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City-specific or generalisable resistances? An urban animal connectivity model performs better when parameterised from two cities

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Research Article

Keywords: urban landscape connectivity, landscape connectivity modelling, context-dependence of landscape resistance, connectivity model parameterisation, habitat requirements, transferability of model parameters

Posted Date: August 12th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-10313062/v1

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Additional Declarations: No competing interests reported.

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Acknowledgements

We are very grateful to Elin Eberl, Elio Lauppe, Florian Mesarek and Daniel Bescher-Stauffer for collecting the data on the common blackbird in Munich and to Amandine Vergondy and Thomas Oulhen for the data collection in Angers.

Abstract

Urban ecological connectivity models are increasingly used to inform conservation decisions, but they often lack observational calibration data, particularly for estimating habitat requirements and landscape resistance. Connectivity parameters are therefore often derived in one city and transferred to another, yet systematic tests of their transferability across cities are lacking. Here, we use observations of the common blackbird in Munich (Germany) and Angers (France) to compare parameter estimates derived from a single city or from both jointly, testing whether habitat requirements and resistance values are transferable across cities and whether joint parameterisation improves predictive performance. We found that transferability of resistance values was limited to their relative order for barriers such as buildings and streets, while absolute values differed. However, resistances derived from the joint dataset moderately outperformed the Munich parameters when predicting independent Munich data, suggesting that combining data from different cities can improve resistance estimates and facilitate transferability to unknown data points. Habitat requirements, by contrast, were already well estimated from single-city datasets. Overall, our study provides evidence that resistance values can be transferred between cities when the aim is to identify the relative importance of barriers. The improved transferability gained by combining data from different cities indicates that blackbird movement is shaped by similar barriers across them. Pooling multiple datasets into the estimation of resistance values can thus substantially enhance the predictive value of connectivity modelling. Further research extending this approach to other species and cities would help establish how broadly these findings generalise.

Keywords

urban landscape connectivity, landscape connectivity modelling, context-dependence of landscape resistance, connectivity model parameterisation, habitat requirements, transferability of model parameters

1. Introduction

Understanding how animals move across and use urban landscapes is essential to guide sustainable urban planning. Since cities are heterogeneous, barrier-rich landscapes, mobile species must navigate fragmented green spaces to access the resources and nesting sites they depend on (Goddard et al. 2010; Kowarik et al. 2025). Maintaining and restoring ecological connectivity within and between these green spaces has therefore become an international conservation priority (Target 12 of the Convention on Biological Diversity; CBD 2022). To support this goal, connectivity modelling is increasingly used by planners to identify key habitat patches and wildlife corridors and to guide biodiversity-friendly urban development (Habrich and Fahrig 2025). Urban ecological connectivity models have the potential to support evidence-based planning, but their effective implementation hinges on obtaining reliable and generalisable parameter estimates that describe how species interact with the urban landscape (Bergsten and Zetterberg 2013).

Connectivity modelling encompasses several approaches, including least-cost path analysis, circuit theory, and individual-based models (Calabrese and Fagan 2004). Regardless of the approach, predicting movement paths across heterogeneous landscapes relies on the accurate definition of key parameters, especially habitat/resource patch identification and land cover resistance values (Diniz et al. 2020). However, estimating these parameters remains challenging since it requires detailed data on the species' ecology in urban environments. Since this data remains limited for most species (Zeller et al. 2012), connectivity models in urban contexts frequently rely on parameters derived from expert opinion (Balbi et al. 2019; Habrich and Fahrig 2025; Hämäläinen et al. 2026). While expert-based parameterisation approaches are pragmatic given the scarcity of empirical data, they may deviate from species' actual behaviour in cities and provide limited opportunities for generating new empirical knowledge on urban-specific connectivity parameters (Foltête et al. 2020; Lookingbill et al. 2022; Merkens et al. 2026).

To overcome the limitations of expert-based parameterisation, methods have been developed to derive connectivity parameters from a variety of data sources (Zeller et al. 2018; Supp et al. 2021; Riordan-Short et al. 2023; Habrich and Fahrig 2025). Models that utilize movement-proxy data, such as direct observations of movements, camera traps, and roadkill records, have recently gained attention as cost-effective alternatives to GPS tracking while still capturing important movement information (Kadoya 2009; Kervellec et al. 2023; Merkens et al. 2026). For example, Merkens et al. (2026) developed an integrated framework deriving habitat/resource requirements, resistance values, and movement distances from such data, using the blackbird in Munich as a model species.

Once connectivity parameters have been empirically calibrated for a given city, a further question is whether they hold beyond it. In practice, resistance values derived in one city have already been transferred to others: The parameters empirically derived for the hedgehog in Zurich (Braaker et al. 2014), for example, have been applied to multiple other European cities (Balbi et al. 2019; App et al. 2022). Such a transfer is appealing because it can extend the

applicability of empirically calibrated connectivity models beyond the single city in which they were derived (Pundsack et al. 2025). Yet whether these parameters are genuinely transferable remains a critical but underexplored question, bearing on their context-dependence and degree of generality across cities (Unnithan Kumar et al. 2022). Existing knowledge, mostly derived from dispersal studies, suggests that movement drivers and associated resistance values may vary across landscapes and regions (Short Bull et al. 2011; Castillo et al. 2016; Vergara et al. 2017; Balbi et al. 2018; Beninde et al. 2018). Across cities, such variability may arise from differences in urban landscape structure and composition, species interactions, or differential behavioural acclimatisation to local urban conditions (Gomez et al. 2025). Yet direct evidence remains scarce, as comparative studies across multiple cities for the same species are rare (Balbi et al. 2018; Miles et al. 2019).

This is a critical issue for urban planning: if resistance values derived in one city cannot be reliably applied to another, the validity of connectivity models built on transferred – or spatially generalised expert-based – parameters may be seriously compromised, potentially leading to the misidentification of key corridors and habitat patches. Addressing this challenge calls for multi-city comparative approaches. Studies based on replicated landscapes have shown that, despite inter-landscape variability, combining information across landscapes improves statistical power and enables the identification of general patterns that single-landscape approaches cannot reveal (Castillo et al. 2016; Balbi et al. 2018). Such replication is therefore key not only to test whether connectivity parameters can be transferred across cities, but also to characterise the degree of generality of these parameters, which is needed to inform urban planning at broader scales.

Defining what such generality, and hence transferability, means, however, requires distinguishing two independent dimensions. On one hand, resistance values may range from being universally applicable – fully capturable from data collected in any single city – to fully context-dependent, that is, city-specific, with no valid transfer possible. In between lies the case where general patterns exist but can only be revealed by pooling data across cities (Unnithan Kumar et al. 2022). On the other hand, even where resistances prove comparable across cities, that comparability may be merely relative, i.e. preserving the ranking or ratios between land cover types but not absolute magnitudes, or fully absolute, meaning raw resistance values are directly transferable without recalibration. Explicitly framing these two dimensions is essential to defining what transferability of connectivity parameters means in practice.

In this study, we test for the context-dependence versus generality of empirically-derived connectivity model parameters for the common blackbird (*Turdus merula*) in two European cities, and evaluate whether parameterisation, and therefore parameter transferability, can be improved by combining data from the two cities. Originally a forest-dwelling species, the blackbird has undergone a remarkable adaptation to urban environments and is now found across the entire European continent (Gliwicz et al. 1994). The blackbird has already been used as a model species in Merkens et al. (2026), where the authors empirically demonstrated that building height constitutes a significant source of resistance to blackbird daily movements in Munich. However, whether these resistances hold across different urban contexts remains

unknown. Using the modelling framework from Merkens et al. (2026), we derive habitat requirements and resistance values from movement-proxy data in Munich (Germany) and Angers (France).

We present, to our knowledge, the first study testing the context dependence versus generality of urban resistance values for an urban bird species, which can serve as a blueprint for further comparable studies. Additionally, we not only compare parameter values, but, in an explicit validation step, evaluate whether these parameter values actually lead to differences in predictive performance for blackbird movement. Thus, on the parameterisation side, we derive parameters independently for each city and from the joint dataset, which allows us to assess whether parameter values are fully context-dependent or exhibit some degree of generality. In the case of generality, we additionally determine whether that generality holds in relative terms (rankings and ratios between land cover types), in absolute terms (raw resistance values), or both. On the validation side, we evaluate how well each set of parameters, city-specific, cross-city transferred, and jointly derived, predicts movement patterns in both cities. Thereby, we directly test the practical transferability of empirically-derived connectivity model parameters and whether pooling data across cities improves predictive performance relative to single-city parameterisation. From both parameterisation and validation, we derive conclusions on the value of joint parameterisation and transferability of habitat requirements and resistance values between cities.

