Urban Ecosystems (2026) 29:121
https://doi.org/10.1007/s11252-026-01948-y

RESEARCH

Sensitivity of habitat suitability-derived connectivity models to three-dimensional measures of urban landscape structure

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Received: 31 October 2025 / Accepted: 3 March 2026
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Abstract

Ecological connectivity models commonly derive resistance surfaces from habitat suitability; however, it remains unclear how two-dimensional (2D) versus three-dimensional (3D) representations of landscape propagate through this modeling pipeline, particularly in urban environments. This study evaluated the sensitivity of habitat suitability and connectivity outputs derived from these models to the inclusion of 3D landscape structure for two bird species with contrasting habitat associations, the Western Bluebird (*Sialia mexicana*) and Acorn Woodpecker (*Melanerpes formicivorus*), in Los Angeles, California, USA. Species distribution models were developed in Maxent using 2D variables and compared to models incorporating 3D variables derived from LiDAR, with connectivity modeled using Omniscape under identical parameterization. Across both species, 2D and 3D Maxent models exhibited similar performance and high niche overlap, indicating limited sensitivity of overall habitat suitability patterns to the inclusion of 3D variables. Likewise, connectivity outputs were highly correlated with high-connectivity values consistently concentrated in protected open spaces, mirroring the patterns seen in the Maxent models. However, the inclusion of 3D variables altered variable importance in the models and produced discernible shifts in spatial configuration of some suitability and high connectivity values, with species-specific differences. The results suggest that even when overall habitat suitability and downstream connectivity outputs are similar, the inclusion of 3D variables still produced discernible differences in the spatial configuration of high connectivity values, having implications for conservation management decisions. More broadly, these results underscore the importance of evaluating how upstream modeling choices related to the dimensional characterization of landscape propagate through connectivity workflows.

Keywords Urban birds · 3D urban form · Built environment · Ecological connectivity · Species distribution models

Introduction

The United Nations Convention on Biological Diversity's Kunming-Montreal Global Biodiversity Framework has set ambitious goals for cities to conserve biodiversity, with increasing ecological connectivity as a primary strategy (Convention on Biological Diversity 2023). Ecological connectivity, encompasses two key aspects: structural connectivity, which is the physical connectedness between habitats, such as green corridors (Lynch 2019; Zhou et al. 2021), and functional connectivity, which refers to how species perceive and use the landscape (Pe'er et al. 2011; Taylor et al. 2006). Much of connectivity research has been conducted in non-urban landscapes; however, cities present landscapes characterized by fine-scale heterogeneity, intense human modification, and vertically varied vegetation and built features (LaPoint et al. 2015; Wentz et al. 2018). Therefore,

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Published online: 23 April 2026

assumptions and metrics developed from non-urban landscapes may not translate directly into urban contexts.

Urban landscapes are characterized by pronounced horizontal and vertical heterogeneity of both vegetation and built features, which differentiates them from non-urban landscapes. Human modifications to the landscape, such as roads and buildings, create a complex matrix of habitats that can act as barriers to movement, both horizontally and vertically, by fragmenting habitats and increasing risks, such as vehicle collisions and bird-window strikes (Kreling et al. 2019; Loss et al. 2014). At the same time, these features can also provide unexpected opportunities for movement and habitat use. Buildings can create updrafts that shape flight paths for migratory birds (Liu et al. 2021) and can provide nesting sites (Reynolds et al. 2019). This duality, in which the same elements of urban built form can both impede and enable movement, underscores the need for analytical approaches that capture the multidimensional nature of urban environments. Capturing this multidimensional nature requires methods capable of representing both horizontal and vertical variation in urban landscapes.

While connectivity research in urban environments is growing, there remain significant gaps in our understanding, partly due to the insufficient representation of urban contexts in existing metrics (LaPoint et al. 2015). The limited incorporation of detailed urban form metrics, particularly those capturing vertical variation, may constrain our ability to fully understand how built environments influence species movement. For example, without integrating 3D data, skyscrapers and single-story buildings may appear identical when viewed only by their horizontal footprints, despite significant differences in height and volume. These differences in building height and volume have important ecological consequences, including increased bird-building collisions, altered flight behaviors, and impacts on animal communication (Hager et al. 2013; Liu et al. 2021; Warren et al. 2006). Similarly, excluding 3D information obscures structural variation among trees in urban landscapes. Research has established that the diversity of tree canopy height plays an important role in woodland bird species richness and forest ecosystem health (Skidmore et al. 2021; Huang et al. 2014), which warrants testing in urban environments. Recent advances in remote sensing, particularly by light detection and ranging (LiDAR) and structure from motion (SfM), now enable fine-scale measurements of the vertical structure of landscapes (Camarretta et al. 2020; Iglhaut et al. 2019), creating an opportunity to incorporate 3D data into connectivity modeling.

Despite the increasing availability of 3D data made possible by LiDAR and SfM, the application of 3D measures of landscape in connectivity modeling remains underutilized, with a few notable exceptions. For example, Casalegno et al. (2017) assess connectivity in urban greenspaces in the United Kingdom using both 2D and 3D data of vegetation (Casalegno et al. 2017), and found that the models predicted different levels of connectivity. A study in a Korean city incorporated 3D data for both buildings and vegetation into their connectivity model, and found strong associations of these structural measures to bird richness when conducting correlation tests (Choi et al. 2021). However, community-level analyses may obscure interspecific differences in mobility and habitat use; therefore, species-specific modeling is required to reveal how 3D urban landscape structure differentially influences connectivity across species. Species differ in how they interact with urban landscapes depending on their dispersal capacity and habitat preferences (Préau et al. 2022), and variation in vertical habitat use further underscores the limits of community-level analyses (Re et al. 2025). These insights highlight the need for species-specific modeling approaches that integrate 3D data to advance understanding and management of ecological connectivity in urban landscapes.

A common assumption in many connectivity studies, particularly when facing data limitations, is the development of resistance surfaces from habitat suitability models (Zeller et al. 2012). In connectivity modeling, resistance surfaces represent landscapes as continuous gradients of movement cost, estimating how landscape features facilitate or constrain a species' movement (Zeller et al. 2012). As direct measurement of movement costs across heterogeneous landscapes is often logistically challenging (Richard and Armstrong 2010; Bélisle 2005), resistance values are frequently estimated using expert opinion or from habitat suitability predicted by species distribution models (SDMs) (Beier et al. 2011; Zeller et al. 2012; Shimazaki et al. 2016). In this instance, areas of high predicted suitability are assigned lower resistance values and areas of low predicted suitability are assigned high resistance values. The assumption inherent in this method is that areas that are more suitable for a species will be easier to move through versus an area with low suitability will be more difficult to traverse. Thus, this approach is not realized movement of the species, but serves as a proxy for potential movement.

While parameterizing resistance layers with actual movement data is preferable when available, such data remains challenging to obtain and particularly scarce in urban environments. In this context, SDMs provide useful approximations for landscape resistance. For example, one study found that while resistance surfaces parameterized with GPS or genetic data performed better than SDMs, the SDMs still captured approximately 65–87% of the dispersal process (Zeller et al. 2018), demonstrating its usefulness when other data cannot be obtained. Despite the fact that habitat suitability does not correspond perfectly to movement, as

it does not directly capture realized dispersal (Zeller et al. 2018; Keeley et al. 2017), it remains the best data available in many instances, necessitating careful evaluation of how they are constructed. Therefore, evaluating how alternative representations of landscape structure propagate through this commonly used modeling pipeline is essential for clarifying the implications of methodological choices in connectivity modeling in urban environments.

This study evaluated the sensitivity of habitat suitability and connectivity outputs derived from these models to the inclusion of 3D landscape structure and compared them to models with conventional 2D data. We incorporated occurrence data from two species with contrasting habitat associations, the Western Bluebird (*Sialia mexicana*) and the Acorn Woodpecker (*Melanerpes formicivorus*). These two species serve as complementary test cases for evaluating how different representations of landscape dimensions propagate through a connectivity modeling pipeline. Specifically, we asked: (1) To what extent are predicted ecological niches sensitive to the inclusion of 3D landscape representations, and does this sensitivity differ by species? and (2) To what extent are connectivity model outputs derived from these models sensitive to 3D representation of landscape features, and does this sensitivity differ by species? We expect that incorporating 3D representations of landscape will alter both habitat suitability and connectivity predictions relative to 2D representations, with larger differences anticipated for the Acorn Woodpecker given its association with dense, mature tree canopy. By examining the sensitivity of habitat suitability models and connectivity outputs derived from these models to the inclusion of 3D landscape representation, this study clarifies how these methodological choices in resistance construction influence comparative connectivity outputs in urban environments, laying the groundwork for future studies that integrate movement data to assess ecological relevance.

Methods

Study area

Our study was conducted in Los Angeles, California, United States (34°03′N 118°15′W), a city with approximately 3.8 million inhabitants that spans 1,214 km^2 (U.S. Census Bureau 2021). The metropolitan area experiences a Mediterranean climate and lies within the California Floristic Province, a region recognized as one of the world's 36 biodiversity hotspots (City of Los Angeles Department of Sanitation & Environment 2022). Los Angeles serves as an ideal testbed because of its diverse range of development intensities and the presence of both highly modified green spaces and natural remnant habitats (Fig. 1).

