Connectivity at home: A data-driven connectivity modeling framework for home range movements in heterogeneous landscapes

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Abstract

1. Landscape connectivity analyses can serve landscape planning with designing functional conservation networks. However, existing frameworks face challenges, such as achieving consistency between integrated data and modeled processes, implementing data-driven parameterization, and addressing connectivity within the home range. We propose restricting connectivity analyses to the home range scale to better relate landscape resistance, barrier effects and resource accessibility to daily movements and home range establishment.
2. We introduce a home range connectivity modeling framework that allows deriving important connectivity parameters empirically. We identify areas that can support home ranges based on available resources and calculate resource patch accessibility using graph and circuit theory. Resistance values, patch isolation distances, and connectivity metrics are selected from statistical models using movement data. We demonstrate the framework's utility through a case study on urban blackbirds and increase its applicability by testing whether the use of simple presence/absence data without additional movement data, and the use of a coarser resolution affect the estimation of parameter values.
3. In statistical analyses, the local connectivity showed a strong significant positive association with the probability of blackbird movement ($\beta = 0.23$, $p < 0.005$). We uncover that the connectivity parameters are better assessed with graph theory-derived metrics when parametrized with movement data. We find a high barrier effect of high buildings and a moderate barrier effect of lower buildings and streets on blackbird movement. However, when assessed with presence/absence data, model parametrization can result in similar values only when using circuit theory metrics. Changing the resolution from 10 to 30 m has minimal impact on parametrization results with movement data.
4. Our study showcases a data-driven parameterization using statistical model selection, which addresses several of the main limitations of recent connectivity modeling approaches. Presence/absence data and coarser resolution can be used judiciously, but independently. Restricting analyses to home ranges yields valuable insights into home range ecology, landscape impacts on movement in highly heterogeneous landscapes, and species distribution.

1. Introduction

International agreements and resolutions increasingly emphasize the critical role of ecological connectivity in sustaining ecosystems and their services to humans (IUCN, 2021; UN General Assembly, 2021). Defined as the "degree to which a landscape facilitates or impedes movement among resource patches" (Taylor et al., 1993), ecological connectivity supports biodiversity and ecological processes from the level of an individual (e.g., resource allocation within home ranges) (Blazquez-Cabrera et al., 2014; Taylor et al., 1993) to the metapopulation (e.g., dispersal and gene flow between subpopulations) (Blazquez-Cabrera et al., 2016; Braaker et al., 2017).

Ecological connectivity models offer valuable insights for landscape planning and aid in nature conservation (Foltête et al., 2014; Molné et al., 2023). They have been instrumental in creating conservation networks, assessing population fragmentation, and designing urban green spaces for both wildlife and humans (Koen et al., 2014; Mimet et al., 2016, 2020). Over the past two decades, numerous connectivity modeling approaches have emerged (Fletcher et al., 2019; McRae et al., 2008; Unnithan Kumar, Kaszta, et al., 2022; Urban et al., 2009; Van Moorter et al., 2023). These approaches encompass a spectrum of complexity, ranging from simple distance analyses of habitat patches (Calabrese & Fagan, 2004; Foltête et al., 2014) to intermediately complex methodologies utilizing graph and circuit theory with habitat patches, links, and resistance surfaces (McRae et al., 2008; Urban et al., 2009), and advanced approaches simulating individual movement (Unnithan Kumar, Kaszta, et al., 2022). Among these, graph and circuit modeling tools strike a balance between data requirements and the generation of sufficiently detailed model results (Calabrese & Fagan, 2004; Martensen et al., 2017), rendering them prevalent at the research-landscape planning interface (Foltête et al., 2014; Koen et al., 2014; Molné et al., 2023). However, the applications of these methodological frameworks suffer from a lack of consistent scales and trustworthy parameter values to ensure reliable results. These limitations undermine confidence in their outputs and consequently hinder their broad applicability (Moilanen, 2011; Unnithan Kumar, Turnbull, et al., 2022). In particular, graph and circuit theory modelling tools face the following challenges:

(i) ***Scale inconsistencies:*** Many methodological approaches to connectivity models do not specify whether they address movement between patches within a home range or between populations at the scale of dispersal (Blazquez-Cabrera et al., 2014). Within-home-range movements occur frequently, take less time, and involve travel between small resource patches, while dispersal movements are infrequent, time-consuming, and connect large, heterogeneous areas of high suitability (Blazquez-Cabrera et al., 2014; Mimet et al., 2016). Often, small and large-scale movements are mixed, ignoring the differences in the animals' motivations, their timescales, and the spatial properties of the movements and the connected areas (Blazquez-Cabrera et al., 2014, 2016). Several studies infer dispersal processes from foraging movements which can result in erroneous parameter values (Zeller et al., 2018). For example, the landscape resistances that mammals experience differ if either data from dispersal or foraging is used for their parameterization (Blazquez-Cabrera et al., 2016; Zeller et al., 2016).

(ii) ***Non-empirical derivation of landscape resistances***: The resistance values of different land cover types are often evaluated based on expert knowledge and literature reviews rather than empirical data (Unnithan Kumar, Turnbull, et al., 2022; Zeller et al., 2012). Conversely, well-parametrized connectivity models use

tracking data of individuals to estimate landscape resistances, but this is expensive, time-consuming and limited to only a few species (Zeller et al., 2012, 2018). Acquiring tracking data for many species and conservation applications, therefore, is unrealistic, despite its necessity for parametrizing connectivity models (Koen et al., 2014; Zeller et al., 2018). In cases with available observational presence/absence data, species distribution models are often used to estimate habitat suitability, from which landscape resistance is directly derived (Keeley et al. 2017; Zeller et al., 2018). However, this practice is contested (Keeley et al., 2017; Zeller et al., 2018). Hence, a systematic parametrization approach is needed to test various landscape resistances and facilitate the use of readily available data (Verbeylen et al., 2003).

(iii) ***Unclear choice of connectivity modeling approach and related connectivity metric:*** The two connectivity modeling approaches graph and circuit theory both link patches in a landscape matrix that introduces resistance to movement between them (McRae et al., 2008; Urban et al., 2009). The two approaches are used equivalently, but the choice between them is rarely empirically-based, despite them having opposite assumptions on animal movement patterns (McClure et al., 2016; Palmer et al., 2011). In graph theory, the movement between two patches follows the least-cost path; the path of lowest cumulative resistance determined from a resistance map (Galpern et al., 2011; Urban et al., 2009), suitable for modeling animals with good memory in familiar areas (Palmer et al., 2011). By contrast, circuit theory models the movement of individuals as an electrical current thereby employing a random walk (McRae et al., 2008) and assuming animals lack prior knowledge, suitable for an unknown landscape or animals with bad memory (McClure et al., 2016). Besides the unclarity about the fitting approach, both approaches, particularly graph theory, offer numerous metrics partly covering similar and partly different aspects of connectivity (Foltête et al., 2012; Rayfield et al., 2010). Their suitability for a specific movement is unclear and untested (Foltête et al., 2012; Rayfield et al., 2010).

(iv) ***Unclear effects of mapping resolution:*** Advancements in remote sensing and geospatial modeling have provided higher-resolution datasets for connectivity modeling (Morin et al., 2022). However, this comes at the cost of increased computational demands which limits the practicality of connectivity modeling in broader conservation planning (Molné et al., 2023). Furthermore, the resolution at which an animal perceives its environment is probably dependent on the species and the body mass (Hostetler & Holling, 2000). The best resolution for modeling the connectivity for a target species is not well researched so far (Zeller et al., 2012). Therefore, it remains largely untested whether the widely available resolutions of 10 m and 30 m provide the same information for a target species (Molné et al., 2023).