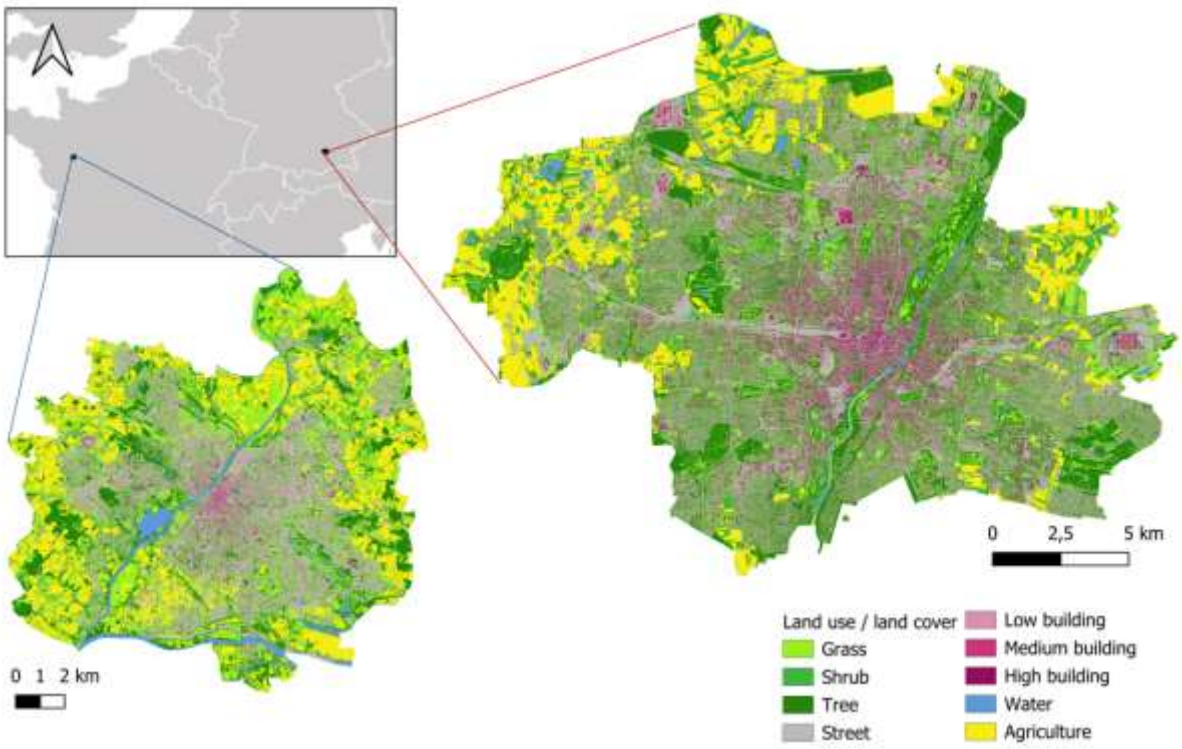
2. Methods

2.1. Study overview and case study cities

In this study, we tested the transferability of connectivity model parameters between the cities of Angers, France, and Munich, Germany. For this, we parameterised ecological connectivity models in both cities independently and jointly, using observations of flying blackbirds collected in both cities.

Munich has the third-largest population in Germany (1.6 million inhabitants) and covers 311 km^2, leading to the highest population density in the country (4,861 people/km^2 in 2023) (Statistisches Bundesamt 2024). It belongs to the warm-temperate climate zone, and its largest park, the English Garden, is famous as being one of the largest inner-city parks worldwide (muenchen.de). Angers in France is substantially smaller than Munich, covering a surface area of 203 km^2. With a population of about 160,000, Angers has a lower population density than Munich (3,724 people/km^2, Wikipedia). Angers belongs to the same warm-temperate climate zone and is known as the greenest city in France, especially for its many parks, which provide important greenery for its inhabitants and support biodiversity (Destination Angers 2026). Repeated ornithological studies in urban parks reveal that, similar to Munich, typical European urban bird species are frequent in Angers (Mühlbauer et al. 2021; Fairbairn et al. 2025; Ville d'Angers).

Despite differences in total area and population size, Munich and Angers show an overall comparable share of vegetation – trees, shrubs, and grass – is similar across cities (Munich 48.88 %, Angers 46.53 %). Similarly, both cities are traversed by a major river – the Maine bisects Angers north-south, as the Isar does with Munich. Moreover, both cities are rather old European cities whose building structure and composition are relatively similar (Fig. 1, Table 1).



177

178 **Fig. 1** Land cover maps of Angers, France (bottom left) and Munich, Germany (top right), the
179 study cities of our analyses. The top left panel shows the location of Angers and Munich in
180 Europe.

181 **Table 1**. Statistical summary of cities: land cover proportions in Munich and Angers

		Share of land cover type to overall urban area land cover in (%)								
	Total Area	Low building	Medium building	High building	Street	Water	Agriculture	Grass	Shrub	Tree
Munich	480.33 km^2	7.88	3.45	1.68	18.39	2.26	17.46	11.22	9.97	27.69
Angers	203.33 km^2	6.22	1.25	0.20	18.11	3.50	19.78	23.14	5.42	17.97

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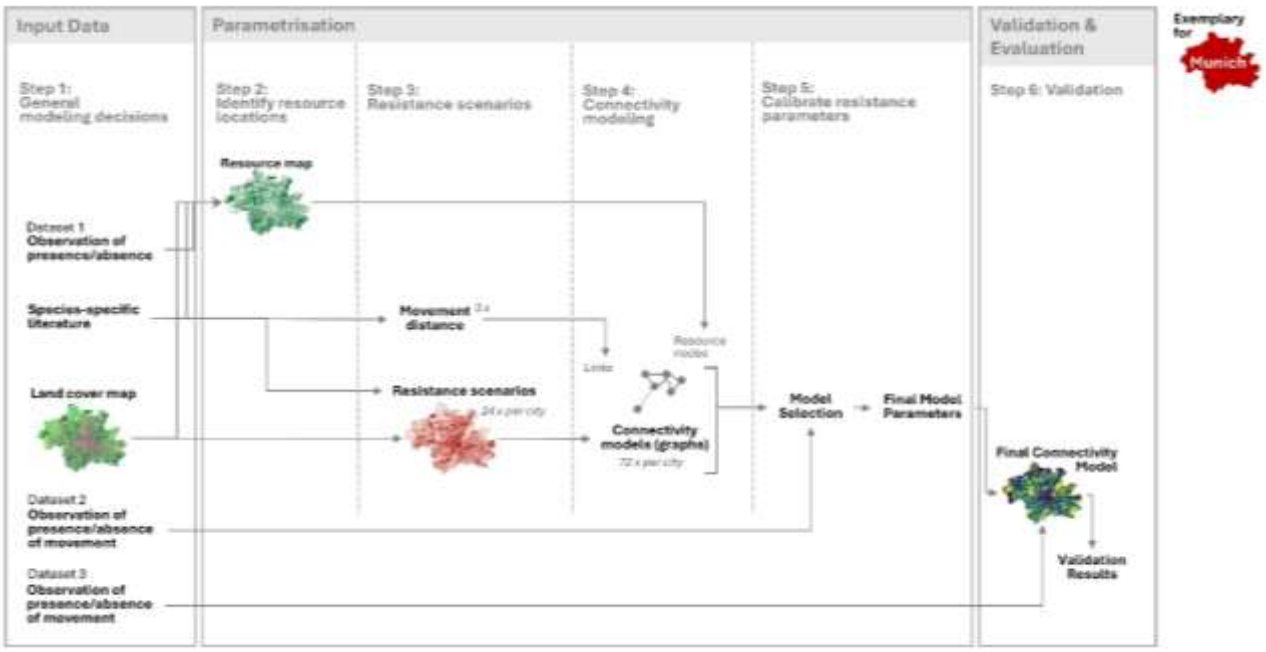


Fig. 2 Illustration of the modelling workflow by Merkens et al. 2026 as applied to single-city data. The workflow proceeds in six steps, divided into three phases, to model connectivity for an urban animal using empirical movement-proxy data. First, input data is obtained (Step 1). Second, resource locations are identified (Step 2), resistance scenarios are created (Step 3), from which connectivity models are built (Step 4) and evaluated, based on their ability to predict movement in the training data (Step 5). Thirdly, the selected connectivity model and its underlying parameters are evaluated using additional movement-proxy data (Step 6), performing a random out-of-sample model validation.

We implemented the modelling framework as described by Merkens et al. (2026) (Fig. 2), which uses movement-proxy data, i.e. data on the observed presence or absence of blackbird movement, and landscape resistance scenarios to determine which resistance values best explain observed blackbird movement. To identify resource locations for the blackbird (Step 2), we refined the approach using a PCA-based methodology introduced by Pundsack et al. (2026). We first compared parameter values derived from Angers' data and Munich's data separately, and then jointly. In the validation step, we tested how well parameter values derived for one city predict observed movements in another, and if parameter values derived from both cities performed better than single-city parameterisation. Analyses and modelling were performed in R v. 4.2.3 (R Core Team 2022) and Graphab v. 2.8 (Foltête et al. 2012) via the graph4lg package (Savary et al. 2023). In this section, we describe how we implemented the steps introduced by Merkens et al. (2026).