Study species

Two indicator species used by the City of Los Angeles to monitor urban biodiversity were selected because of their contrasting habitat associations to serve as test cases for evaluating how the representation of landscape in 3D influences habitat suitability and downstream connectivity predictions. Western Bluebirds are small insectivorous thrushes commonly associated with open woodlands, low-lying vegetation, and suburban landscapes (Guinan et al. 2020). They nest in natural or human-provided cavities, such as tree holes and nest boxes (Collar and Christie 2014), and are generally considered territorial (Guinan et al. 2020). Acorn Woodpeckers are associated with oak woodlands and forests, feed on insects and acorns, and store them in granary trees, utility poles, and buildings (MacRoberts and MacRoberts 1976). Acorn Woodpeckers excavate their own nesting cavities and exhibit highly social and territorial behavior (Koenig et al. 2019, 2023). Given that Western Bluebirds are more commonly associated with open areas and suburban habitats (Guinan et al. 2020), we would expect habitat suitability and downstream connectivity outputs to be less sensitive to variation in canopy height compared to the Acorn Woodpecker, which is associated with mature tree canopy (MacRoberts and MacRoberts 1976). Together, these two species provide complementary lenses through which to assess how 2D versus 3D representation of urban landscape structure propagates through a connectivity modeling pipeline.

Habitat suitability modeling

To assess the behavior of habitat suitability models when incorporating 3D representation of urban landscapes, the machine learning algorithm Maxent was selected for model construction and comparison. Maxent is widely used for presence-only data and has demonstrated competitive predictive performance relative to alternative SDMs (Elith et al. 2006, 2011; Phillips and Dudik 2008; Yan et al. 2025). Maxent estimates the probability distribution of species presence from occurrence records and environmental predictors across a study area (Phillips et al. 2006). This method, when using the complementary log–log link function, generates a continuous probability of occurrence output, which can be interpreted as habitat suitability for each raster cell, with values ranging from 0 (least suitable) to 1 (most suitable). As the objective of this study was to evaluate how 2D versus 3D representations of urban landscape influence habitat suitability and downstream connectivity outputs, we held the model constant to avoid introducing more variation.

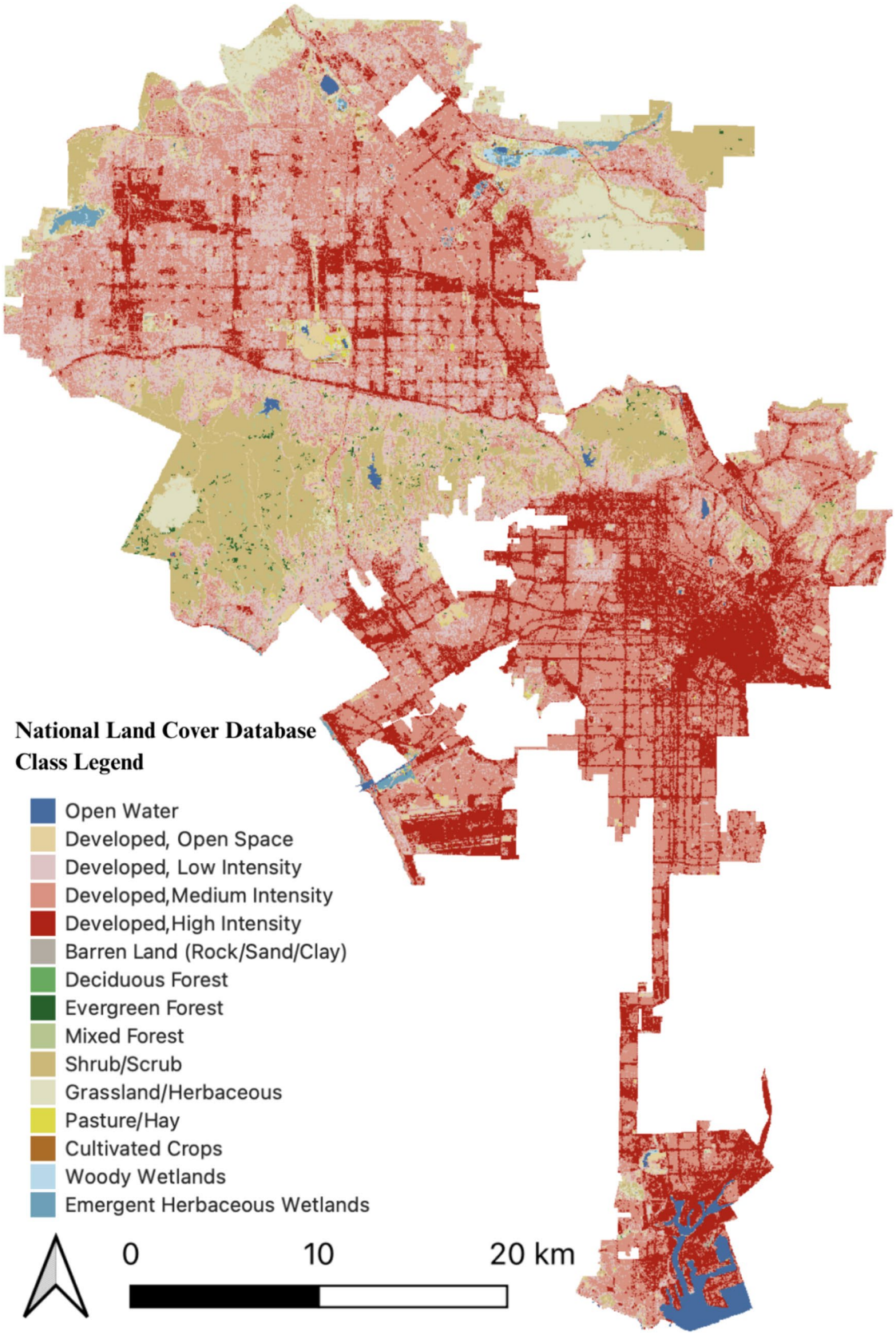

Fig. 1 Land cover for the City of Los Angeles from the 2021 National Land Cover Database (NLCD)

Thus, we selected a single, well-established SDM approach, for comparison of 2D and 3D outputs.

Environmental variables

Two sets of environmental variables were developed for modeling. The first set included only 2D representations of landscape. The second set included the 2D variables and additional 3D variables representing building and vegetation structure (Table 1). All variables had a resolution of 30 m or finer and were aggregated to 100 m pixel resolution (i.e., grain size). The pixel resolution was chosen to align to the resolution of occurrence data (as defined by coordinate uncertainty; see Sect. "Occurrence data"), consistent with best practices (Sillero and Barbosa 2021), and to capture the heterogeneity of the habitat structure within 1 km. For connectivity modeling, we defined a 1 km moving window to represent local-scale movement (see Sect. "Connectivity modeling"). Acorn Woodpecker movements are generally on the order of 1 km, with occasional movements of several kilometers during the breeding season (Koenig et al. 2000), supporting the use of this scale. Movement distances for Western Bluebirds are less well quantified (Guinan et al. 2020); however, given their smaller body size relative to Acorn Woodpeckers and the general scaling of dispersal distance with body size because distance traveled generally increases with body size (Sutherland et al. 2000), a 1 km window likely represents a conservative estimate of local movement for this species. Thus, the 100 m grain size captures the heterogeneity of the landscape within 1 km.

Only environmental variables with a native spatial resolution equal to or finer than the selected 100 m grain size were considered to avoid artificially inflating spatial precision through resampling (Sillero and Barbosa 2021). Continuous predictors were aggregated using mean values. Categorical land cover classes were converted to continuous values by calculating the proportional cover of each class within a 100 m grid cell using area-weighted aggregation. Using continuous land cover variables aligns with best practices because models based on continuous predictors typically outperform those based on categorical data (Coops and Wulder 2019; Cushman et al. 2010; Nawrocki et al. 2020; Ahmer and Ostendorf 2025).

Following best practices for habitat suitability modeling, multicollinearity among variables was determined using the raster.cor.matrix function in ENMTools v1.1.2 (Warren & Dinnage 2024) in R v4.4.3, in combination with the raster package (Hijmans et al. 2025a, b; Simons et al. 2022; Barber et al. 2022; R Core Team 2024). Variables with pairwise Pearson correlation coefficients exceeding $|r|>0.7$ were considered highly correlated. Rather than removing all correlated variables, we constructed candidate model sets in which one variable from each highly correlated pair was retained. We then calculated the variance inflation factor (VIF) for each candidate model, removing variables with VIF exceeding a threshold of 7 (Feng et al. 2024; Dormann et al. 2013). This approach allowed us to evaluate competing combinations of 2D and 3D variables (see Supplementary Material S1 for candidate models).

Occurrence data

Occurrence data for both study species, the Western Bluebird and Acorn Woodpecker, were obtained from iNaturalist, a community science platform, via the Global Biodiversity Information Facility (GBIF.org 2025). Recent studies have shown that community science data, when filtered to address temporal and spatial biases, can produce reliable species distribution estimates across diverse taxa (Beninde et al. 2023; Dutko et al. 2023; Henckel et al. 2020). Records were filtered to include only “research grade” observations with valid geographic coordinates for the years 2020–2024. This five-year window coincided with the timing (i.e., data collection) of the vegetation structure data. The CTrees data were generated in 2022 (CTrees 2026). Accordingly, we selected occurrence records from several years prior to and following this date. This window balances the need for temporal coherence with the need to retain sufficient sample sizes to support the robust modeling using community science data. Additionally, Los Angeles experienced major wildfires in early 2025, significantly altering vegetation. Only records with a reported coordinate uncertainty parameter were retained, which represented the radius within which the observation was spatially accurate. To retain a sufficient number of occurrences while ensuring spatial accuracy, we retained only records with a reported uncertainty equal to or less than 50 m.