(v) ***Lack of home range connectivity modeling frameworks:*** The scale of the home range, defined as “the area or volume over which [an individual] normally travels in pursuit of its routine activities” (Okubo & Levin, 2001), is rarely considered in connectivity analyses (LaPoint et al., 2013; Mimet et al., 2020). Most connectivity modeling approaches target dispersal, i.e. “[circumstances] in which individuals leave their existing home ranges and do not return” (Stenseth & Lidicker, 1992). Connectivity does, however, also affect daily movements in home ranges (Koen et al., 2014; LaPoint et al., 2013; Zeller et al., 2016) and their size, formation, and

shape (Bevanda et al., 2015; Sutherland et al., 2015; Walter et al., 2009). In very heterogeneous landscapes like cities, connectivity is crucial for a species' access to resources distributed across patches (Kirk et al., 2018), thereby influencing home range establishment and species distributions. Moreover, territories in such areas are relatively small compared to a vertebrate's home range and their size corresponds more to one or few sub-populations than a metapopulation (Beninde et al., 2016; Braaker et al., 2017). Consequently, dispersal has limited explanatory power for the species' distribution and movement. Studying connectivity at the home range scale is more justified for compact and heterogeneous territories and emphasizes its essential role in home range establishment.

This study aims to address these limitations by introducing a modeling framework for building and parametrizing home range connectivity models, thereby enhancing their applicability and reliability for planning and conservation (Foltête et al., 2014). Our two-step modeling framework is inspired by the hierarchy of habitat selection that distinguishes between the lower-order process of selecting a home range within the geographical range and the higher-order process of choosing specific habitat components within the home range based on availability and accessibility (Johnson, 1980). By applying this hierarchical approach, our framework assesses two critical resource conditions impacting the occurrence of home range movements: resource amount (sufficient resources for home range establishment) and resource accessibility (the accessibility of resources in different patches through an individual's movement). In a first step, areas that could support home ranges are delineated based on a species' minimum resource requirements. In a second step, connectivity between resource patches within these potential home range areas is modeled. Our framework utilizes statistical model selection to derive *key connectivity parameters*, including the amount and the type of resources that constitute a home range and a resource patch (home range resource map), resistance values of land cover types, maximum isolation distances between resource patches, and the most appropriate metric for movement description. This statistical approach expands and structures the methodology demonstrated by Verbeylen et al. (2003).

We illustrate the utility of our modeling framework in a case study on the common blackbird (*Turdus merula*) in the city of Munich. Cities epitomize extreme environmental conditions with very heterogeneous landscapes, offering valuable insights into the fundamental mechanisms in the interplay between landscape structure, movement, and connectivity (Breuste et al., 2008).

2. Methods

2.1 Modeling framework

The modeling framework introduced in this study generates home range scale connectivity maps using four empirically-derived *key connectivity parameters* (Figure 1). It employs a raster representation of the landscape that consists of a resource and a resistance landscape finally depicted in a home range resource and a resistance map (Table 1). Resource patches, identified from a land cover map, represent resources/foraging sites and comprise various vegetation types or water bodies. Potential home ranges, derived from the land cover map, consist of multiple pixels and indicate areas with sufficient resources for home range establishments without considering accessibility or disturbance. The resource landscape details resource patches within each home range and, therefore, requires a fine resolution. The resistance landscape quantifies the landscape's resistance to an individual's movement based on local land cover types and necessitates the same resolution as the resource landscape.

Table 1: Definition of important terms used in the model description

Landscape	**Term**	**Definition**
Resource landscape	Home range	"The area or volume over which [an individual] normally travels in pursuit of its routine activities" (Okubo & Levin, 2001). Home ranges can be approached by a circle defined by a species-specific radius, the home range radius (Arthur et al., 1996).
	Resource cell	A pixel of a land cover type on the land cover map that provides resources for the target species (e.g. food, shelter)
	Resource patch	Connected resource cells between which the animal can move without traversing a cell without resources
	Home range circle	A circle with the size of a home range (Arthur et al., 1996) that is discretized on a raster map. This circle must not necessarily represent a home range; it is used to estimate the amount of resources available if a home range was located there.
	Home range resource map	Identifies the resource patches located in areas providing sufficient resources for home range establishment
Resistance landscape	Resistance value	Quantified resistance that is assigned to a specific land cover type. Resistance values are also assigned to resource cells
	Resistance map	Map of resistance values in each cell that are determined from the local land cover types. If there are different land cover types in a cell, the resistance of a cell is the sum of the resistance values of the land cover types present in a cell weighted by their coverage.

	Maximum patch isolation distance	Maximum distance between patches that the target species crosses during home range movements

Parametrization of the model requires observational presence/absence data of the target species and additional literature information on the species' ecology (i.e., vegetation type used for foraging, home range size) as well as a list of connectivity metrics to be calculated. The data used is limited to presence/absence information since the presence of a home range hinges on meeting minimal resource requirements and ensuring sufficient accessibility (connectivity). Abundance data is inappropriate as abundance only increases after critical thresholds of resource amount and accessibility are surpassed and, thereby, introduces unnecessary complexity (see Appendix 1 for more details). The initially required information is retrieved in *Step 0* of the analysis (Figure 1, Table 2). Parametrization is done in two modeling steps reflecting the hierarchical process of habitat selection (Johnson, 1980) (Figure 2):

Step 1 – Creating a *Home Range Resource Map.*

This step identifies resource patches within potential home ranges in the landscape. The output is the home range resource map that serves as an input for the connectivity model developed in *Step 2* (Foltête et al., 2012; McRae et al., 2016). *Step 1* consists of ten sub-steps and first processes a land cover map to attain a suitable modeling resolution (Table 2). To obtain the home range resource map, a first dataset with information on the presence/absence of the species is used to determine areas with sufficient resources for the species to sustain a home range (the "home range resource map" *key parameter*). Other necessary parameters include the land cover type providing resources for the target species and the species' minimum home range radius (Figure 1).

Step 2 – Parametrizing the *Connectivity Model*.

This step integrates species movement and resource accessibility through connectivity modeling. *Step 2* consists of nine sub-steps and requires the home range resource map from *Step 1* and a second dataset on the presence and absence of movement (Figure 1, Table 2). *Step 2* models the connectivity for movement between resource patches within home ranges, excluding connectivity to patches outside (Figure 2). The aim of this modeling step is to determine *key connectivity parameter*s, in particular resistance values of land cover types, maximum isolation distance between resource patches, and the best connectivity metric through statistical model selection (Figure 1). *Step 2* creates connectivity maps for all reasonable combinations of the *key connectivity parameters* and then selects the parameter values that best explain the presence/absence of movement of the target species (Table 2). In a final step, it calculates connectivity maps based on the best parameter values (Table 2).

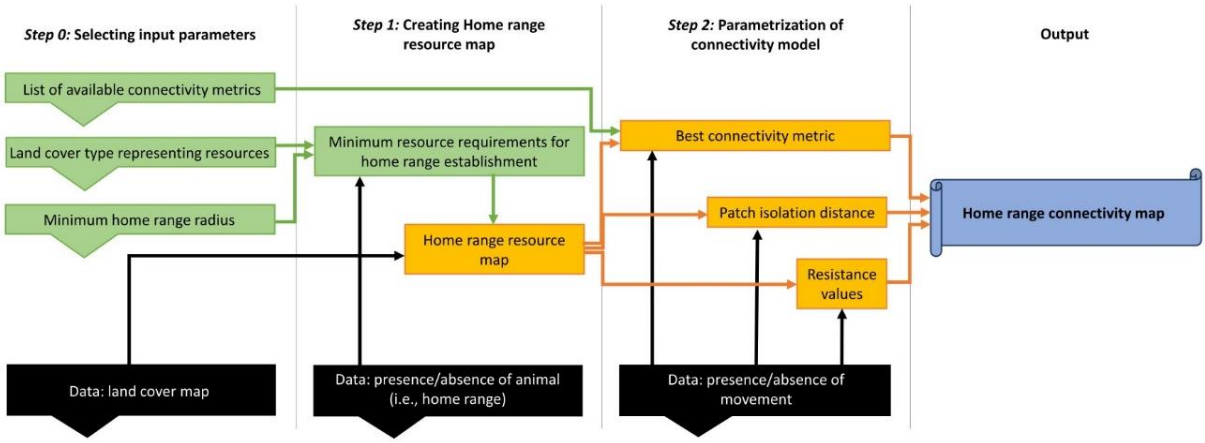


Figure 1: Parametrization procedure for the home range connectivity model in this study. Boxes with triangles represent either external data for parameter selection (black) or initial literature-based input parameter (green). Simple green boxes indicate empirical data chosen from the literature and orange boxes show key connectivity parameters *empirically derived from the parametrization procedure.*

