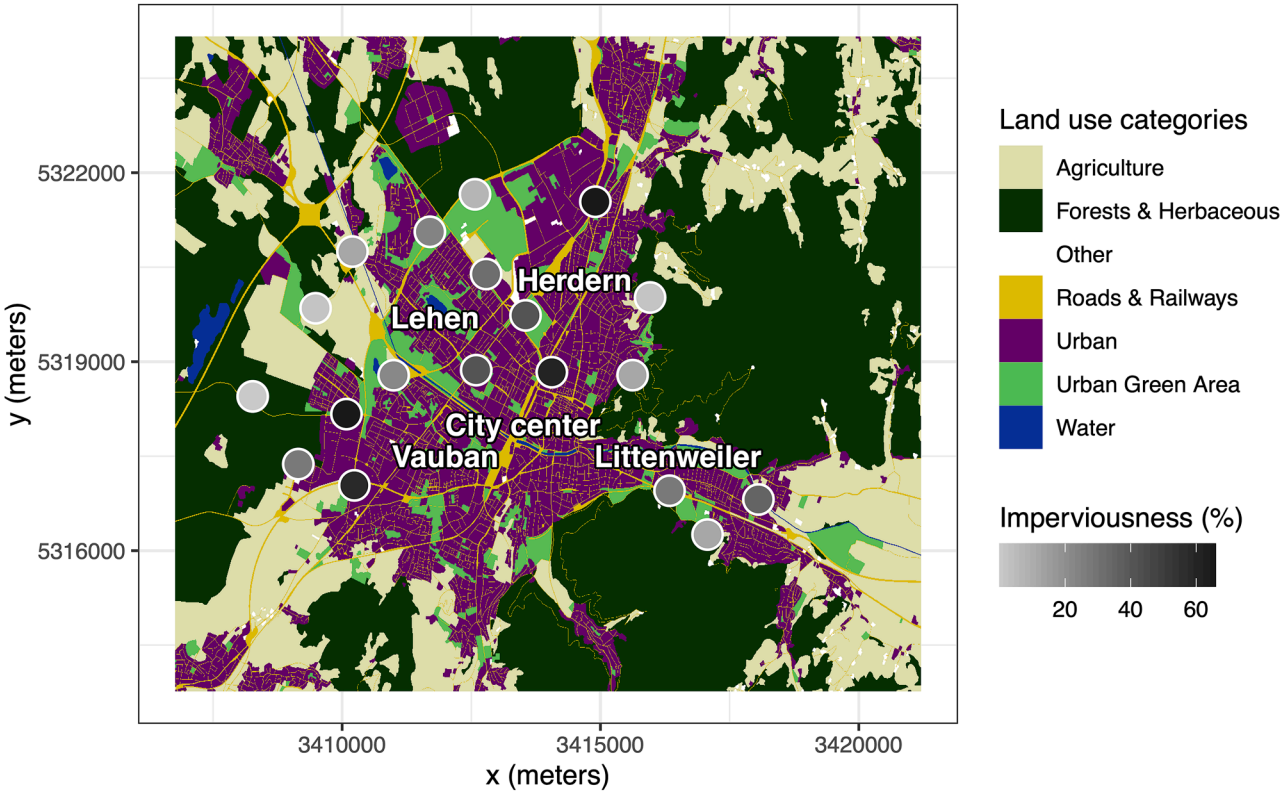


Figure 1. Overview of the camera locations. The locations are colored based on their mean surrounding impervious surface cover proportion (in %) calculated in a concentric circle with radius 500 m around the camera trap location. Find further information on the land use categories in the Supporting information.

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Table 1. Details on the taxa investigated in the analysis.

Species name	Scientific name	Common name	Predominant diet	Predominant behavior	Sources
European hare	*Lepus europaeus*	hare	herbivore	urban adapter	Reichlin et al. 2006, Hackländer et al. 2011
Roe deer	*Capreolus capreolus*	deer	herbivore	urban avoider	Jedrzejewska and Jedrzejewski 1998, Torres et al. 2012
Wild boar	*Sus scrofa*	boar	herbivore	urban avoider	Jedrzejewska and Jedrzejewski 1998, Schley and Roper 2003, Stillfried et al. 2017
European hedgehog	*Erinaceus europaeus*	Hedgehog	insectivore	urban exploiter	Hof et al. 2012, van de Poel et al. 2015
European badger	*Meles meles*	Badger	omnivore (invertebrates, fruit, vertebrates, scavenge)	urban avoider	Harris 1984, Kowalczyk et al. 2003
Stone marten	*Martes foina*	Marten	omnivore (plant material, vertebrate prey, invertebrates, scavenge)	urban exploiter	Apathy 1998, Ruette et al. 2015
Red fox	*Vulpes vulpes*	fox	omnivore (scavenge, vertebrate prey, invertebrates, fruit)	urban adapter	Contesse et al. 2004, Iossa et al. 2008

the interpretation, species occurring in less than four locations were removed (Cao et al. 2001). The final selected species were European hare *Lepus europaeus* (hereafter hare), roe deer *Capreolus capreolus* (hereafter deer), wild boar *Sus scrofa* (hereafter boar), European badger *Meles meles* (hereafter badger), stone marten (hereafter marten), red fox (hereafter fox) and hedgehog (Table 1). The categorization of the species' predominant behavior was based on findings from previous authors (Harris 1984, Apathy 1998, Jedrzejewska and Jedrzejewski 1998, Contesse et al. 2004, Hackländer et al. 2011, Hof et al. 2012).

The covariates were measured at the camera locations and their surroundings (Table 2). These covariates were subsequently categorized into measurements of connectivity, fragmentation, urbanization and vegetation.

To proxy fragmentation, we selected patch density in a concentric circle around the camera location with a radius of 500 m (hereafter 500-m buffer). We investigated buffers of different radii (50, 100, 250 m) which resulted in high VIF values. We used the 'landscapemetrics' package, where the FRAGSTAT landscape metric calculations are implemented for R (*lsm_c_pd()* function, ver. 1.5.4; Hesselbarth et al. 2019). To calculate the urbanization proxy, we determined the average proportion of impervious surface cover within a 500-m radius. We calculated the proportion of specific land use types in a buffer of 500-m radius surrounding the camera locations as easily accessible measures of habitat composition. The index for vegetation was the vegetated patch size (in m^2).

Calculation of the species-specific structural connectivity proxy

The predictor variables additionally contained a species-specific connectivity proxy, the area-weighted least-cost distance (*aw.lcd*). This variable is measured combining the camera location patch's area (in m^2), the least-cost distance (Supporting information) to the easiest reachable green patch (hereafter referred to destination patch), and the destination patch's area (in m^2). The area-weighted least-cost distance was calculated based on the equation proposed by Magle and Fidino (2018):

$$aw.lcd = \frac{\left(a_i \times a_j\right)^{0.7}}{d_{ij}^{1.7}}$$

Where a_i denotes the area of the origin patch, a_j represents the area of the destination patch, and d_{ij} indicates the distance between the two patches. In accordance with research indicating that species often exhibit non-linear responses to alterations in isolation (Kerkhoff et al. 2000, Brown et al. 2002), Magle et al. (2009), applied an exponent of 0.7 to the area terms and an exponent of 1.7 to the distance between fragments (Sapoval et al. 2004, Theobald 2006). In Magle et al. (2009), d_{ij} is defined as the Euclidean distance, which we substituted by the least-cost distance. The cost distance is derived from the summed friction values of each traversed raster pixel from the origin – that is, the camera location – to a specific raster pixel. The raster data layer containing the cell-specific friction values is referred to as the friction surface. Increases in area-weighted least-cost distances are indicative of increases in patch connectivity.

