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Faculty for Environment and Natural Resources

Is Connectivity the Key?

Analysis of Mammal Diversity in Urban Green Areas

MASTER THESIS

Marius Paul Huber | May 2022

Matr.No. 370 4992

Supervisor: Prof. Dr. Ilse Storch

Second examiner: Prof. Dr. Peter Biedermann

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Abstract

Urbanization is known to have ambiguous effects on biodiversity. While the consequential degradation, fragmentation, and loss of habitat via urbanization decreases species diversity, connectivity is assumed to mitigate the consequences of changes in habitat quality. Urban biodiversity is a well-studied topic, however there are only few multi-species analyses on urban mammal diversity. Therefore, this study aimed to understand the effect of patch connectivity in combination with proxies on fragmentation, urbanization, and vegetation on urban mammal diversity. I used an information-theoretical approach to find the proxies' effects, their direction, and their ranking in predicting species richness and species-specific occurrences in generalized linear models and generalized least squares models. I calculated species-specific area-weighted least-cost distances to assess functional patch connectivity. Urban mammal species richness was best predicted by distance to the city boundary, increasing by one species every 62.5m. European hare (*Lepus europaeus*), red fox (*Vulpes vulpes*), roe deer (*Capreolus capreolus*), and stone marten (*Martes foina*) occurrences were found to be associated with functional connectivity, while European hedgehogs (*Erinaceus europaeus*), roe deer, and wild boar (*Sus scrofa*) are affected by surrounding vegetation cover proportion. The study highlights the negative influence of urbanization on mammal diversity while emphasizing the importance of even small patches of greenery in the urban landscape. Further research could include multiple cities and more data points to investigate the found associations more profoundly.

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1 Introduction

Urbanization is an ongoing trend: Currently, more than half of the world's population lives in cities, which is predicted to become 68% by 2050 (UN DESA, 2018). As the urban population increases, an expansion of human settlement is expected to continue, resulting in the conversion of natural areas into artificial ones (Angel et al., 2011; UN DESA, 2018). On the one hand, such urban sprawl is a major driver of habitat degradation, fragmentation, and loss (Aronson et al., 2014). On the other hand, urban development can result in highly heterogeneous landscape structure and diversity in land-use can offer a variety of ecological niches (Savard et al., 2000). There is, thus, increasing interest to understand the opportunities to enhance biodiversity in cities (Rands et al., 2010).

Urban landscapes – comprising urban green areas like parks, cemeteries, and different-sized gardens – can provide habitat for a variety of wildlife species (Faeth et al., 2011). The animal species found in urban and peri-urban areas may vary concerning species-specific ecology and behavior (Baker & Harris, 2007). Based on their response to urbanization, animal species associated with urban areas are grouped into "urban exploiters", "urban adapters" and "urban avoiders" (Blair, 2001). Urban avoiders are sensitive species that are susceptible to land-use conversion. They are the first species to become locally extirpated due to the conversion of natural ecosystems to urban ones. Urban adapter species use intermediately urbanized habitats and their resources. Urban exploiters benefit from an anthropogenic supply of resources and can occur in higher abundances in cities than in any other habitats. Due to urban exploiter species, studies on the biodiversity of different animal taxa generally show a pattern of increasing animal abundance in urban context, but species richness and diversity generally decline due to increasing urbanization (Faeth et al., 2011).

Besides species-specific traits, local environmental factors contribute to shaping urban animal species occurrences and overall richness. The most important driver of urban bird, insect, and plant species richness has been found to be the area size of urban green patches (Beninde et al., 2015). Garden et al. (2006) found habitat loss to be the most influential factor affecting Australian terrestrial mammals (53.3%), followed by structural or functional patch connectivity (46.7%), surrounding vegetation and habitat heterogeneity (20%), and patch area (13.3%). Accordingly, a more recent review on urban biodiversity corroborates the importance of habitat loss as a driver of decreasing vertebrate species richness in urban landscapes (McKinney, 2008), and the importance of patch area is supported for European urban mammals as well (Baker & Harris, 2007).

However, multi-species investigations on mammals are found to be lacking (Faeth et al., 2011). An existing global review on urban biodiversity studies reported that only 6.5% of literature considered mammals (Faeth et al., 2011). Mammals can provide crucial ecosystem services, irrespective of the landscape context (e.g., nutrient cycling, pest control, or seed dispersal) (Lacher Jr. et al., 2019). A lack of consistent knowledge and insight into urban mammal ecology can lead to species diversity loss as well as human-wildlife conflicts in cities (Rands et al., 2010). Due to this research gap and the benefit of urban mammal diversity, I focused my study on mammals. As connectivity is found to be an influential factor in the occurrence of urban mammals (Baker & Harris, 2007), I specifically focus on the role of patch connectivity, investigating structural and functional measures.

1.1 Connectivity and fragmentation

Landscape connectivity is defined as “the degree to which the landscape facilitates or impedes movement of organisms among resource patches” (Taylor et al., 1993; Tischendorf & Fahrig, 2000, p. 7). It can be classified as structural or functional connectivity. Structural connectivity represents the landscape structure and composition as a physical attribute. It is quantified in landscape metrics or the availability of linear features acting as inhibitors or facilitators of animal movement (LaPoint et al., 2015). Conversely, functional connectivity considers the studied organism’s behavior to conclude whether habitat patches are connected or not (Theobald, 2006).

Contrasting to the theory of island biogeography, landscape connectivity accounts for the influence of habitat matrix quality on animal movement. The island biogeography theory compares patches of suitable habitat to islands isolated by an ocean of unsuitable matrix, viewing landscape binarily as habitat or non-habitat (MacArthur & Wilson, 2016). However, habitat matrix quality significantly contributes to the effective isolation of suitable habitat patches (Ricketts, 2001). Habitat matrix quality is defined here as the structure and composition of landscape between habitat patches, i.e., patches that enable animal colonization and persistence (see Hanski, 1998).

As landscape connectivity accounts for the habitat matrix, it is necessarily affected by habitat fragmentation. Habitat fragmentation is the process of transforming large habitat patches into a multitude of smaller-sized patches intersected by matrix differing from the original habitat (Wilcove et al., 1986). Habitat fragmentation results in the loss of habitat area and the separation of large patches into smaller, more isolated patches (Laurance, 2008). The latter is called fragmentation per se and its effect on biodiversity is often confounded with the habitat loss resulting from fragmentation. While the effects of fragmentation per se and habitat loss are complex to investigate separately, Fahrig (2003) found that most of the biodiversity loss attributed to fragmentation is caused by habitat loss, not fragmentation per se.

For studies of urban biodiversity, concepts from the island biogeography theory (MacArthur & Wilson, 2016) and metapopulation dynamics (Hanski, 1998) are popular theories on populations and movement biology. Despite these models' immense impact on fragmentation research, particularly the island biogeography theory's application in highly fragmented landscapes was found to be lacking. Among other simplifications, the island biogeography theory misses the crucial effects of corridors and matrix habitat (Laurance, 2008). Therefore, I analyzed the highly fragmented urban ecosystem based on a landscape ecological approach following Forman and Godron (1981). The landscape is assumed to consist of a mosaic of patches, matrix, corridors, and human habitations. In this study, I include human habitations as a specific matrix type since the urban ecosystem consists mostly of human habitation areas.

An addition to this conceptualization of landscape ecology is the organism-based landscape resistance, reflecting the organism-centered aspect of functional connectivity (Tischendorf & Fahrig, 2000). Different habitat types are assumed to affect organism movement according to the organism's biology and behavioral response. Therefore, state-of-the-art connectivity measures incorporate the species-specific effects of matrix habitat on organism-based movement facilitation or impediment in addition to the interpatch distance (Kupfer, 2012). In functional connectivity measures, landscape ecology and its organism-specific influence are often incorporated by landscape resistance values for landscape features, thus reflecting effective barriers or corridors (Adriaensen et al., 2003). Combining the importance of patch area for urban biodiversity (Beninde et al., 2015) with the biologically more meaningful functional connectivity measures (see Chardon et al., 2003; Theobald, 2006), I introduce the area-weighted least-cost distance as patch connectivity estimator in this study.

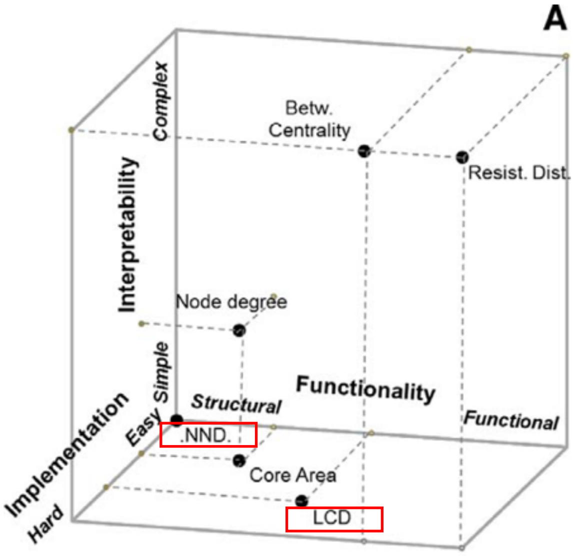

Figure 1: Diagram of landscape and connectivity metrics as a function of their ease of implementation and interpretation and structural or functional connectivity viewpoint from Kupfer (2012). Visualized are patch/ element metrics. Measures occurring in this thesis are marked red: NND = Euclidean nearest neighbor distance; LCD = least-cost distance

1.2 Aims & objectives

In my thesis, I aimed to understand the effect of patch connectivity on urban mammals. Specifically, I focused on the species richness and species-specific occurrence of medium to large-sized-mammals as a function of patch connectivity. The study site is the highly fragmented urban landscape of one of Germany's greenest cities, Freiburg im Breisgau. The city is surrounded by large, unfragmented forest patches with a multitude of smaller, presumably well-connected urban green area fragments located closer to the city center. Thus, this cityscape offers a gradient of natural to urban landscape features that could provide insight for the investigation of the effects of connectivity, fragmentation, urbanization, and vegetation on urban mammal diversity. Analyzing this study location, I assessed three research questions:

1) How does the proximity to different landscape features affect urban mammal species richness and species-specific probability of occurrence of medium to large-sized urban mammals?
2) How does increasing patch size influence urban mammal species richness and species-specific occurrence probability?
3) Is the impact of patch connectivity on species richness and species-specific occurrence probability more pronounced in higher fragmented areas?

I hypothesize that the occurrence of mammal species is affected by the proximity of landscape features according to their behavioral response to urbanization: I predict that the species categorized as urban avoiders will be affected negatively by impervious surface cover proportion as proxy of urbanization and positively by surrounding vegetation cover proportion. Since they can adapt to life in urban context, I predict that the occurrence probability of urban adapter species is not significantly affected by impervious cover. Lastly, I predict that urban exploiter species are more probable to occur in higher levels of urbanization. Since this simplistic approach will not fully explain the species-specific occurrence, the distance to other landscape features could add to the understanding of the species' occurrence.

According to the findings on the importance of patch size for urban biodiversity, I hypothesize that patch size impacts mammal species richness and mammal occurrences. Specifically, I predict that total species richness and mammal species' occurrence will be affected positively by patch size. Conversely, I expect that species favoring a high spatial heterogeneity will be affected negatively by increasing patch area size.

I hypothesize that, explicitly in sites with small, fragmented patches, the effect of patch connectivity is stronger. I, therefore, predict that in locations with increasing surrounding fragmentation, greater patch connectivity will favor total species richness and all mammal species irrespective of their behavioral response to urbanization and habitat prerequisites. Summarizing previous authors' findings, I also predict that increasing patch connectivity will also be positively associated with species richness, regardless of the interaction with fragmentation.

2 Material and methods

2.1 Study area & site selection

To assess how connectivity influences mammal species richness, I collected camera trap records of medium and large mammal species occurring along an urbanization gradient. The study area was Freiburg im Breisgau, located in the South of Baden-Württemberg, Germany (47°59’45” N; 7°51’07” E). The city covers an area of approximately 15,300 ha comprised of 3,464 ha of agricultural sites, 6,533 ha of forest area, and 670 ha of sports, leisure, and recreational areas, including urban green areas. There are approximately 230,000 inhabitants in Freiburg im Breisgau (Amt für Bürgerservice und Informationsmanagement, 2021), with a population density of about 1,500 inhabitants per km^2.