Because the true location of an observation may lie anywhere within this uncertainty radius and no directional information is available, we adopted a conservative approach and defined the effective spatial resolution of the occurrence records as the full diameter of the uncertainty circle (i.e., 100 m). Environmental variables were therefore aggregated to a 100 m spatial resolution to ensure that the grain of environmental variables matched the spatial resolution of the occurrence data, following best practices (Sillero & Barbosa 2021). Additionally, occurrence records were spatially thinned to one occurrence per raster cell to reduce spatial clustering arising from sampling bias using the Rpackage spThin (Beninde et al. 2023; Simons et al. 2020; Aiello-Lammens et al. 2015). After spatial thinning, 280 occurrence records remained for the Western Bluebird and 199 records for the Acorn Woodpecker (see Supplementary Material S2).

Table 1 Environmental variables considered for 2D and 3D habitat suitability models

Model	Variable	Description	Native resolution	Source	Rationale
2D & 3D	Developed, Open Space	Proportion of developed, open space cover within 100 m pixel	30 m	National Land Cover Database (Dewitz 2023)	Land cover/Land use variables are the most used in resistance parameterization (Zeller et al. 2012), as they represent landscape composition relevant to species' habit associations and have been shown to strongly influence species occurrence patterns (Saunders et al. 2022)
2D & 3D	Grass	Proportion of grass cover within 100 m pixel			
2D & 3D	Shrub	Proportion of shrub cover within 100 m pixel			
2D & 3D	Water	Proportion of water cover within 100 m pixel			
2D & 3D	Impervious	Proportion of impervious cover within 100 m pixel			
2D & 3D	Annual Mean NDVI	Normalized Difference Vegetation Index was derived by computing NDVI for each cloud-masked scene and averaging values across the calendar year	10 m	Sentinel-2 Level-2A surface reflectance imagery for 2022 (European Space Agency 2022)	NDVI represents vegetation greenness and productivity, capturing variation in urban habitat quality that may not be fully reflected by land cover/land use (Bino et al. 2008; Amini Tehrani et al. 2020)
2D & 3D	Protected Open Space	Proportion of protected open space within 100 m pixel	Vector parcel-based dataset	California Protected Areas Database (GreenInfoNetwork, 2020)	Protected open space was included as a proxy for urban green spaces, which serve as important habitat for many species, including birds, in highly modified urban landscapes (Beninde et al. 2015; La Sorte et al. 2020)
2D & 3D	Tree Canopy	Proportion of tree canopy within 100 m pixel	Vector layer derived from 60 cm resolution liDAR	High-resolution tree canopy height dataset for Los Angeles, CA (CTrees 2026)	Tree canopy is a significant predictor of bird species richness (Beninde et al. 2015)
3D only	Mean Tree Height	Average tree height within 100 m pixel	60 cm	High-resolution tree canopy height dataset for Los Angeles, CA(CTrees 2026)	Canopy height has strong associations with bird occurrence and species richness (Coops et al. 2016; Melin et al. 2016)
3D only	Standard Deviation of Tree Height	Vertical variability of tree height within 100 m pixel			Vertical variability in canopy structure has strong associations with bird occurrence and richness (Bae et al. 2014; Coops et al. 2016; Eldegard et al. 2014)
3D only	Mean Building Height	Average building height within 100 m pixel	Vector layer derived from 60 cm resolution liDAR	Building Footprints within the City of Los Angeles captured through LARIAC4 (Los Angeles GeoHub 2017)	Measures of building height and volume have been shown to have strong associations with bird occurrence and species richness (Choi et al. 2021; Liu et al. 2021; Buenaño-Mariño et al. 2025)
3D only	Standard Deviation of Building Height	Vertical variability of building height within 100 m pixel			
3D only	Total Building Volume	Total building volume within 100 m pixel			

Model tuning and validation

The models were parameterized using the complementary log–log (cloglog) link function and optimized using the ENMevaluate function from the ENMeval R package (Kass et al. 2025), following the recommendations of Merow et al. (2013) and Laszlo et al. (2022). All combinations of feature classes were tested across regularization multipliers ranging from one to five. Model tuning employed spatial block cross-validation, which divides occurrence records into four geographically structured folds to reduce the inflation of performance metrics due to spatial autocorrelation. The optimal feature class and regularization multiplier were selected based on the lowest corrected Akaike Information Criterion (Burnham and Anderson 2002). Presence-only models such as Maxent estimate habitat suitability by contrasting environmental conditions at occurrence locations with those at background locations. When occurrence records are spatially biased, as is common for community science gathered data, uniformly sampled background points may introduce environmental bias into model estimation (Phillips et al. 2009). Following Phillips et al. (2009), we generated a kernel density-based bias surface using a two-dimensional Gaussian kernel implemented via the kde2d function from the MASS package (Venables and Ripley 2002) in R v4.1.3 (R Core Team 2024) to weight background sampling according to the spatial distribution of observation effort. From this bias surface, 10,000 background points were drawn for model calibration. Final models were refitted in Maxent using the selected tuning parameters and evaluated across 10-fold cross-validation. In each iteration, 90% of the occurrences were used for training and 10% for testing, with predictions averaged across folds to generate the final habitat suitability output.

Model performance was assessed using the Area Under the Curve (AUC) for both training and test data (Huntley et al. 2006). Model generality was measured as the difference between the training and test AUC, where smaller differences indicate greater generalizability (Warren and Siefert 2011). Predictive discrimination was additionally evaluated using the True Skill Statistic (TSS) (Phillips and Dudík 2008; Allouche et al. 2006). All analyses were implemented in R using a custom automation script (Banta 2024), with Maxent executed using the Maxent function in the dismo package (Hijmans et al. 2024).

Comparing 2D and 3D habitat suitability outputs

To compare the differences between the 2D and 3D habitat suitability outputs, we compared spatial predictions using similarity metrics that capture different aspects of agreement. First, we calculated the Hellinger niche similarity index after normalizing each habitat suitability raster to represent a probability distribution across the landscape (Warren et al. 2008). The Hellinger niche similarity index quantifies the global distributional overlap between two suitability outputs (Robert et al. 2016). As it is derived from the Hellinger distance, this metric emphasizes the proportional similarity in habitat suitability across the landscape, capturing whether the two models allocate suitability to similar regions overall. The Hellinger distance (H) was calculated as:

$$\mathrm{H} = \sqrt{\sum\left(\sqrt{P_x} - \sqrt{P_y}\right)^2}$$

where p_x and p_y represent the normalized suitability values for the corresponding pixels in the two rasters. The Hellinger similarity index was derived as:

$$I = 1 - \frac{1}{2}H$$

yielding values ranging from 0 (no overlap) to 1 (identical distributions).

Second, to evaluate spatial congruence, we calculated the Spearman's rank correlation between raster cell values (Henckel et al. 2020). Spearman's coefficient assesses the strength of a monotonic association between ranked suitability values rather than their raw magnitudes. By ranking predictions prior to comparison, Spearman's correlation isolates agreement in the order of habitat suitability across space, regardless of differences in magnitude. To further visualize potential spatial restructuring of predictions, we mapped the difference between Spearman ranked 3D and 2D predictions, allowing the identification of regions where incorporation of 3D variables altered habitat suitability values compared to 2D.

Connectivity modeling

Connectivity was modeled using the Omniscape.jl package in Julia, a wall-to-wall connectivity algorithm that applies circuit theory to assess potential movement pathways across heterogeneous landscapes (McRae 2016; Landau et al. 2021). Omniscape computes connectivity using a moving-window approach, in which the window size determines the spatial scale of the analysis. For this study, the moving window was set to 1 km to capture local movement patterns consistent with the movement behavior of the focal species (see Sect. "Environmental variables"). To evaluate how the dimensional representation of urban landscape structure propagates through the connectivity modeling pipeline,

connectivity analyses were conducted using 2D and 3D habitat suitability outputs with identical algorithm settings.

Two rasters are required for model execution: (1) a source layer representing the likelihood of each pixel serving as an origin or destination for movement, and (2) a resistance layer quantifying the ease or difficulty of movement through the landscape. Habitat suitability rasters serve as the source layers under the assumption that areas of higher predicted suitability correspond to greater potential movement into and out of these locations (Beninde et al. 2023). Resistance layers were derived from habitat suitability outputs under the commonly used assumption that areas of higher predicted suitability correspond to lower relative movement resistance (Keeley et al. 2017). Habitat suitability rasters were produced using the cloglog output from Maxent and were therefore already scaled between 0 and 1. These values were converted to resistance values using a linear inverse transformation as follows:

$$R = 1 + (1 - H) \times (R_{max} - 1)$$

where R represents resistance, H is habitat suitability, and R_{max} was set to 100. In this transformation, resistance decreases proportionally with increasing suitability. A linear transformation was selected to minimize assumptions about nonlinear or threshold-based movement responses and to focus comparisons on differences in dimensional landscape representation. Although alternative nonlinear transformations have been proposed and may better approximate realized movement (Zeller et al. 2018), data were not available for focal species to validate different resistance transformations and were out of the scope of this study. Instead, the goal of this study is to test model sensitivity rather than realized movement.