The cost distance is a calculation based on graph theory with the need for a friction map (also referred to as 'cost surface' in literature) to base the calculation on. The friction map is a species-specific raster dataset where every raster grid cell has a friction value (also referred to as 'cost value' in literature) based on its influence on the species movement. Grid cells consisting of landscape features that inhibit movement, e.g. by being bare of vegetation cover or by being steep, have a higher friction value than grid cells with features that facilitate movement, e.g. flat, vegetated patches. The cost distance is based on the summed friction values of each traversed raster pixel from the origin (i.e. the camera location) to a certain raster pixel. Therefore, the minimal cost distance is not necessarily the connection between two green patches with the minimal Euclidean distance, but instead the

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Table 2. Resistance values assigned to the classes of the weight factor land use categories. The Roman numbers refer to the literature cited: (I) Duduś et al. (2014), (II) Mayer and Sunde (2020), (III) Harris 1984, (IV) Stillfried et al. (2017), (V) Loro et al. (2016), (VI) Driezen et al. (2007). Resistance values are based on the ranking of land use types. Bold values are added, values in non-bold format taken from the literature unchanged.

Land use category	Fox (I)	Marten (I)	Hare (II)	Badger (III)	Boar (IV)	Deer (V)	Hedgehog (VI)
Urban > 80%	**140.00**	**1.00**	**90.00**	**144.00**	**130.00**	153.13	5.00
Urban 50–80%	**140.00**	**1.00**	**90.00**	**144.00**	**130.00**	153.13	5.00
Urban 30–50%	**30.00**	**50.00**	**1.00**	**144.00**	**130.00**	114.84	5.00
Urban 10–30%	**1.00**	**12.00**	**100.00**	**144.00**	**90.00**	114.84	5.00
Urban < 10%	**1.00**	**12.00**	**100.00**	**144.00**	**90.00**	114.84	5.00
Isolated structures	**90.00**	**150.00**	**50.00**	**2.20**	**35.00**	50.00	**2.00**
Industrial, commercial, public, military and private	**25.00**	**100.00**	**70.00**	**7.60**	**75.00**	114.84	**2.00**
Fast transit roads	**200.00**	**200.00**	**200.00**	**200.00**	**200.00**	153.13	150.00
Other roads	**140.00**	**150.00**	**100.00**	**144.00**	**140.00**	131.25	20.00
Railways	**140.00**	**150.00**	**50.00**	**36.00**	**140.00**	131.25	150.00
Port areas	**-**	**-**	**-**	**-**	**-**	-	-
Airports	**40.00**	**25.00**	**50.00**	**1.60**	**35.00**	114.84	2.00
Mineral extraction	**25.00**	**100.00**	**70.00**	**10.30**	**75.00**	153.13	**2.00**
Construction sites	**25.00**	**100.00**	**70.00**	**10.30**	**75.00**	153.13	**2.00**
Land without current use	**90.00**	**150.00**	**50.00**	**2.20**	**35.00**	50.00	**2.00**
Green urban areas	**40.00**	**25.00**	**50.00**	**1.60**	**35.00**	114.84	2.00
Sports and leisure facilities	**40.00**	**25.00**	**50.00**	**1.60**	**35.00**	114.84	2.00
Arable land	**80.00**	**30.00**	**50.00**	**1.60**	**150.00**	**49.50**	100.00
Permanent crops	**80.00**	**30.00**	**50.00**	**1.60**	**150.00**	**49.50**	100.00
Pastures	**90.00**	**150.00**	**50.00**	**1.60**	**150.00**	**49.50**	1.00
Complex and mixed cultivation	**80.00**	**30.00**	**50.00**	**1.60**	**150.00**	**49.50**	2.00
Orchards – urban fringe	**80.00**	**30.00**	**50.00**	**144.00**	**35.00**	**49.50**	2.00
Forests	**40.00**	**25.00**	**95.00**	**1.00**	**1.00**	**1.00**	2.00
Herbacious vegetation associations	**40.00**	**25.00**	**95.00**	**1.00**	**1.00**	**1.00**	2.00
Open space with little or no vegetation	**90.00**	**150.00**	**50.00**	**2.20**	**35.00**	50.00	1.00
Wetlands	**-**	**-**	**-**	**-**	**75.00**	-	-
Water	**200.00**	**200.00**	**200.00**	**200.00**	**200.00**	**200.00**	150.00

connection with the lowest cumulative movement inhibition (Adriaensen et al. 2003).

To assess which weight factors to integrate into the friction surface, we did model-averaging of the global models consisting of the response variable as function of surrounding agricultural land use (agri.500), urban green area (green.500), forest (forest.500), and impervious surface cover proportions (imp.500) in per cent based on a concentric circle around the cameras with radius 500 m. These models will be referred to as 'global friction models' hereafter. The predictors that were calculated to affect the response variables measurably, were incorporated in the species-specific friction value calculation. If none of the covariates included in the global models were found to exhibit a measurable effect on the response variable, the friction values consisted of resistance values assigned to the land-use classes only.

The species-specific friction values were based only on the land-use categories for the majority of the species. Otherwise, the friction values (friction) were calculated as

$$friction = R_1 \times W_1 + R_2 \times W_2$$

Here, W denotes the weight factors and R the resistance values. Weight factors are parameters facilitating or inhibiting the species' movement, such as certain land-use types, topography, or surrounding vegetated area proportion (Etherington 2016). The resistance values are numeric values assigned to the classes contained in the weight factor parameters ranging from 1 to 200 in this study. Lower resistance values represent lower movement resistance. Beier et al. (2009) provide further information on the selection of weight factors and assignment of resistance values. It is essential not to mistake a resistance value assigned for a feature class of a landscape parameter with the total friction value, i.e. the sum of multiple weighted resistance values.

Whenever possible, calculated resistance values from previous studies were assigned to the land use types and validated values were preferred over values resulting from expert estimation. For the species with multiple weight factors in the friction value calculation, the weight values were based on the results from the model selection. If no calculated resistance values from previous studies were available, land use categories' resistance values were calculated by the authors based on occurrence data in certain land use categories found in a

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literature review on the species' habitat preferences and landscape features' barrier effects. The formula for the calculation was:

$$resistance = \frac{1}{(n.obs_{\text{l.u.}} + 1) \times (max(n.obs_{\text{l.u.}}) + 1)^{-1}}$$

With resistance being the resistance value calculated for a specific land use category and $\text{n.obs}_{\text{l.u.}}$ the species-specific number of observations in the land use category found in the literature (Table 3). This calculation, although based on a small database was a more data-driven approach than the estimation of resistance values used by fellow scientists (Bunn et al. 2000, Beier et al. 2009, Etherington et al. 2014) (Table 3). However, for hares, boars and hedgehogs, the necessary data was not fully available and the missing values were estimated by the authors. Beier et al. (2009) conducted an uncertainty analysis, resulting in the finding that the results of least-cost modelling was robust to uncertainty in resistance values and factor weights, supporting preceding literature (Quinby et al. 1999, Schadt et al. 2002, Larkin et al. 2004, Kautz et al. 2006, Adriaensen et al. 2007).