Following the suggestions of the Urban Wildlife International Network (sUWIN) study design, 24 motion-triggered cameras (hereafter: camera traps) were placed in green spaces in and around the city of Freiburg (Figure 2). The sites were selected in a grid approach. Therefore, the city area was divided into 1.5 x 1.5-km grid cells. Hereby, the suggested Euclidean distance of at least 1000 m between camera trap locations was maintained (Urban Wildlife Information Network, 2020). One camera trap that was too close to its next neighbor was excluded from the analysis. To assure the appropriate incorporation of a gradient ranging from peri-urban to urban landscape, the grid cell’s average impervious cover was calculated based on the Global Man-made Impervious Surface Dataset From Landsat (Brown de Colstoun et al., 2017). The site selection focused on an even distribution of cameras in different levels of impervious cover proportion. However, due to restrictions from the green area management and private properties, there were fewer cameras installed in medium and higher urbanized areas than in lower intensity urban districts (Figure 2).

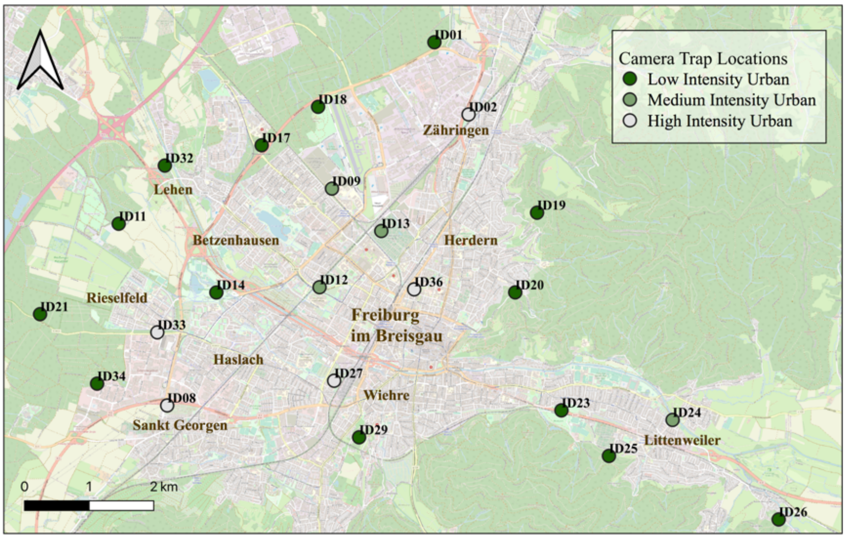

Figure 2: Overview of the camera trap locations included in the analysis. The imperviousness classes are low intensity urban (< 30 % surrounding impervious cover), medium intensity urban (30 – 50 % surrounding impervious cover), and high intensity urban (> 50 %).

2.2 Data collection & data preparation

The species data was collected with camera traps (Bushnell Trophy Cam Essential E3 (119837); Lenexa, Kansas State, USA, 2016). Before the installation at the study sites the camera settings were adjusted similarly to the UWIN study design (Urban Wildlife Information Network, 2020). Details on the camera settings used can be found in Table 1.

Table 1.

Non-default settings used for the camera traps.

Set Mode	Setting
Mode	Camera
Image Size	3 Megapixels
Pictures per Sequence	2 Photos
Interval	30 s
Sensor level	Normal

The camera traps were installed on trees or poles at the study sites (Figure 3). Exact camera trap locations were chosen using the following criteria: a minimum distance of 10 m to the next path, orientation towards a clearing or a site with minimum vegetation, and low visibility from the closest path to prevent theft. After 11 to 15 days, the batteries and SD-cards of the cameras were exchanged, and after 28 trap nights the cameras were retrieved.

Figure 3: One of the installed camera traps. Photo by Marufa Sultana.

For the classification of the camera trap records, TIMELAPSE2 picture classification software was used following a template created specifically the camera trap photo classification. Each camera trap photo was controlled and classified for animal and site-specific information manually (Table 2). Photos with domesticated, non-mammalian, or small-sized mammals and those without animals were deleted from the analyzed records.

Table 2.

Classification template parameters.

Parameter	Comment
Date & Time	Time and date when the picture was taken; automatically recognized by the software
Image quality	Dropdown list; information on whether the photo was acceptable or not (e.g., too dark)
Delete	Markable option to select the picture as irrelevant for the analysis
Species	Dropdown list of potentially occurring mammal species; based on the citizen science platform Wilde Nachbarn
Number	Number of the recognized individuals on the picture
Money shot	Markable option to highlight the picture as particularly aesthetic
Comment	Used for notes, e.g., on the taxa of irrelevant species
Urban gradient	Dropdown list of three different levels of urbanization (low urban, medium urban, high urban)
Analyst	Name of the person classifying the picture

2.2.1 Response variables

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. The species richness measure was expressed as alpha-diversity, the number of distinct species present in each location. The species included in the analysis were all mammal species with a body mass greater than or equal to that of a European hedgehog (hereafter: hedgehog). Because rare species add statistical noise to the modeling while providing little additional input for the interpretation, species occurring in less than 4 locations were removed (Cao et al., 2001). More information on the analyzed study taxa can be found in Table 3. The categorization of the species' predominant behavior was based on findings from previous authors. Species found to avoid urban context were classified as urban avoiders, species that were found to adapt as urban adapters, and species profiting from and therefore seeking anthropogenic proximity as exploiters. Additionally, the classification was based on habitat selection in the urban context (inner- vs. outer urban) and abundances observed (higher abundance in rural landscape versus higher abundance in urban landscape) (*sensu* Blair, 1996). I checked for sampling completeness with a species accumulation curve (*specaccum*-function, *vegan*-package, *v.2.5.7*) (Oksanen et al., 2020).

Table 3.

Details on the taxa investigated in the analysis

Species name	Predominant diet	Predominant behavior	Sources
European hare (*Lepus europaeus*)	Herbivore	Urban adapter	Hackländer et al., 2011; Reichlin et al., 2006
Roe deer (*Capreolus capreolus*)	Herbivore	Urban avoider	Jedrzejewska & Jedrzejewski, 1998; Torres et al., 2012
Wild boar (*Sus scrofa*)	Herbivore	Urban avoider	Jedrzejewska & Jedrzejewski, 1998; Schley & Roper, 2003; Stillfried et al., 2017
European hedgehog (*Erinaceus europaeus*)	Insectivore	Urban exploiter	van de Poel et al., 2015; Hof et al., 2012
European badger (*Meles meles*)	Omnivore (Invertebrates, fruit, vertebrates, scavenge)	Urban avoider	Harris, 1984; Kowalczyk et al., 2003
Stone marten (*Martes foina*)	Omnivore (Plant material, vertebrate prey, invertebrates, scavenge)	Urban exploiter	Apathy, 1998; Ruette et al., 2015
Red fox (*Vulpes vulpes*)	Omnivore (Scavenge, vertebrate prey, invertebrates, fruit)	Urban adapter	Contesse et al., 2004; Iossa et al., 2008

2.2.2 Site-specific predictor variables

Independent variables were measured at the camera locations and their surroundings. These variables were categorized into measurements of connectivity, fragmentation, urbanization, and vegetation. I measured the Euclidean distance to different Urban Atlas features in QGIS as easily measurable, structural connectivity indicators (Kupfer, 2012), and additionally to the area-weighted least-cost distances (chapter 2.3.1). As a fragmentation proxy, I selected patch density. Therefore, the patch density of each 500-m buffer around the camera location was calculated. I used the *landscapemetrics*-package, where the FRAGSTAT-landscape metric calculations are implemented for R (*lsm_c_pd*-function, *version 1.5.4*, Hesselbarth et al., 2019). As an urbanization proxy, I used the average proportion of impervious surface cover within a 500-m buffer. As an index for vegetation, I chose the vegetation cover proportion within a 500-m buffer around the camera locations. I calculated the vegetation cover as the proportion of vegetated Urban Atlas features in the 500-m buffer. The feature classes “forest”, “urban green area”, “airports”, and “sports and leisure facilities” were comprised in the vegetated Urban Atlas features. Table 4 shows further information on the sources and specifications of the site-specific measurements.

Table 4.
Information on the measured site-specific predictor variables.

Category	Variable	Explanation	Data type	Source resolution	Source
Urbanization	Land use (*l.use*)	Land use categories of the polygons contained in the attribute table	Categorical	10 m x 10 m	Copernicus Land Monitoring Services, 2018
	Impervious surface cover proportion (*imp500*)	Average proportion of impervious surface cover (%) in a 500-m buffer around the camera location with the extract-function (R, raster-package)	Continuous	30 m x 30 m	Brown de Colstoun et al., 2017
Connectivity	Distance to agricultural area (*d.agri*)	Edge-to-edge distance to the closest agricultural feature (m) measured with the NNJOIN-plugin in QGIS	Continuous	10 m x 10 m	Copernicus Land Monitoring Service 2018
	Distance to city boundary (*d.city*)	Edge-to-edge distance to Freiburg's city boundary (m)– the boundary between the urban land-use categories and forest or agricultural sites – measured with the NNJOIN-plugin in QGIS	Continuous	10 m x 10 m	Copernicus Land Monitoring Service 2018
	Distance to forest (*d.forest*)	Edge-to-edge distance to the closest forest feature (m) measured with the NNJOIN-plugin in QGIS	Continuous	10 m x 10 m	Copernicus Land Monitoring Service 2018
	Distance to green urban area (*d.green*)	Edge-to-edge distance to the closest urban green area or leisure and sports facilities feature (m) measured with the NNJOIN-plugin in QGIS	Continuous	10 m x 10 m	Copernicus Land Monitoring Service 2018
	Distance to road (*d.road*)	Edge-to edge distance to the nearest road (m) measured with the NNJOIN-plugin in QGIS	Continuous	10 m x 10 m	Copernicus Land Monitoring Service 2018
Vegetation	Surrounding vegetation cover proportion (*veg500*)	Average proportion of forests, urban green areas or leisure and sports facilities (%) in a 500-m buffer around the camera location calculated with intersect function & field calculator in QGIS	Continuous	10 m x 10 m	Copernicus Land Monitoring Service 2018
Fragmentation	Patch density (*p.dens*)	Number of polygon features inside a 500-m buffer around the camera location calculated in R with lsm_c_pd (landscapemetrics package)	Continuous	10 m x 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 m x 10 m	Copernicus Land Monitoring Service 2018

2.3 Statistical analysis

I applied generalized linear models (hereafter: glms) and generalized least square models (hereafter: gls) to investigate the relationships between species richness and species presence or pseudo-absence (hereafter: presence data or occurrence) and vegetation, urbanization, green connectivity, and fragmentation measures.

The model inference to assess the influence of these factors' proxies was based on the corrected Akaike's Information Criterion AICc (Burnham & Anderson, 2002). To find out the importance of the proximity of landscape features, model selection was applied. The model with the best fit – i.e., the lowest AICc value – was selected as the model best explaining the response variable. For the research questions on patch size and fragmentation, pre-defined models were used. For the inference, the models were tested against the null model (likelihood-ratio-test) and the predictors' effects were checked for significance and direction. The model assumptions were checked with the standard diagnostic plots for the gls (residuals versus fitted; quantile-quartile plot) and additionally with the simulated residuals for the glms (*DHARMa*-package, *v.0.4.4*; Hartig, 2021).

For the analysis, I used the statistics software R, version *4.0.1* in its environment RStudio, version *1.3.1093* (R Core Team, 2020; RStudio Team, 2020), and the geographic information system software Quantum Gis (QGIS), version *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 resolution of the spatial analysis is 10 m x 10 m raster cell size, based on the resolution of the land-use data.

2.3.1 Species-specific predictor variables

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

$$aw.lcd = \frac{(a_i * a_j)^{0.7}}{\mathrm{d}_{ij}^{1.7}}$$

With a_i being the area of the origin patch, a_j the area of the destination patch, and d_{ij} the distance between the two patches. In Magle & Fidino (2018), d_{ij} is the Euclidean distance, which I substituted by the least-cost distance. Increasing area-weighted least-cost distances indicate increasing patch connectivity.

The cost distance is a calculation based on graph theory with the need for a friction map (also called "cost surface" in other research) to base the calculation on. The friction map is a species-specific raster dataset where every raster grid cell has a friction value (also called "cost value" in other research) 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. An example of a friction map is shown in Figure 4. 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 connection with the lowest cumulative movement inhibition (Adriaensen et al., 2003).

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

$$friction = R_1 * W_1 + R_2 * W_2$$

With W being weight factors and R resistance values. Weight factors are parameters facilitating or inhibiting the species' movement, such as certain land-use types, topography, or surrounding green area proportion. 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, Majka & Newell (2009) provide further information on the selection of weight factors and assignment of resistance values. It is important 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.