2.2. Input data

Step 1: General modeling decisions on studied movement type

Land cover and biological data need to be targeted to the movement of the model species. As studied behavioural process, we focus on short, directed blackbird movements within the home

range, aimed at accessing resources, such as shelter, nesting sites, or food (Merkens et al. 2026). To set spatial scales that fit the behavioural process, we selected a 10 m cell size as a suitable modelling resolution and tested 30, 90, and 150 m as possible maximum movement distances between resource cells. To implement this modelling resolution, we aggregated the Munich and the Angers land cover maps to a 10 m cell size. For every 10 m cell, we extracted the proportion of each land cover type within the cell to define possible resource patches and resistance maps. Following literature indicating that urban birds can use relatively small vegetation patches for foraging (Bourgeois et al. 2024; Martin et al. 2026), we set a minimum threshold of 20 m^2 for a cell to be considered a potential resource cell, which proved robust in prior analyses (Bourgeois et al. 2024; Merkens et al. 2026).

Land cover maps. As input for the connectivity models, we used land cover maps generated from locally available remote sensing data (Fig. 1). We created the maps with slightly different spatial resolutions (40 cm for Munich, 50 cm for Angers) and different data sources because very high-resolution land cover maps were not available from supranational sources (Pundsack et al. 2025). For Munich, the classification was obtained from orthophotos and digital surface and height models (Merkens et al. 2026). For Angers, the classification was obtained using land cover information from CoSIA (IGN 2023a), refined with a digital terrain model (IGN 2020) and height model (IGN 2023b) to extract building and vegetation height classes. For both cities, we identified land cover types relevant to the animal (Pundsack et al. 2025), i.e., different vegetation classes (grass, shrub, and tree), low (< 10 m), medium (10 – 18 m) and high (< 18 m) buildings, streets, water, and agricultural surfaces (Fig. 1).

Bird observations. We used two observational datasets, one to derive information on the resources that attract common blackbirds (Fig. 2, Step 2) and the second to quantify and validate resistance to blackbird movement in Munich and Angers (Fig. 2, Step 3-6). The biological observations need to be spatially sufficiently dispersed to cover the main barriers and resource patches. The two datasets differ in their behavioural interpretations and sampling designs and were collected in both cities using a standardised methodology (Table 2).

Dataset 1 consists of visual and acoustic detections of blackbird presence/absence and was used to determine which land cover types provide resources for blackbirds (Fig. 2, Step 2). The data was collected through random point observations along gradients of traffic density and vegetation cover in both cities.

Dataset 2 represents observations of the presence or absence of blackbirds flying across 50 m street transects (thus movement-proxy data sensu Merkens et al. (2026)), which are easily observed without visual barriers. Dataset 2 served to parameterise resistance and to validate connectivity models in a 10-fold random out-of-sample validation (Fig. 2, Step 5-6, Fig. 3). To achieve those two goals, we randomly split the Munich and joint datasets, i.e., the dataset combining data points from Angers and Munich, into two halves (50:50 split): a training and a test dataset. The Angers dataset was too small to reliably estimate parameters from a 50% subset; we therefore used only the Angers data for training, and no within-Angers validation was performed (Fig. 3). We ensured that both the train and test data covered vegetation

248 gradients, so that neither contained a substantially higher proportion of vegetation that attracts
249 blackbirds.

250 **Table 2.** Specifications on the methodology of the collection of bird observations in Angers and
251 Munich. Adapted from Merkens et al. (2026).

	Dataset 1 (simple presence/absence)	**Dataset 2 (movement-proxy data)**
Data type	Presence/absence of blackbird in area	Number of moving blackbirds across street transect
Sampling of observation points	Random sampling along gradients of traffic density and greenness	Random sampling along gradients distance from city centre and greenness
# Data points	104 points in Munich, 68 in Angers	217 transects in Munich, 190 in Angers
Observed area	Point observations; perimeter of 50 m	Transect observations on 50 m transects across a street
Observation	A trained ornithologist noted whether blackbird was seen or heard	Trained ecologists counted the number of blackbirds crossing the street
Use in modelling	Identification of resources used (Step 1)	Determination of best node isolation and resistance scenario and validation across cities (Steps 4 and 6)

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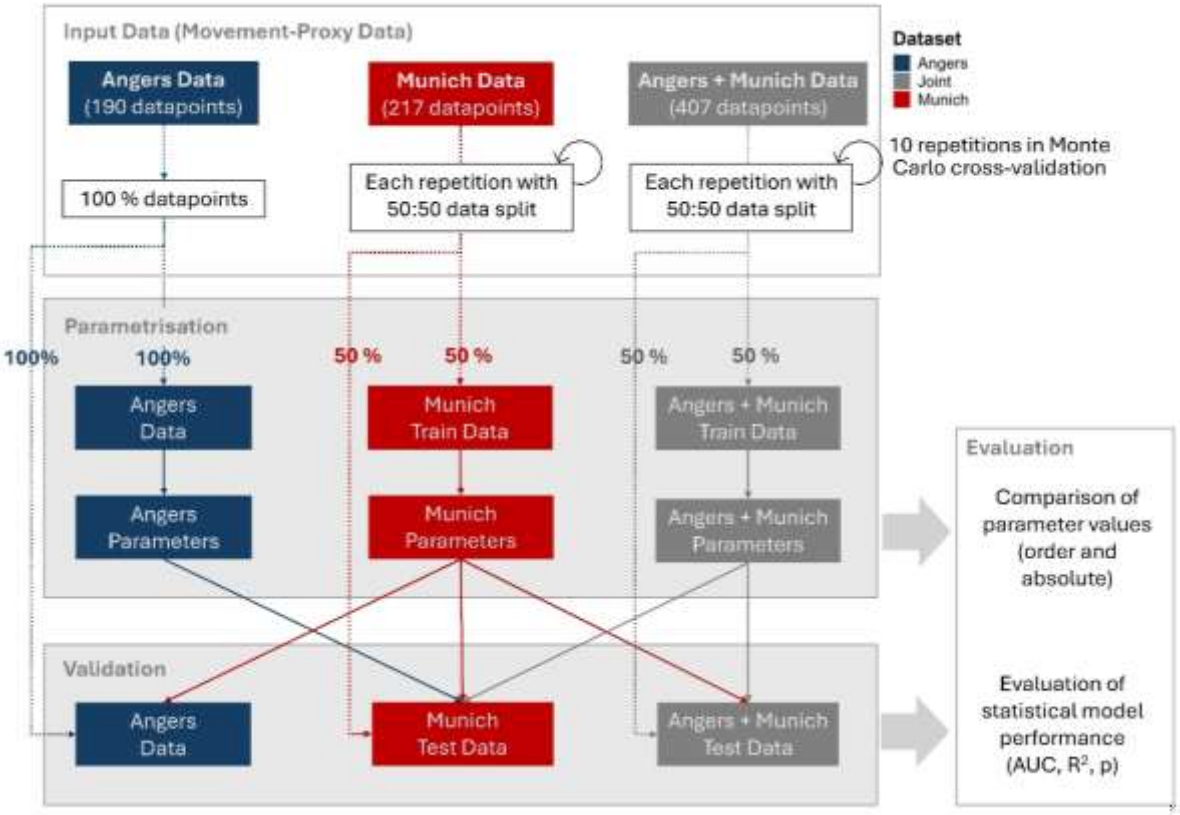


Fig. 3 Overview of the workflow applied to compare the parameterisation and validation results between Angers, Munich, and the joint dataset. This refers to Steps 3 to 6 of the overall modelling workflow (Fig. 1). There is no city-specific nor joint validation for the Angers parameters because the parameterisation was conducted on the entire dataset due to data limitations and no independent validation could be ensured.

2.3. Parameterisation

Step 2: Identification of resource locations

Identifying the areas that can serve as resources for animal species is crucial for determining possible locations to which the animals might move, i.e., the nodes in a landscape graph (Fig. 2, Step 2). For this, we used a PCA followed by Classification and Regression Trees (CARTs) (Mimet et al. 2019; Pundsack et al. 2026). From these steps, possible resource locations can be identified in a resource map (Fig. 2, Step 2).

The workflow leverages Dataset 1 from each city and land cover types identified in the literature as potential resources for the common blackbird (i.e., grass, shrubs, and trees) (Snow 2008; Mohring et al. 2021). We extracted the proportions of these potential resource types around the observation points in both cities to identify the crucial vegetation types for blackbird presence and their minimum required proportion and composition. Because land cover proportions were collinear, a condition known to induce variable selection instability by causing correlated predictors to be interchangeably selected across model runs, we conducted a PCA on resource proportions prior to fitting the CART model (Pundsack et al. 2026). PC scores were then used

as predictors in the CART to identify which vegetation proportions and compositions were associated with blackbird presence (Mimet et al. 2019). We conducted a sensitivity analysis on the radii used for vegetation proportions extraction and the hyperparameters used for the CARTs to ensure robustness of the results (Supplementary Methods, Fig. S1).