The least-cost distances were calculated in QGIS using the *leastcostpath()* function (FlowMap Group@SESS-PKU 2020). This function needs an origin object, a destination object, and a fiction surface for the calculation algorithm. The origins were the camera locations, and the destinations were points located on the polygon edge of vegetated patches in a 1000 m concentric circle around the camera locations. The distance between the destination points was selected to be 500 m apart from each other. For every camera location, a destination point layer was created in QGIS. The *leastcostpath()* function returns destination coordinates and the least-cost distances between the origins and each destination. The species-specific minimal least-cost distance value at each location was used as d_{ij} for the calculation of the area-weighted least-cost distance.

Statistical analysis

We conducted Pearson correlation analysis and checked for multicollinearity of variables using the variance inflation factor (VIF; Fox and Weisberg 2019). We chose a conservative VIF-threshold of VIF < 3. From variables showing a VIF ≥ 3, the less biologically relevant variable was excluded for the model analysis (O'Brien 2007).

We applied generalized linear models (GLMs) to evaluate our hypotheses. To address the first research question, the covariates included in the species-specific models addressing the land use effects on species occurrences were the mean surrounding proportions of impervious surface cover, urban green areas, agricultural land use, and forest area, each calculated from a 500 m concentric circle around the camera trap locations. If the model resulted in a predictor's significant ($p < 0.05$) association with the species-specific occurrence probability, this predictor was incorporated as factor for the species-specific resistance calculation – referred to as the friction surface (Theobald 2006, Gharibi et al. 2021, Kwon et al. 2021). Consequently, these models will be referred to as 'friction models' hereafter.

To address the second research question, the global models incorporated the following predictors: area-weighted least-cost distance, patch density, patch area, and surrounding impervious cover proportion. The area-weighted least-cost distance was log-transformed to improve the distribution of residuals.

Table 3. Information on the measured site-specific variables.

Variable	Explanation	Data type	Source resolution	Source
Land use (*l.use*)	Land use categories of the polygons contained in the attribute table (Supporting information)	categorical	10 × 10 m	Copernicus Land Monitoring Services 2018
Impervious surface cover proportion (*imp.500*)	Average proportion of impervious surface cover (%) in a 500-m buffer around the camera location with the *extract()* function ('raster' R package)	continuous	30 × 30 m	Brown de Colstoun et al. 2017
Agricultural land use proportion (*agri.500*)	Average proportion of agricultural land use (%) in a 500-m buffer around the camera location	continuous	10 × 10 m	Copernicus Land Monitoring Service 2018
Forest proportion (*forest.500*)	Average proportion of forest (%) in a 500-m buffer around the camera location	continuous	10 × 10 m	Copernicus Land Monitoring Service 2018
Urban green area proportion (*green.500*)	Edge-to-edge distance to the closest urban green area or leisure and sports facilities feature (m) measured with the NNJOIN-plug in in QGIS	continuous	10 × 10 m	Copernicus Land Monitoring Service 2018
Patch density (*p.dens*)	Number of polygon features inside a 500-m buffer around the camera location calculated with function *lsm_c_pd()* ('landscapemetrics' R package)	continuous	10 × 10 m	Copernicus Land Monitoring Service 2018
Patch area (*p.area*)	Area (m^2) of the camera trap green patch contained in the attribute table	continuous	10 × 10 m	Copernicus Land Monitoring Service 2018

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To analyze the response variable of species richness, we utilized GLMs with a Poisson error distribution. The species richness refers to the location-specific α-diversity, i.e. the sum of study species detected in the location's camera trap pictures. This approach is appropriate for count data such as species richness, allowing for the modelling of the number of different species observed at each site. For modelling the response variable species richness, the site-specific minimal value of the species-specific area-weighted least-cost distance was employed as a connectivity proxy.

For the investigation of species-specific occurrence probabilities, we applied GLMs with a binomial error distribution. This modeling framework is suitable for binary response variables, such as the presence or absence of a particular species at a given camera trap location.

Model inference

Model inference was based on the corrected Akaike information criterion (ΔAICc) and Akaike weights (*Wi*) (Burnham and Anderson 2002). To assess the influence of the predictors and address the research questions, we applied model averaging. Candidate models with ΔAICc ≤ 2 were selected and included in the model averaging set (Δ-2-set). Top-ranked models were selected based on the lowest ΔAICc and highest *Wi*. We examined the model-averaged coefficient estimates, their 95% confidence intervals (CI), the significance of the covariates, and the proportion of variation (pseudo-R^2) explained by the models. The model assumptions were checked with the standard diagnostic plots for the glms (residuals versus fitted; quantile–quartile plot).

For our analysis, we used R ver. 4.1.0, in the RStudio environment, ver. 1.4.1717 (www.r-project.org), and the geographic information system software Quantum GIS (QGIS) (ver. 3.10.7; QGIS Development Team 2021). All geographical operations were performed in the coordinate reference system DHDN/ 3-degree Gauss–Kruger zone 3 (EPSG: 5677). The spatial analysis was conducted at a resolution of 10 × 10 m raster cell size, which was determined based on the resolution of the land-use data.

Results

Proportion of land use categories' effect on species occurrence

We conducted a power analysis on a sample size of 19, and the calculated statistical power for high effect sizes (d = 0.8) ranged from 0.33 to 0.49 for the logistic GLMs. To achieve a statistical power of 0.8, sample sizes from 40 to 64 locations would have been ideal. However, the geospatial extent of Freiburg (i.e. a medium-sized city), in combination with UWIN's study design (i.e. at least 1 km distance between cameras), limited the quantity of potential camera trap locations. The number of sampling sites was further restricted by the availability of landowner permission for the study.

Badgers were present in 8 sites, boars photographed in 5, deer in 6, foxes in 16, hares in 8, hedgehogs in 14, and martens in 18 sites. Badgers, hares, hedgehogs, foxes and martens were observed across varying levels of surrounding impervious cover. In contrast, boars and deer were exclusively found in areas with low levels of surrounding impervious cover (Fig. 2C). Higher species richness values were observed in lower levels of surrounding impervious cover, close to forest locations adjacent to the city area (Fig. 2A–B). In the following paragraphs, additional information on the species' top-ranked models, defined as the models with the lowest AICc values resulting in a ΔAIC of 0 is provided. The coefficient estimates as well as their confidence intervals mentioned were the result of the conditional model-averaging.

The models in the badger's Δ-2-set contained the predictors impervious surface, urban green area, agricultural land, and forest proportion (McFadden pseudo-R^2 of the candidate models: 0.13 to 0.19; Table 4). The covariates included in the top-ranked model (*Wi*: 0.38, pseudo-R^2: 0.188) were surrounding agricultural land-use, urban green area and impervious surface cover (Table 4). Impervious surfaces decreased badger occurrence probability (coefficient estimate: −0.04, 95% CI: −0.08 to −0.01; Table 5), whereas forest proportion increased it (coefficient estimate: 0.02, 95% CI: 0.00–0.03; Table 5).