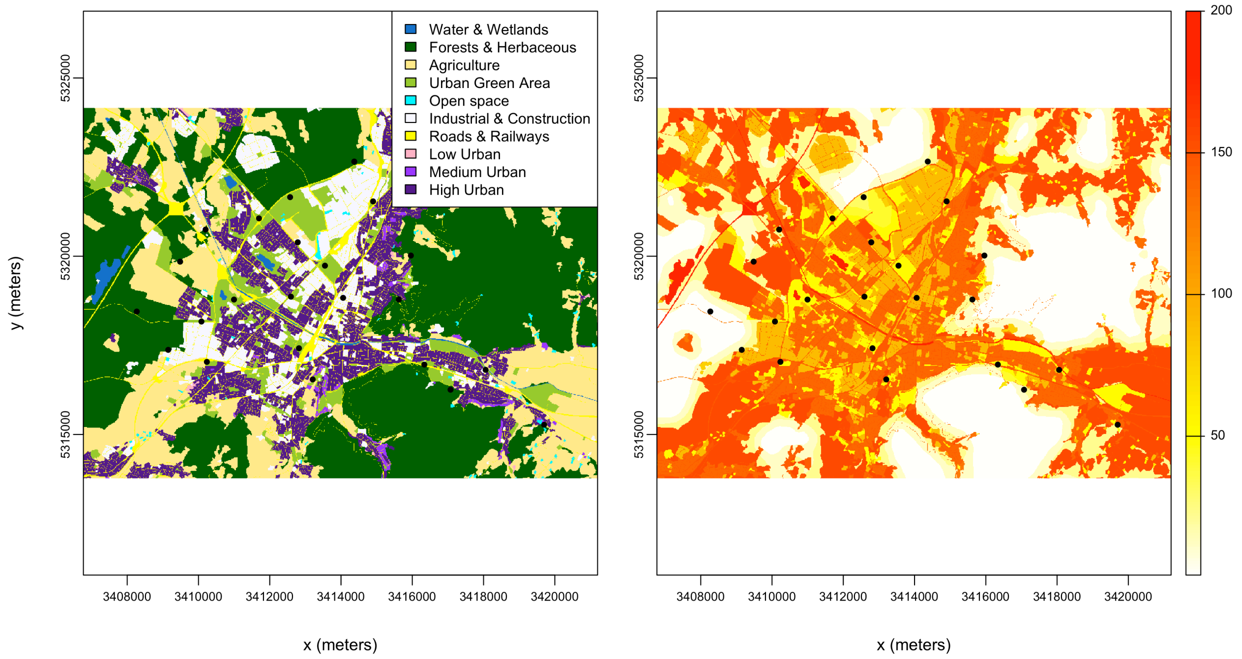

Figure 4: Map of Freiburg im Breisgau with the landscape features (**A**) and example of a friction map (**B**), i.e., the friction values calculated for the wild boar, as result from the landscape features and further significant predictors (chapter 3.2.1).

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. A complete table with the assigned resistance values for each land-use category and its source is available in the appendices (appendix A.1). For the species with multiple weight factors in the friction value calculation, the weight values were based on the results from the model selection (chapters 2.3.2 & 3.2.1 – friction models).

The least-cost distances were calculated in R with the function *shortestPath* from the *gdistance*-package, *v.1.3.6* (van Etten, 2017). This function needs an origin object, a destination object, and a transition layer for the calculation algorithm. The origins were the camera locations, and the destinations were ten random points per vegetated patch in a 1000 m concentric circle around the camera locations. For every camera location, a destination point layer was created in QGIS. The transition layer is a raster layer containing a function informing the algorithm about the calculation of the least-cost distances. In this case, the reciprocal of the cost surface's mean ($mean(cost)^{-1}$) was used as the calculation function. This reciprocal calculates the landscape permeability or movement inhibition. This calculation is the example function from the package documentation of the used *gdistance*-package (van Etten, 2017).

The output of the *shortestPath*-function was specified as a *spatialLines*-object, therefore it returned 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 selected for the calculation of the area-weighted least-cost distance.

2.3.2 Model inference

For modeling the species richness and spatially autocorrelated species presence data as response variables, I applied generalized least squares models with correction for spatial autocorrelation (Dormann, 2007). For the other species-specific presence data, I used logistic regression models (Corlatti, 2021). Further information on the models can be found in Table 5 as well as chapter 3.2 and the subchapters therein.

To account for the possible bias of spatially non-independent data, I checked the species presence data for spatial autocorrelation with Moran's I (Gittleman & Kot, 1990). For the species whose occurrence was found to be spatially autocorrelated ($P < 0.05$), I incorporated the spatial dependency. Dormann (2007) found that spatial dependency in data strongly influences model inference and significance values. Therefore, I used gls models with an exponential correlation function and the Euclidean distance as weights for the response variables with autocorrelation issues (following Diniz-Filho et al., 2003).

Following the spatial autocorrelation check, I checked for multicollinearity of variables. I used the variance inflation factor (hereafter: VIF) (Fox & Weisberg, 2019) . I chose a conservative VIF-threshold of VIF < 3. From variables showing a VIF ≥ 3, the less biologically relevant variable was excluded from the models (R. M. O'Brien, 2007). The exclusion was done in a stepwise manner, excluding one variable at a time and then re-checking the VIF-values.

To assess which weight factors to integrate into the friction surface, I selected the best-fitting model based on the AICc value. The input models were the species-specific global models (Table 5, Table 8, chapter 3.2.1). I investigated the best-fitting model for the predictors' effects on the species-specific probability of presence. When the top-ranked/ best-fitting model contained predictors with an at least marginally significant effect ($P < 0.1$) on the probability of species-specific presence and the model showed a significantly better fit than the null model in the likelihood-ratio test ($P < 0.05$), the most influential predictor was incorporated in the species-specific cost surface. If not, the cost surface values consisted of the land-use classes only. Which predictor was considered influential was based on the predictor's relative occurrence in the models with a difference in AICc values of less than 2.

For analysis of the response variable species richness, I used the site-specific minimal area-weighted least-cost distance when it needed to be incorporated as a predictor in the model formula. For the model analysis, the area-weighted least-cost distance was log-transformed to get a better distribution of residuals.

Table 5.
Formulas of the analyzed global friction and distance models.

Mammal species	Formula - Global friction model (**I**)	Formula - Global distance model (**I**)
European badger	~ d.roads + d.forest + d.city + d.water + veg500	~ d.agri + d.city + d.forest + d.green + d.roads + d.water
European hare	~ d.roads + d.water + veg500	~ d.agri + d.city + d.forest + d.green + d.roads + d.water
European hedgehog	~ d.forest + d.water + imp500 + veg500	~ d.agri + d.forest + d.green + d.roads + d.water
Red fox	~ d.city + d.forest + d.roads + imp500 + veg500; Exponential spatial correlation: ~ Latitude + Longitude	~ d.agri + d.city + d.forest + d.green + d.roads + d.water; Exponential spatial correlation: ~ Latitude + Longitude
Roe deer	~ d.roads + d. water + veg500	~ d.roads + d. water + veg500
Stone marten	~ d.forest + d.roads + d.water + imp500 + veg500; Exponential spatial correlation: ~ Latitude + Longitude	~ d.agri + d.city + d.forest + d.green + d.roads + d.water; Exponential spatial correlation: ~ Latitude + Longitude
Wild boar	~ d.city + d.roads + d.water + veg500	~ d.agri + d.forest + d.green + d.roads
Species richness total	-	~ d.agri + d.city + d.forest + d.green + d.roads + d.water; Exponential spatial correlation: ~ Latitude + Longitude

I: The response variables are the species-specific presence data or the species richness for the last row.

3 Results

3.1 Data collection & data preparation

The 24 camera traps took 11,026 photos within four weeks. In total, the cameras were active for 672 trap nights and ~16 pictures were taken per trap night. The majority of the pictures contained birds, domestic animals, or no animals at all. 424 images contained wild mammal observations of 11 species. In addition to the study taxa, a stoat (*Mustela erminea*), brown rats (*Rattus norvegicus*), red squirrels (*Sciurus vulgaris*), and further rodent species (order Rodentia) were detected. Figure 5 shows that with 23 sampled sites the species accumulation curve has reached its horizontal asymptote and the sampling is complete.

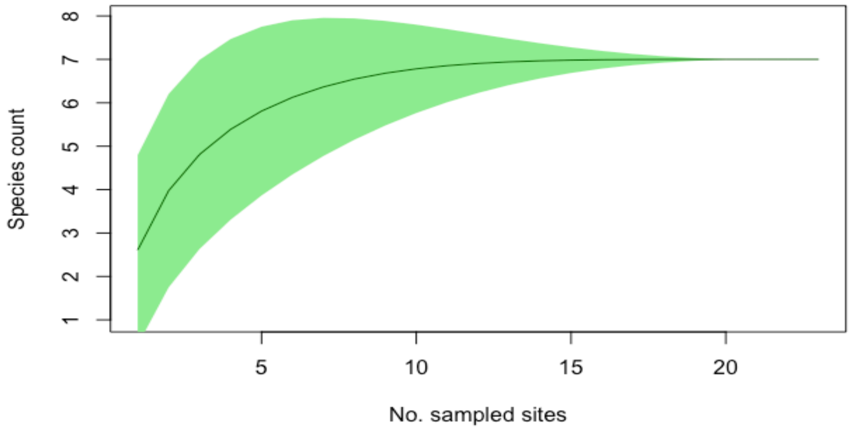

Figure 5: Species accumulation curve.

The maximum observed species richness concerning only the selected study taxa per site was 5, the minimum 1, and the mean approximately 3 with a standard deviation ("*SD*") of ± 1. Values over 3 were only observed in low-intensity urbanized locations. The mean of species richness in low-intensity urban was 3 ± 1 SD. All the medium-intensity urban locations had a species richness value of 2 (mean = 2 ± 0 SD). In highly urban locations with an impervious surface proportion higher than or equal to 50% species richness 1 and 3 were observed once and the value 2 three times (mean = 2 ± 1 SD) (Figure 6B). The map shows the spatial distribution of the richness values (Figure 6A). Higher species richness values occurred on the urban outskirts. However, the difference in species richness as a function of the classified urban gradient is not significant (Anova: P > 0.1).

At the species level, stone martens (hereafter: martens) were the most observed species followed by red foxes (hereafter: foxes) and hedgehogs, observed in 17, 15, and 9 locations respectively. These species were the only species observed in all imperviousness classes. European badgers (hereafter: badgers), roe deer, and wild boars were only observed in locations with low surrounding impervious surface cover. European hares (hereafter: hares) were detected in low- and medium-intensity urban sites. Although they occurred only in low-intensity urban sites, roe deer were still detected more frequently than hares, occurring in 6 versus 5 sites respectively. The species that were occurring in the fewest sites were the badger and the wild boar, being detected in 4 sites each (Figure 6C).

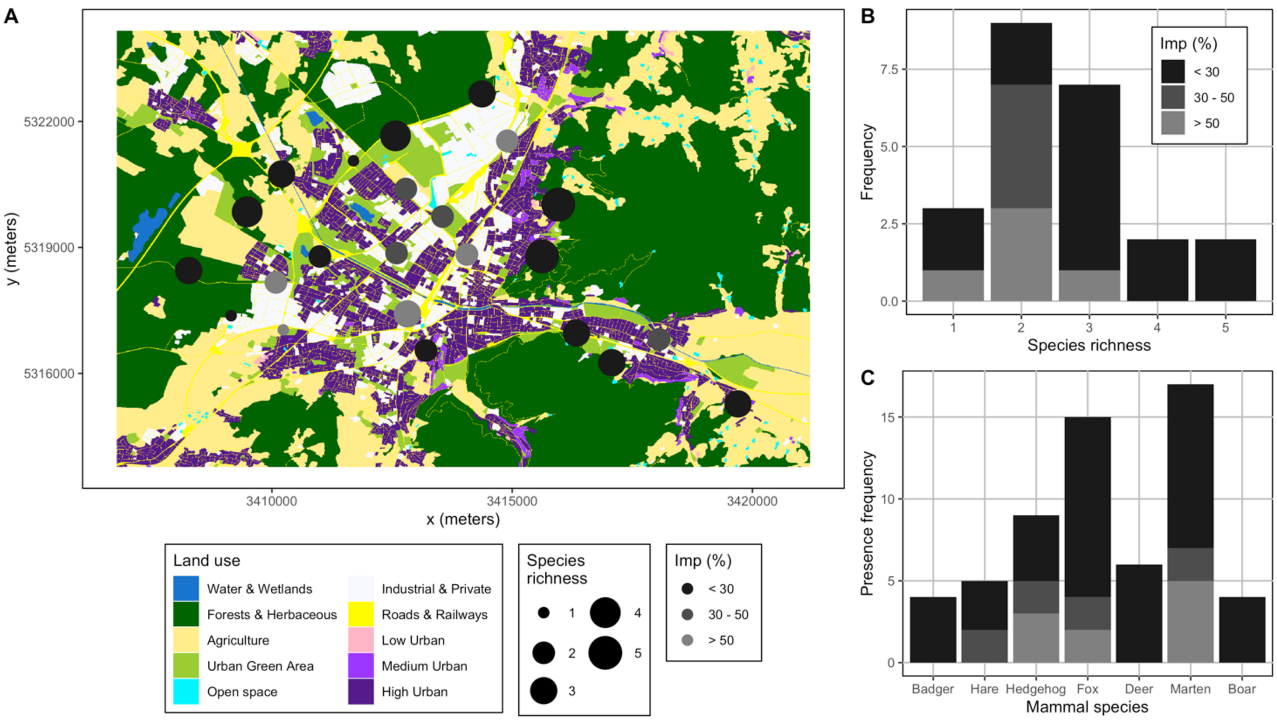

Figure 6: Overview of the data collection results. **A**: Map of the camera locations according to the observed mammal species richness and the surrounding impervious surface proportion. **B**: Histogram of the species richness categorized in impervious surface proportion classes. **C**: Species-specific occurrence frequency following the same classification and color scheme as **B**.