To assess whether the CART results and the captured vegetation gradients are transferable across cities, we ran the CARTS three times: (1) for Munich, (2) for Angers, and (3) for both cities combined (Supplementary Information; Fig. S1). For each run, we selected the CART model that best predicted blackbird presence, based on sensitivity, accuracy, and the decision tree's parsimony. In case of multiple CARTs performing equally well, the least complex tree was selected (Supplementary Methods). We compared the three final CARTs for Angers, Munich, and both cities combined and assessed consistency across datasets.

Step 3: Resistance scenarios

This workflow follows the logic of systematically creating several plausible resistance scenarios and selecting the ones that best explain the movement-proxy data (Fig. 2, Step 3). We created the same 24 scenarios to test the resistance of different urban land covers as suggested by Merkens et al. (2026) (Table 3). The 24 resistance maps were obtained by multiplying each land cover's proportion within the 10 m cell by its resistance value, for each scenario. We included maximum inter-patch movement distances of 30, 90, and 150 m for each resistance scenario, following the literature (Ferry et al. 1981; Török and Ludvig 1988). This ensures that our resistance parameter estimation is not restricted by a single assumed maximum movement distance, still allowing some flexibility.

Table 3. Tested resistance scenarios

Land cover	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	R11	R12
Low buildings	10	10	10	10	10	10	10	10	10	10	10	10
Medium buildings	100	100	100	10	10	10	100	100	100	10	10	10
High buildings	1000	1000	1000	10	10	10	100	100	100	100	100	100
Streets	10	100	1000	10	100	1000	10	100	1000	10	100	1000
Water	10	10	10	10	10	10	10	10	10	10	10	10
Agriculture	10	10	10	10	10	10	10	10	10	10	10	10
Grass	1	1	1	1	1	1	1	1	1	1	1	1
Shrub	1	1	1	1	1	1	1	1	1	1	1	1
Tree	1	1	1	1	1	1	1	1	1	1	1	1

Land cover	R13	R14	R15	R16	R17	R18	R19	R20	R21	R22	R23	R24
Low buildings	100	100	100	100	100	100	100	100	100	1000	1000	1000
Medium buildings	100	100	100	1000	1000	1000	100	100	100	1000	1000	1000
High buildings	100	100	100	1000	1000	1000	1000	1000	1000	1000	1000	1000
Streets	10	100	1000	10	100	1000	10	100	1000	10	100	1000
Water	10	10	10	10	10	10	10	10	10	10	10	10
Agriculture	10	10	10	10	10	10	10	10	10	10	10	10
Grass	1	1	1	1	1	1	1	1	1	1	1	1
Shrub	1	1	1	1	1	1	1	1	1	1	1	1
Tree	1	1	1	1	1	1	1	1	1	1	1	1

Step 4: Connectivity modelling

For each combination of resistance scenarios (and the three maximum movement distances), we generated connectivity maps by calculating link-based BC, resulting in 72 candidate models. We modelled connectivity using landscape graphs connected by least-cost paths rather than circuit theory, as the former is well-suited to contexts in which animals are assumed to navigate actively within a well-known environment (McClure et al. 2016). This corresponds to our data, which capture frequent short-distance movements within a home range. We used a cell-based landscape graph, as suggested by Drielsma et al. (2007) and Saura and Pascual-Hortal (2007), meaning that one resource patch was divided into several equally sized resource cells matching the modelling resolution. Thereby, we could account for redundant pathways (Goicolea et al. 2021; Van Moorter et al. 2023) between larger resources patches in the city.

To quantify landscape connectivity and create connectivity maps using graph models, we calculated link-based Betweenness Centrality (BC). A high BC value indicates that the link is more likely to be used to pass from one node to another, given the other possible surrounding paths and the spatial configuration of the patches (Bodin and Saura 2010). The link-based connectivity metric better fits our observational data than its node-based equivalent, as it reflects movements between patches rather than just patch occupancy (Girardet et al. 2015). For a given link l, BC is defined as

$$\boldsymbol{BC(l)} = \sum_{A=1}^{N} \sum_{B=1, B>A}^{N} \mathbf{1}_{l \in L_{AB}} \, e^{-\alpha \, d_{AB}} \qquad (1)$$

Where L_{AB} is the set of links traversed by the least-cost path between nodes A and B and the indicator function $1_{l \in L_{AB}}$ ensures that only links occurring on the path are included. The weighting term $e^{-\alpha d_{AB}}$ reflects movement probability along the path with cost distance d_{AB}, with the decay parameter α defined as:

$$\boldsymbol{\alpha = \frac{-\log(\varphi)}{d_{iso}}} \qquad (2)$$

so that movement probability drops to φ at node isolation d_{iso}, the maximum distance our target species is able to move from one resource cell to another (Bodin and Saura 2010).

Step 5: Calibrate resistance parameters

We created a continuous connectivity map across Angers and Munich for all resistance scenarios by interpolating the link-based BC-values using the Graphab interpolation tool. The modelled connectivity is extracted at points of observed presence/absence of animal movement. Movement presence/absence was then statistically modelled as a function of the local connectivity value for all 72 candidate models and their parameter combinations. Using AIC-based model selection, the resistance scenarios that best explain the observed movement presence/absence are identified, used to compute average resistances, and to create a final connectivity map (Fig. 2 Step 5; Fig. 3). The statistical model differed slightly in parameterisation between the single-city and joint datasets.

For the single-city parameterisation, we built Generalised Linear Models (GLMs) with a logit-link function to identify the best parameter combination for the Angers and Munich movement-proxy data independently. The model followed this structure:

$$PA_{movingBird} \sim \log(connectvity + 1) + pedestrians$$

In this model, the presence/absence of flying blackbirds was modelled as a function of the BC values averaged across the full area of the observation transects. BC values were log-transformed to account for their highly skewed distribution. Pedestrians represent the number recorded during the blackbird observation period and were included because we do not separately account for them in our model, despite them potentially reducing the probability of observing birds (Fairbairn et al. 2024). To improve the comparability of statistical results between cities, we aimed for the same model formulation in the two cities. We tested several versions of this GLM, also accounting for the surrounding resource cover and the observer as a random factor. Based on the AIC values, we found that this was the most stable and parsimonious model formulation while remaining the most informative across the two cities.

For the joint parameterisation, we identified the parameter combination best explaining the joint observation dataset using a Generalised Linear Mixed-Effects Models (GLMMs) with a logit link function. For this dataset, we also tested different model formulations and adopted the version with the lowest overall AIC across all resistance and movement distance scenarios. The model followed the structure:

$$PA_{movingBird} \sim \log(connectvity + 1) + pedestrians + city + (1|observer)$$

As with the GLMs, the presence/absence of a moving bird was modelled as a function of connectivity and the number of pedestrians. Additionally, we could account for the city and the observer. We included the city as a fixed effect because we assumed that general connectivity levels can differ between cities, and a random observer effect to reflect potential biases arising from the different observers in France and Germany.

Deriving resistance values from model selection. Based on our 72 statistical models (24 resistance maps * 4 movement distances), we performed the model selection three times – once for Angers, once for Munich and once for the joint dataset to identify the best resistance values per dataset. Since several resistance maps could appear within a delta-AIC range of 2 of the best model, we could not always identify a single best set of parameter values. Instead, we averaged the resistance values with a delta-AIC < 2. Finally, we assessed whether resistance values were consistent across the three datasets (Angers, Munich, joint) by visually comparing the derived parameter values and their standard deviations.

All statistical models were built using the lme4 package (Bates et al. 2015). For all statistical models, we tested for overdispersion, zero inflation and homoscedasticity using the DHARMa package (Hartig 2022).

Step 6: Validation

To test how well the different parameters derived for Munich, Angers, and across both cities predicted unknown data, we performed model validation on independent datasets, using a 10-times repeated, out-of-sample approach (Braaker et al. 2014). Because analyses with the Angers dataset revealed that after a data split, robust parameterisation or validation was not possible, the validation was restricted to the Munich and joint test datasets (Fig. 3).

To evaluate the practical transferability of dataset-specific parameters, we tested how well the parameter combinations from Munich, Angers, and the joint dataset could predict independent movement data, in Angers, Munich and the combined cities, using the same models as in the parameterisation step (GLM for single-city validation, GLMM for the joint dataset). We evaluated and compared the predictive power of the dataset-specific parameters using R2 and AUC, as well as the p-values for the connectivity predictor in these statistical models.