For boars, the predictors contained in the candidate models with ΔAICc ≤ 2 were surrounding impervious cover, urban green area and forest proportion. However, the contained predictors were uninformative, without significant effects on the response variable (Table 5). The candidate models' McFadden pseudo-R^2 ranged from 0.18 to 0.22 (Table 4). The top-ranked model with the lowest AICc value (AICc: 38.71, *Wi*: 0.35, pseudo-R^2: 0.177) contained surrounding imperviousness as the only predictor (Table 4).

The candidate models with ΔAICc ≤ 2 for deer included the same set of predictors as those for badgers', the candidate models' predictors consisted of the impervious surface cover, agricultural land-use, forest, and urban green area proportion. The selected candidate models' pseudo-R^2 ranged from 0.47 to 0.53 (Table 4). The top-ranked model (AICc: 46.25, *Wi*: 0.43, pseudo-R^2: 0.520) included the covariates of surrounding agricultural land-use and impervious surface cover (Table 4). The surrounding impervious surface cover proportion was shown to affect deer occurrence probability negatively (coefficient estimate: −0.20, 95% CI: −0.31 to −0.08; Table 5).

For foxes, the candidate models incorporated all the global model's predictor variables (range of McFadden pseudo-R^2: 0.24 to 0.25; Table 4). The model predicted by surrounding forest and surrounding imperviousness was rated the highest (AICc: 81.81, *Wi*: 0.46, pseudo-R^2: 0.237; Table 4). Surrounding imperviousness was found to have a measurable, negative effect on fox occurrence probability (coefficient estimate: −0.04, 95% CI: −0.07 to 0.00; Table 5).

The candidate models with ΔAICc ≤ 2 for hares contained the imperviousness, agricultural, and forest cover proportion (range of McFadden pseudo-R^2: 0.11–0.12; Table 4). For hares, akin to foxes, the model predicted by surrounding forest and surrounding imperviousness was rated best (AICc: 87.87, *Wi*: 0.61, pseudo-R^2: 0.109; Table 4). Surrounding

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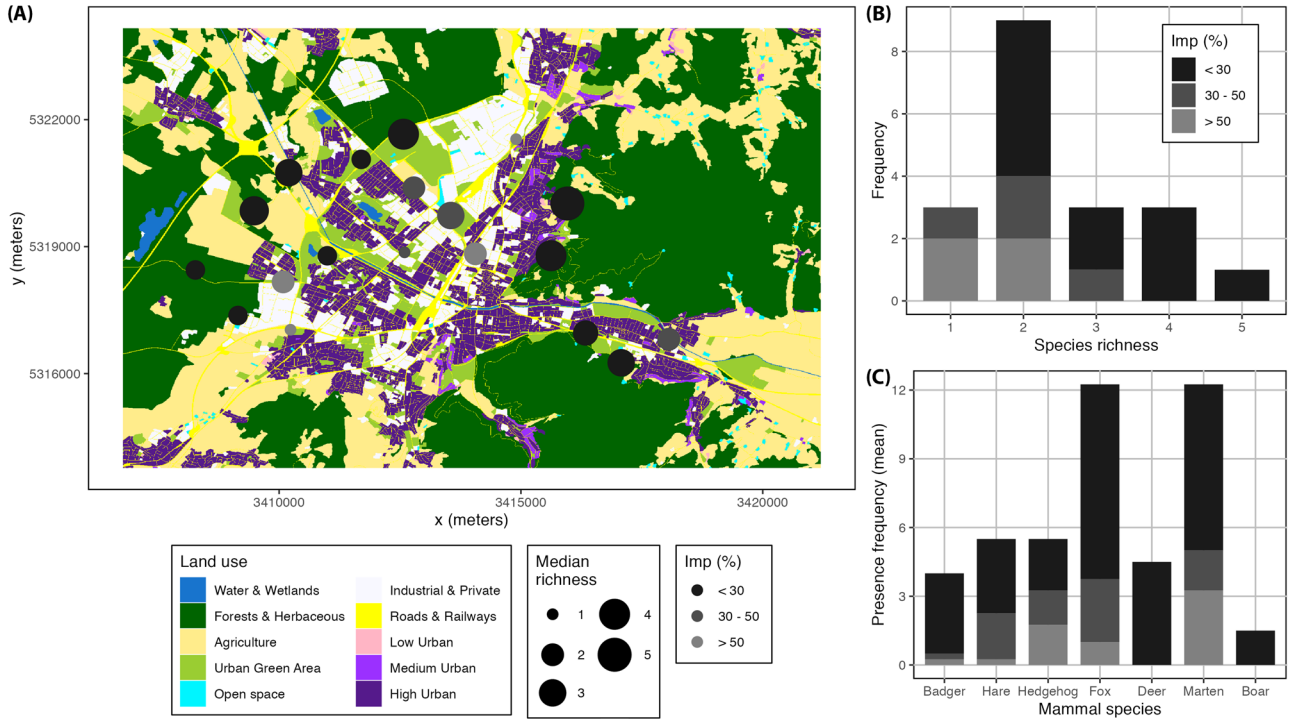


Figure 2. Overview of the results per site. (A) Richness medians as a function of their spatial location and the surrounding impervious surface cover proportion (in categories). (B) Frequency (no. sites) of observed species richness values as a function of the categorized surrounding impervious surface cover proportion. (C) Species-specific mean number of occurrence sites per season as a function of imperviousness. Imp (%) = mean surrounding impervious surface cover proportion in a 500-m radius concentric circle around the camera location.

imperviousness exerts a measurable, negative effect on probability of hare occurrence (coefficient estimate: −0.05, 95% CI: −0.08 to −0.01, Table 5).

For hedgehogs the proportions of impervious surface, forest area, urban green area and agricultural land use were included in the candidate models (pseudo-R^2: 0.07 to 0.10, Table 4). None of the parameters showed measurable influence on the probability of hedgehog occurrences (Table 5). The top-ranked model (AICc: 89.22, *Wi*: 0.20, pseudo-R^2: 0.070) was the univariate model including the covariate of surrounding forest area (Table 4). For a complete list of the friction models' selection and averaging results, see the Supporting information. The resulting friction surface calculation is available in Table 6.

Effects of urbanization, patch connectivity, fragmentation, and patch size

The urbanization proxy, the proportion of surrounding impervious surface cover, was shown to have a measurable negative effect on the species-specific probability of occurrence of badgers, deer, foxes, and the overall measured species richness (Fig. 3A, C–D, H, Table 7). The candidate models with ΔAICc ≤ 2 for deer, foxes, and species richness also contained additional predictors. The top-ranked model for badgers (*Wi*: 1.0, pseudo-R^2: 0.188) contained surrounding imperviousness; deer (*Wi*: 0.61, pseudo-R^2: 0.223) contained surrounding imperviousness and patch density. The top-ranked model for foxes (*Wi*: 0.66, pseudo-R^2: 0.520) contained surrounding imperviousness and the area-weighted least-cost distance. The top-ranked model for overall species richness (*Wi*: 0.48, pseudo-R^2: 0.080) contained surrounding imperviousness and patch area, respectively (Table 7). However, for all these response variables, exclusively the impervious surface cover proportion exerted a measurable effect, which was estimated to be negative for badgers (coefficient estimate: −0.04, 95% CI: −0.08 to −0.01; Table 7, Table 8), deer (coefficient estimate: −0.15, 95% CI: −0.25 to −0.05; Table 7, Table 8), foxes (coefficient estimate: −0.07, 95% CI: −0.13 to −0.02; Table 7, Table 8), and species richness (coefficient estimate: −0.01, 95% CI: −0.02 to 0.00; Table 7, Table 8). The urbanization proxy was also shown to exert a measurable, positive influence on the occurrence probability of hedgehogs (coefficient estimate: 0.03, 95% CI: 0.00 to 0.06, Fig. 3F, Table 7, Table 8) and was contained in the hedgehog's top-ranked model (*Wi*: 0.53, pseudo-R^2: 0.109; Table 6, Table 7).