3.1.1 Spatial autocorrelation & multicollinearity checks

The calculation of Moran's I showed that the majority of the species' occurrence data is not significantly spatially autocorrelated. Only the presence data of fox and marten showed significant spatial autocorrelation (P < 0.05). Because these species were included in the analysis of the total species richness, I chose a generalized least square model for this response variable as well.

Table 6.

Results of the spatial autocorrelation check.

Species	Calculated Moran's I	Expected Moran's I	P-value
European badger	-0.050	-0.045	0.869
European hare	-0.058	-0.045	0.631
European hedgehog	-0.029	-0.045	0.532
Red fox	**-0.111**	**-0.045**	**0.014 (*)**
Roe deer	-0.045	-0.045	0.999
Stone marten	**-0.098**	**-0.045**	**0.045 (*)**
Wild boar	-0.081	-0.045	0.161

The multicollinearity check resulted in the global models used for the model selection. For each species and the species richness value, there was a distance-model that was predicted by the distance to Urban Atlas features. The species-specific friction surface models included the vegetation proxy surrounding vegetation cover proportion (*veg500*). The distance to vegetated areas (urban green areas and forests) combined with the vegetation proxy resulted in high VIF-values. Due to the assumption that the surrounding vegetation cover proportion is more direct for the prediction, this variable was preferred for the species-specific global friction surface models.

3.1.2 Species-specific predictor variables

The results of the model selection of the global friction models for the badger, the hare, and the marten showed that the null model ranked highest and the other models did not have a higher likelihood ratio. Therefore, the null hypothesis cannot be rejected. None of the uni- or multivariate models consisting of different combinations of the global friction model's predictors were found to have a significant influence on the probability of these species' presence.

For hedgehogs, the model selection resulted in the multivariate model with distance to water and surrounding vegetation as predictors ranked first (AICc = 24.14; ΔAICc to the null model (hereafter: $\Delta AICc_0$) = 8.84; P-value likelihood-ratiotest (hereafter: P_{lrt}) < 0.001; McFadden pseudo-R-squared (hereafter: R^2) = 0.452). The predictor coefficients of the unscaled model are both negative (d.water = -0.0029 ± 0.0015 Standard Error ("SE"); veg500 = -0.0495 ± 0.0301 SE) and marginally significant (d.water and veg500: $P < 0.1$). The distance to water was also found in the second and third-ranked models and was therefore incorporated in the friction surface.

The top-ranked friction model predicting the probability of fox presence was the univariate gls model with the surrounding vegetation cover proportion as predictor (AICc = 35.20; $\Delta AICc_0 = 2.55$; $P_{lrt} < 0.05$; $R^2 = 0.181$). The effect of the parameter's coefficient in the unscaled model is slightly positive (0.008 ± 0.003 SE) and significant ($P = 0.026$).

For roe deer, the top-ranked model consisted of the predictor surrounding vegetation cover proportion (AICc = 18.75; $\Delta AICc_0 = 9.843$; $P_{lrt} < 0.001$; $R^2 = 0.464$). The parameter has a significant positive effect, the coefficient is 0.1074 ± 0.0539 SE ($P < 0.05$).

Wild boar presence data was also best predicted by the surrounding vegetation cover proportion model (AICc = 19.74; $\Delta AICc_0 = 3.709$, $P_{lrt} < 0.05$; $R^2 = 0.288$). The surrounding vegetation cover proportion has a positive, marginally significant effect (coefficient = 0.0649 ± 0.0347 SE, $P < 0.1$). Based on these findings, I incorporated the additional weight factors in the species-specific friction surfaces and classified those into resistance value classes. The friction values for the aforementioned four species with multiple weight factors were calculated as follows:

Table 7.

Friction surface specifications.

Species	Formula	Maximal land use resistance ("max.lu")	Weight factor classes apart from l.use	Resistance value
European hedgehog	friction = 0.9 * l.use + 0.1 * d.water	150	d.water < 312 m	1
			312 ≤ d.water < 740	0.5 * max.lu
			d.water > 740	1.0 * max.lu
Red fox	friction = 0.9 * l.use + 0.1 * veg500	200	veg500 > 35	1
			veg500 ≤ 35	0.5 * max.lu
Roe deer	friction = 0.65 * l.use + 0.35 * veg500	200	veg500 > 65	1
			52 ≤ veg 500 ≤ 65	0.5 * max.lu
			veg500 < 52	1.0 * max.lu
Wild boar	friction = 0.9 * l.use + 0.1 * veg500	200	veg500 > 84	1
			63 ≤ veg500 ≤ 84	0.5 * max.lu
			veg500 < 63	1.0 * max.lu

The threshold values for the weight factor classes were based on the modelled probability of presence: Presence probability > 0.66 → Resistance value = 1; 0.33 < presence probability ≤ 0.66 → resistance = 0.5 * max.lu; presence probability < 0.33 → resistance value = 1 * max.lu

I used the species' friction surface to calculate the minimal least-cost distances and the resulting area-weighted least-cost distances. Despite the calculation based on species-specific friction surfaces, neither the least-cost distances nor the area-weighted least-cost distances differed significantly between the species (Anova: $P = 1$; Anova: $P = 0.897$ respectively; Figure 7). The minimal least-cost distance is 40 m which is the same for all mammal species for location 32, and the corresponding area-weighted least-cost distance is $\log(-0.77) = 0.46$. The maximum value of the least-cost distances is 1052.8 m calculated for wild boar in location 34, with an area-weighted least-cost distance of $\log(-7.08) = 0.00084$. The maximum area-weighted least-cost distance value $\log(-0.15) = 0.86$ was found in location 20 for wild boar and roe deer, location 20 being one of the locations in the forest with little surrounding impervious surface and high surrounding vegetation proportion. The badger has the smallest range in area-weighted least-cost distance values, as< seen in its boxplot's whiskers, while the hare has the widest, followed by the hedgehog and the fox (Figure 7B).

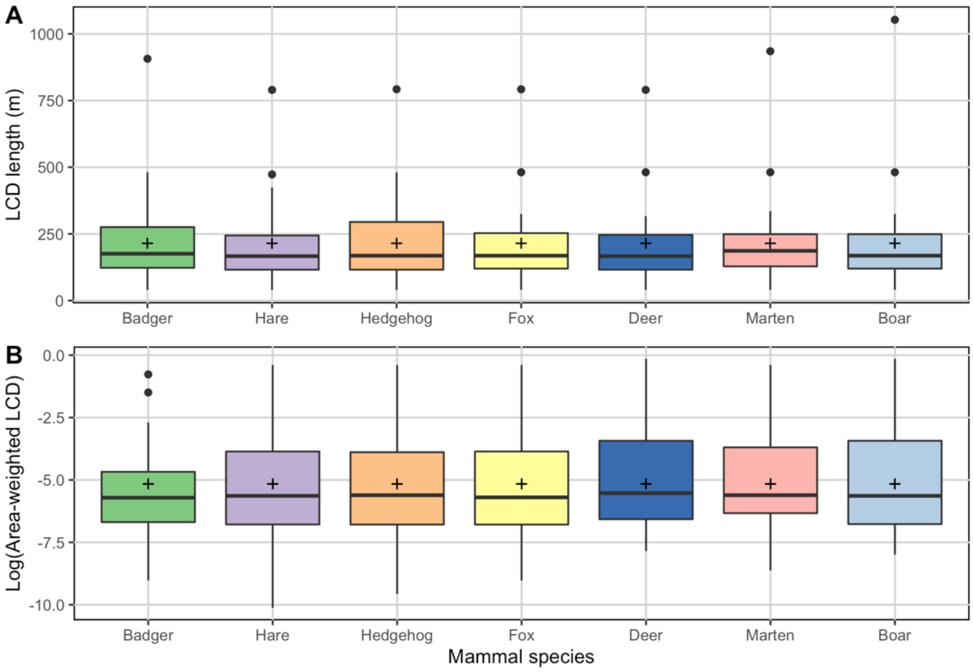

Figure 7: Boxplots of the species' least-cost distance length (**A**) and logarithmic area-weighted least-cost values (**B**). The lower limit of the box represents the 25-percentileand the upper boundary represents the 75-percentile. The lower and upper whisker ends show the 2.5- and 97.5-percentile respectively. The crosses show the mean.

Figure 8 shows an example map of the camera locations, the calculated minimal least-cost distances, and the easiest reachable destination point. The base map is the friction surface for the hedgehog. Equivalent maps for the other mammal species can be found in the appendices (appendix A.2).

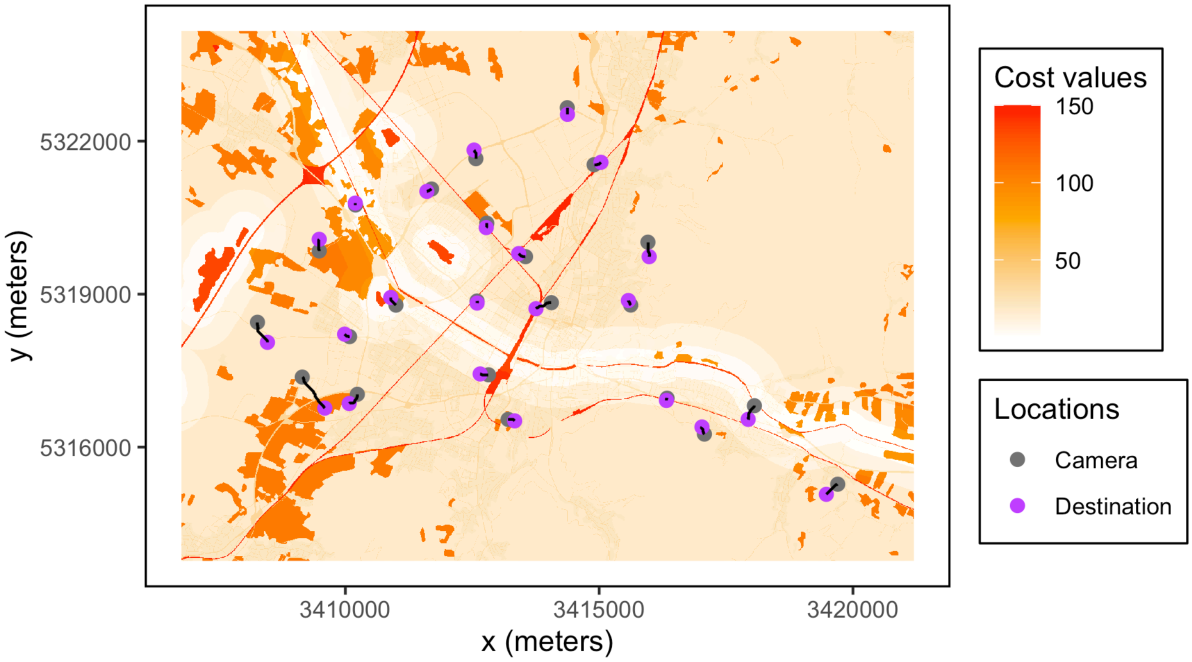

Figure 8: Example lcd-map for the European hedgehog. The black connections between camera and destination points show the route of the calculated minimal least-cost distance.

3.2 Model inference

3.2.1 Landscape features

To assess the effect of landscape features' proximity, I investigated the friction models. In addition, I created the global distance models and used model selection to analyze the variables' effects on species-specific presence probability and mammal species richness in urban vegetated areas. If it passed the multi-collinearity check, a multivariate model including the predictors species-specific area-weighted least-cost distance (or minimal area-weighted least-cost distance for the dependent variable species richness) and surrounding imperviousness were investigated as well (hereafter: aw.lcd-model).

For the badger, in the model selection approaches of the global friction and the global distance model, the null model was top-ranked. In the model selection of the aw.lcd-model for the European badger, the impervious surface cover proportion model was ranked first ($AICc = 21.63$; $\Delta AICc_0 = 1.81$; $P_{lrt} < 0.05$; $R^2 = 0.199$). Still, the predictor's coefficient is not significant ($P > 0.1$). Therefore, it cannot be assumed that the urbanization proxy surrounding impervious surface cover proportion is a significant influence factor on badger presence probability from this data.