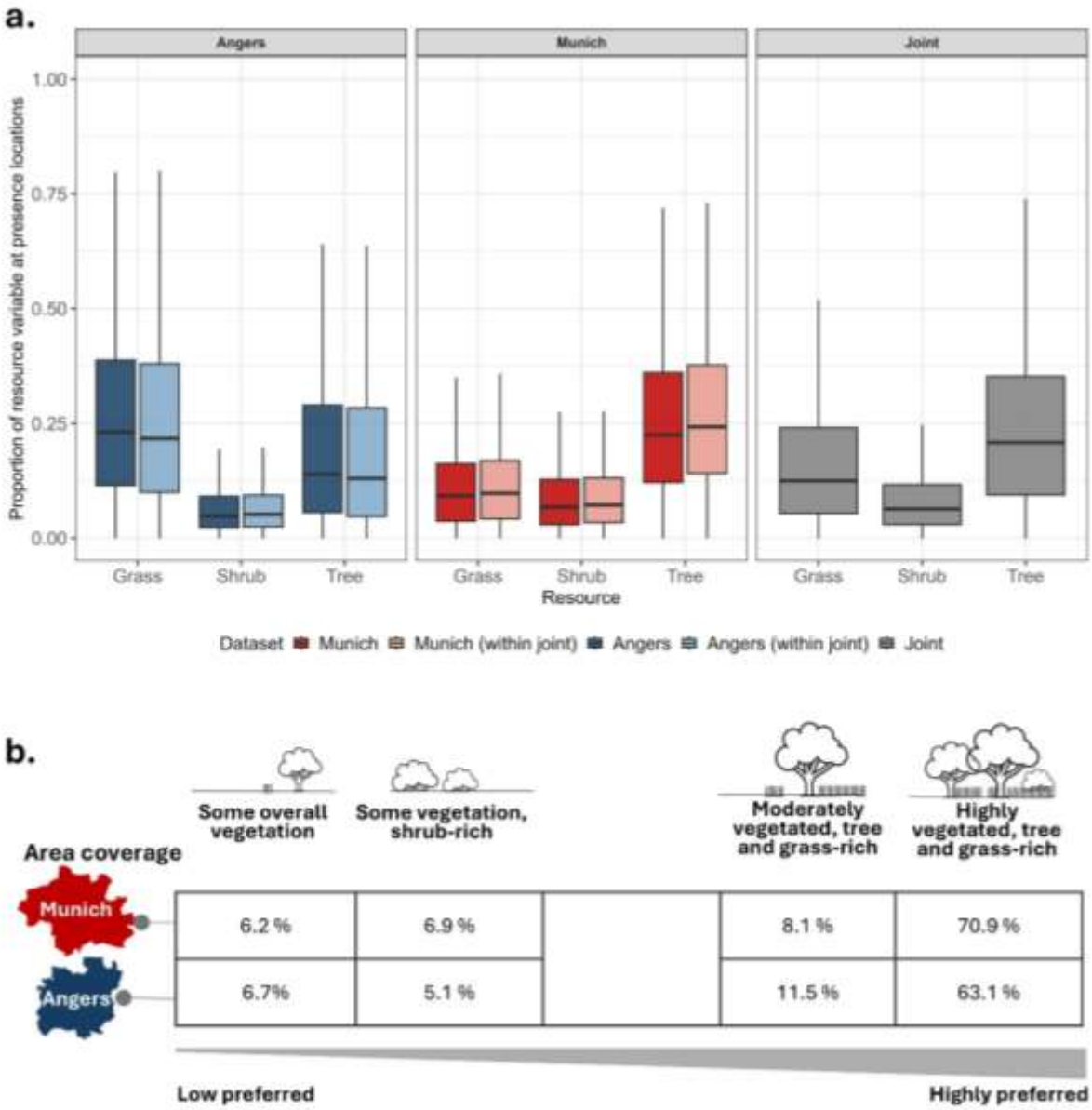
Results

3.1 Comparison of model parameters

3.1.1 Resource parameters

The identification of resource locations based on the CARTs revealed that, across all three datasets, common blackbird presence was most strongly associated with sites of substantial cover of all three vegetation types, tree, shrub, and grass (Fig. 4b; PC1, Supplementary material Fig. S2c). Crucially, the resource profiles recovered for each city were largely the same whether estimated from that city's data alone or from the joint dataset: For both Munich and Angers, single-city and joint models yielded near-identical median resource proportions at predicted presence locations (Fig. 4a). Pooling the two datasets thus neither distorted nor substantially altered the resource composition recovered for either city. This equivalence also held for predictive performance: all models accurately identified areas of blackbird presence (Sensitivity = 1). The joint model (Accuracy = 0.70) performed comparably to the best single-city model for Munich (Accuracy = 0.77), while exceeding the single-city fit for Angers (Accuracy = 0.52), suggesting it captured most of the city-specific predictive power in Munich while still generalising reasonably to Angers (Supplementary material Fig. S2).

The two cities nonetheless differed in the relative importance of individual resources: Predicted presence in Munich was associated with higher tree cover than in Angers (median 24% vs. 13%) and lower grass cover (13% vs. 21%), with comparable shrub cover (6% vs. 5%; Fig. 4a). These city-specific contrasts were preserved in the single-city and joint estimates alike and are averaged out only in the pooled dataset (Fig. 4a), which reflects the combined composition of both cities and should therefore be read as an aggregate rather than as representative of either city individually. Because it predicted consistently across both cities, we use the joint model to map the spatial coverage of predicted presence: Projected back into each city, areas whose resource proportions match those associated with the highest predicted presence probability cover 70.9% of Munich and 63.1% of Angers (Fig. 4b).



405

406 **Fig. 4** Results from resource parameterisation on joint, Munich and Angers blackbird
407 occurrence data: (a) Boxplots show median and interquartile range (Q3-Q1) of resources across
408 areas with predicted blackbird presence according to selected CARTS decision tree by dataset
409 and resource type. (b) Areas within each city that correspond to the final nodes and their
410 resource compositions. The highest likelihood of blackbird presence is in areas with high
411 overall vegetation, especially grassy and tree-rich habitats.

412 Buffering all predicted-presence locations by a 170 m radius, the home range size of an urban
413 blackbird (Snow 2008), all areas within these cities appear suitable for our generalist model
414 species. Therefore, all resource patches within our two cities became nodes in our landscape
415 graphs. We conducted an extensive sensitivity analysis to assess the robustness of our findings
416 (Carboni et al. 2007), revealing that the results and the selected threshold remained consistent
417 across changes in certain parameters, such as extraction radius (51 m was constantly identified
418 as best radius) or CART hyperparameters (Supplementary Material Fig. S1).

3.1.2 Resistance parameters

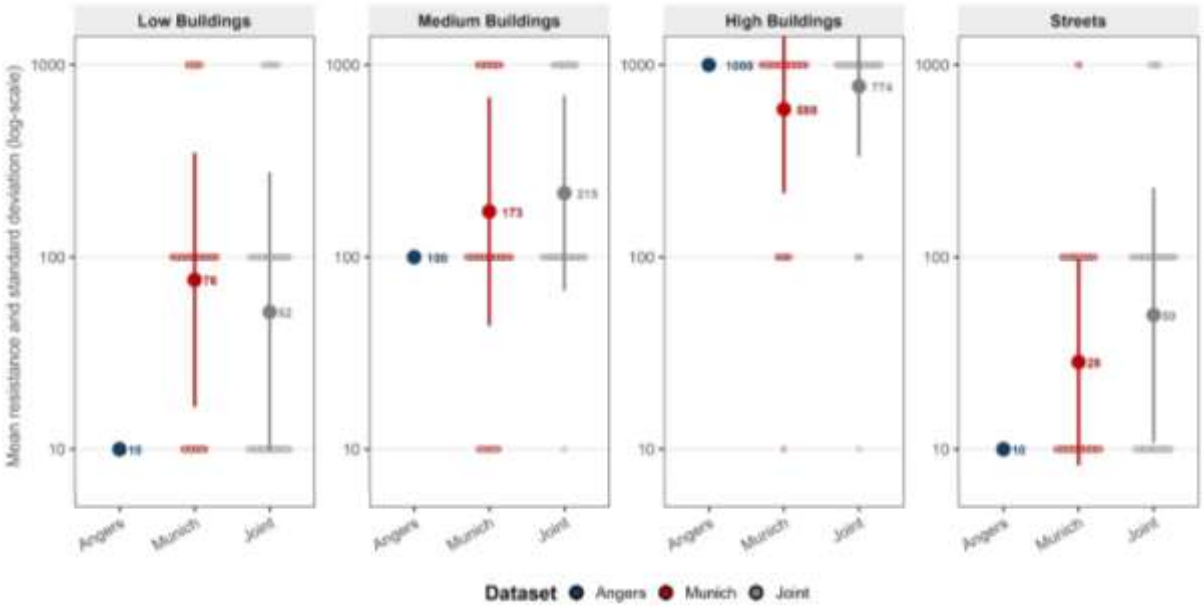
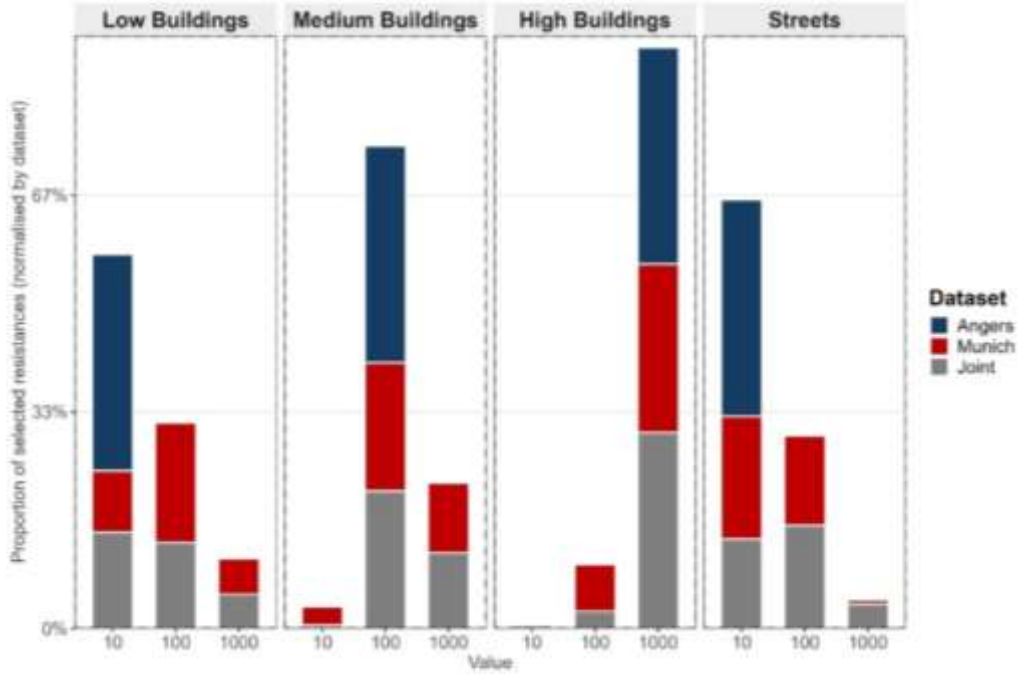