The species-specific area-weighted least-cost distance was identified as a predictor in the candidate models with ΔAICc ≤ 2 for boar, deer, fox, hare, and hedgehog. Exclusively for the boars, the patch connectivity predictor was shown to affect the species' occurrence probability measurably – in a positive effect direction (coefficient estimate: 0.42, 95% CI: 0.05 to 0.79; Table 7, Table 8). The pseudo-R^2 values of the candidate models with ΔAICc ≤ 2 ranged from 0.28 to 0.29. The top-ranked model for boars (*Wi*: 0.48, pseudo-R^2: 0.151) contained the area-weighted least-cost distance as a predictor (Table 7, Table 8).

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Table 4. Selected candidate models with ΔAICc ≤ 2 from the friction models addressing land-use effects on species-specific occurrence and species richness. ΔAICc refers to the corrected Akaike information criterion. Models with the lowest ΔAICc and the highest Akaike weights (*Wi*) for each response variable are shown in bold to indicate the top-ranked model. Pseudo-R^2refers to the variation explained by the models. The models included site-specific covariates. Here, agri.500 = surrounding agricultural land use proportion (500-m radius), green.500 = surrounding urban green proportion (500-m radius), imp.500= surrounding impervious surface cover proportion (500-m radius), forest.500 = surrounding forest proportion (500-m radius).

Response variable	Model formula	*Wi*	AICc	ΔAICc	Pseudo-R^2
Badger occurrence	**~ 1 + agri.500 + green.500 + imp.500**	**0.38**	**72.10**	**0.00**	**0.188**
	~ 1 + green.500 + imp.500	0.28	72.76	0.65	0.151
	~ 1 + agri.500 + imp.500	0.19	73.49	1.39	0.142
	~ 1 + forest.500 + green.500	0.15	74.04	1.94	0.134
Boar occurrence	**~ 1 + imp.500**	**0.35**	**38.71**	**0.00**	**0.177**
	~ 1 + green.500 + imp.500	0.31	38.95	0.23	0.223
	~ 1 + forest.500 + green.500	0.19	39.93	1.21	0.200
	~ 1 + forest.500 + imp.500	0.16	40.30	1.59	0.191
Deer occurrence	**~ 1 + agri.500 + imp.500**	**0.43**	**46.25**	**0.00**	**0.520**
	~ 1 + agri.500 + forest.500 + imp.500	0.21	47.67	1.42	0.530
	~ 1 + agri.500 + green.500 + imp.500	0.18	48.04	1.79	0.526
	~ 1 + imp.500	0.18	48.05	1.80	0.473
Fox occurrence	**~ 1 + forest.500 + imp.500**	**0.46**	**81.81**	**0.00**	**0.237**
	~ 1 + forest.500 + green.500 + imp.500	0.29	82.70	0.90	0.250
	~ 1 + agri.500 + forest.500 + imp.500	0.25	83.01	1.20	0.247
Hare occurrence	**~ 1 + forest.500 + imp.500**	**0.61**	**87.87**	**0.00**	**0.109**
	~ 1 + agri.500 + forest.500 + imp.500	0.39	88.79	0.92	0.123
Hedgehog occurrence	**~ 1 + forest.500**	**0.20**	**89.22**	**0.00**	**0.070**
	~ 1 + imp.500	0.20	89.22	0.00	0.070
	~ 1 + forest.500 + imp.500	0.18	89.48	0.26	0.091
	~ 1 + forest.500 + green.500	0.11	90.40	1.17	0.081
	~ 1 + green.500 + imp.500	0.11	90.44	1.21	0.080
	~ 1 + forest.500 + green.500 + imp.500	0.10	90.60	1.38	0.103
	~ 1 + agri.500 + imp.500	0.09	90.92	1.70	0.075
Marten occurrence	**~ 1**	**0.48**	**100.95**	**0.00**	**0.000**
	~ 1 + imp.500	0.27	102.11	1.16	0.010
	~ 1 + forest.500	0.26	102.20	1.25	0.009
Species richness	**~ 1 + imp.500**	**0.52**	**251.59**	**0.00**	**0.193**
	~ 1 + green.500 + imp.500	0.48	251.76	0.16	0.225

The fragmentation parameter, patch density, was included in the candidate models for boar and marten. While it did not exert a measurable impact on boar occurrence probability, it was significantly associated with marten occurrence probability (coefficient estimate: 0.70, 95% CI: 0.01 to 1.38; Table 7, Table 8). The top-ranked model (*Wi*: 0.64, pseudo-R^2: 0.070) for martens was the model consisting of the predictors patch area and patch density (Table 6, Table 7).

Patch size was included in the candidate models for boar, hare, hedgehog, and species richness; however, it was not found to have a significant impact on any of these response variables. The top-ranked model for hare (*Wi*: 0.39, pseudo-R^2: 0.526) contained the connectivity proxy as a predictor (Table 6, Table 7).

Further information on the selected candidate models with ΔAICc ≤ 2 is available in Table 7, Table 8, and the Supporting information.

Discussion

Overall, our study in Freiburg indicated a significant decline in mammal species richness in relation to surrounding impervious surface cover (i.e. the proportions of developed surface), a proxy of urbanization. Particularly, the occurrence probability of four species, badgers, deer, foxes, and hares, decrease with increasing impervious surface. In case of badger, the occurrences probability increases with higher proportions of forest cover.

In Freiburg, patch connectivity positively impacted the occurrence probability of wild boars. Stone marten's (one of the most frequently observed species) higher probability of occurrence was associated with increasing patch density in the city. No other factors were found to have a significant impact on the species' occurrence probability in the city of Freiburg.

Proportion of land use categories' effect on species occurrence

Badgers' occurrence probability was found to be negatively associated with increasing levels of impervious surface cover proportion and positively associated with higher levels of surrounding forest cover. These findings align with the findings of Piza-Roca et al. (2015), who conducted a literature review of badger sett locations. The reviewed literature indicated a preference for woodland areas, whereas other land use types were

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Table 5. Average coefficient parameters in the candidate models with ΔAICc ≤ 2 from the the species-specific friction models. ΔAICc refers to the corrected Akaike information criterion. The models included site-specific covariates. Here, agri.500 = surrounding agricultural land use proportion (500 m radius), green.500= surrounding urban green proportion (500 m radius), imp.500 = surrounding impervious surface cover proportion (500 m radius), forest.500 = surrounding forest proportion (500 m radius).