The model selection of the global friction and the global distance model for the hare yielded the null model ranked first as well. The model inference of the aw.lcd-model ranked the univariate model with the logarithm of the area-weighted least-cost distance on top ($AICc = 23.20$; $\Delta AICc_0 = 3.076$; $P_{lrt} < 0.05$; $R^2 = 0.228$). The coefficient of the logarithmic area-weighted least-cost distance is positive (0.56 ± 0.271 SE) and significant ($P < 0.05$). No other predictor variables were found to significantly affect hares. The effects of the most important predictors resulting from the model selection concerning mammal presence and richness as a function of proximity to features are shown in Figure 9.

For the probability of hedgehog presence, the distance to water was found to be an influential predictor. It was contained in the top-ranked models of the model selection for the global friction and the global distance model. The best-fitting model of the distance set contained the distance to water and the distance to agriculture as predictors. The simulated residuals of the selected distance model showed violations of the model assumptions. Therefore, the top-ranked model of the friction set was selected as the better model (~ d.water + veg500). This model has an AICc value of 24.14 ($\Delta AICc_0 = 8.839$; $P_{lrt} < 0.001$) and a McFadden pseudo R^2 of 0.452. Table 8 shows further information on the models.

The univariate generalized least squares model with the logarithmic fox area-weighted least-cost distance had the best fit for the fox (AICc =34.44; $\Delta AICc_0 = 3.313$; $P_{lrt} < 0.05$; $R^2 = 0.206$). It was a better fit than the top-ranked friction model (presence ~ veg500; AICc = 35.20, ΔAIC = 0.760) and the top-ranked distance model (presence ~ d.city; AICc = 36.61; ΔAICc = 2.170). The distance to the city boundary and the surrounding vegetation cover proportion are not strongly correlated with the area-weighted least-cost distance (Pearson's r: $|r| < 0.1$ for both). Therefore, the most important effect can be attributed to the patch connectivity proxy area-weighted least-cost distance. Its coefficient has a significant positive effect on the presence probability of foxes ($P < 0.05$ and log(aw.lcd)-coefficient = 0.094 ± 0.036 SE).

For the roe deer global friction model, the univariate surrounding vegetation cover proportion model was top-ranked (AICc = 18.75; $\Delta AICc_0 = 9.214$; $P_{lrt} < 0.001$; $R^2 = 0.440$). The surrounding impervious surface cover proportion model was the best-fitting model for the model selection based on the aw.lcd-model and had an almost equal fit concerning the AICc value (ΔAICc = 0.629), but the model predicted by the surrounding vegetation cover proportion was assumed to predict the deer behavior more directly. Additionally, the predictors surrounding vegetation cover proportion and surrounding impervious cover proportion are strongly negatively correlated ($r = -0.713$). The surrounding vegetation cover proportion model predicts a significant ($P < 0.05$; coefficient = 0.10 ± 0.054 SE) increase of 11.3 % per percent increase in surrounding forest and green area proportion.

For the marten's global friction model, the univariate generalized least square model predicted by the logarithmic area-weighted least-cost distance had the best fit with regard to predicting marten occurrences (AICc = 30.64; $\Delta AICc_0 = 3.678$; $P_{lrt} < 0.05$; $R^2 = 0.245$). The model predicts a significant, negative effect of the logarithmic area-weighted least-cost distance (coefficient = -0.103 ± 0.038 SE; $P < 0.05$).

The best model predicting probability of wild boar presence consists of the predictor distance to urban green area (AICc = 14.24; $\Delta AICc_0 = 9.202$; $P_{lrt} < 0.001$; $R^2 = 0.546$). The model predicts a positive, marginally significant effect of the distance to urban green area (coefficient = 0.011 ± 0.006 SE; $P < 0.1$). This model is also much better fitted than the top-ranked models from the global friction model and the global aw.lcd-model ($\Delta AIC_{veg500} = 5.493$ and $\Delta AIC_{imp500} = 6.151$ respectively).

Two models predicted total mammal species richness almost equally well. Nevertheless, I chose the univariate gls with the predictor distance to the city boundary as the better model over the univariate surrounding impervious surface cover model due to a slightly lower AICc and a slightly higher McFadden pseudo R^2 (AICc = 69.08 & $R^2 = 0.128$ compared to AICc = 69.36 & $R^2 = 0.123$). The distance to the city boundary model is also significantly better than the null model ($\Delta AICc_0$ =

5.645; Plrt < 0.01). The coefficient of distance to the city boundary is positive and significant (0.015 ± 0.005 SE; P < 0.01), predicting an increase of species richness by 1 every 62.5 m. Other models consisting of combinations of the global models' predictors have a ΔAICc > 2, so no other combinations of predictors are as influential as the surrounding impervious surface cover proportion and the distance to the urban boundary. Taking the almost equal fit into account, it is worth mentioning that the imperviousness has a significant negative effect (-0.029 ± 0.009 SE; P < 0.01). The surrounding impervious surface cover proportion and the distance to the urban boundary are negatively correlated (r = -0.62).

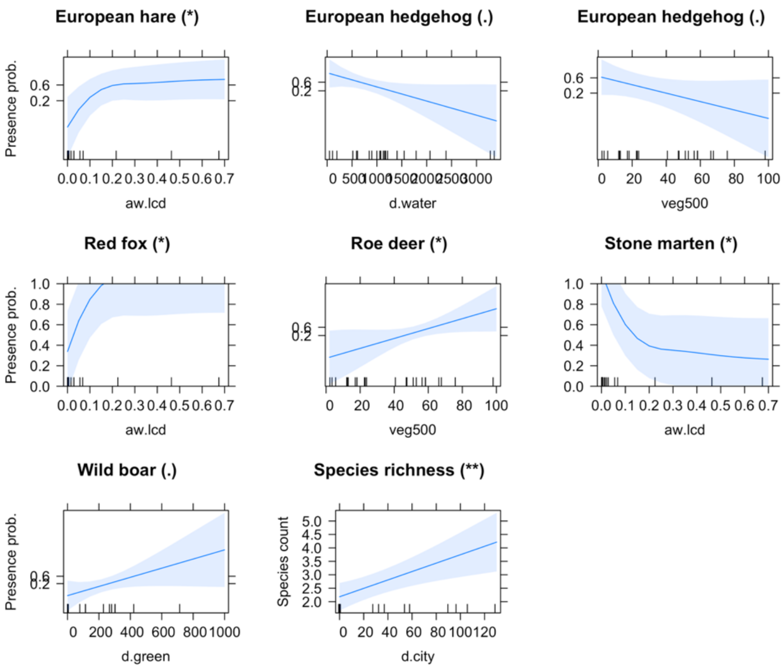

Figure 9: Visualization of the effects of influential predictors and significance level on the species-specific probability of presence and the species richness. The line is the calculated regression line, the shaded area shows the coefficient's (x-axis-label) 95% confidence interval. Significance levels: P < 0.1 (.); P < 0.05 (*); P < 0.01 (**).

Table 8.

Results of the model inference for the friction-, distance-, and aw.lcd.-models.

Response variable	Predictor set	Top-ranked model	AICc	ΔAIC_0	R^2	P_{lrt}	Predictor	Coefficient/ Odds-ratio
European badger	Friction model	~ + 1	23.44	0.000	-	-	Intercept	-1.558 ± 0.5501 (**)
	Distance model	~ + 1	23.44	0.000	-	-	Intercept	-1.558 ± 0.5501 (**)
	Aw.lcd-model	**~ + imp500**	**21.63**	**1.810**	**0.199**	**0.040 (*)**	**imp500**	**-0.077 ± 0.049**
European hare	Friction model	~ + 1	26.28	0.000	-	-	Intercept	-1.281 ± 0.5055 (*)
	Distance model	~ + 1	26.28	0.000	-	-	Intercept	-1.281 ± 0.5055 (*)
	Aw.lcd-model	**~ + log(aw.lcd)**	**22.67**	**3.601**	**0.25**	**0.014 (*)**	**log(aw.lcd)**	**8.406 ± 5.0607 (.)**
European hedgehog	**Friction model**	**~ + d.water + veg500**	**24.14**	**8.839**	**0.452**	**0.001(***)**	**d.water**	**-0.003 ± 0.0015 (.)**
							veg500	**-0.050 ± 0.0301 (.)**
	Distance model	~ + d.agri + d.water	24.95	8.028	0.425	0.001 (**)	d.agri	0.003 ± 0.0017
							d.water	-0.003 ± 0.0015 (*)
	Aw.lcd-model	~ + 1	32.98	0.000	-	-	Intercept	-0.4412 ± 0.4272
Red fox	Friction model	~ + veg500	35.20	2.550	0.181	0.0189 (*)	veg500	0.008 ± 0.0035 (*)
	Distance model	~ + d.city	36.61	1.139	0.134	0.0429 (*)	d.city	0.005 ± 0.0023 (*)
	Aw.lcd-model	**~ + log(aw.lcd)**	**34.44**	**3.313**	**0.206**	**0.0123 (*)**	**log(aw.lcd)**	**0.094 ± 0.0361 (*)**

Table 8 continued.

Response variable	Predictor set	Top-ranked model	AICc	ΔAIC_0	R^2	P_{lrt}	Predictor	Coefficient/ Odds-ratio
Roe deer	**Friction-model**	**~ + veg500**	**18.75**	**9.843**	**0.464**	**0.0005 (***)**	**veg500**	**0.107± 0.0539 (*)**
	Distance model	-	-	-	-	-	-	-
	Aw.lcd model	~ + imp500	19.38	9.214	0.44	0.001 (***)	imp500	-0.151 ± 0.0688 (*)
Stone marten	Friction model	~ + 1	34.32	0.000	-	-	Intercept	0.751 ± 0.1097 (***)
	Distance model	~ + d.green	32.43	1.888	0.179	0.0277 (*)	d.green	-0.001 ± 0.0004 (*)
	Aw.lcd-model	**~ + log(aw.lcd)**	**30.64**	**3.678**	**0.245**	**0.01 (*)**	**log(aw.lcd)**	**-0.103 ± 0.0379 (*)**
Wild boar	Friction model	~ + veg500	19.74	3.709	0.288	0.013(*)	veg500	0.065 ± 0.03473 (.)
	Distance model	**~ + d.green**	**14.24**	**9.202**	**0.546**	**0.001 (***)**	**d.green**	**0.011 ± 0.0062 (.)**
	Aw.lcd model	~ + imp500	20.39	3.051	0.257	0.019 (*)	imp500	-0.097 ± 0.0570 (.)
Species richness	**Distance model**	**~ + d.city**	**69.08**	**5.645**	**0.128**	**0.003 (**)**	**d.city**	**0.016 ± 0.0047 (**)**
	Aw.lcd model	~ + imp500	69.36	5.370	0.123	0.004 (**)	imp500	-0.028 ± 0.0094 (**)

Bold: Species-specific models and richness model with the lowest AICc resulting from the model selection of the predictor sets. Significance levels: P < 0.1 (.); P < 0.05 (*); P < 0.01 (**); P < 0.001 (***)

3.2.2 Patch size

Concerning the influence of patch size and patch connectivity on the species and the species richness, I investigated models containing combinations of the distance to urban green area or the distance to forest site, area-weighted least-cost distance, and patch area. I also included the confounding factor surrounding impervious cover proportion when the multicollinearity check allowed for it.

For the detected badgers, hares, hedgehogs, foxes, and wild boars, this combination of parameters does not add any findings. The model selection shows that the parameters that were found to predict the animals' presence in chapter 3.2.1 have more influential effects than patch size. The same holds true for the investigation of total mammal species richness.

In the combination of the aforementioned parameters, the roe deer occurrence could not be predicted by any model containing the predictor distance to forest. The models had the issue of complete separation. Therefore, this parameter was left out of the model building and the surrounding impervious cover proportion variable had to be left out as well due to multicollinearity with the predictors of interest, logarithmic area-weighted least-cost distance and patch size. The model with the combination of these predictors had an AICc value of 20.0 ($\Delta AICc_0 = 8.588$; $P_{lrt} < 0.01$; $R^2 = 0.517$) and a $\Delta AICc$ of 1.25 worse than the surrounding vegetation cover model. Still, the pseudo-R^2 value suggests a very good model fit and, therefore, the suggested positive effect of area-weighted least-cost distance on the verge of significance is not negligible (coefficient = 0.63 ± 0.323 SE; $P < 0.1$).

For martens, the multivariate model of logarithmic area-weighted least-cost distance and patch size as predictors is in the second rank after the aforementioned univariate model with the logarithmic area-weighted least-cost distance as a single predictor ($\Delta AIC = 0.82$). This multivariate model shows a significant effect of the logarithmic area-weighted least-cost distance ($P < 0.05$) and a non-significant effect of the patch area with a coefficient of 0.00 ± 0.000 SE.