Table 2 Model evaluation metrics and the three environmental variables with the highest permutation importance for 2D and 3D Western Bluebird habitat suitability models

Model	AUC train	AUC test	AUC diff	TSS	Top 3 predictors by permutation importance (%)
2D	0.82	0.80	0.02	0.55	Proportion of Protected, Open Space (53.7), Proportion of Impervious (21.3), Proportion of Tree Canopy (11.5)
3D	0.85	0.83	0.02	0.57	Proportion of Protected, Open Space (58.1), Proportion of Impervious (16.1), Mean Building Height (9.3)

Area Under the Curve (AUC) is reported for both training and test data; AUC Diff represents the difference between training and test AUC values and reflects potential overfitting. True Skill Statistic (TSS) summarizes model discrimination. Permutation importance measures how much model performance declines when that variable's values are randomized. Complete results of permutation importance are provided in Supplementary Material S3

Connectivity was assessed using the cumulative current flow output, which represents the total predicted connectivity across the landscape. To quantify the similarity between the 2D and 3D connectivity models, the outputs were standardized using Z-scores to remove differences in absolute current magnitude. Pearson's correlation coefficients were then calculated between standardized rasters to assess the similarity in spatial patterns of predicted connectivity (Phillips et al. 2021). In addition, the overlap of high-connectivity areas (defined as the top 10% of current flow values within each model) was calculated to evaluate whether dimensional representation altered the spatial configuration or extent of priority areas. Raster operations were conducted in R using the Terra package (Hijmans et al. 2025a, b).

Results

Following multicollinearity screening, all 2D environmental variables were retained except NDVI, which was excluded due to high correlation with impervious cover and tree canopy (Supplementary Material S1). For the 3D models, six candidate model configurations were evaluated based on alternative combinations of correlated predictors identified during multicollinearity testing (Supplementary Material S1). The top-ranked 3D model for each species included all retained 2D predictors along with two structural variables: standard deviation of tree canopy height and mean building height for the Western Bluebird, and mean tree canopy height and mean building height for the Acorn Woodpecker. Results are presented by species to enable direct comparison of 2D and 3D model outputs.

2D and 3D habitat suitability models for Western Bluebird

The 2D model for the Western Bluebird performed well and was considered useful as it exceeded validation metric thresholds of AUC above 0.7, small AUC difference, and a TSS above 0.40 (Table 2). The best performing 3D model, also exceeded the validation metric thresholds (Table 2). This indicates that both models have minimal overfitting and reflect agreement between the predicted and observed occurrences. Both models used the LQHP feature classes (i.e., Linear, Quadratic, Hinge, Product) and performed similarly.

The permutation of importance of the environmental variables in the 2D versus 3D models for the Western Bluebird, varied slightly (Table 2). The most important variable in both models was the proportion of protected open space, which had an outsized influence (53.7 and 58.1 in 2D and 3D, respectively). The second most influential predictor

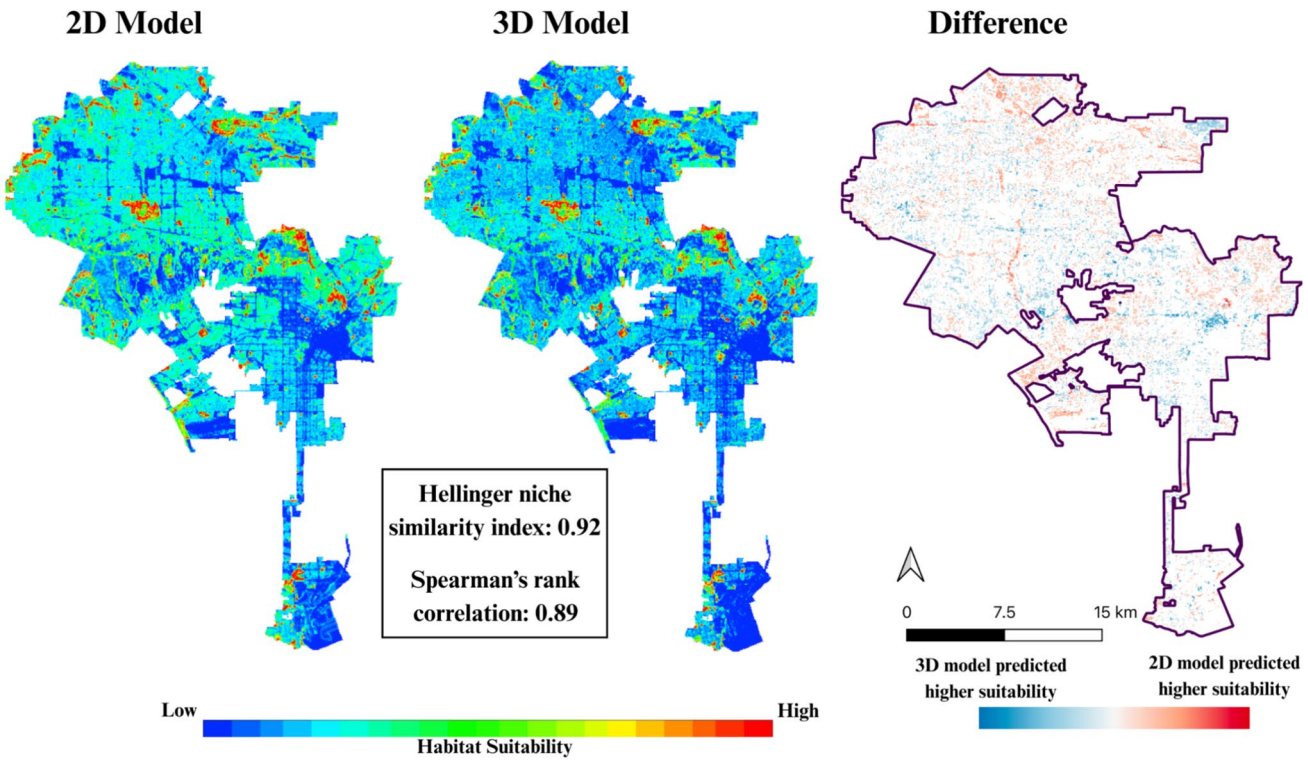

Fig. 2 Predicted habitat suitability from 2D and 3D models for the Western Bluebird, and the spatial differences in predicted suitability comparing these two models

in both models was the proportion of impervious cover, although the 3D model dropped from the 2D model 21.3 to 16.1. The standard deviation of tree canopy height and mean building height influenced the 3D model more than the rest of the 2D variables at 7.3 and 9.3, respectively. In particular, the proportion of tree canopy was less important in the 3D model at 1.8, compared to the 2D model at 11.5 (see Table 2 and Supplementary Materials S3).

When comparing the 2D and 3D habitat suitability outputs visually, there is some variation in the predictions (Fig. 2). Some minor clusters of values show minimal predicted differences. This was confirmed by both the Hellinger Similarity Index and Spearman's rank correlation tests, which found high ecological niche overlap (0.92) and high correlation (0.89).

2D and 3D habitat suitability models for acorn woodpecker

Similarly, both the 2D and 3D models for the Acorn Woodpecker exceeded the validation metric thresholds. The best performing 3D model was slightly different from the Western Bluebird model, with the inclusion of mean tree height instead of the standard deviation of tree height. Both the 3D Western Bluebird model and the 3D Acorn Woodpecker model included the mean building height. This variable outperformed models with the standard deviation of building height. Both the 2D and 3D Acorn Woodpecker models had slightly higher validation metrics than the Western Bluebird models; however, both sets of models performed well and are considered suitable for prediction. The 2D model used LQHPT (i.e., Linear, Quadratic, Hinge, Product, Threshold) feature classes, whereas the 3D model used LQHP (Table 3).

Table 3 Model evaluation metrics and the three environmental variables with the highest permutation importance for 2D and 3D Acorn Woodpecker habitat suitability models

Model	AUC train	AUC test	auc diff	TSS	Top 3 predictors by permutation importance (%)
2D	0.86	0.87	−0.1	0.64	Proportion of Protected, Open Space (52.8), Proportion of Tree Canopy (20.8), Proportion of Impervious (11.6)
3D	0.86	0.87	−0.00	0.63	Proportion of Protected, Open Space (57.9), Mean Tree Canopy Height (13.2), Proportion of Impervious (7.9)

Area Under the Curve (AUC) is reported for both training and test data; AUC Diff represents the difference between training and test AUC values and reflects potential overfitting. True Skill Statistic (TSS) summarizes model discrimination. Permutation importance measures how much model performance declines when that variable's values are randomized. Complete results of permutation importance are provided in Supplementary Material S4

As with the Western Bluebird models, the most influential variable in both models for the Acorn Woodpecker was the proportion of protected open space (Table 3). However, unlike the Western bluebird models, the second variable of importance differed. For the 2D model, it was tree canopy, and for the 3D model, it was mean tree canopy height. While the proportion of impervious cover was the second most important variable in both models for the Western Bluebird, it dropped to third for the Acorn Woodpecker. Interestingly, mean building height had little influence in the 3D model for the Acorn Woodpecker (0.9) compared to the Western Bluebird (9.3) (Table 3, Supplementary Material S4).