Response variable	Coefficient	95% confidence intervals		Estimate	SE
		2.50%	97.50%		
Badger	(Intercept)	−1.45	1.63	0.09	0.78
	imp.500	−0.08	−0.01	−0.04	0.02
	agri.500	−0.09	0.01	−0.04	0.02
	green.500	−0.08	0.01	−0.04	0.02
	forest.500	0.00	0.03	0.02	0.01
Boar	(Intercept)	−3.20	0.56	−1.32	0.95
	imp.500	−0.15	0.01	−0.07	0.04
	green.500	−0.20	0.05	−0.07	0.06
	forest.500	−0.01	0.04	0.02	0.01
Deer	(Intercept)	0.37	4.68	2.52	1.09
	imp.500	−0.31	−0.08	−0.20	0.06
	agri.500	−0.09	0.00	−0.04	0.02
	forest.500	−0.04	0.02	−0.01	0.02
	green.500	−0.07	0.04	−0.02	0.03
Fox	(Intercept)	−0.11	2.89	1.39	0.75
	imp.500	−0.07	0.00	−0.04	0.02
	forest.500	0.00	0.07	0.03	0.02
	green.500	−0.04	0.01	−0.02	0.01
	agri.500	−0.03	0.09	0.03	0.03
Hare	(Intercept)	−0.77	2.04	0.64	0.71
	imp.500	−0.08	−0.01	−0.05	0.02
	forest.500	−0.04	0.00	−0.02	0.01
	agri.500	−0.02	0.06	0.02	0.02
Hedgehog	(Intercept)	−2.94	0.21	−1.37	0.80
	forest.500	−0.05	0.00	−0.02	0.01
	imp.500	0.00	0.06	0.03	0.01
	green.500	−0.01	0.04	0.01	0.01
	agri.500	−0.03	0.06	0.01	0.02
Marten	(Intercept)	−0.14	1.24	0.55	0.35
	imp.500	−0.01	0.03	0.01	0.01
	forest.500	−0.02	0.01	−0.01	0.01
Richness	(Intercept)	0.99	1.48	1.23	0.12
	imp.500	−0.02	0.00	−0.01	0.00
	green.500	−0.01	0.00	−0.01	0.00

Table 6. Formulas of each species' friction surface calculation. imp.500 = surrounding impervious surface cover proportion in a 500-m radius, l.use = resistance value assigned to the land use categories. Following Beier et al. (2009), the impervious surface cover was split in three classes: low (imp.500 < 30%), medium (30% ≤ imp.500 < 50%), and high (imp.500 ≥ 50%). Due to the measurable negative effect on the species, the low imperviousness class had the lowest resistance value, the medium class an intermediate value, and the highest class the maximum value, corresponding to 1, 100 and 200, respectively.

Response variable	Friction map formula
Badger	friction = l.use × 0.8 + imp.500 × 0.2
Boar	friction = l.use × 1.0
Deer	friction = l.use × 0.5 + imp.500 × 0.5
Fox	friction = l.use × 0.8 + imp.500 × 0.2
Hare	friction = l.use × 0.8 + imp.500 × 0.2
Hedgehog	friction = l.use × 1.0
Marten	friction = l.use × 1.0

selected less frequently in comparison to their availability. Our study's results support the increase in badger occurrence with increasing vegetation. Conversely, a comprehensive review of the extant literature on urban carnivores revealed that badgers are present in high population density within urban environments (Šálek et al. 2015). One potential explanation for this phenomenon is that badgers may actively colonize urban landscapes in response to their population density (Harris 1984, Bateman and Fleming 2012). The urbanization categories in which badgers occurred (Fig. 2C), indicate that the badger population density close to Freiburg could be sufficiently small to be inhabited in the surrounding natural areas. While we categorize the badgers occurring in the forest adjacent to the city core as 'urban avoiders', a multi-city assessment, incorporating confounding factors such as city extent and surrounding badger population, could offer further insights into the factors accelerating urban colonization by European badgers.

The negative association of deer occurrence and increasing impervious surface cover proportion was consistent with

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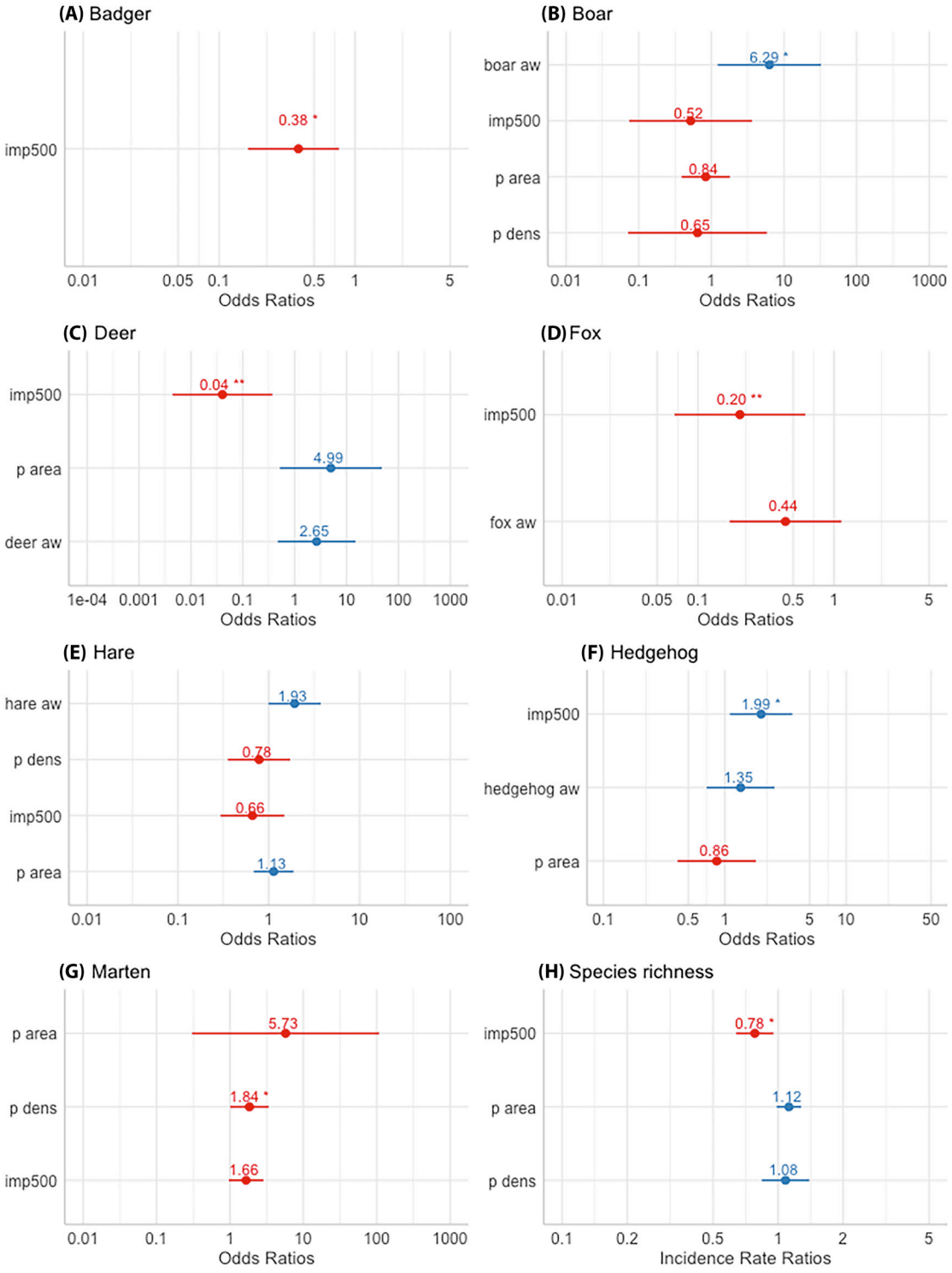


Figure 3. Resulting scaled coefficients and confidence intervals of the model averaging for the investigated species. For the single-species investigations, the x-axis shows odds ratios. Odds ratios < 1.0 signify a negative impact. Aw = area-weighted least-cost distance; p.dens = patch density; p.area = patch size; imp.500 = surrounding impervious surface cover proportion (500-m radius).