Fig. 5 Mean selected resistance values (± standard deviation shown as error bars) by urban land cover type for the common blackbird per dataset on a logarithmic scale. Individual points show the resistance values for all model parameterisations selected within 2 AIC units of the best model in each Monte Carlo cross-validation repetition

A general trend is detectable in the resistances best describing the barrier effects of the four anthropogenic land cover types to blackbird movement: Resistance values increase with building height across datasets and thus cities (Fig. 5). For high buildings, the mean resistance values across all three datasets are between 500 and 1000 (Munich 588, Angers 1000, Joint 774), while for medium buildings, they tend to be in the lower hundreds (Munich 173, Angers 100, Joint 215). Overall, the mean resistance values indicate a generally similar order across the three datasets, except for the mean resistance of low buildings and streets. They differ slightly across datasets, with (nearly) equal resistance values in the Angers dataset (both 10) and the joint dataset attributed a mean of 52 to low buildings and 50 to streets. In Munich, we observed higher resistance in low buildings (76) than in streets (28).



435

436 **Fig. 6** Empirically derived resistance parameters for the common blackbird. Display of the
437 proportion of the resistance values selected across all 10 folds for the Joint dataset, Munich
438 datasets, and the full Angers dataset (no folds, see Fig. 2). The displayed proportions are stacked
439 and normalised within each dataset, totalling 100 % across all three datasets. Percentages
440 indicated in text may not sum up to 100 % due to rounding.

441 The proportions of selected resistances across these four anthropogenic land covers support this
442 finding. For high buildings, 89% of the best models across all three datasets assigned a
443 resistance value of 1000, followed by medium buildings, where about 74% of the best models
444 assigned a resistance value of 100, indicating high consistency (Fig. 6). A higher variability in
445 the selection of resistance values for streets and low buildings could be observed, although
446 typically concentrating on two resistance values. Detailed results on the statistical models
447 created for identifying the best parameter values are provided in Supplementary Material S2
448 and Supplementary Material S3.

449 These resistance values from the different parameterisation datasets yield specific resistance
450 and connectivity maps (Fig. 7). For most of Munich, the mean resistance values derived from
451 the three datasets are similar, so the only differences between the parameter estimates are visible
452 in the city centre (Fig. 7). The differences in connectivity values do not show a clear spatial
453 pattern, with differences being dispersed across the whole study area (Fig. 7). However, the
454 results demonstrate that, in general, connectivity values are higher when applying the Angers
455 parameterisation. Also, the spatial correlation between connectivity values was very high, with
456 the Pearson correlation coefficient for the worst-performing connectivity map pair (Angers-
457 Munich) being 0.87 ($p < 0.0001$).

458 Overall, the results of the parameter analysis reveal that the relative order of resistance values
459 is quite consistent between the datasets (Fig. 5, Fig. S3), whereas the absolute values show a

certain consistency for high and medium-sized buildings, but especially for small buildings and streets are not well-aligned (Fig. 6). Therefore, discrepancies in the resistance maps derived from the different parameterisation datasets concentrate in the city centre of Munich (Fig. 7), but overall, connectivity values are still spatially similarly distributed.