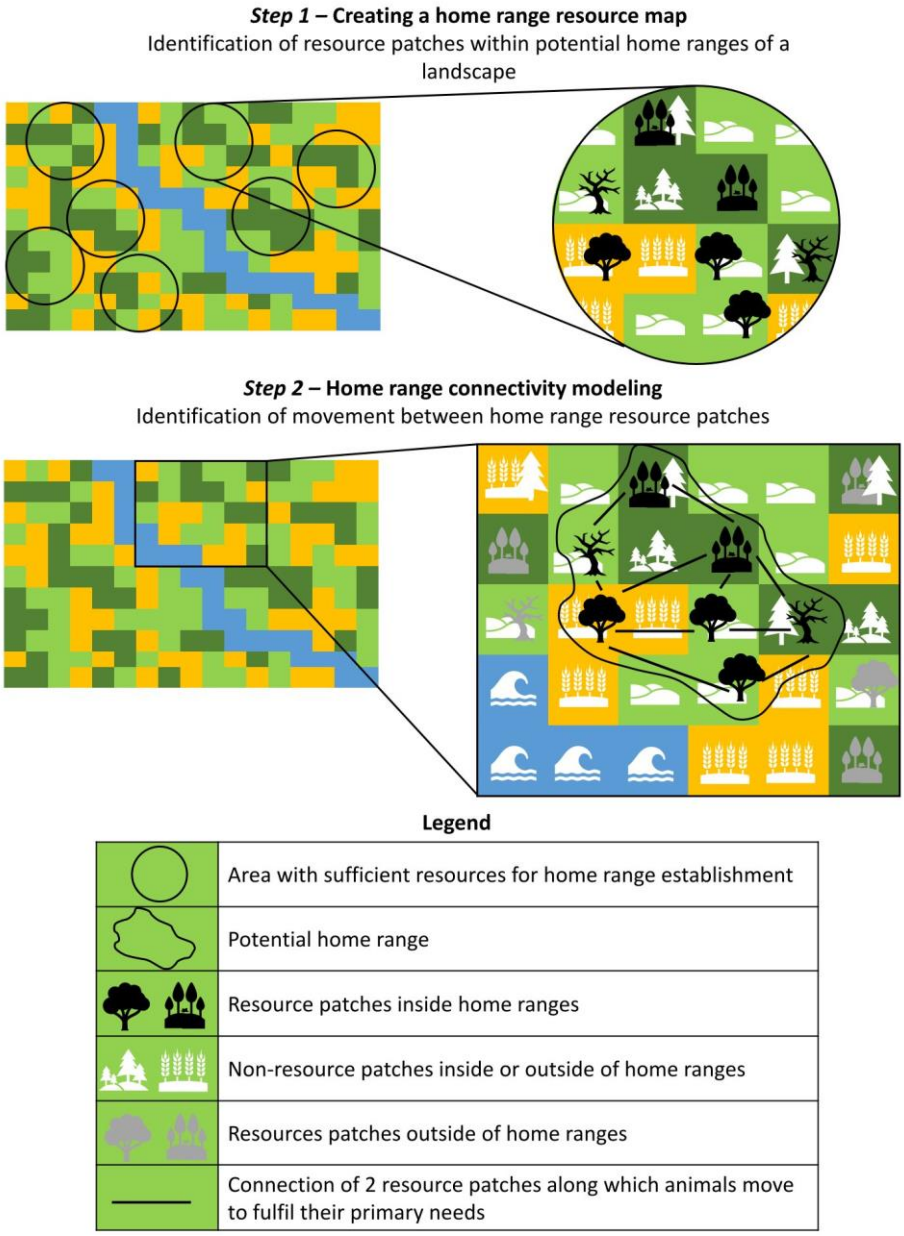


Figure 2: Graphical representation illustrating the two modeling steps for a hypothetical species dependent on deciduous trees. Patches with deciduous trees are therefore resource patches (dark green pixels). We assume that the species can cross meadows (light green pixels) and agricultural fields (yellow pixels) but cannot cross rivers (blue pixels). In Step 1 *of the algorithm, suitable home ranges (black circles) and the resource patches within them (black pictograms) are identified. Note that* Step 1 *also identifies the minimum amount of resources needed (in this example the number of patches with deciduous trees).* Step 2 *models connectivity for movement between resource patches (black pictograms) within home ranges (black lines), excluding connectivity to patches outside (grey pictograms).*

Table 2: General description and adaptation to the case study of the input parameters, steps and sub-steps of the modeling framework parametrization procedure

	General description	Model input or parameter	Source	Case study
Step 0: Selecting input parameters				
0.1 Set minimum home range size	Defines the minimum home range radius for the target species.	Minimum home range radius	From literature	The average male blackbird home range in the city is approximately a 180 m radius circle (Ferry et al., 1981). It varies between sexes, and the most intensely used area is substantially smaller (Snow, 1966). We selected a radius of 100 m as a conservative value for the minimum home range size.
0.2 Identify land cover types with resources	Defines the land cover types where resources (for food, nesting, shelter) for the target species occur	Land cover types	From literature	The initial highly resolving land cover map of Munich differentiates the following land cover types: buildings of different heights, streets, agricultural areas, water bodies, grass, shrubs and trees. Grass, shrubs, and trees are blackbirds' resources for feeding and/or nesting and land use types containing these resources can be defined as resource cells (Snow, 1966). For description of creation of land cover map of Munich, see appendix 2.
0.3 Define what amount of resources constitutes a resource patch	Defines the amount of all resources (in m2) that is sufficient to constitute at resource patch. Treats all identified resources (from step 0.2) equivalently independent of their initial vegetation or land cover type. The amount of resources should be small enough to identify important features in the landscape (e.g. a fully-grown tree). A very small threshold increases the computational requirements. The threshold is determined from visual inspection of the highly-resolved land cover map.	Resource threshold	User-defined	Resource cells that contain at least 20 m2 of vegetation to reflect the size of a well-grown tree (Konijnendijk, 2023)

0.4 Retrieve connectivity metrics to be tested	Retrieves connectivity metrics that will be used to calculate entire raster maps with connectivity values for every cell. The available metrics depend on the used modeling tool. To test whether graph or circuit theory is more suitable to model the movement of a target species, connectivity metrics from both approaches should be selected.	Connectivity metric	From literature	We decided to use metrics from both graph and circuit theory modeling tools and used the modeling tool Graphab (Foltête et al., 2012) for graph-theory-based analyses and the Julia-package Omniscape (Landau et al., 2021) for circuit theory. Both modeling tools allow for a landscape graph with many patches and omnidirectional movement (Foltête et al., 2012; Phillips et al., 2021). For graph theory, we chose the four local connectivity metrics that are available in Graphab for extrapolation to the landscape, namely Flux (F), Interaction Flux (IF), corridors, and Betweenness Centrality (BC) (Clauzel et al., 2022). Only these metrics allow to produce raster maps of connectivity (Clauzel et al., 2022). For circuit theory, we selected two connectivity metrics available in the Julia-package Omniscape (Landau et al., 2021), Cumulative Current Flow (CF) and Normalized Current Flow (NCF) (for further description of metrics, see Appendix 3).
Step 1: Creating home range resource map				
1.1 Aggregate land cover map to suitable resolution	Aggregates the land cover map from initially very high resolution to the pixel size chosen for computation. For every land cover type, its proportion within the larger pixel is stored.	Coarse-resolution land cover map	User-defined	Considering the minimum home range radius of 100 m and computational power, we aggregated the land cover map with an initial resolution of 40x40 cm to 10x10 m.
1.2 Create map of resource cells	Applies the resource threshold defined in step 0.2 to the coarse-resolution land cover map to obtain a map of resource and non-resource cells.	Map of resource cells	Derived from step 0.3 and step 1.1	Map of Munich with resource and non-resource cells.
1.3 Calculate amount of resources per home range	Calculates the amount of every resource type in a home range circle from the coarse-resolution land cover map. This calculation is performed for every home range circle that geometrically fits into the map.	Map of amount of resources in all home ranges circles	Derived from step 0.1 and step 1.1	The amount of grass, shrub, and tree in a 100 m circle was calculated. The amount of resources was assigned as a value to the center cell of each circle.
1.4 Define classes of resource amount per home range	Discretizes the resource amount per home range circle to extract lower and upper thresholds of resource amount per resource type for a potential home range. For every resource type, several classes are created. The classes are defined by visual inspection of the statistical distribution of the amount of the different resources in home range circles around the points of species presence/absence.	Classes of resource amount	User-defined	The following classes were created: - 5 possible classes of grass: 0-5%, 5-20%, 20-30%, 30-50%, 50-100% - 3 possible classes of shrub: 0-5%, 5-15%, 15-100 % - 4 possible classes of tree: 0-5%, 5-15%, 15-40%, 40-100% Note that every home range has a value for these classes
1.5 Assign resource amount classes to every home range circle	Assigns the classes defined in step 1.4 to every home range circle	Map of resource classes	Derived from steps 1.3 and 1.4	Each home range circle was classified into a grass, a shrub, and a tree class according to the proportion of each of these three resources in the 100 m radius.