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Table 7. Selected candidate models with ΔAICc ≤ 2 addressing the effects of urbanization, patch connectivity, fragmentation and patch size on species-specific occurrence probabilities and species richness. ΔAICc refers to the corrected Akaike information criterion. Models with the lowest ΔAICc and the highest Akaike weights (*Wi*) for each response variable are shown in bold to indicate the top-ranked model. Pseudo-R^2refers to the variation explained by the models. Here, Boar.aw = area-weighted least-cost distance for boars; deer.aw = area-weighted least-cost distance for deer; fox.aw = area-weighted least-cost distance for foxes; hare.aw = area-weighted least-cost distance for hares; hedgehog.aw = least-cost distance for hedgehogs; p.dens = patch density; p.area = patch size; imp.500 = surrounding impervious surface cover proportion (500-m radius)

Response variable	Model formula	*Wi*	AICc	ΔAICc	Pseudo-R^2
Badger occurrence	**~ 1 + imp.500**	**1.00**	**74.30**	**0.00**	**0.188**
Boar occurrence	**~ 1 + log(boar.aw)**	**0.46**	**34.48**	**0.00**	**0.151**
	~ 1 + imp.500 + log(boar.aw)	0.20	36.14	1.66	0.142
	~ 1 + log(boar.aw) + p.area	0.17	36.42	1.94	0.134
	~ 1 + log(boar.aw) + p.dens	0.17	36.48	2.00	0.177
Deer occurrence	**~ 1 + imp.500 + p.area**	**0.61**	**39.05**	**0.00**	**0.223**
	~ 1 + imp.500 + log(deer.aw) + p.area	0.39	39.91	0.86	0.191
Fox occurrence	**~ 1 + imp.500 + log(fox.aw)**	**0.66**	**82.91**	**0.00**	**0.520**
	~ 1 + imp.500	0.34	84.23	1.32	0.530
Hare occurrence	**~ 1 + log(hare.aw)**	**0.39**	**88.59**	**0.00**	**0.526**
Hare occurrence	~ 1 + p.dens + log(hare.aw)	0.16	90.36	1.77	0.473
	~ 1 + imp.500	0.15	90.46	1.87	0.237
	~ 1 + imp.500 + log(hare.aw)	0.15	90.49	1.90	0.250
	~ 1 + p.area + log(hare.aw)	0.15	90.51	1.92	0.247
Hedgehog occurrence	**~ 1 + imp.500**	**0.53**	**89.22**	**0.00**	**0.109**
	~ 1 + imp.500 + log(hedgehog.aw)	0.28	90.50	1.28	0.123
	~ 1 + imp.500 + p.area	0.20	91.21	1.99	0.070
Marten occurrence	**~ 1 + p.area + p.dens**	**0.64**	**93.65**	**0.00**	**0.070**
	~ 1 + imp.500 + p.area	0.36	94.77	1.12	0.081
Species richness	**~ 1 + imp.500 + p.area**	**0.48**	**250.89**	**0.00**	**0.080**
	~ 1 + imp.500	0.34	251.59	0.70	0.103
	~ 1 + imp.500 + p.area + p.dens	0.19	252.74	1.85	0.075

prior research findings. Torres et al. (2012) found that roe deer avoid human settlements if they are not dependent on anthropogenic feeding located close to houses. Roe deer, like wild boar, are considered a game species. Consequently, they are susceptible to anthropogenic disturbance, which is perceived as a mortality risk due to hunting and road mortality (Forman and Alexander 1998, Lone et al. 2014).

The impervious surface cover proportion negatively affecting the fox occurrence probability was contradictory to our predictions, in which we categorized foxes as urban adapter species. However, this finding supports the conclusion of Červinka et al. (2014) suggesting that red fox are likely to avoid highly urbanized areas. The preferred habitat is characterized by a greater degree of naturalness and a lesser degree of urbanization. Despite its preference for areas with substantial surrounding vegetation cover, presumably forest sites, fox occurrences were detected in every level of surrounding imperviousness cover (Fig. 2C). Nevertheless, foxes were found to occur preferentially in lower values of surrounding impervious surface cover in Freiburg. One potential explanation for this phenomenon could be the proximity of forest sites within the urban environment, which offer higher quality habitat. Investigating genetic distance of fox subpopulations in the metropolitan area of Berlin, Germany, Kimmig et al. (2020) found the urban landscape impeding gene flow and resulting in genetic differentiation of urban and rural conspecifics. The authors find indications of foxes using linear, anthropogenic structures such as roads or railways to migrate into the city, while Fletcher et al. (2025) demonstrate the increased use of anthropogenic food items in city-dwelling foxes. It seems that the smaller spatial extent of Freiburg decreases its movement impediment resulting in fox ability to exploit human food resources while inhabiting the adjacent forest sites. We encourage the assessment of fox occurrence and genetic distance in different-sized cities in a multi-city study.

The presence of hares was predominantly observed within low and medium urban camera trap sites. This observation was found to be a measurable effect, suggesting that the surrounding impervious cover may play a role in influencing the occurrence probability of European hares. This finding aligns with the conclusions drawn from earlier studies. Pavliska et al. (2018) also noted hares avoiding urban settlements and found a habitat preference for semi-natural grasslands and forests. The European hare population in Freiburg displays a comparable behavioural pattern to other urban and peri-urban conspecifics (Roedenbeck and Voser 2008, Mayer and Sunde 2020) in this regard. The absence of further significant findings concerning the surrounding land use categories' effect on hare occurrence supports the hares' behavioural flexibility to exploit different landscapes in a manner that adapts to the urban environment (Fulgione et al. 2009).

The analysis of the land uses' cover proportions resulted in a significant increase in hedgehog occurrence probability with higher levels of surrounding impervious surface cover proportion. Our categorization of hedgehogs as urban exploiters aligns with research showing higher population density in urban areas (Hubert et al. 2011). Recent studies

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Table 8. Average coefficient parameters in the candidate models with ΔAICc ≤ 2 addressing the effects of urbanization, patch connectivity, fragmentation, and patch size on species-specific occurrence probabilities and species richness. ΔAICc refers to the corrected Akaike information criterion. Here, Boar.aw = area-weighted least-cost distance for boars; deer.aw = area-weighted least-cost distance for deer; fox.aw = area-weighted least-cost distance for foxes; hare.aw = area-weighted least-cost distance for hares; hedgehog.aw = least-cost distance for hedgehogs; p.dens = patch density; p.area = patch size; imp.500 = surrounding impervious surface cover proportion (500-m radius).