Similar to the visual comparison of the Western Bluebird models, the Acorn Woodpecker models appear very similar, with some minor clusters of values that are different (Fig. 3). The results of the Hellinger Similarity Index and Spearman's rank correlation tests confirm this with 0.92 and 0.93, respectively. The Acorn Woodpecker model has the same ecological niche overlap between the 2D and 3D models as the Western Bluebird at 0.93 but a slightly higher Spearman's rank correlation in the spatial distribution of values at 0.93 compared to the Western Bluebird at 0.89.

Connectivity models

The connectivity outputs are closely aligned with the habitat suitability outputs, as the predicted connectivity for the 2D and 3D models for both species demonstrated a high degree of correlation (Fig. 4). Specifically, the Pearson correlation coefficient was 0.93 for the Western Bluebird and 0.96 for the Acorn Woodpecker. There is a notable consensus that higher connectivity values are concentrated in larger urban green spaces and natural remnant habitats for both species. This pattern was also reflected in the Maxent models. The Acorn Woodpecker's predicted connectivity was concentrated in a few areas, whereas the Western Bluebird exhibited intermediate connectivity values throughout the study area. This pattern was also evident in the habitat suitability models. The behavior of the connectivity models mirrors that of the habitat suitability models, following similar patterns and showing substantial similarities between the 2D and 3D models.

When examining the top 10% connectivity values, some differences emerged between the 2D and 3D models for both the Acorn Woodpecker and Western Bluebird (Fig. 4). The largest differences can be observed in the mountainous northwest portion of the study area. For both the Western Bluebird and Acorn Woodpecker connectivity models, the 2D models predicted a greater extent of this region within the top 10% of connectivity values compared to the 3D models. However, for the Acorn Woodpecker, the 3D model also redistributed high-connectivity values within this region, with some areas identified in the 2D top 10% no longer retained in 3D and others emerging as newly prioritized.

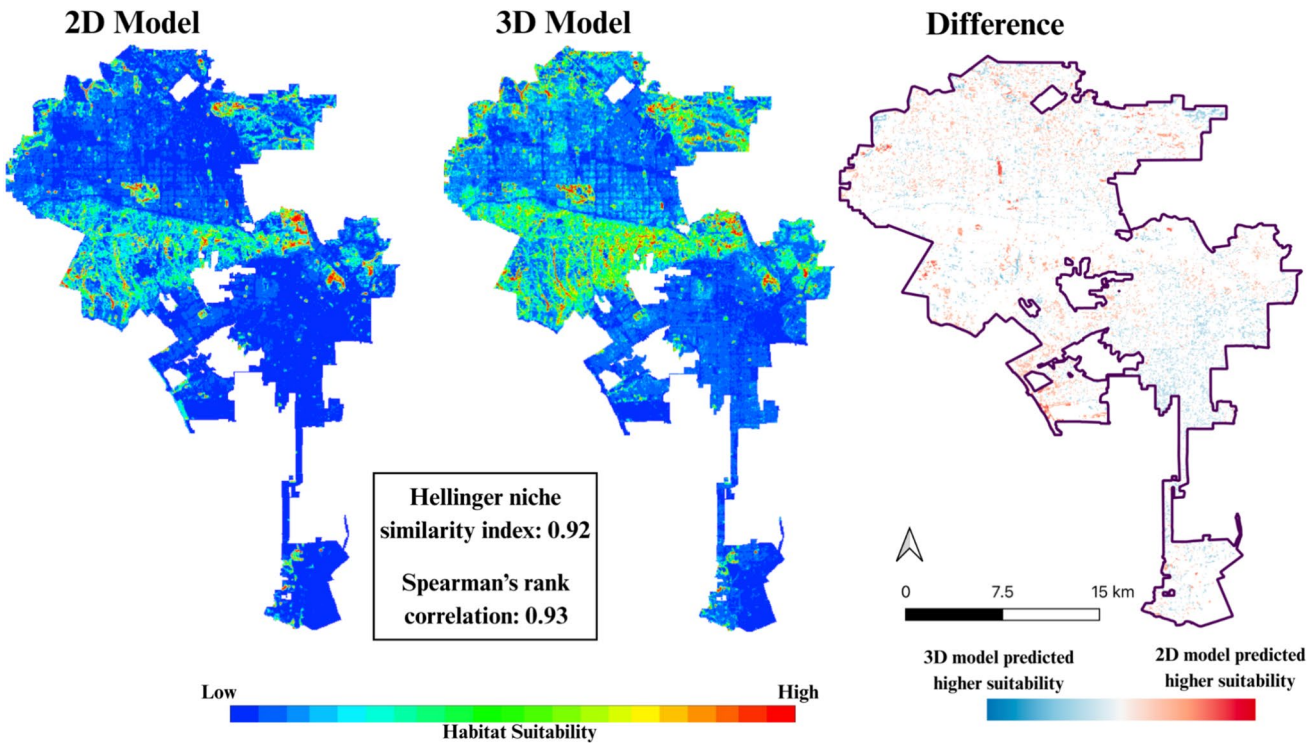

Fig. 3 Predicted habitat suitability from 2D and 3D models for the Acorn Woodpecker, and the spatial differences in predicted suitability comparing these two model

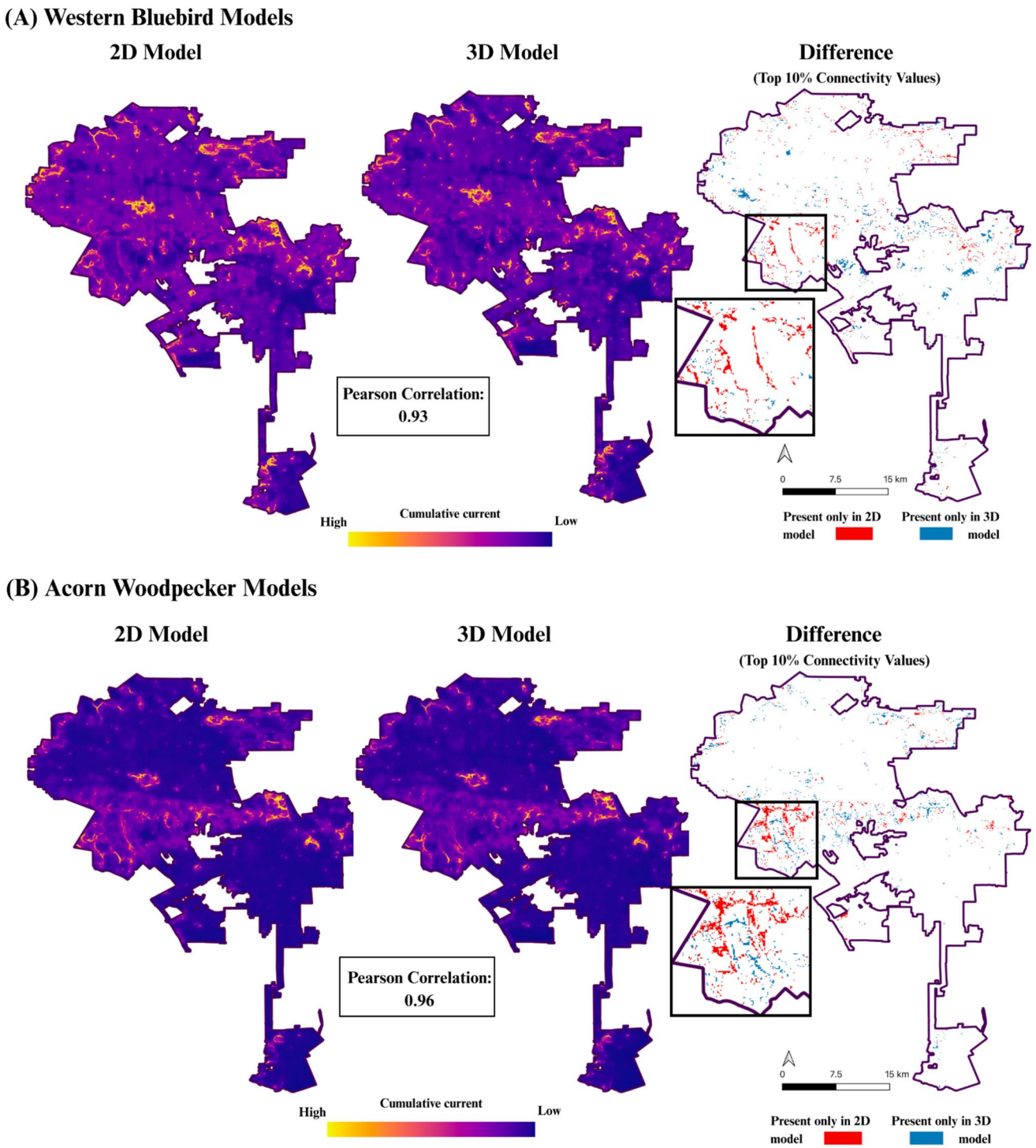

Fig. 4 Cumulative current flow from 2D and 3D connectivity models for (A) Western Bluebird and (B) Acorn Woodpecker. Spatial differences in predicted high-connectivity areas (top 10% of cumulative current flow) are shown to highlight divergence between models. Insets display the mountainous northwest portion of the study area, where the greatest differences in high-connectivity spatial prioritization were observed between models

Discussion

This study evaluated the sensitivity of habitat suitability and connectivity outputs derived from these models for Western Bluebird and Acorn Woodpecker to the inclusion of 3D measures of urban landscape structure. Across both species, 2D and 3D habitat suitability models performed similarly according to standard validation metrics, exceeding the commonly accepted thresholds for Area Under the Curve (AUC) and True Skill Statistic (TSS) (Allouche et al. 2006; Laszlo et al. 2022), suggesting that the addition of the two 3D variables to the model did not significantly improve model fit. Niche overlap between 2D and 3D models was high for both species, and Spearman rank correlations were similarly strong, suggesting that while there are some differences between the models, they largely agree on the distribution of suitability values. Downstream connectivity outputs derived from these suitability models were also highly correlated, indicating that predicted connectivity values were largely stable to the inclusion of 3D representation of the landscape. However, differences emerged in the variable importance and in the spatial configuration of some high-connectivity values. Together, these results suggest that while the inclusion of 3D variables does not substantially alter model performance or overall spatial agreement of outputs, it does alter the spatial patterns in some areas.