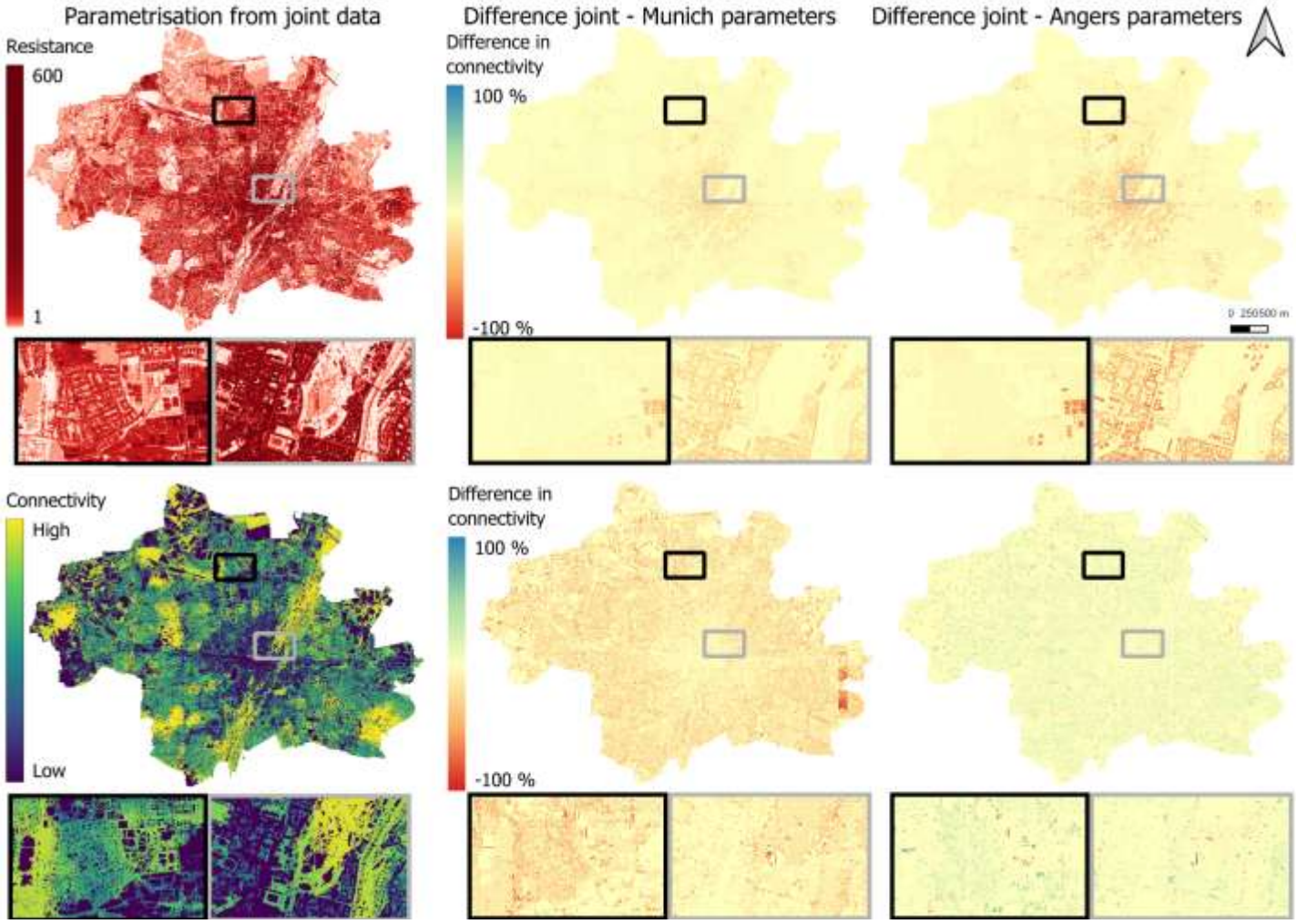
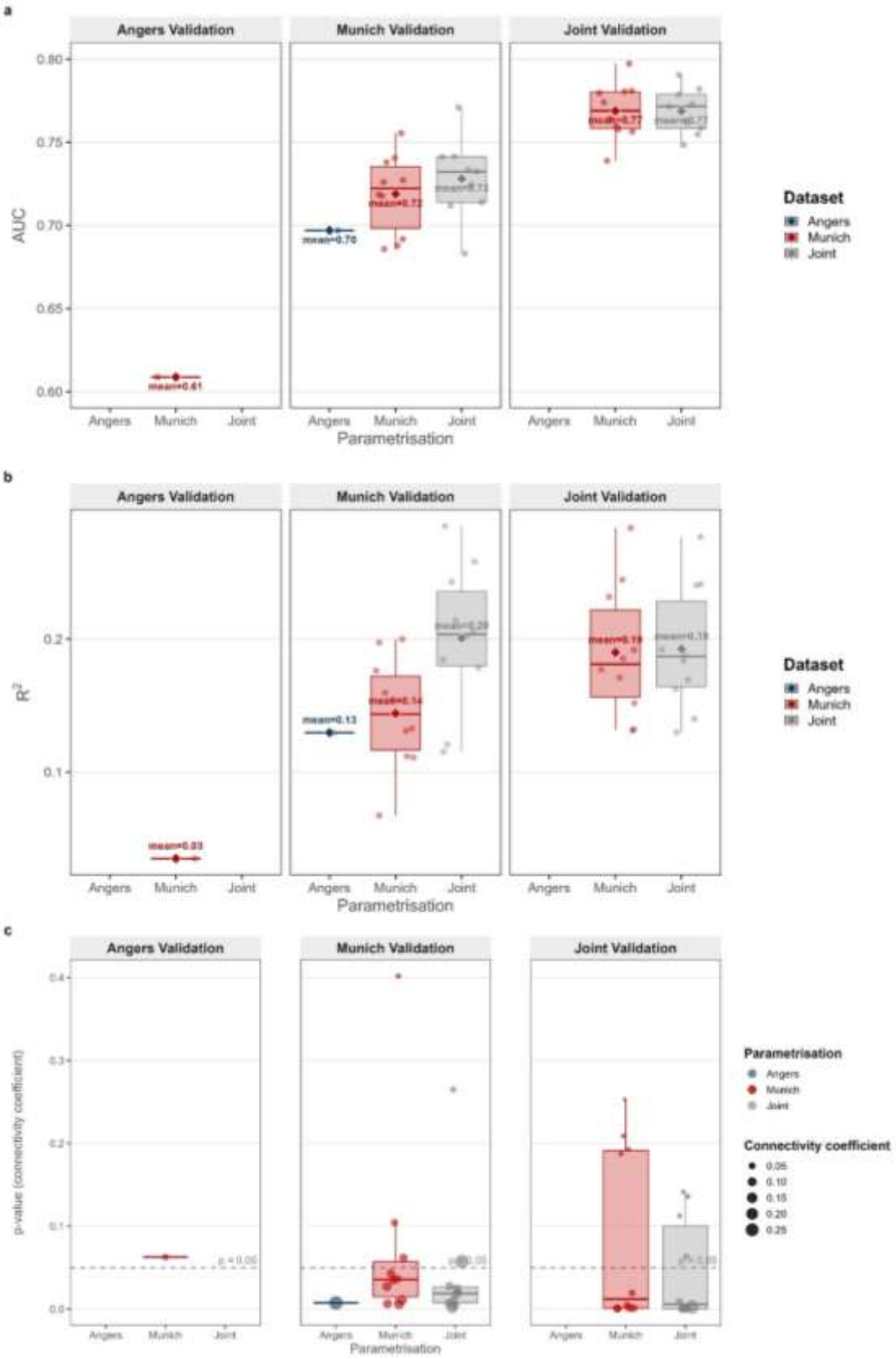


Fig. 7 Resistance (upper half) and connectivity maps (lower half) for Munich derived from parameterisation using datapoints from both cities jointly (left column), Munich (centre column), and Angers (right column). The maps in the centre and right columns demonstrate the difference between the Munich and Angers parameterisation and the parameterisation results from the joint dataset (left column)

468 **3.2 Comparison of predictive performances**



469

470 **Fig. 8** Out-of-sample validation of empirically-derived parameters across three datasets
471 (Angers, Munich, joint). **a**. AUC values indicate the overall model fit to accurately discriminate
472 between blackbird presence and absence when applying the different parameters. The AUC

across all models ranged from 0.61 to 0.79, indicating that some models perform well, while others are only marginally better than random. **b.** R^2 values indicate the proportion of variance in blackbird movement explained by the model. **c.** P-values of the connectivity coefficient as a fixed variable in the GLMM. Where no data were shown, validation was not possible due to Anger's data constraints (Fig. 3)

Overall, the best-performing models are those from the joint validation, probably because the large dataset size facilitates the detection of statistical effects. Using the Munich parameters and the joint data yields a mean AUC of 0.77, indicating a decent parameterisation (Fig. 8a). R^2 ranged around 0.19, and p-values for the connectivity parameter are overarchingly significant (Fig. 8b, c). The Munich parameters applied to the joint dataset seem to perform equally well as those derived for the joint dataset, indicating that here, the single-city parameters were transferable to cross-city models.

For validation in Munich, we observe that the parameters from the joint data perform best among the parameters used (mean AUC = 0.73) and explain 20 % of the variability in the blackbird movement data, while the connectivity predictor variable is mostly significant (Fig. 8). These parameters also moderately outperform those derived from the Munich parameterisation (AUC = 0.72; R^2 = 0.14), indicating that using parameters derived from more data points, even from distinct cities, improves the predictive ability and generalisability of our connectivity model to unknown data points. The parameter values derived from the Angers data perform less well in Munich (AUC = 0.70; R^2 = 0.13; connectivity predictor not significant). When applying the Munich parameters to Angers for validation, we observe poor results (AUC of 0.61). The model accounted for only 3 % of the variability in the blackbird movement dataset (R^2 = 0.03), and the connectivity predictor variable was not significant at our defined significance threshold (Fig. 8c). Detailed results on the statistical models and coefficients used for validating the connectivity model parameter with the different datasets are provided in Supplementary Material S2 and Supplementary Material S4.

These results suggest that, especially between the joint and Munich datasets, parameter transfer yielded connectivity models with decent performance. Interestingly, using the joint dataset for parameterisation improved out-of-data prediction in Munich. Finally, the validation in Angers was not very successful and was difficult to interpret, since repeated tests were impossible due to weaknesses in the dataset's performance.

4. Discussion

In this study, we tested whether landscape resistance in different European cities was similar, both in absolute values and relative order, for the common blackbird, a generalist European urban bird species. To derive landscape resistance, we made use of movement-proxy observations from Munich, Germany, and Angers, France, as well as a joint dataset for both cities. Additionally, we tested whether the parameter values derived from one dataset could predict movement at another study site. Our analyses revealed that the relative order of selected resistance values was generally stable between cities, while absolute resistance values differed more between Munich and Angers. However, validation indicated that including multiple cities in the parameterisation improved the connectivity model's performance compared to a single-city parameterisation, suggesting that resistance values may be more general across cities than previously assumed. Also, the land cover types that determine urban blackbird occurrence and which form the nodes of the landscape graphs are similar between the parameterisation datasets. In the following, we will discuss the implications of these results regarding the generality and transferability of urban resistance values, their context dependence, their use in urban planning, and the limitations of our study.

4.1. Transferability through joint parameterisation

For resistance parameters, the models derived from the joint dataset outperformed those derived from single-city datasets in out-of-sample validation in Munich, yielding higher AUC and R^2 values and a more frequently significant connectivity predictor than when using Munich-derived parameters alone. This improvement is likely attributable to two complementary mechanisms: first, to a larger number of data points during parameterisation, which increases statistical power to detect the effect of connectivity on movement; and second, to wider coverage of landscape conditions over which resistance values must be estimated. Notably, the resistance values derived from the joint dataset were not simply intermediate between those independently estimated for Angers and Munich (for medium buildings and streets, joint resistance estimates exceeded those of both single-city datasets). This could indicate that pooling data across cities does not merely average city-specific signals but brings additional information that enables more accurate estimation of parameter values. Taken together, these findings support a joint parameterisation approach for deriving more reliable and generalisable connectivity model parameters.