Response variable	Coefficient	95% confidence intervals		Estimate	SD
		2.50%	97.50%		
Badger	(Intercept)	−1.16	0.58	−0.29	0.44
	imp500	−0.08	−0.01	−0.04	0.02
Boar	(Intercept)	−11.03	−1.54	−6.28	2.38
	log(boar.aw)	0.05	0.79	0.42	0.19
	imp500	−0.12	0.06	−0.03	0.05
	p.area	0.00	0.00	0.00	0.00
	p.dens	−3.01	2.01	−0.50	1.26
Deer	(Intercept)	−3.49	3.27	−0.11	1.71
	imp500	−0.25	−0.05	−0.15	0.05
	p.area	0.00	0.00	0.00	0.00
	log(deer.aw)	−0.15	0.53	0.19	0.17
Fox	(Intercept)	0.49	7.14	3.81	1.68
	imp500	−0.13	−0.02	−0.07	0.03
	log(fox.aw)	−0.63	0.04	−0.29	0.17
Hare	(Intercept)	−3.69	0.35	−1.67	1.02
	log(hare.aw)	0.00	0.49	0.24	0.12
	p.dens	−1.18	0.62	−0.28	0.45
	imp500	−0.06	0.02	−0.02	0.02
	p.area	0.00	0.00	0.00	0.00
Hedgehog	(Intercept)	−4.28	−0.08	−2.18	1.06
	imp500	0.00	0.06	0.03	0.01
	log(hedgehog.aw)	−0.13	0.35	0.11	0.12
	p.area	0.00	0.00	0.00	0.00
Marten	(Intercept)	−0.12	2.08	0.98	0.55
	scale(p.area)	−1.19	4.68	1.75	1.47
	scale(p.dens)	0.01	1.21	0.61	0.30
	scale(imp500)	−0.03	1.05	0.51	0.27
Richness	(Intercept)	0.83	1.41	1.12	0.15
	imp500	−0.02	0.00	−0.01	0.00
	p.area	0.00	0.00	0.00	0.00
	p.dens	−0.20	0.38	0.09	0.15

indicate an urbanization optimum, for example, Turner et al. (2022) reported that hedgehogs in London thrive at intermediate impervious surface levels but decline at higher levels and human population densities. The study also indicated that hedgehogs prefer urban allotments, gardens, parks, and terraced housing (Turner et al. 2022, Fung et al. 2024). Hubert et al. (2011) noted a positive link between hedgehog abundance and anthropogenic food, while Williams et al. (2018) found negative implications of badger presence on hedgehog occupancy. The increasing presence of hedgehogs in urban environments has been the subject of recent research, with the underlying reasons for this phenomenon being extensively studied.

Effects of urbanization, connectivity, fragmentation and patch size

The findings of our study indicate an adverse impact of urbanization on total mammal species richness. A measurable negative effect on species richness exerted by the predictor surrounding impervious surface cover proportion is in accordance with the prediction. In accordance with these results, various reviews emphasize the decrease in mammal species richness with increasing urbanization (McKinney 2008, Faeth et al. 2011). Gallo et al. (2017) identified that sites situated within the urban forest adjacent to the urban boundary exhibited the highest species richness values among the investigated urban green area types. In contrast to our predictions, the other investigated predictors did not affect species richness measurably, a finding that is particularly noteworthy concerning the assumed importance of connectivity for the conservation of urban mammal diversity. The existing literature on connectivity supports the hypothesis that increasing patch connectivity leads to an increase in the occurrence of mammal communities by facilitating dispersal (Vergnes et al. 2013). In the city of Cape town, connectivity was identified to be the most important factor to explain different species richness values in urban nature reserves (Schnetler et al. 2021). Furthermore, studies have demonstrated that wild boars possess the capacity to colonize urban forest sites and establish subpopulations that exhibit genetic distinctions from their rural conspecifics (Stillfried et al. 2017). In Freiburg, we did not observe deer and boars in camera trap locations with

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medium to high levels of surrounding impervious surface cover proportions. The reason for the absence of camera traps recording these species in higher urbanized locations could be the relatively compact spatial extent of the city. The city's adjacent forest sites combined with its small extent and its small-scale urban green areas result in a lack of natural and near-natural green areas within the city borders, i.e. urban wooded areas like city forests. While the forest-dwelling species lack shelter inside the urban boundaries, the limited scope of Freiburg possibly mitigates the barrier effect cities pose to wildlife immigration in and out of the settlement to exploit human resources (Červinka et al. 2014). This pattern suggests that our study's results could possibly differ in cities with larger spatial extent, where the distance between city center and neighboring forest or vegetation patches pose a higher movement impediment. Whether the size of cities contribute to a greater importance of patch connectivity could be object of future research investigating mammal occurrence as function of the interaction of impervious surface cover, city area and patch connectivity in a multi-city study.

The area-weighted least-cost distance exhibited a positive effect on the boar's occurrence probability. This finding underscores the heightened sensitivity of boars to increased road density, a phenomenon that has been previously documented in the literature (Forman and Alexander 1998, Grilo et al. 2009). The finding regarding the connectivity proxy's effect adds to former studies showing the species' preference for near-natural vegetated sites, even in urban environments (Stillfried et al. 2017), and the boar mobility under the given circumstance of step-stone forest cover (Rutten et al. 2019).

Conclusion

Our study emphasizes the negative effect of urbanization on mammal species richness. The findings deviate from those of urban wildlife studies, particularly regarding the significance of patch connectivity and fragmentation. In this city, surrounded by forest and agricultural land use, the role of connectivity and fragmentation is of lesser importance. It can be hypothesized that urban green spaces offer the potential for both urban adapters and urban avoiders to reside in neighboring forest patches while exploiting anthropogenic resources.

The analysis suggests that some of the investigated species occurs with increasing probability in lower urbanized landscapes regardless of the inter-patch connectivity. However, hedgehogs were the exception as they seem adapt to urbanization in Freiburg, maybe due to the supplementary feeding by gardeners (Benjamin et al. 2025). A future investigation on this species separately through multi-city assessment including larger sample size would be necessary to confirm this. European badgers and wild boars have been observed to both colonize cities and exhibit behaviors that indicate avoidance of urban areas. It is therefore imperative to consider the urban extent and the quality of urban green areas when assessing the impact of urbanization on species populations. The inter-patch connectivity is likely to be of greater significance in urban landscapes characterized by green spaces that are isolated from adjacent forests. Therefore, the present study highlights the crucial importance of urban green areas forming step-stones within urban landscapes.

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Author contributions

Marius Huber: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Ilse Storch**: Conceptualization (equal); Funding acquisition (lead); Resources (lead); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Geva Peerenboom**: Conceptualization (supporting); Data curation (supporting); Funding acquisition (supporting); Methodology (supporting); Project administration (supporting); Writing – review and editing (supporting). **Marufa Sultana**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j9kd51cvz (Huber et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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