Sensitivity of habitat suitability models to the inclusion of 3D representations of landscapes

Across both species, incorporating representation of 3D urban landscape structure did not substantially improve habitat suitability model performance relative to 2D models, as reflected by similar AUC and TSS values. Interpreting these results in relation to prior work is not straightforward because explicit 2D-3D comparisons for bird habitat suitability models remain relatively limited, in part due to the relatively recent availability of LiDAR and SfM remote sensing products. The studies that do exist span different species (Bae et al. 2014; Hagar et al. 2020; Lawrence 2024), are often focused on forest ecosystems (Burns et al. 2020; Basile et al.2021), and analysis spans different scales, which makes direct comparison challenging. Within this emerging literature, some studies report improved performance when LiDAR-derived metrics are included. For example, Hazel Grouse (*Tetrastes bonasia*) models using LiDAR-derived metrics outperformed models based on aerial photography (Bae et al. 2014), and LiDAR-derived forest structure metrics improved habitat suitability modeling for species such as the Northern Spotted Owl (*Strix Occidentalis Caurina*) (Hagar et al. 2020) and Red-cockaded Woodpecker (*Dryobates Borealis*) (Lawrence 2024). Other work suggests that performance gains are modest and that the more consistent effect of adding 3D metrics is a reweighting of predictor importance, which then refines habitat suitability values by capturing more detailed information on habitat quality, particularly for canopy and forest associated species (Burns et al. 2020). Similarly, another study reported that incorporating 3D metrics improved SDM performance for some species, with the magnitude varying substantially among bird species (Davison et al. 2023).

Results from the present study align with the broader patterns reported in Burns et al. (2020) and Davison et al. (2023). Incorporating 3D metrics produced limited gains in overall model performance gain but meaningful shifted variable importance, most notably mean tree height for the Acorn Woodpecker, a canopy associated species (MacRoberts and MacRoberts 1976), resulting in a reorganization of suitability values in some areas. Mean canopy height emerged as an influential predictor for the Acorn Woodpecker, consistent with evidence that vertical canopy structure is especially informative for canopy associated species (Burns et al. 2020), where vegetation structure captures relevant habitat quality (Beninde et al. 2015). Meanwhile, mean building height contributed more strongly to Western Bluebird models, a species more often associated with open areas and suburban landscapes in cities (Guinan et al. 2020), indicating that sensitivity to vertical attributes may be species-specific and can reflect not only vegetation structure but also built structure (Davison et al. 2023; Buenaño-Mariño et al. 2025). This result is consistent with emerging broad-scale evidence that building height can be an important predictor for birds; for example, a study found that across 298 U.S. cities building height was among the strongest predictors for bird richness (Buenaño-Mariño et al. 2025).

Differences between this study and the SDM studies that reported larger performance gains with the incorporation of LiDAR-derived metrics (Bae et al. 2014; Hagar et al. 2020; Lawrence 2024) likely reflects differences in model parameterization, particularly the grain size at which environmental predictors were calculated (Connor et al. 2018). While our study calculated environmental predictors at 100 m, the previous studies mentioned (Bae et al. 2014; Hagar et al. 2020; Lawrence 2024), calculated environmental predictors ranging from 2.4 to 25 ha. Meanwhile, the prior studies mentioned that had results more closely aligned with our study results (Burns et al. 2020; Davison et al. 2023), calculated environmental predictors ranging from 150 to 1000 m. Evidence from multiple studies shows that model results can shift depending on the grain size at which analyses are conducted (Connor et al. 2018; Manzoor et al. 2018; Frazier et al. 2021), and that optimal grain sizes can be species-specific (Seavy et al. 2009). Given the results of this study

and others showing that model outcomes can shift across grain sizes in species-specific ways, identifying the grain at which 3D measures of urban landscape structure are most informative, especially by species, is an important next step for interpreting and applying 3D metrics in habitat suitability modeling.

Sensitivity of connectivity outputs to the inclusion of 3D representations of urban landscapes in habitat suitability models

As expected, connectivity outputs closely mirrored the patterns of habitat suitability, with both 2D and 3D connectivity models demonstrating a strong agreement for both species (Popescu et al. 2021; McCluskey et al. 2024). However, a previous study, while not comparing 2D to 3D connectivity, found that varying Omniscape moving window sizes (i.e., the spatial scale of dispersal analyzed) can have a larger effect on predicted connectivity than changes to the input resistance layer (Belote et al. 2022). In this study, connectivity was modeled using a 1 km moving window to represent local-scale connectivity (see Methods), and this parameter was held constant to isolate sensitivity to 2D versus 3D landscape representation. However, given the sensitivity reported by Belote et al. (2022), differences between 2D and 3D outputs may be larger or smaller under alternative window sizes. Therefore, we recommend that future studies assess the sensitivity of 3D connectivity model to varying window sizes, which may reflect larger changes between 2D and 3D model outputs.

Areas of high predicted connectivity were consistently located within protected open spaces and remnant natural habitats across both 2D and 3D models, underscoring the significant influence of the protected open space variable in the underlying habitat suitability models. The models reinforce the ecological importance of protected open space for providing habitat for species (Beninde et al. 2015; La Sorte et al. 2020). At the same time, because occurrence data were derived from community science observations, residual sampling bias toward greenspaces (e.g. parks) may contribute to the prominence of these areas in model predictions, even with bias correction, spatial thinning, and spatially structured validation (Dimson and Gillespie 2023; Tulloch and Szabo 2012). Notably, another study parameterized resistance using land-use intensity and a habitat quality index (vegetation type quality and patch size), rather than deriving from species-specific habitat suitability models, yet protected open spaces were similarly identified as important to connectivity in Los Angeles (Brown 2019). Together, these findings suggest that while sampling bias may influence the magnitude of predicted connectivity in protected open areas, their consistent prominence across modeling approaches and support in the literature as important places of habitat reflects their importance for connectivity (Brown 2019; Beninde et al. 2015; McCluskey et al. 2024; Kang et al. 2015).

Despite the overall agreement in the prominence of protected open spaces in the 2D and 3D connectivity outputs, differences emerged in the spatial prioritization of high-connectivity values. Although few studies have directly compared 2D and 3D connectivity models, prior work incorporating LiDAR-derived metrics into resistance inputs for connectivity modeling have also documented spatial shifts in predicted high-connectivity (Choi et al. 2021; Casalegno et al. 2017). For example, Casalegno et al. (2017) found that incorporating vegetation height into connectivity modeling led to the 3D model to predict a smaller extent of connected area compared to the 2D model. A similar pattern emerged in the mountainous northwest portion of our study area, where tree canopy height varied. In this area, the 2D models identified a greater extent of high connectivity values compared to the 3D models for both species. However, a species-specific difference was evident for the Acorn Woodpecker, with the 3D model reprioritizing high connectivity values toward locations corresponding to higher mean tree canopy. These patterns mirror the broader habitat suitability predictions and likely reflects differences in habitat associations, with the Western Bluebird more broadly associated with open and suburban environments (Guinan et al. 2020) and the Acorn Woodpecker more associated with dense, mature forests (MacRoberts and MacRoberts 1976). These findings highlight how alternative representations of landscape structure can propagate species-specific habitat associations from habitat suitability models through the resistance surface, resulting in redistribution of some high connectivity values in connectivity outputs.

We recommend interpreting our results within the context of the commonly used practice of deriving resistance surfaces from habitat suitability models in connectivity analyses. In this common modeling pipeline, areas of higher predicted suitability are assumed to facilitate movement and are therefore assigned lower resistance values, producing connectivity outputs that represent potential rather than realized movement pathways (Zeller et al. 2012). In data-limited systems, resistance surfaces are frequently derived from expert opinion or habitat suitability models because direct measurement of movement costs across heterogeneous landscapes is logistically challenging (Beier et al. 2011; Shimazaki et al. 2016). Empirically estimating movement costs would require tracking individuals using high-resolution telemetry data and quantifying how specific structural attributes alter movement behavior and path selection through approaches such as step selection or path selection functions (Zeller et al. 2016). Connectivity modeling in

urban landscapes is rarely empirically validated, and more studies are needed to understand the ecological value and implications of connectivity in urban landscapes (Lookingbill et al. 2022). Thus, the results of this study do not support inference of movement behavior; rather, they clarify how 2D versus 3D representation of urban landscape structure within in habitat suitability modeling propagate through the connectivity modeling pipeline. These findings underscore the importance of transparently evaluating model sensitivity to methodological choices of landscape dimensional representation. Future research integrating empirical movement data for parameterization and validation of connectivity models is an important next step toward better understanding of how 3D structure of urban landscapes influences connectivity for different species.