Table 9.

Results of the model inference of patch size & patch connectivity models.

Response variable	Top-ranked model	AICc	ΔAIC_0	R^2	P_{lrt}	Predictor	Coefficient/ Odds-ratio
European badger	~ + imp500	21.63	1.810	0.199	0.040 (*)	imp500	-0.077 ± 0.0488
European hare	~ + log(aw.lcd)	22.67	3.601	0.25	0.014 (*)	log(aw.lcd)	8.406 ± 5.0607 (.)
European hedgehog	~ + imp500	33.33	-0.353	0.067	0.152	imp500	0.030 ± 0.0218
Red fox	~ + log(aw.lcd)	34.44	3.313	0.206	0.012 (*)	**log(aw.lcd)**	**0.094 ± 0.0361 (*)**
Roe deer	~ + p.area + log(aw.lcd)	20.00	8.588	0.517	0.001 (**)	p.area	0.000 ± 0.0000
						log(aw.lcd)	**0.627 ± 0.3227 (*)**
Stone marten	~ + log(aw.lcd)	30.64	3.678	0.245	0.010 (*)	**log(aw.lcd)**	**-0.103 ± 0.0379 (*)**
Wild boar	~ + imp500	20.39	3.051	0.257	0.019 (*)	imp500	-0.097 ± 0.0570 (.)
Species richness	~ + imp500	69.36	5.370	0.123	0.0039 (**)	**imp500**	**-0.029 ± 0.0094 (**)**

Bold: significant predictor effects. Significance levels: $P < 0.1$ (.); $P < 0.05$ (*); $P < 0.01$ (**); $P < 0.001$ (***)

3.2.3 Fragmentation & patch connectivity

To investigate the effect of fragmentation and patch connectivity, patch density and logarithmic area-weighted least-cost distance were combined into a multivariate additive formula. I checked the model's diagnostics and, when no violations of the model assumptions occurred, I tested it against the null model.

For the European badger and the roe deer presence data as well as the total species richness as the response variables, the model did not predict better than the null model. The likelihood-ratio-test was non-significant ($P_{lrt} > 0.1$), and the AICc value showed a worse fit than the null model. This suggests that for the mentioned species and the total species richness, this combination of predictors does not have any predictive value.

Investigating the European hare data, the model is significantly better than the null model (AICc = 25.27; $\Delta AICc_0 = 1.004$; $P_{lrt} < 0.05$ (*); $R^2 = 0.252$). However, the effect of patch density is not significant ($P > 0.1$), and the effect of the logarithmic area-weighted least-cost distance is mitigated to marginal significance ($P < 0.1$). The model without the fragmentation proxy, exclusively consisting of the logarithmic area-weighted least-cost distance as a predictor, has a better fit ($\Delta AICc = 2.072$), although it has a slightly lower pseudo-R^2. The parameter fragmentation explains some variance in the data but does not have a significant effect. Similar results were achieved from the investigation of the effect of the fragmentation proxy and the patch connectivity proxy on foxes and martens. The combined models provide better predictions than the null model but have a higher AICc value than the univariate model without the fragmentation proxy. For wild boars, the model was also significantly better than the null model ($P < 0.05$), but the model's summary did not show any significant parameter effects.

The European hedgehog model was found to be violating model assumptions by checking the standard diagnostic plots. The residuals showed a trend in their distribution. The model was not significantly better than the null model ($P_{lrt} > 0.1$).

Table 10.

Results of the model inference of fragmentation and patch connectivity models.

Response variable	Model formula	AICc	ΔAIC_0	R^2	P_{lrt}	Predictor	Coefficient/ Odds-ratio
European badger	~ + log(aw.lcd) + p.dens	25.33	-1.883	0.15	0.2029	p.dens	-1.847 ± 1.250
						log(aw.lcd)	-0.363 ± 0.397
European hare	~ + log(aw.lcd) + p.dens	25.27	1.004	0.252	0.0479 (*)	p.dens	-0.453 ± 0.652
						log(aw.lcd)	**0.514 ± 0.2723 (*)**
European hedgehog	~ + log(aw.lcd) + p.dens	37.08	-4.096	0.032	0.6137	p.dens	0.294 ± 0.4465
						log(aw.lcd)	-0.091 ± 0.1971
Red fox	~ + log(aw.lcd) + p.dens	37.57	0.185	0.212	0.0397 (*)	p.dens	-0.037 ± 0.0930
						log(aw.lcd)	**0.089 ± 0.0391 (*)**
Roe deer	~ + log(aw.lcd) + p.dens	28.41	0.179	0.199	0.0724 (.)	p.dens	-0.097 ± 0.5071
						log(aw.lcd)	**0.479 ± 0.2426 (*)**
Stone marten	~ + log(aw.lcd) + p.dens	33.50	0.816	0.262	0.029 (*)	p.dens	0.053 ± 0.0845
						log(aw.lcd)	**-0.097 ± 0.0399 (*)**
Wild boar	~ + log(aw.lcd) + p.dens	20.76	2.683	0.365	0.021 (*)	p.dens	-3.456 ± 2.2302
						log(aw.lcd)	0.113 ± 0.2878
Species richness	~ + log(aw.lcd) + p.dens	75.44	-0.717	0.082	0.0624 (.)	p.dens	-0.212 ± 0.2016
						log(aw.lcd)	**0.166 ± 0.0898 (*)**

Bold: significant predictor effects. Significance levels: $P < 0.1$ (.); $P < 0.05$ (*); $P < 0.01$ (**); $P < 0.001$ (***).

4 Discussion

My study aimed to assess the influence of patch connectivity, fragmentation, urbanization, and vegetation on mammal diversity in a peri-urban to urban landscape gradient. The study put a special focus on the investigation of the effect of patch connectivity. I investigated species-specific statistical models to ascertain which variables significantly contribute to the species’ occurrences. Based on these parameters, I calculated least-cost distances which I incorporated in my patch connectivity estimator, the area-weighted least-cost distance. Following this, I applied model selection to address my research questions, hypotheses, and predictions.

The analysis showed that proximity to features or patch connectivity affected the presence of the majority of the species at least marginally significant. The most influential predictors depend on the species. While I could establish the importance of patch connectivity and the proximity to landscape features, the investigation of the effect of patch size did not support the hypotheses of this variable’s impact on mammal presence and species richness. The same holds true for the importance of fragmentation as a predictor.

4.1 Discussion of methods

For the data collection, 24 camera traps were deployed, 23 of which were located at least 1 km distant from each other and, thus, were included in the analysis. The species accumulation curve shows that the sampling for Freiburg im Breisgau is complete and the species richness can be analyzed unconditionally. A challenge for studies based on camera trap data is the assumption of complete detection, meaning animal species may be present in the camera location but not cross the camera’s viewing area, and may, therefore, not be photographed (T. G. O’Brien & Kinnaird, 2011). However, this is a trade-off of most camera trap studies and will not be focused on.

The distance between the camera locations was selected according to the UWIN protocol (Urban Wildlife Information Network, 2020). It is assumed that 1 km exceeds the home range extent of the majority of mammals inhabiting urban landscapes (Fidino et al., 2020). To control the assumption of spatial independence of the sampling locations, I checked for spatial autocorrelation using Moran’s I. If the assumption was violated signaled by a significant P-value, I incorporated the spatial autocorrelation following Diniz-Filho et al. (2003). The generalized least squares model calculates a linear regression instead of a binomial one – which is suggested for binary presence data (Corlatti, 2021). Still, the use of a spatial model is supported by Dormann's findings (2007). He found out that P-values and calculated coefficients are more precise when incorporating the spatial context in spatially autocorrelated data. The trial of applying generalized linear mixed models with spatial parameters (location, latitude and longitude, urbanization intensity class) as random effects failed as the models did not converge. This can possibly be attributed to there being too few data points (n = 23). Based on the model diagnostics, I found that the models did not violate any general model assumptions if not otherwise mentioned. I also added the calculated McFadden pseudo-R^2 for a better comparison of fit, as suggested by Allison (2014). The models mostly exceed a pseudo R^2 of 0.2, which makes them reasonable. Some have a pseudo-R^2 over 0.4, which is considered very high (Veall & Zimmermann, 1994).

I calculated a patch connectivity estimator that is based on the minimal cost-distance of various least-cost paths between an origin and various possible destinations. The patch connectivity estimator takes the patches' area into account and was modified after the area-weighted distance (Magle & Fidino, 2018). While the Euclidean nearest neighbor distance is easy to implement and interpret, it defines the patch connectivity in a purely structural manner. The least-cost distance is more complex to implement but as simple to interpret and more functional, in addition (Figure 1). The cost-distance was found to be superior at predicting the presence of model species over the Euclidean distance (Chardon et al., 2003; Verbeylen et al., 2003). In general, graph-based functional connectivity measures are assumed to be more biologically meaningful than structural ones (e.g., Adriaensen et al., 2003; Sawyer et al., 2011; Theobald, 2006). Most connectivity studies consider a larger scale and fewer investigate the urban context. Still, Magle & Fidino (2018) showed the advantage of functional over structural connectivity measures in predicting animal persistence in an urban landscape.

The most complex challenge in the implementation of graph-based connectivity measures is the need for a friction surface and the difficulty in selecting robust factor weights and resistance values (Etherington, 2016). The selection of factors and assignment of values is mostly based on expert opinion and therefore not objective (Etherington, 2016). Therefore, the importance of validation and the need for multiple, organism-based weight factors is stressed (Sawyer et al., 2011). I selected additional weight factors based on their predictive importance and effect on the organisms' presence or pseudo-absence. Thereby, I established which factors to add to the friction surface with a statistical and objective approach. I was not able to validate the assumed factor weights and had to assign some resistance values myself, creating uncertainty and subjectivity. Still, most of the resistance values for the land use types were available in literature or derived from it (Appendix A.1). Beier et al. (2009) found that least-cost models are robust to uncertainties in factor weights and resistance values. Therefore, despite lacking profound expert knowledge concerning the species' movement behavior, the least-cost paths can still provide a reasonable proxy.

In my approach to creating location-specific destination layers, large, unfragmented patches have a lower density of randomized destination points. The distance between the camera and the patch edge is also greater in large patches than in small ones. This results in two factors biasing the connectivity estimation and in the possible assumption that larger patches have lower connectivity while they should actually have a higher one (Fahrig, 2003). Therefore, and for the finding of the area being an influential factor for urban biodiversity (Beninde et al., 2015), the area-weighting is incorporated. While the structural connectivity measures 'distance to green area' and 'distance to forest' are not included in any of the top-ranked models, the area-weighted least-cost distance predicts various species' presence best (chapter 3.2), supporting the utility of the measure and the superiority of functional over structural connectivity measurements.

I selected the location-specific, minimal area-weighted least-cost distance of all species as the predictor for total mammal species richness. This conservative approach seemed more ecologically reasonable than taking the median or mean into consideration, especially since it was suggested by an expert concerning ecological statistics (C. F. Dormann, personal communication, January 20, 2022). Selecting the minimum value was based on "Liebig's Law of the Minimum" (Hooker Jr, 1917). Although Liebig's Law of the Minimum is not defined in a precise wording, it states that growth is always limited by the limiting factor – the scarcest resource – and is often applied in an ecological context (e.g., Danger et al., 2008; De Baar, 1994; Dolman & Wiedner, 2015). The assumption is that if the mammal with the lowest location-specific patch connectivity occurs in one site, the other mammals having higher patch connectivity values can move around less impeded. The trade-off in this approach is that urban avoiders' area-weighted least-cost distance values are taken into consideration in inner-city locations as well. The species European badger, roe deer, and wild boar have not been detected in locations with higher surrounding imperviousness cover proportion than 30%. Still, their area-weighted least-cost distance might be taken into account as a predictor for locations where they were not detected and probably will not visit, restricted by their behavioral response to urbanization. An additional specification for the patch connectivity estimator for total species richness could be to select the minimal value from exclusively the detected species for each location. However, the area-weighted least-cost distances were not significantly different between species (Anova: P = 0.897; Figure 6). The bias from the mentioned shortcoming is therefore assumed to be negligible.

Many of the observed effects from the model analysis were only marginally significant. I assume that this is owed to the small sample size (n = 23). Therefore, significant variables must have a strong effect (Dormann, 2017). To further investigate the effect of patch connectivity and additional factors, the number of samples could be increased by including data from multiple seasons or cities.