1.6 Create the combinations of resource amount classes	Creates all possible combinations of resource amount classes. A combination of resource amount classes encompasses one class for every resource type. For every resource type, several classes can be taken together. The number of possible combinations is directly derived from the classes created in 1.4	All possible combinations of resource amount classes	Derived from step 1.4	900 possible combinations of resource amount classes. Examples: - grass: classes 1 to 2, shrub: classes 1 to 1, tree: classes 1 to 4 - grass: classes 2 to 5, shrub: classes 1 to 3, tree: classes 1 to 1
1.7 Create the home range maps to be tested	Creates maps of potential home ranges for each combination of resource amount classes by mapping all the home range circles from step 1.3 that meet a combination of resource amount classes.	Prediction map for each possible combination of resource amount classes	Derived from steps 1.3 and 1.6	900 home range maps.
1.8 Identify the resource amount classes for home range establishment	Finds the combination of resource amount classes that best explains a presence/absence dataset. Each observation site is characterized by the presence/absence of the target species and a percentage of home range coverage as predicted from each combination of resource amount class. As the locations of an animal observation are very likely within a home range and unlikely outside, all presences are considered to indicate the presence of a home range. The selection of the combination of resource amount classes is based on the comparison of the contingency tables of the observed versus predicted presence/absence. It consists of selecting the combination(s) that best predicts (i) the observed presence of the target species and (ii) lowers the number of false predicted absences. The user must define a minimum home range coverage value to use as threshold to consider the site to be in/out potential home ranges.	Resource amount class for home range establishment	Empirically derived	We used dataset 1 for presence/absence data of blackbirds (for description, Appendix 5). For each of the 900 combinations of resource amount classes, we considered a 10% home range site coverage threshold as a conservative threshold excluding sites where the blackbird observations were unlikely.
1.9 Create the home range map	Creates the home range map by mapping the home ranges that meet the requirements of the resource amount classes that best explains the presence/absence dataset determined in step 1.8	Home range map	Derived from steps 1.3 and 1.8	Home range map for Munich
1.10 Create the home range resource map	Creates the home range resource map by intersecting the map of resource cells from step 1.2 and the home range map from step 1.9.	Map of resource patches within home ranges	Derived from step 0.5 and 1.7	Home range resource map for Munich
Step 2: Parametrization of connectivity model				

2.1 Create sets of resistance values to be tested	Creates sets of resistance values for the land cover types of interest which are tested for the target species' movement. The sets should be built to test competing solutions where the resistance values of land cover types vary relative to each other. Sets of resistance values should follow a species-specific logic (e.g. building height should not matter for a cursorial animal but could matter for a flying one). The logic helps to reduce the number of sets of resistance values and thereby to limit the computational effort.	Sets of resistance values for the different landscape elements	From literature	We were interested in the barrier effect of urban land cover types, so we fixed the resistance values for resource patches at 1 and for agriculture and water at 10 because open areas are more resistant to bird movement (Shimazaki et al., 2016; Tremblay & St. Clair, 2009). A resistance value between 10 and 1000 was attributed to buildings according to their height and streets. We decided that a high building's resistance cannot be lower than the resistance of a lower building but had no prior assumption on the relative resistance of buildings and streets. By applying this rule and the range of resistance values, we produced 24 sets of resistance values to be tested (Appendix 4).
2.2 Create resistance maps to be tested	Creates a resistance map from the coarse-resolution land cover map derived from step 1.1 for each set of resistance values defined in step 2.1. For each cell, the resistance value is computed as the sum of the resistance values of the land cover types present in the cell of the coarse-resolution land cover map weighted by their coverage.	Resistance map for each set of resistance values to be tested	Derived from step 2.1	We obtained 24 resistance maps with resistance values ranging from 1:10 to 1:1000.
2.3 Define maximum isolation distance between resource patches to be tested	Defines the maximum patch isolation distances that are tested for best explanation of the target species' movement. Fixed maximum isolation distances between resource patches are selected based on literature values of typical movement distances and home range sizes of the animal. For logical reasons, the highest selected value should not be higher than two times the minimum home range radius.	Maximum patch isolation distances for the target species	From literature	We fixed maximum patch isolation distances at 30, 60, 90, and 150 m according to the literature on blackbird movement and home range sizes (Ferry et al., 1981).
2.4 Derive connectivity models for all combinations of resistance values and patch isolation distances to be tested	Derives (circuit and graph theory-based) connectivity models for the home range resource map using all possible combinations of resistance maps and maximum patch isolation distances. The graph theory-based model is pruned by the Euclidean maximum patch isolation distance. The circuit-theory-based connectivity is calculated allowing flow only between resource cells within the search radius of the patch isolation distance. The maximum size of a patch should be defined to equal the resolution of the input home range resource and resistance maps. This ensures that the resolutions of the inputs and movement modeling correspond to each other and that all resource patches are comparable in area and in their underlying ecological role and associated species movements.	One connectivity model for each possible combination of resistance values and maximum patch isolation distances from home range resource map	Derived from steps 1.10, 2.2 and 2.3	We used all 96 combinations of resistance maps and patch isolation distances to build connectivity models using graph (R package Graph4lg v. 1.8) (Savary et al., 2023) and circuit (Julia package Omniscape v. 0.5.8) (Landau et al., 2021) theory. For details on the model settings, see Appendices 8-9.

2.5 Derive connectivity metrics and maps for all combinations of resistance values and patch isolation distances to be tested	Derives and maps connectivity metrics for all connectivity models created in step 2.4.	Connectivity metrics and maps	User-defined	We computed the following metrics from graph theory (Clauzel et al., 2022): Flux (F), Interaction Flux (IF), Betweenness Centrality (BC), and Corridors (for description, see Appendix 3). We furthermore computed the following metrics from circuit theory (Landau et al., 2021): Cumulative Current Flow (CF), and Normalized Current Flow (NCF). We produced one connectivity map for every metric, resistance map, and isolation distances (24 resistance maps * 4 isolation distances * 6 metrics = 576 maps).
2.6 Build logistic regression models for extraction of values for *key connectivity parameters*	Runs logistic regression models for all connectivity models and metrics. This step uses data on the presence/absence of movement and the connectivity value at the observation location that is obtained from the connectivity maps created in step 2.5. This logistic regression model is used to explain the presence/absence of movement. More explanatory variables can be included.	One logistic regression model for each combination of isolation distance, resistance values, and connectivity metric	Derived from step 2.5	We built 576 binomial Generalized Linear Mixed Effect Models (GLMMs) using data on the presence and absence of moving blackbirds in potential home ranges as response variables (dataset 2, detailed description in Appendix 6). We averaged the connectivity values across the observation transects and included this as a fixed factor. Other fixed factors added were the proportion of resource patches in the transects to account for the effect of local vegetation on bird presence and the number of pedestrians and the temperature during observations to control for other effects on bird presence. To exclude possible observer bias or date-related effects, we included these terms as random factors. We applied the R package lme4 v.1.1-33 (Bates et al., 2015) to build the binomial GLMMs with a logit link function and tested for outliers, overdispersion, and zero inflation using the R package DHARMa v.0.4.6 (Hartig, 2022). For more details on the statistical models, see Appendix 10.
2.7 Extract values for *key connectivity parameters* using statistical model selection	Extracts the resistance values of landscape elements and the maximum isolation distance from the best models (step 2.6) and finds the connectivity metric that best explains the presence/absence of movement data. This step uses a model selection procedure on the logistic regression models created in step 2.6.	Maximum patch isolation distance, resistance values, connectivity metric	Derived from step 2.6	We selected the resistance maps and patch isolation distances from the logistic regressions with the lowest AIC and within a delta-AIC of 2 (across metrics). We averaged their input parameters (resistance values and maximum isolation distance) to obtain the final resistance values and patch isolation distances. As the resistance values scale exponentially, we applied a log10 transformation before calculating the mean and standard deviation. We evaluated the AIC values per metric across resistance maps and isolation distances to obtain the metric with the highest explanatory power for our data. We considered a metric better when its lowest AIC value was lower than the delta-AIC of 2 of the lowest AIC value of other metrics.