Furthermore, these results indicate that resistance values, in particular, can be more general than previously assumed. This finding nuances the prevailing view that resistance-based connectivity parameters are strongly context-dependent (Unnithan Kumar et al. 2022); a perception that has been established based on a few comparative studies showing that parameters derived in different cities tend to diverge (Balbi et al. 2018; Beninde et al. 2018). The strong validation results for parameters derived from the joint dataset in Munich indicate that combining observational data from multiple cities improves the predictive ability of resistance values, thereby challenging the prevailing perception of context-dependent resistance values. This could indicate that the context dependence observed when parameterising

resistance independently for each city reflects limited sampling of environmental gradients in each city rather than a substantial difference in the species' response to the urban environment.

4.2. Limited transferability for single-city parameterisation

Unlike resistance parameters, resource identification did not benefit from unifying the datasets from multiple cities. The joint CART recovered the same city-specific resource profiles as the single-city trees and predicted blackbird presence comparably well, without distorting the resource composition of either city. A single city was therefore sufficient to identify the land cover types at which the nodes of the landscape graph should be placed. The joint dataset only extended the analysis across a broader gradient of vegetation conditions, reflecting the greater heterogeneity of the pooled environments without improving performance. Within this shared structure, the two cities nonetheless differed in the resources most associated with blackbird presence, tree cover in Munich and grass cover in Angers, a result also found in other studies (Larson et al 2024). Nevertheless, in both cities, presence was associated with a mixture of all three vegetation types, consistent with the common blackbird's generalist nature. Future work could differentiate resources by quality, rather than cover alone, and by their associated probability of blackbird presence.

Resistance parameters showed a more nuanced picture than resource identification regarding the parameter similarity derived in the two cities. Their transferability from one city to another depended on whether resistance was considered in absolute or relative terms. Considering the derived resistance values from the complementary perspectives of absolute magnitude and relative order reveals two distinct patterns. In absolute terms (Fig. 5, Fig. 6), the resistance value assigned to high buildings is by far the most robust estimate. The other three land cover types also show a clearly dominant value within each dataset, but with comparatively lower consensus. For the relative order of resistance values (Fig. 5, Fig. 6), the ordering of resistance by building height (low < medium < high) is consistent across Angers, Munich, and the joint dataset, indicating similar ecological behaviour of the species with respect to building height across cities. The resistance of streets relative to low buildings is less clearly parameterised between the datasets, with Angers and the joint dataset showing quite similar resistance, and Munich leaning towards higher resistance of low buildings. This could reflect differences in traffic-associated disturbance between cities (Pundsack et al. 2026): Birds avoid high traffic noise (McClure et al. 2013), which varies markedly between European cities (European Environment Agency 2026), owing, for instance, to differences in local land cover distribution (Kang 2000). Taken together, these results suggest that, for the blackbird, the relative ranking of resistance among land cover types is more reliably estimated and more consistent across cities than the precise absolute resistance values themselves, with the exception of high buildings. As a consequence, resistance values derived from single-city datasets might not be fully transferable in absolute terms.

Despite differences in predictive performance between Munich and Angers parameters, the spatial correlation of connectivity values was remarkably high, with the lowest correlation coefficient in the Angers-Munich dataset being 0.87. Even where predictive performance was

weak, the resulting connectivity surfaces remained spatially congruent, indicating that differences in resistance parameters translate into only limited differences in the spatial distribution of connectivity values. Given that the relative order of resistance proved more transferable across cities and that their spatial distribution remains quite similar, single-city parameters may still provide a sufficient basis for planning applications primarily aimed at locating green infrastructure (Balbi et al. 2019; App et al. 2022).

4.3. Limitations

Our approach and the conclusions we can draw for the blackbird remain dependent on the amount and quality of available data, as well as on the structural characteristics of the cities studied. First, our results stem from a single, highly urban-adapted generalist species that is presumably among those least constrained by urban barriers (Gliwicz et al. 1994). Despite this, we detected a significant connectivity signal, suggesting that species less common or less mobile in cities might exhibit an even stronger response to landscape resistance, which remains to be tested (Devictor et al. 2008; Callaghan et al. 2019).

Second, our test of context-dependence rests on only two cities that, despite their differences in size and population, share a number of conditions: a common climate zone, a similar latitude, and a comparable history of urbanisation for the blackbird, which started around the same period (1820-1830) (Evans et al. 2010). The generality we observe once data are pooled may therefore partly reflect this underlying similarity in macro-scale conditions and urban adaptation process of the blackbird, rather than a property that would hold across more divergent settings or species following another urbanisation model (Evans et al. 2010). Testing cities that differ more in climate, latitude, or the timing and degree of blackbird urbanisation would help establish whether the generality identified here extends beyond environmentally and historically similar contexts.

Third, the comparable amount of movement-proxy observation points available in Angers and Munich was nonetheless insufficient to reliably parameterise the model for Angers, preventing us from splitting the Angers dataset and validating model performance independently in this city. As a result, model transferability could only be confidently assessed for Munich. Why a comparable sample size led to such different parameterisation outcomes between the two cities might be explained by the interplay between sampling design and city structure. In Angers, our movement-proxy data were collected along typically narrow street transects bordered by tall buildings, and largely devoid of vegetation – conditions under which modelled connectivity is consistently low or null. This spatial overlap between sampling locations and high resistance may have reduced the variance in connectivity values, thereby limiting the ability to detect an effect. However, in Munich, data collection was mainly conducted on streets with bordering frontage zones that supported significant vegetation cover (Micklewright et al. 2026), resulting in substantial modelled connectivity at the observation site. Consequently, the variance in connectivity values at observation sites in Munich was higher than in Angers, which has probably facilitated the detection of connectivity effects on blackbird flights in Munich.

Fourth, as discussed above, our treatment of streets as a single static category likely contributes to the inter-city variability observed in their relative resistance (Pundsack et al. 2026). Despite their possible importance, the incorporation of data representing street use heterogeneity, like traffic density and traffic noise data, however, was hampered by the unavailability of common data for the two cities, thereby limiting the pooled analysis beyond the street's physical footprint (Beaugeard et al. 2020).

These latter two aspects highlight that observed differences across cities in parameter and connectivity values can be independent of any differences in the species' behaviour and are instead specific to the data used. Observed differences could be heavily influenced by the configuration of the studied city and how sampling is distributed within it, and therefore by the number of data points required to detect a connectivity effect. This further strengthens the case for combining data across cities, as it increases the likelihood of capturing sufficient variance in landscape conditions to reliably estimate parameters.

4.4 A blueprint to derive connectivity model parameters transferable across cities

Taken together, our findings offer a blueprint for deriving connectivity model parameters that are both empirically grounded and usable beyond the city in which they were collected. Our results suggest that, once important movement properties are appropriately constrained, e.g. a single species and movement type, in cities of broadly similar urban form and climate, a degree of stationarity in resistance values may emerge. As our analysis rests on a single species and two cities, this should be regarded as a working hypothesis, but it suggests that context dependence can be addressed empirically by deliberately sampling the conditions under which generality is sought.

In practical terms, connectivity parameters should ideally be derived from movement-proxy data pooled across multiple cities, since this both improved predictive performance and revealed values unattainable from any single city. When this is not feasible, parameters derived from one well-sampled city can still provide a useful first approximation, provided the target city does not depart too far from the source city's urban structure, climate, and urbanisation history. For urban planning, our results provide an applied demonstration that empirically derived connectivity parameters, once established for a given species and movement type, can support biodiversity-friendly planning decisions beyond their original calibration city (Lookingbill et al. 2022; Habrich and Fahrig 2025).

Data availability

The common blackbird data from Munich are available online:
https://doi.org/10.5281/zenodo.19049212.

The common blackbird data and land cover data from Angers are available online:
https://zenodo.org/records/21283611

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Statements and Declarations

Funding

This French-Bavarian collaboration was kindly funded by the BayFrance programme, project "Beyond city parks: Ecological connectivity modelling to enhance biodiversity across urban landscapes" (funding period 2025-2026, FK 28). Additionally, LM and MP were funded by the Co-Creational Cohabitation Network (CoCoNet) project of the Driving Urban Transitions (DUT) Partnership, co-funded by the European Commission (EC) under the Horizon Europe framework program, the Austrian Research Promotion Agency (FFG), the German Aerospace Center (DLR), the Bundesministerium for Forschung, Technologie und Raumfahrt, and the Swiss National Science Foundation (SNSF, 10DU--_224163/1) that also supported WW. The Master's thesis of Damien Gourmelon was funded by the Région Pays de la Loire through the PULSAR project VitalConnect (2024_05894**)** that also supported AM.

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Author contributions

877 L.M., M.P., A.M, and W.W. conceived the study design and the research question. L.M., M.P.,
878 and A.M. developed the methodological approach. D.G. collected the data on the common
879 blackbird in Angers. L.M., M.P., A.M. and D.G. processed the observational data. L.M. and
880 M.P. conducted the connectivity and statistical modelling. L.M., M.P. and A.M. wrote the first
881 draft of the manuscript. All authors commented on previous versions of the manuscript. All
882 authors read and approved the final manuscript.

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