Limitations and future directions

As with all modeling studies, we note several limitations of our study to consider when interpreting these findings. First, the connectivity model inputs were not parameterized or validated using actual movement data. Although species occurrence data were used for both training and validation, and separate datasets were employed following best practices, this approach does not capture behavioral responses or movement pathways directly (Creech et al. 2024). For example, a study evaluating different methods for estimating resistance surfaces found that for pumas (*Puma concolor*) in Southern California, models based on GPS collars or genetic data outperformed those based on presence-only data (Zeller et al. 2018). Notably, presence-only models still yielded useful results when applied within a circuit theory based model, such as Omniscape, but actual movement derived models still achieved better predictive performance overall. The authors concluded that while GPS or genetic data are ideal for resistance surface calibration, presence-only SDMs may still be a practical alternative in data-limited contexts (Zeller et al. 2018). The intention of this study was to test model sensitivity to the inclusion of 3D representations of landscape rather than test whether the outputs predicted actual movement. Future research integrating telemetry, experimental movement studies, or genetic data could provide important opportunities to evaluate how 3D landscape structure shapes connectivity for species.

Second, the representation of 3D landscape structure was constrained by spatial scale and multicollinearity among LiDAR-derived variables. Environmental variables were derived at a 100 m grain and were highly correlated at this grain size, leaving a small subset of vegetation and building height variables for the inclusion in the models, whereas previous studies often incorporated multiple 3D variables and computed them over larger spatial extents (e.g., Bae et al. 2014; Hagar et al. 2020; Lawrence 2024). These scale and collinearity constraints may have reduced the ability of the 3D variables to capture different aspects of vertical heterogeneity of the landscape. Future work could test the sensitivity of 3D variables to alternative grain sizes to determine the spatial scales at which 3D urban landscape structure most strongly influences habitat suitability and connectivity.

Finally, our study focused on only two species with contrasting habitat associations, which allowed evaluation of differential sensitivity to 2D versus 3D landscape representation in habitat suitability modeling and its downstream connectivity outputs, but limits the generality of these findings. Expanding to species across different functional groups and habitat associations will be important, as previous research indicates that the ecological effects of urbanization can differ depending on species traits (Rogers 2022; Gray et al. 2007; Haight et al. 2025). Given that much of this work is based on 2D land cover/land use data, it is expected that capturing the added heterogeneity introduced with 3D landscape measures would show even more variation in species responses. Pairing such multi-species modeling with empirical movement data would be particularly valuable for linking 3D urban landscape structure to ecological outcomes (Milanesi et al. 2017). Additionally, since 2D habitat suitability models are sensitive to spatial grain, connectivity models are sensitive to moving window size, and species responses vary across ecoregions, it is reasonable to expect that the influence of 3D landscape representation will likewise depend on these methodological choices and the species (Lin et al. 2021; Connor et al. 2018; Manzoor et al. 2018; Frazier et al. 2021). Further research could therefore evaluate 3D variables across alternative spatial scales in habitat suitability modeling, varying moving window sizes in connectivity modeling, and multiple species across ecoregions to better understand how 3D landscape measures behave under different modeling parameters.

Conclusion

The Kunming-Montreal Global Biodiversity Framework calls for cities to conserve biodiversity and identifies ecological connectivity as a primary strategy (Convention on Biological Diversity 2023). Cities are characterized by fine-scale heterogeneity, intense human modification, and high vertical variation of vegetation and built landscape features (Grimm et al. 2008; Wentz et al. 2018; Cadenasso et al. 2007). As a result, metrics and modeling assumptions developed for non-urban systems may not be directly applicable to urban environments (LaPoint et al. 2015). Connectivity studies in urban areas are limited and more

research is needed to understand the ecological value and implications of connectivity in urban landscapes (Lookingbill et al. 2022). Additionally, with the growing availability of high-resolution 3D datasets, there is an opportunity to gain a deeper understanding of how species respond to vertical landscape structure, which is particularly relevant for species that navigate vertical space such as birds (Liu et al. 2021). Despite the growing availability of these datasets, these data are rarely integrated into habitat suitability and connectivity models, representing an important methodological and conceptual gap (Merrick et al. 2013; Elliott et al. 2025).

This study addressed this methodological gap by evaluating the sensitivity of habitat suitability and connectivity outputs to the inclusion of 3D representations of urban landscape structure within a commonly used habitat suitability to resistance layer input for connectivity modeling pipeline. The results of the study show that even when overall habitat suitability and downstream connectivity outputs are broadly similar, the inclusion of 3D variables still produced discernible differences in the spatial configuration of high connectivity values. Because connectivity maps are often used to prioritize areas for conservation (Rudnick et al. 2012), even subtle differences in spatial configuration may influence management decisions in urban landscapes. More broadly, these results underscore the importance of evaluating how upstream modeling choices propagate through connectivity workflows. As high-resolution 3D data from LiDAR and SfM become increasingly available in urban environments, the intentional inclusion and transparent evaluation of 3D data will be important for interpreting model behavior.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11252-026-01948-y.

Acknowledgements This research originated as part of the corresponding author's dissertation at the University of California, Los Angeles. The corresponding author thanks her dissertation committee, Drs. V. Kelly Turner, Kirsten Schwarz, Thomas Gillespie, Morgan Tingley, and Amy Frazier for their guidance and valuable feedback throughout the development of this work. The corresponding author also thanks Raffaella D'Auria and Joshua Banta for technical assistance in troubleshooting model execution on the Hoffman2 Cluster. This research benefited from the computational and storage resources provided by the Hoffman2 Cluster, operated by the UCLA Office of Advanced Research Computing's Research Technology Group, and was supported by funding from the Graduate Division of the University of California, Los Angeles.
Subsequent revisions, additional analyses, and manuscript development were conducted at the University of California, Santa Barbara, and benefited from the intellectual environment and resources of the Spatial Conservation and Landscape Ecology (SCALE) Lab.
The authors thank CTrees for providing access to their high-resolution tree canopy height dataset for Los Angeles, which was integral to the 3D structural analyses conducted in this study. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

Author contributions Morgan L. Rogers: Conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, validation, visualization, writing - original draft, writing - review and editing.
Amy E. Frazier: Supervision of conceptualization and analysis, Writing - Review & Editing.
Amanda J. Zellmer: Writing - Review & Editing.
Susannah B. Lerman: Writing - Review & Editing.

Funding This work was supported by a fellowship grant from the Division of Graduate Education at the University of California, Los Angeles.

Data availability All data and code used in this study, including scripts used to process the environmental data, are publicly available at https://github.com/mlrog/suitability-connectivity-2D-3D. Access to the CTrees dataset can be requested directly from CTrees (info@ctrees.org).

Declarations

Competing interest The authors declare no competing interests.

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References

Ahmer I, Ostendorf B (2025) Harnessing the power of categorical maps for spatial modelling – a case study for soil type using Maxent. Ecol Modell 508:111096. https://doi.org/10.1016/j.ecolmodel.2025.111096

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP, Bjornson R, Weston S (2015) spThin: functions for spatial thinning of species occurrence records for use in ecological models (Version 0.2.0) [Computer software]. https://cran.r-project.org/web/packages/spThin/index.html. Accessed Feb 2026

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43(6):1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Amini Tehrani N, Naimi B, Jaboyedoff M (2020) Toward community predictions: multi-scale modelling of mountain breeding birds' habitat suitability, landscape preferences, and environmental drivers. Ecol Evol 10(12):5544–5557. https://doi.org/10.1002/ece3.6295

Bae S, Reineking B, Ewald M, Mueller J (2014) Comparison of airborne lidar, aerial photography, and field surveys to model the

habitat suitability of a cryptic forest species – the hazel grouse. Int J Remote Sens 35(17):6469–6489. https://doi.org/10.1080/01431161.2014.955145

Banta JA (2024) How to run Maxent using R [Computer software]. Patreon. https://www.patreon.com/collection/625696. Accessed May 2025

Barber RA, Ball SG, Morris RKA, Gilbert F (2022) Target-group backgrounds prove effective at correcting sampling bias in Maxent models. Divers Distrib 28(1):128–141. https://doi.org/10.1111/ddi.13442

Basile M, Storch I, Mikusiński G (2021) Abundance, species richness and diversity of forest bird assemblages – the relative importance of habitat structures and landscape context. Ecol Indic 133:108402. https://doi.org/10.1016/j.ecolind.2021.108402

Beier P, Spencer W, Baldwin RF, McRAE BH (2011) Toward best practices for developing regional connectivity maps. Conserv Biol 25(5):879–892. https://doi.org/10.1111/j.1523-1739.2011.01716.x

Belote RT, Barnett K, Zeller K, Brennan A, Gage J (2022) Examining local and regional ecological connectivity throughout North America. Landscape Ecol 37(12):2977–2990. https://doi.org/10.1007/s10980-022-01530-9

Beninde J, Delaney TW, Gonzalez G, Shaffer HB (2023) Harnessing iNaturalist to quantify hotspots of urban biodiversity: the Los Angeles case study. Front Ecol Evol. https://doi.org/10.3389/fevo.2023.983371