2.8 Create the final connectivity map from the values of the *key connectivity parameters*	The values for the *key connectivity parameters* determined in step 2.7 and the home range resource map created in step 1.10 are used to create a final connectivity map. The connectivity map is calculated using the best connectivity metric identified in step 2.7.	Final connectivity map	Derived from steps 1.10 and 2.7	One connectivity map for blackbirds in Munich based on the *key connectivity parameters* determined in step 2.7 and the home range resource map from step 1.10

2.2 Case study: Blackbirds in Munich

Our case study has two primary objectives: The first objective is to demonstrate the applicability of our framework for deriving the values of the *key connectivity parameters* (home range resource map, resistance values, patch isolation distance, connectivity metrics) from movement and high-resolution land cover data (10 m). The applicability is also evaluated statistically by examining the importance of connectivity for explaining the movement of blackbirds. The second objective is to assess the feasibility of retrieving these values of the *key parameters* using widely accessible data, i.e. a coarser resolution (30 m) and simple presence/absence data.

2.2.1 Study area

Munich (48° 8' 23" N, 11° 34' 28" E, 529 m asl) is Germany's third-largest city with a population exceeding 1.5 million and the highest population density among German municipalities (5100 persons/km2 in 2022) (Stadtverwaltung, n.d.). Despite its urban character, Munich's green spaces cover approximately 13.4% of the city's total area with the English Garden encompassing 375 ha that connect the city center with outer areas (muenchen.de, n.d.).

2.2.2 The common blackbird

The common blackbird, an urban dweller frequently found in European cities, was initially a forest species (Mohring et al., 2021). Blackbirds primarily feed on earthworms, invertebrates, and fruits on the ground, in open areas or under canopies (Snow, 1966). Both males and females establish territories, with suitable nest-sites in trees or shrubs being crucial for territory establishment (Snow, 1966). The radius of home ranges for male blackbirds in cities is up to 180 m, but it varies with sex and building density (Ferry et al., 1981; Snow, 1966). Due to its distinctive look and song, the common blackbird is an easily identifiable urban species and, therefore, an ideal study subject.

2.2.3 Data

2.2.3.1 Land cover map for Munich

We obtained the following high-resolution remote sensing data from the Bavarian State Office for Digitization, Broadband and Surveying (https://www.ldbv.bayern.de/index.html): a digital elevation model at 1 m resolution, a surface model at 40 cm resolution, and color-infrared orthophotos at 20 cm resolution. These were used to create a 40 cm resolution land cover map for Munich in 2017. The map encompasses vegetation classes (grass, shrubs, trees), building height classes (< 10 m, 10 – 18 m, > 18 m), streets, agricultural areas, and water bodies (Appendix 2). We aggregated the land cover data at a 10 m resolution by extracting the percentage of each land cover class per 10 m raster cell.

2.2.3.2 Observational blackbird data

In our case study, we employed three distinct sets of blackbird data (Appendices 5-7). All three datasets were collected on and around 103 urban squares in Munich that cover a gradient of tree density, square size and proximity to the city center (Fairbairn et al., 2023; Mühlbauer et

al., 2021). Datasets 1 and 2 were used to target the first objective whereas dataset 3 was applied for the second objective.

For dataset 1 (Mühlbauer et al., 2021), a trained ornithologist acoustically and visually determined bird species for 20 minutes on the 103 squares during three sessions in spring 2017. We utilized dataset 1 to create the home range resource map and to estimate the minimum resource requirements for home range establishment in *Step 1* within the first objective.

For dataset 2, ecologists recorded the number of blackbirds flying across 217 10 x 60 m street transects adjacent to the 103 Munich squares within four minutes. The movement data in dataset 2 was applied for the parametrization in *Step 2* within the first objective.

Dataset 3 was retrieved from acoustically monitoring all bird species using bird recorders on the 103 squares for 24 hours and determining the species using the BirdNET algorithm (Kahl et al., 2021). This dataset served as a comparative dataset to assess the potential replacement of the movement dataset (dataset 2) in the second objective (retrieving the values of the *key connectivity parameters* from more widely data).

2.2.4 First objective: Applicability of modeling framework

The applicability of our modeling framework was tested by applying it to the blackbird in Munich. For every modeling step, we described the application to the blackbird case study in Table 2 in the last column. In the table, we also justified the selection of input parameters and the development of the statistical models. We derived the input parameters (*Step 0*), the resource requirements necessary for home range establishment and the home range resource map (*Step 1*) as well as the values for the other *key connectivity parameters* (resistance values, maximum patch isolation distance, connectivity metric) (*Step 2*).

In *Step 2.6*, we utilized binomial General Linear Mixed Effect Models (GLMMs) to select the values of the *key connectivity parameters* (resistance values, patch isolation distance, connectivity metric) and then evaluated the significance of the local connectivity value for whether a blackbird moved at a location or not (dataset 2). Thus, the movement of a blackbird across a street transect (0/1), was modeled as a function of the fixed factors connectivity value averaged across the street transect, the proportion of resource patches in the street transect, observed pedestrian count, and temperature, and the random factors observer and date (more details in Appendix 10). This comprehensive approach enabled us to examine whether the connectivity value significantly accounted for variations in blackbird movement, and whether this influence differed from that of proportion of resource patches within the same area. The values of the *key connectivity parameters*, obtained using movement data and averaging the best models, were considered as reference values in the second objective.

2.2.5 Second objective: Retrieving values of *key connectivity parameters* using widely accessible data

The second objective of the case study was to test the impact of using widely accessible data, i.e. a coarser resolution (30 m instead of 10 m) and presence/absence data instead of movement data, on resistance values and patch isolation distances, comparing them to reference values obtained from the first objective. We first tested their effect individually and

then in a combined analysis, i.e. we modeled connectivity at 30 m resolution using movement data, at 10 m resolution using presence/absence data, and at 30 m resolution using presence/absence data.

To assess the effects of coarser resolution, we aggregated the land cover map from 40 cm to 30 m instead of 10 m and repeated all modeling steps, starting with the calculation of the home range resource map (Table 2, *Step 1.1*).

To assess the effect of using presence/absence instead of movement data, we built binomial GLMMs using the 95 datapoints from dataset 3 located within potential home ranges determined in step 1. The presence/absence in dataset 3 was recorded with acoustic recorders that detect singing birds within a circle of up to 50 m radius. Therefore, we averaged the connectivity value across a circle with 50 m radius for building the GLMMs. We included the proportion of resources in the 50 m circle to account for the effect of local vegetation on bird presence and temperature as additional fixed and date as random factors. The methodology to extract the parameters with the highest explanatory power follows the procedure described in Table 2, *Step 2.7* (mode details in Appendix 10).