4.2 Discussion of results

I wanted to analyze the effect of the proximity of different landscape features, green patch size and fragmentation on urban mammal species richness and species-specific occurrences. Concerning the distance to landscape features, I predicted that urban avoiding species less adapted to human proximity are negatively affected by urbanization. For urban exploiter species, I predicted that their occurrence probabilities would increase with higher-intensity urbanization. Additionally, I predicted that urban adapter species would not be significantly affected by increasing impervious surface cover proportion as proxy for urbanization. Other landscape features were predicted to be adding further insights especially into species-specific occurrences. For the second research question, I predicted that mammal species richness, as well as the occurrence of area-sensitive species, would be positively associated with increasing patch size. On the other hand, I predicted that the occurrence of species like the stone marten, which favors a high spatial heterogeneity, would be affected negatively. I also wanted to assess the importance of patch connectivity exclusively and in the interaction with fragmentation. Thus, I predicted that connectivity would favor all species irrespective from fragmentation but also and especially with increasing fragmentation.

4.2.1 Landscape features

Of the species investigated, badgers, roe deer, and wild boars were found to express an urban avoiding behavior – exclusively occurring in locations with low surrounding imperviousness cover proportion. Roe deer occurrence was found to be positively affected by surrounding vegetation, and negatively affected by surrounding impervious cover proportion. This supports the prediction that urban avoider species occur in less intensely urbanized and more vegetated areas. However, the model selection for the species European badger, which I predicted to be an urban avoider species, as well, contrasted the prediction. Badgers were found to be significantly affected by neither surrounding vegetation cover nor surrounding imperviousness cover proportion. Therefore, my prediction could be neither completely corroborated nor falsified for the grouped urban avoiders. This suggests investigating urban avoiders at the species level rather than grouping these taxa could provide further insights.

The occurrence of wild boar was best predicted by the distance to urban green areas, stressing a habitat selection against this land-use type. This could be caused by the characteristics of this category – managed green space offering only little cover and human proximity. However, the positive effect of increasing distance to green area on wild boar occurrence is contradicted in the literature. Stillfried et al. (2017) compared habitat use in urban and rural wild boars and both groups used green areas according to their availability. Houses and houses with gardens were found to be selected less than available, supporting the species' choice against high-intensity urban settlements. The reason for the wild boar's apparent avoidance of urban green areas in my study could be a confounding effect of this land-use type occurring mainly in the city center. Therefore, the urban green areas are less easily reachable from the forest patches on the outskirts, that are frequented by wild boar specimens. Another reason might be the lack of cover in urban green areas compared to forest sites, which is essential to mitigate predation risk and enable resting (Tolon et al., 2009), and the increased disturbance and mortality due to higher road density (Forman & Alexander, 1998; Grilo et al., 2009). The study area of Stillfried et al. (2017) was located in Berlin and Brandenburg where the presence of Eurasian wolf (*Canis lupus lupus*) packs might create a "landscape of fear" that could shift the habitat selection of wild boar towards urban and peri-urban areas (Laundré et al., 2001).

The roe deer occurrence in more vegetated and less urbanized sites is in line with previous findings. Torres and colleagues (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 a game species. Therefore, they are subject to anthropogenic disturbance, which is perceived as a mortality risk due to hunting and road mortality (Forman & Alexander, 1998; Lone et al., 2014). Although cities might not increase the mortality by hunting, the additional effect of light pollution encourages the habitat selection for natural and less urbanized green areas (Ciach & Fröhlich, 2019). The main reason for roe deer occurring in the forest rather than urban green areas around Freiburg is probably their herbivorous diet in combination with the absence of top predators like the Eurasian lynx (*Lynx lynx*) or the Eurasian wolf. The density of species-specific food items increases with higher surrounding vegetation cover, while roe deer occurrence in forest sites is not limited by the aforementioned top predators.

The European badger was not found to be significantly influenced by any of the predictors included in the logistic regression model. This finding is surprising and contrasts with the literature. Harris (1984) conducted a thorough analysis of urban badger ecology in Britain and found the habitat selection in urban landscapes to be non-random with badger setts mainly located in "wooded banks, woodlands" and "waste land, scrub, disused gardens" (Harris, 1984, Table 1) and concluded via a review that badgers occur in urban landscapes mainly in combination with high badger population densities in the surrounding. Huck et al. (2008) investigated badger sett distribution and found that it was best predicted by the habitat in which the sett was located. They found a habitat selection preference for "scrub, wasteland, woodland and allotments" (p. 193). My categorization of the badger as an urban avoider is discussable, as well, since the literature is not very explicit either. While Harris (1984) found the badger to be maximally a visitor on the urban fringes, that avoids urban areas, a recent review of urban carnivores by Šálek et al. (2015) found European badgers to occur in high densities in urban landscapes, expressing a typical urban exploiter characteristic. Contrary to the review, badgers in Freiburg im Breisgau were only detected in areas of low urban intensity, supporting the avoiding classification. One explanation could be that European badgers start to actively colonize urban landscapes dependent of their population density (Bateman & Fleming, 2012; Harris, 1984). Another crucial point is the scale of investigation (Pautasso, 2007). While I count the European badgers occurring in the forest adjacent to the city core as urban avoiders, a more large-scale investigation could categorize all of the animal detections as urban adapter species, since they occur adjacent to the urban settlement. Considering the small sample size and the badger occurrence count, my results concerning the opportunistic, random habitat use of European badgers do not suffice to falsify the findings of the previous studies. A multi-city assessment over several seasons could provide more robust results.

I predicted that the European hare and red fox, which I categorized as urban adapter species, would not be significantly affected by the degree of urbanization because of their behavioral plasticity enabling them to adapt to urban landscapes. I found red foxes to be positively associated with surrounding vegetation cover and negatively associated with impervious cover. The most important positive effect occurred with increasing patch connectivity. The presence of hares was found to be significantly higher in better connected green patches. None of the other independent variables significantly affected the probability of presence of hares. Thus, for the fox, the results contradict my prediction whereas the findings for the European hare support it.

None of the predictor variables except for the logarithmic area-weighted least-cost distance showed a significant association with European hare occurrences. This suggests a generalist habitat selection. For a rural European hare population, Fulgione et al. (2009) had issues finding meaningful ecological variables to predict habitat suitability for the European hare. While they argued that this was to be expected for such an adaptable species, the findings for urban and peri-urban European hare populations speak against the generalist habitat use (Mayer & Sunde, 2020; Roedenbeck & Voser, 2008) (see also chapter 4.2.3). In Freiburg im Breisgau, in addition to the importance of patch connectivity, the hare occurrences were located exclusively in low- and medium-urbanized sites (Figure 6C). This non-significant trend is supported by previous studies. Roedenbeck & Voser, (2008) found that hares avoid urban settlements and selected semi-natural grasslands and forests. These landscape features are found in a higher proportion in Freiburg im Breisgau's less urbanized outskirts (Figure 6A). However, the trend is not statistically supported but is exclusively shown in descriptive statistics. Thus, the results for hares in Freiburg im Breisgau support the prediction that urban adapter species are minimally affected by increasing urbanization. While the positive association of hare occurrences with increasing patch connectivity could be established here, multi-season data could again provide insight into whether the European hare population in Freiburg im Breisgau expresses a more generalist habitat use like rural conspecifics or whether the selection for the less urbanized area is significant.

The best explanatory variables for the fox occurrence were the patch connectivity estimator, followed by the surrounding vegetation cover. Since the surrounding vegetation cover increases the probability of fox occurrence, the negatively correlated impervious surface cover proportion as a proxy for urbanization could affect it negatively, contradicting my prediction that urban adapter species are minimally affected by urbanization. The positive influence of surrounding vegetation on red fox occurrence is in accordance with the literature. Červinka et al. (2014) found that the fox is the urban carnivore species with the most selective habitat choice of all their study taxa. The preferred habitat is more natural and less urbanized. Despite the preference for areas with high surrounding vegetation cover, presumably forest sites, red fox occurrences were detected in every level of surrounding imperviousness cover (Figure 6C). This could result from the mitigated barrier effect of medium-sized cities not inhibiting immigration into the settlement as effectively as in larger cities (Červinka et al., 2014). Despite their ability to den in urban environments and the anthropogenically supplied food that red foxes can profit from (Bateman & Fleming, 2012), Freiburg im Breisgau's foxes are modeled to occur preferentially in proximity to higher surrounding vegetation cover proportion.

I categorized European hedgehogs and stone martens as urban exploiters, according to the literature. The results of my study suggest European hedgehogs are significantly associated with distance to water, as well as surrounding vegetation cover proportion, and stone martens with patch connectivity. The results on marten occurrences oppose the prediction that urban exploiter species benefit from increasing urbanization intensity with the impervious surface cover proportion as a proxy. Whereas the negative influence of surrounding vegetation cover on the probability of hedgehog occurrence corroborates the prediction.

The top-ranked model on European hedgehog occurrence contains the independent variables distance to water and surrounding vegetation cover. Although the distance to water is not mentioned explicitly as an important factor for European hedgehog habitat suitability, it contributes to crucial behaviors performed by the species (e.g. "Drinking, grooming, […] swimming") (Riber, 2006, Table 2). Additionally, the positive association of European hedgehogs with water may be explained by their diet consisting to a notable degree of earthworms and invertebrates abundant in moist green areas such as leys and pastures (Driezen et al., 2007; Hof, 2009). Additionally, this habitat type is assumed to facilitate their movement (Driezen et al., 2007). However, hedgehogs occurred in all the imperviousness classes (Figure 6C) and surrounding vegetation was found to decrease the probability of hedgehog occurrence. The reasons for this may lie in the hedgehog's generalist habitat use as suggested by Driezen et al. (2007) and in its most important predator, the European badger (Doncaster et al., 2001), occurring presumably more often in Freiburg im Breisgau's forest sites. This could cause the behaviorally plastic European hedgehog to reside in closer proximity to urban settlements, which was found by Hof et al. (2012).

The model selection for stone martens did not show any significant effect from the urbanization proxy on the occurrence of stone martens. Investigating habitat selection in martens, Červinka et al. (2014) found that, overall, martens express an opportunistic habitat selection in a gradient of natural versus urban landscape. That could explain stone marten occurrence in all three levels of urbanization intensity and the weak predictive power of the urbanization proxy. Although the prediction that urban exploiters such as stone martens are positively affected by the surrounding imperviousness cover's analysis, the study contributed interesting findings concerning stone marten response to increasing patch connectivity (chapters 3.2.3 & 4.2.3).

Concerning the total mammal species richness, the results show a significant association of species richness with distance to the city boundary, while decreasing surrounding imperviousness cover also significantly increases the species richness. These findings highlight a negative influence of urbanization on total mammal species richness. In accordance with these results, various reviews emphasize the decrease in mammal species richness with increasing urbanization (e.g., Faeth et al., 2011; McKinney, 2008). More specifically, Gallo et al. (2017) found that, of different investigated urban green area types, natural areas have the highest medium to large-sized mammal species richness, superior to cemeteries, city parks, and golf courses. The natural areas in this study are the sites located in the urban forest adjacent to the urban boundary with high surrounding vegetation cover and low surrounding imperviousness cover. These locations had the highest species richness (Figure 6A and 6B). The effect is likely increased by the species European badger, roe deer, and wild boar – approximately 43% of analyzed mammal species – exclusively occurring in these low-intensity urbanized locations. In other studies (e.g., Harris, 1984; Huck et al., 2008; Stillfried et al., 2017), European badgers and wild boars are reported to occur within the urban boundaries. The reason for the absence of these species could be the small spatial extent of the city of Freiburg im Breisgau resulting in a lack of natural and near-natural green areas within the city borders, i.e. urban wooded areas like city forests. Therefore, I suggest the investigation of the effect of the interaction of spatial extent of cities and urban green area type on urban mammal species in a multi-city assessment, considering various spatial urban extents.

4.2.2 Patch size

Concerning the effect of patch size, I predicted that increasing patch size is associated with higher species richness as well as with a higher probability of species-specific occurrences. I predicted that species that prefer high structural heterogeneity, such as the stone marten, form the exception. The results show that patch size was not an influential predictor for any of the response variables. Thereby, the hypotheses about the relation of patch size and mammal species' occurrences as well as mammal species richness cannot be corroborated by this study.

The top-ranked model on stone marten occurrence as function of patch size and patch connectivity had a non-significant coefficient of 0 ± 0.00. This suggests that the investigated stone marten population is not significantly affected by patch area, which is reasonable concerning stone marten preference for structural heterogeneity (Virgós et al., 2000), their exploitation of anthropogenic resources (Bateman & Fleming, 2012; Herr et al., 2010), and their generalist habitat use (Červinka et al., 2014). The same coefficient is found in the roe deer model, which is surprising considering the species' sensitivity to fragmentation. Roe deer are thought to be a forest-dwelling species dependent on large, unfragmented patches and sensitive to fragmentation impacts, since e.g., road mortality is an important mortality factor (Corlatti et al., 2009). The reason for the lack of significance for patch size's effect on roe deer and the other urban avoider species of the analysis is likely caused by too few observations ($n_{\text{roe deer}} = 6$; $n_{\text{European badger}} = 4$; $n_{\text{wild boar}} = 4$; Figure 6C). The same could hold for the European hare, which was found to select for large patches in rural (Roedenbeck & Voser, 2008) and urban contexts (Mayer & Sunde, 2020).