We evaluated the ability of coarser resolution and presence/absence data to retrieve reference parameters values using a point-based system. This system compared parameter values from 10 m resolution modeling with movement data to results obtained for 30 m resolution modeling and presence/absence data individually for each connectivity metric. The evaluation included both relative (relative order of the resistance values of the urban land cover type) and absolute assessments of resistance values, and absolute assessment of patch isolation distances. We assigned one point if high buildings had the highest resistance value and one point for every urban land cover type whose resistance was lower than that of high buildings. We added one point for each urban land cover type and the patch isolation distance when the standard deviation of the value overlapped with the reference value. The final evaluation was the sum of points for each metric, resolution, and datatype combination. More points, therefore, indicate a closer match to the reference values (more details in Appendix 11).

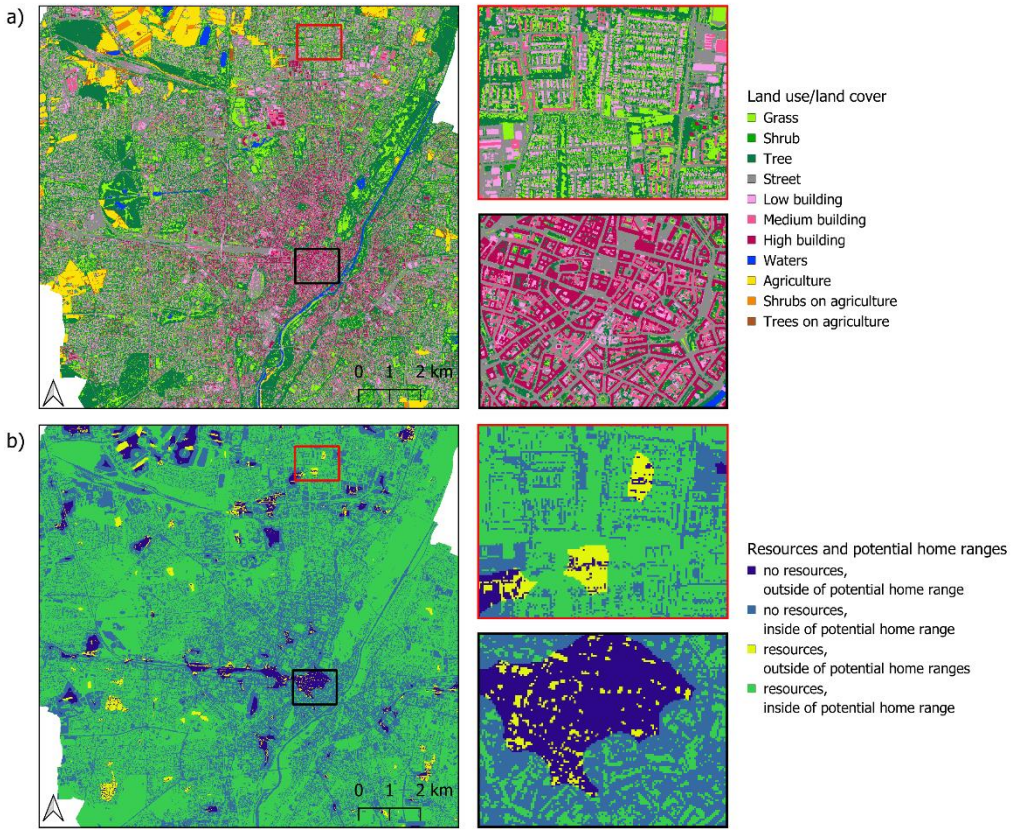
All analyses were conducted in R v.4.1.3 and v.4.2.3 (R Core Team, 2022).

3. Results of the case study

3.1 First objective: Applicability of modeling framework

3.1.1 Minimum resource requirements for home range establishment of blackbirds

We identified suitable conditions for blackbird home range establishment. The home range for blackbirds should have 5-40% tree cover, a maximum of 20% shrub cover, and no specific limitations for grass proportion (all measured within a 100-meter radius). Munich generally provided favorable conditions for potential home range establishment, with some less suitable areas in the city center and in the North where buildings or agriculture predominate (Fig. 3a, Fig. 3b).



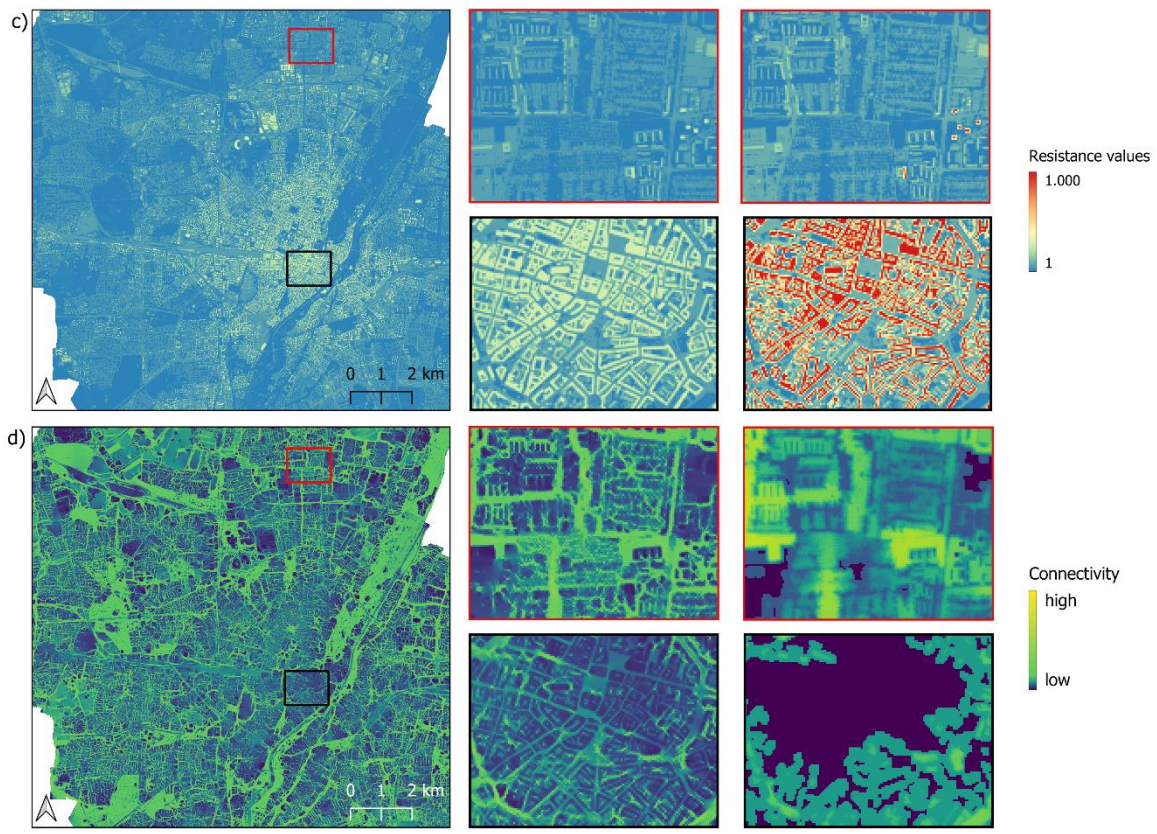


Figure 3: Map of central Munich left and zooms in the smaller panels with colored frames showing a) land use, b) the home range resource maps derived from Step 1*, i.e., mapped resources within potential home range areas, c) resistance values derived from* Step 2*, and d) associated final connectivity maps. For c and d), the parameters used to create the large maps and the left zooms are obtained from presence/absence data using the Normalized Current Flow metric from circuit theory and the right zooms from movement data and the Flux metric from graph theory representing the reference maps.*

3.1.2 Statistical evaluation of importance of connectivity for blackbird movement

We used binomial GLMMs to retrieve the connectivity maps that best explain the observed movement of blackbirds using statistical model selection. The connectivity modeling and subsequent model selection procedure from the GLMMs resulted in the selection of eight best connectivity maps with comparable AIC values. We found a significant effect of the connectivity values in all eight maps on the probability of observing a moving blackbird indicating that movement within the home range of a blackbird is more likely where connectivity is high ($\beta = 0.144$ to $\beta = 0.23$, SE = 0.067 to SE = 0.043, $p < 0.005$). The probability of movement was lower with an increasing number of pedestrians ($\beta = -0.044$ to $\beta = -0.052$, SE = 0.7 to SE = 0.73, $p = 0.03$ to $p = 0.06$). At the same time, no significant effects of the proportion of resources and temperature on the probability of movement across the street transects were detected, indicating that the effect of resources was already accounted for by the home range resource analysis and, therefore, did not significantly contribute to the movement of blackbirds. The marginal R^2 values ranged from 0.22 to 0.25, suggesting that a substantial proportion of the observed movement could be explained by the included fixed factors (more details in Appendix 12).

3.1.3 Resistance values, patch isolation distance and connectivity metric for blackbirds

In this analysis, we derived reference resistance values and patch isolation distances from the best eight connectivity maps (delta-AIC < 2) parametrized using movement data at 10 m resolution and all six metrics. High buildings had the highest resistance value (mean of 1000 across all eight best GLMMs), followed by medium buildings (mean 178, ranging from 100 to 1000), streets (mean 100 across all eight best GLMMs), and low buildings (mean 75, ranging from 10 to 100) (Fig. 4). The standard deviation of resistance values for high buildings did not overlap with other urban land cover types, suggesting robustly higher resistance values for high buildings. In contrast, the standard deviations for all other urban land cover types overlapped, making resistance rankings uncertain. The reference patch isolation distance between resource patches varied from 90 to 150 m, with a mean of 127.5 m (Fig. 5).

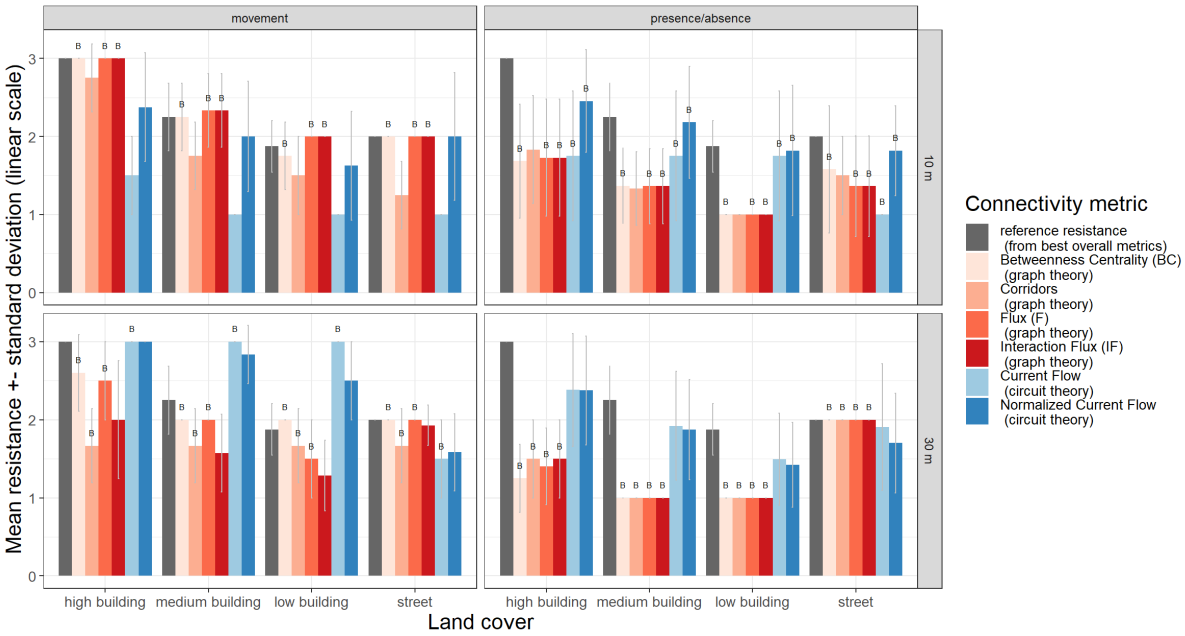


Figure 4: Mean and standard deviation of log10-transformed resistance values for streets, high, medium, and low buildings. Black bars represent reference resistance values (10 m resolution, in-flight data, averaged across best metrics). Colored bars indicate mean values per metric, datatype, and resolution, averaged across the best models for each combination of metric, datatype, and resolution. A 'B' above a bar signifies one of the best models for a specific combination of resolution and datatype.

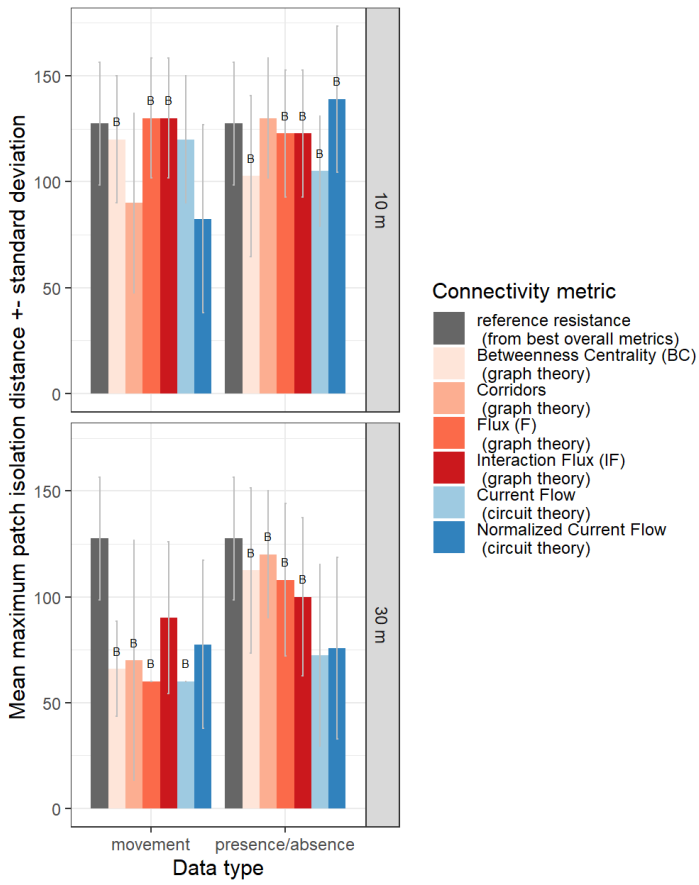


Figure 5: Mean and standard deviation of maximum patch isolation distances. Black bars represent reference values (10 m resolution, in-flight data, averaged across best metrics). Colored bars indicate mean values per metric, datatype, and resolution, averaged across the best models for each combination of metric, datatype, and resolution. A 'B' above a bar signifies one of the best models for a specific combination of resolution and datatype.

The metrics used to evaluate the reference resistance values and maximum isolation distance (i.e., selected in the best eight models explaining the movement data at 10 m resolution) were the Betweenness Centrality, Flux, and Interaction Flux derived from graph theory (Fig. 4, Fig. 5). They produced similar absolute values (Fig. 4, Fig. 5).

3.2 Second objective: Retrieving values of *key connectivity parameters* using widely accessible data

When either presence/absence instead of movement data with 10 m resolution ***OR*** when movement data but a coarser of 30 m resolution was used, reference values were retrieved, but this feasibility depended on the used metric. Using both presence/absence data and a coarser resolution reduced their match to the reference values compared to the individual application of either presence/absence data or a coarser resolution.

Betweenness Centrality and Flux performed best in aligning with reference resistance values when movement data was used for model selection, showing overlapping resistance values and matching order at both resolutions. However, they fell short in replicating the reference

patch isolation distance at 30 m resolution. In contrast, the Normalized Current Flow excelled in retrieving both reference resistance values and patch isolation distance when using presence/absence data but underestimated the patch isolation distance at 30 m resolution (Fig. 4, Fig. 5). Nevertheless, Normalized Current Flow proved to be the best performing metric across all datatype and resolution combinations (Table 3). Current Flow delivered satisfactory results for presence/absence data at 30 m resolution as well (Fig. 4, Fig. 5) but had mixed results when considering all combinations of datatype and resolution (Table 3). Corridors consistently performed the weakest across all combinations of datatype and resolution (Table 3, more detailed results in Appendix 13).

Table 3: Performance (in points) of the six connectivity metrics in reproducing the reference resistance values and reference patch isolation distance.