The result that patch size did not significantly predict any of the response variables is unexpected. For multiple taxa, patch size was shown to be the most influential factor in increasing total urban species richness (Beninde et al., 2015). A possible explanation for the lack of significance could be the quality of the Urban Atlas Data. Comparing Figure 2 and Figure 6A, one can see that the background map of Figure 2 (Open Street Map) classifies the landscape features at a finer scale. Therefore, the patch size of the camera patches might not be precise, biasing the analysis. Also, in my study's case, the surrounding imperviousness cover proportion has a stronger association with species richness, opposing the results of Beninde et al. (2015). However, the mentioned analysis is based on various taxas' pooled data, while I investigated mammals exclusively. Due to their inability to fly and, therefore, being more sensitive to increasing road density, the barrier-effect of the urban boundary (Červinka et al., 2014; Ciach & Fröhlich, 2019) could be more pronounced for medium and large-sized mammals. Exclusively adapted mammal species occurred in the highly urbanized city core with small fragmented green patches (Figure 6C), whereas in the forests outside the urban boundary so-called urban avoiders could be found as well.

4.2.3 Fragmentation & patch connectivity

Concerning the importance of fragmentation, I predicted that especially interacting with increasing fragmentation, patch connectivity is an important predictor of mammal occurrences and species richness. Since none of the response variables were found significantly associated with fragmentation this prediction was not supported by my study's results. However, for selected species, the patch connectivity estimator predicted the species presence most precisely. Therefore, the second prediction concerning the patch connectivity's effect irrespective of fragmentation is supported.

The model selection concerning patch size and patch connectivity's effects showcased that when leaving the effect of urbanization out, roe deer occurrence is positively associated with patch connectivity. The aforementioned point concerning roe deer habitat selection towards forest patches (chapter 4.2.1) provides an explanatory approach here as well. Its habitat use is defined by avoiding human disturbance (Ciach & Fröhlich, 2019), thus the high predictive importance of surrounding vegetation and imperviousness. To a lesser extent, patch connectivity may define roe deer habitat selection. Coulon et al. (2004) found the genetic distance of observed roe deer pairs positively associated with calculated least-cost distances. Thereby, they showed the importance of landscape connectivity for roe deer dispersal. As a species whose movement is inhibited by roads and mainly forest-dwelling, Corlatti et al. (2009) emphasize the need for landscape connectivity to counter genetic pauperization of animal populations and contribute to population persistence.

The European hare occurrences were found to be significantly associated with patch connectivity of urban green areas and peri-urban forest sites. The results show a positive effect of patch connectivity on the occurrence probability of urban European hares. The importance of patch connectivity is in accordance with the literature. European hares include different habitat types, as e.g., foraging or resting habitat, in their home ranges to fulfill their needs (Schai-Braun & Hackländer, 2014 and references therein). Thus, high patch connectivity is necessary to maintain landscape permeability between different types of habitats. The investigation of patch connectivity and fragmentation concerning the hare resulted in this multivariate model with a slightly higher pseudo-R^2 than the univariate patch connectivity model. This could suggest that European hares are somewhat sensitive to fragmentation although the effect is not of significance. Ullmann et al. (2020) found smaller range adjustments in European hares after management in more complex agricultural landscapes. This suggests a positive influence of fragmentation per se in a higher quality matrix. However, this study's urban landscape consists mostly of a lesser quality matrix (Figure 6A) (Mayer

& Sunde, 2020). This could explain why the fragmentation proxy here was calculated to have a negative influence on European hare occurrence. The non-significance of this emphasizes the need for further investigation.

Red fox occurrences were found to be positively associated with patch connectivity. This could be caused by the mobility of this species and its discrimination in resting, denning, and foraging habitats (Marks & Bloomfield, 2006). While they preferably den in vacant dens dug by other animals in less disturbed forests with limestone ground in Southwestern Germany (Weber, 1982), red foxes exploit the urban core by foraging on anthropogenic food resources. Contesse et al. (2004) found anthropogenic refuse present in over 50% of investigated (sub-)urban red fox stomachs. Patch connectivity possibly plays a crucial role in maintaining the red foxes' mobility between the urban city center and the forest on the urban fringes. The importance of vehicular accidents as the second most important mortality factor in urban red foxes (Bateman & Fleming, 2012, Figure 2) adds to the necessity of high patch connectivity for red fox population persistence in proximity to intensely urbanized landscapes with high road densities.

Stone martens respond negatively to the patch connectivity proxy. Since the patch connectivity estimator is area-weighted, larger, less fragmented areas increase patch connectivity values. The negative response to increasing patch connectivity possibly reflects the stone marten's selection for sites with increasing spatial heterogeneity instead of unfragmented, large-sized green areas (Virgós et al., 2000). More urbanized landscapes provide a diverse mosaic of various types of green space adjacent to densely built areas and impervious surface cover (Pautasso, 2007). Stone martens were found to use anthropogenic denning sites on 98.5% of days in cities (Herr et al., 2010) and green space was found to be crucial for foraging and resting (Santos & Santos-Reis, 2010). Therefore, the urban mosaic contains the necessary heterogeneity to inhabit behaviorally plastic stone martens. These biological characteristics combined with the additional benefit of anthropogenic food sources (Bateman & Fleming, 2012) could reasonably explain the negative effect of increasing patch connectivity that seems surprising at first.

Contrasting to the expectations based on the literature on landscape connectivity, the patch connectivity estimator does not show a significant influence on the total species richness. Although other studies come to the same conclusion (Beninde et al., 2015, Figure 4), the applied connectivity measure from these researchers was a basic, structural measurement, the Euclidean distance to the closest green patch. Since various others showed the superiority of functional connectivity measures (e.g., Chardon et al., 2003; Verbeylen et al., 2003), I assumed that my patch connectivity proxy could be a more meaningful predictor. My results also oppose my prediction concerning the increasing effect of connectivity in higher fragmented city parts. The results suggest that urbanization – decreasing the surrounding vegetation – and distance to the city boundary have stronger effects than patch connectivity does on urban mammal species richness. The reason for this may lie in the disturbance sensitivity of particular model species (Ciach & Fröhlich, 2019). Considering that more than 40% of the study organisms are herbivorous (Table 3) results in the importance of vegetation in foraging sites. Therefore, the findings concerning the negative influence of urban settlements as substitution of vegetated areas could be expected. This supports the findings of Fahrig (2003) showcasing that habitat loss, not fragmentation per se, causes detrimental pauperization of species richness.

5 Conclusion

I showed that for Freiburg’s medium to large-sized urban mammal species richness, the distance to the urban boundary is the most influential positive association, followed by the surrounding imperviousness cover’s negative influence. However, to stop sealing (semi-)natural surface cover and to increase the population density in the existing urban boundary seems theoretical, escapist, and too idealistic. Meanwhile, contact with nature in urban proximity enhances the psychological wellbeing of city dwellers and mammals can contribute to crucial ecosystem services. Therefore, my analysis emphasizes the necessity for sustainable urban planning including the prerequisites of the aforementioned taxon.

For a multitude of species, not only those occurring outside the urban boundary, the surrounding vegetation cover was shown to express an influential effect on the probability of presence. This highlights the need not for only urban forests on the city’s fringes but also for an urban landscape consisting of a mosaic of sufficiently green infrastructure in between sealed surfaces. The analysis showed that for small cities, green patch availability is of greater importance than the size of the patches. Urban development should, therefore, focus on the conservation and creation of even small-sized urban green infrastructure. The necessary consequence is increased patch connectivity, which was shown to positively influence a multitude of analyzed study species.

While green space is beneficial to most mammal species, other land-use types result in differences in species-specific perception of landscape resistance. Urban planning should therefore contribute to the creation of a diverse landscape consisting of various land-use types with different physical characteristics. Consequently, heterogeneity-dependent species could further exploit the benefits of urban proximity, while the functional patch connectivity for other species increases with diversity in habitat types – facilitating their movement.

Furthermore, urban mammals depend not only on the facilitation of movement but also on structures that offer forage, cover, and shelter. The conclusion is the crucial importance of conservation, maintenance, and creation of animal-benefitting structures in urban contexts. The urban-dwelling population should therefore be aware of the profit their heaps of leaves can bring, while urban planning should consider, e.g., lower-intensity hedgerow management. Urban biodiversity conservation is a responsibility of a multitude of stakeholders, and on a planet growing increasingly urbanized, everyone can contribute her or his part.

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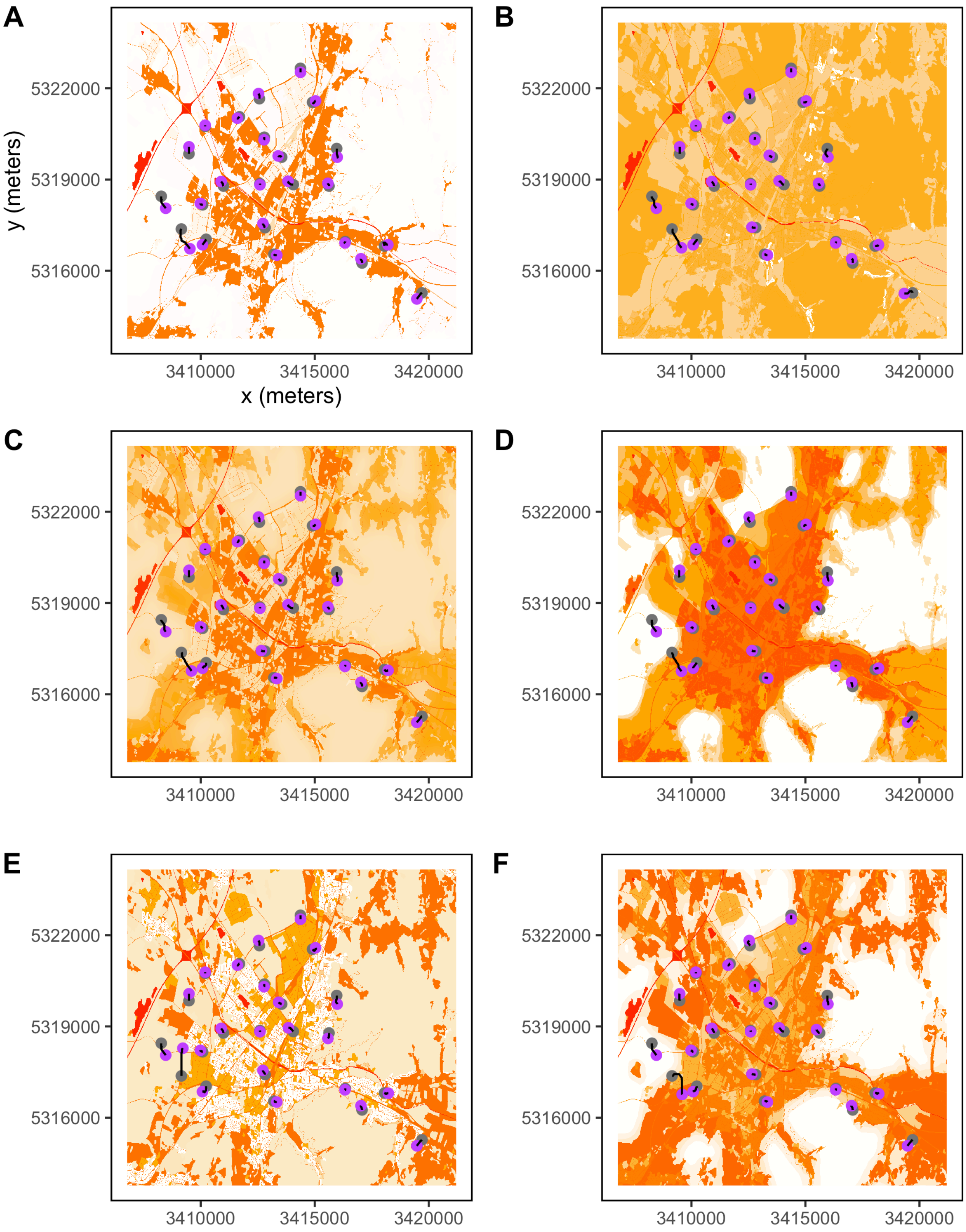
Appendices

Appendix A.1.

Resistance values assigned to the classes of the weight factor land use

Land use category	Red fox (**I**)	Stone marten (**I**)	European hare (**II**)	European badger (**III**)	Wild boar (**IV**)	Roe deer (**V**)	European 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 & 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

I: Duduś et al., (2014); **II**: Mayer & 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.



Appendix A.2: Lcd-maps for European badger (**A**); European hare (**B**); red fox (**C**); roe deer (**D**); stone marten (**E**); wild boar (**F**); symbols as in Figure 8.