Metric	**Overall performance in percentage of total points**
Betweenness Centrality (graph theory)	50 %
Current Flow (graph theory)	41 %
Corridors (graph theory)	37 %
Flux (graph theory)	50 %
Interaction Flux (circuit theory)	44 %
Normalized Current Flow (circuit theory)	57 %

4. Discussion

In this paper, we introduce a novel modeling framework for data-driven home range connectivity models addressing key limitations in current connectivity research. We restricted our analyses to home range movements to explore how they are impacted by connectivity and to ensure the model's robustness by distinguishing foraging from dispersal movement. Our parametrization procedure utilizes readily available empirical presence-absence data to derive landscape resistance and incorporates a data-driven selection of connectivity theory and metrics. To tackle computational challenges, we explored whether coarser resolutions yield comparable parameter values to fine-scale resolutions.

For our case study on common blackbirds, we aimed to test the framework's applicability (first objective) and extend its use. Our investigation involved utilizing blackbird presence/absence data and coarser resolution modeling to approximate reference parameter values typically derived from finer resolution and movement data (second objective).

4.1 Applicability of the modeling framework (first objective)

4.1.1 Relation to other connectivity modeling frameworks

Our connectivity analyses focus exclusively on home range scale movements (LaPoint et al., 2013; Mimet et al., 2020). This approach aligns with the small-scale movement as modeled in Mimet et al. (2016). Unlike this study, we explicitly use data on movement within the home range, capturing its specific distances and landscape resistances (Blazquez-Cabrera et al., 2016; Zeller et al., 2016). Our modeling framework is particularly suited for small-scale case studies, where home range movement predominantly explains species occurrences and individual movement, rendering a meta-patch approach unnecessary (Mimet et al., 2020).

The presented parametrization procedure extends the statistical model selection introduced by Verbeylen et al. (2003) and employs it for resistance values, patch isolation distance, and connectivity metric identification. This approach can be adapted for other parameters, including randomization parameters in randomized shortest paths models (Van Moorter et al., 2023). Unlike habitat suitability-based resistance estimations, our methodology avoids assuming that the properties of an area supporting an individual’s observation are necessarily the same as the ones supporting its movement (Keeley et al., 2017; Zeller et al., 2018). While tracking data applied to resource selection functions yield the most accurate connectivity models (Blazquez-Cabrera et al., 2016; Zeller et al., 2018), their limited availability underscores the value of our more accessible yet robust methodology. Alternative data sources like camera traps or road kills could be employed (Koen et al., 2014; LaPoint et al., 2013)..

4.1.2 Realism of approach

Our case study not only highlights the utility of our modeling framework but also assesses its results. Statistical analysis from the model selection procedure revealed a strongly significant positive relation between connectivity and the probability of blackbird movement and underlines the robust predictive power of our connectivity models. Interestingly, the proportion of resources showed no such correlation. This indicates that local resource accessibility, rather

than quantity, influences the occurrence of blackbird movement. This may be attributed to *Step 1* of our analysis that already accounts for landscape-wide resource availability.

The outcomes of our case study align with our understanding of blackbird ecology. The observed higher resistance values for urban land cover types within home ranges, especially buildings over 18 m, indicate strong avoidance that could be caused by increased energy costs and mortality (Loss et al., 2014; Robertson & Radford, 2009). The findings are in accordance with studies on urban bird movement which found that streets and buildings are less likely to be crossed by birds than vegetation, providing support for our model results (Shimazaki et al., 2016; Tremblay & St. Clair, 2009).

4.1.3 Connectivity metric for blackbird home range movement

We evaluated the predictive power of various connectivity metrics from both graph and circuit theory. Connectivity maps generated through the least-cost path approach in graph theory outperformed those from the random walk approach in circuit theory in explaining blackbird movement. This finding aligns with the hypothesis that blackbirds depend on memorized pathways within their home range that matches the tendency of birds to re-use routes (Biro et al., 2004; Wallraff, 2005).

Despite their theoretical differences in reflecting connectivity (Rayfield et al., 2012), the graph theory metrics Flux, Interaction Flux, and Betweenness Centrality demonstrated equivalent predictive power for blackbird movement. They resulted in the selection of similar values of *key connectivity parameters*, indicating their interchangeability for depicting home range movement. However, the computation of Betweenness Centrality was computationally intensive.

4.2 Second objective: Retrieving values of *key connectivity parameters* from widely accessible data

Our modeling framework can be used for pinpointing crucial patches and barriers for small-scale movement in fragmented landscapes and assessing the impact of development plans (Foltête et al., 2014). We explored the potential use of coarser resolution and readily available data, such as simple presence/absence data, to enhance the accessibility of our modeling framework for planning and conservation applications.

4.2.1 Using a coarser resolution

While we investigated the impact of coarser resolution (30 m instead of 10 m) on connectivity models to address high computational demands, we found that resistance values were qualitatively similar for the graph theory metrics Flux and Betweenness Centrality when using movement data. However, none of the metrics produced a patch isolation distance comparable to the reference value using the coarser resolution of 30 m. The results suggest that, with careful consideration of the chosen connectivity metric and maximum patch isolation distance, coarser resolution parametrization could be suitable, albeit with a potential underestimation of the patch isolation distance.

4.2.2 Using presence/absence data

We explored the use of simple presence/absence data for model selection to enhance accessibility. Comparing reference resistance values derived from movement data with those from presence/absence data showed that presence/absence data can approximate reference values effectively with the right connectivity metric. Most metrics, whether from graph or circuit theory, maintained a consistent rank order for resistance values with presence/absence data, which is known to be more important than absolute values for comparable connectivity outcomes (Beier et al., 2009). In particular, when using Normalized Current Flow, a circuit theory metric, absolute resistance values with reference values overlapped. This suggests that most connectivity metrics can retrieve the most important aspect, the reference rank order of connectivity values, and that especially the circuit theory models are robust for parametrization based on simple presence/absence data (Zeller et al., 2018). Nevertheless, presence/absence data yielded a wider range of resistance values per urban land cover type.

4.2.3 Limitations for using widely accessible data

Our comparisons of the reference values retrieved from movement data and 10 m resolution modeling with more accessible presence/absence data and 30 m modeling reveal that it is possible to cautiously obtain the values of *key connectivity parameters* using these more available data sources. However, several limitations apply:

i) ***Species specificity and generalization:*** Our study focused on the common blackbird; thus, generalizing findings regarding the use of more accessible data and connectivity metrics requires replication across diverse species.

ii) ***Data type and resolution:*** Movement data and finer resolution appeared preferable for deriving the values of *key connectivity parameters* for the home range scale where small elements can play a major role. Movement data and fine resolution showed a greater consistency in parametrization results.

iii) ***Combining presence/absence data and coarse resolution:*** In our case study, combining presence/absence data with coarse resolution led to strongly deviating parameter values. Those results indicate that a choice between the two should be made.

iv) ***Metric for movement data and coarser resolution:*** For movement data and coarser resolution, the Flux from graph theory appears as a good choice due to its predictive accuracy and lower computational requirements. Retrieving patch isolation distances from coarser resolution was more complicated and is not recommended in the current state of framework development.

v) ***Metric for presence/absence data and fine resolution:*** Normalized Current Flow from circuit theory appeared as a robust metric for determining *key connectivity parameters* from simple presence/absence data and a fine resolution (Zeller et al., 2018).

vi) ***Uncertainty assessment:*** We suggest using the means and standard deviations of parameter values calculated in the framework's workflow to assess uncertainty of the modeling results and visualize it in a map of standard deviations (Beier et al., 2009).

Despite these challenges, we believe a robust parametrization procedure can bridge the gap between the need for user-friendly, data-driven connectivity models and the high data demands of individual-based models.

In this paper, we introduced a home range connectivity modeling framework for analyzing the impact of local resource amounts and small-scale barriers on animal movements. It can be applied to any animal species. It requires a land cover map fine enough to map resources within home ranges and capture important barriers to movement. We tested the model using data on the common blackbird, but application to other species and landscapes will allow a more comprehensive understanding of how local movements restrict the occurrence of species in a heterogenous environment.

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