Beninde J, Veith M, Hochkirch A (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecol Lett 18(6):581–592. https://doi.org/10.1111/ele.12427

Bino G, Levin N, Darawshi S, Van Der Hal N, Reich-Solomon A, Kark S (2008) Accurate prediction of bird species richness patterns in an urban environment using Landsat-derived NDVI and spectral unmixing. Int J Remote Sens 29(13):3675–3700. https://doi.org/10.1080/01431160701772534

Bélisle M (2005) Measuring landscape connectivity: the challenge of behavioral landscape ecology. Ecology 86(8):1988–1995. https://doi.org/10.1890/04-0923

Brown IT (2019) Managing cities as urban ecosystems: analysis tools for biodiversity stewardship in Los Angeles [UCLA]. https://escholarship.org/uc/item/4c81w4nr#metrics. Accessed May 2024

Buenaño-Mariño CdelP, Barratt Heitmann J, García-Esparza JA, Mason BM, Callaghan CT (2025) Does building height influence bird diversity in urban landscapes? Landscape Ecol 41(1):5. https://doi.org/10.1007/s10980-025-02247-1

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach (2nd ed.). Springer. https://doi.org/10.1007/b97636

Burns P, Clark M, Salas L, Hancock S, Leland D, Jantz P, Dubayah R, Goetz SJ (2020) Incorporating canopy structure from simulated GEDI lidar into bird species distribution models. Environ Res Lett 15(9):095002. https://doi.org/10.1088/1748-9326/ab80ee

Cadenasso ML, Pickett STA, Schwarz K (2007) Spatial heterogeneity in urban ecosystems: reconceptualizing land cover and a framework for classification. Front Ecol Environ 5(2):80–88. https://doi.org/10.1890/1540-9295(2007)5[80:SHIUER]2.0.CO;2

Camarretta N, Harrison PA, Bailey T, Potts B, Lucieer A, Davidson N, Hunt M (2020) Monitoring forest structure to guide adaptive management of forest restoration: a review of remote sensing approaches. New Forest 51(4):573–596. https://doi.org/10.1007/s11056-019-09754-5

Casalegno S, Anderson K, Cox DTC, Hancock S, Gaston KJ (2017) Ecological connectivity in the three-dimensional urban green volume using waveform airborne lidar. Sci Rep 7(1):45571. https://doi.org/10.1038/srep45571

Choi H, Song Y, Kang W, Thorne JH, Song W, Lee DK (2021) LiDAR-derived three-dimensional ecological connectivity mapping for urban bird species. Landscape Ecol 36(2):581–599. https://doi.org/10.1007/s10980-020-01165-8

City of Los Angeles Department of Sanitation & Environment. (2022). LA biodiversity index baseline report 2022. City of Los Angeles. https://www.lacitysan.org/cs/groups/public/documents/document/y250/mdc2/~edisp/cnt076756.pdf. Accessed Oct 2025

Collar N, Christie DA (2014) Western Bluebird (Sialia mexicana). In: del Hoyo J, Elliott A, Sargatal J, Christie, DA, de Juana E (eds) Handbook of the birds of the world alive. Lynx Edicions. https://birdsoftheworld.org/bow/historic/hbw/wesblu/1.0/introduction. Accessed May 2025

Connor T, Hull V, Viña A, Shortridge A, Tang Y, Zhang J, Wang F, Liu J (2018) Effects of grain size and niche breadth on species distribution modeling. Ecography 41(8):1270–1282. https://doi.org/10.1111/ecog.03416

Convention on Biological Diversity. (2023). Kunming-Montreal global biodiversity framework. Secretariat of the convention on biological diversity. https://www.cbd.int/gbf/goals. Accessed Feb 2026

Coops NC, Tompaski P, Nijland W, Rickbeil GJM, Nielsen SE, Bater CW, Stadt JJ (2016) A forest structure habitat index based on airborne laser scanning data. Ecol Indic 67:346–357. https://doi.org/10.1016/j.ecolind.2016.02.057

Coops NC, Wulder MA (2019) Breaking the habit(at). Trends Ecol Evol 34(7):585–587. https://doi.org/10.1016/j.tree.2019.04.013

Creech TG, Brennan A, Faselt J, Stabach JA, Keeley ATH (2024) Validating connectivity models: a synthesis. Curr Landscape Ecol Rep 9(4):120–134. https://doi.org/10.1007/s40823-024-00102-8

CTrees.org (2026) 2022 Sub-Meter Canopy Tree Height of Los Angeles Urban Area, CA [Dataset]. Accessed 29 Jan 2026

Cushman SA, Evans JS, McGarigal K, Kiesecker JM (2010) Toward Gleasonian landscape ecology: from communities to species, from patches to pixels. Res. Pap. RMRS-RP-84. Fort Collins, CO: U.S. Department of agriculture, forest service, rocky mountain research station 12:84. https://doi.org/10.2737/RMRS-RP-84

Davison CW, Assmann JJ, Normand S, Rahbek C, Morueta-Holme N (2023) Vegetation structure from LiDAR explains the local richness of birds across Denmark. J Anim Ecol 92(7):1332–1344. https://doi.org/10.1111/1365-2656.13945

Dewitz J (2023) National Land Cover Database (NLCD) 2021 Products. U.S. Geological Survey. https://www.mrlc.gov/data/references/national-land-cover-database-2021-landcover-imperviousness-nlcd2021

Dimson M, Gillespie TW (2023) Who, where, when: observer behavior influences spatial and temporal patterns of iNaturalist participation. Appl Geogr 153:102916. https://doi.org/10.1016/j.apgeog.2023.102916

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36(1):27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dutko K, Villa L, Squier B, Mahadi A, Thomas L, White J, Ha E, Saum J, Harris M (with Beninde J, MacDonald Z) (2023) Quantifying and validating habitat connectivity across greater Los Angeles. UCLA institute of the environment and sustainability. https://www.ioes.ucla.edu/project/quantifying-and-validating-habitat-connectivity-across-greater-los-angeles/. Accessed May 2025

Eldegard K, Dirksen JW, Ørka HO, Halvorsen R, Næsset E, Gobakken T, Ohlson M (2014) Modelling bird richness and bird species presence in a boreal forest reserve using airborne laser-scanning

and aerial images. Bird Study 61(2):204–219. https://doi.org/10.1080/00063657.2014.885492

Elith J, H. Graham C, P. Anderson R, Dudík M, Ferrier S, Guisan A, J. Hijmans R, Huettmann F, R. Leathwick J, Lehmann A, Li J, G. Lohmann L, A. Loiselle B, Manion G, Moritz C, Nakamura M, Nakazawa Y, McC. M. Overton J, Townsend Peterson A,…, E. Zimmermann N (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29(2):129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17(1):43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Elliott JM, Flaherty EA, Swihart RK, Jung J, Fei S (2025) Application of lidar and camera traps to model wildlife habitat. J Wildl Manage 89(8):e70093. https://doi.org/10.1002/jwmg.70093

European Space Agency (2022) Harmonized sentinel-2 MSI: MultiSpectral instrument, level-2A (SR). https://www.esa.int/Applications/Observing_the_Earth/Copernicus/Sentinel-2. Accessed Feb 2026

Feng H, Banerjee AK, Guo W, Yuan Y, Duan F, Ng WL, Zhao X, Liu Y, Li C, Liu Y, Li L, Huang Y (2024) Origin and evolution of a new tetraploid mangrove species in an intertidal zone. Plant Divers 46(4):476–490. https://doi.org/10.1016/j.pld.2024.04.007

Frazier AE, Honzák M, Hudson C, Perlin R, Tohtsonie A, Gaddis KD, de Sousa C, Larsen TH, Junker J, Nyandwi S, Trgovac AB (2021) Connectivity and conservation of Western Chimpanzee (*Pan troglodytes verus*) habitat in Liberia. Divers Distrib 27(7):1235–1250. https://doi.org/10.1111/ddi.13270

GBIF.org (2025) GBIF occurrence download. Global biodiversity information facility. https://www.gbif.org/. Accessed May 2025

Gray MA, Baldauf SL, Mayhew PJ, Hill JK (2007) The response of avian feeding guilds to tropical forest disturbance. Conserv Biol 21(1):133–141. https://doi.org/10.1111/j.1523-1739.2006.00557.x

GreenInfoNetwork (2020) California Protected Areas Database (CPAD), Version 2020b. https://www.calands.org. Accessed Feb 2026

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. Science 319(5864):756–760. https://doi.org/10.1126/science.1150195

Guinan JA, Gowaty PA, Eltzroth EK (2020) Western Bluebird (Sialia mexicana), version 1.0. In: Poole AF (Ed.) Birds of the world. Cornell Lab Ornithology. https://doi.org/10.2173/bow.wesblu.01

Hagar JC, Yost A, Haggerty PK (2020) Incorporating LiDAR metrics into a structure-based habitat model for a canopy-dwelling species. Remote Sens Environ 236:111499. https://doi.org/10.1016/j.rse.2019.111499

Hager SB, Cosentino BJ, McKay KJ, Monson C, Zuurdeeg W, Blevins B (2013) Window area and development drive spatial variation in bird-window collisions in an urban landscape. PLoS One 8(1):e53371. https://doi.org/10.1371/journal.pone.0053371

Haight JD, de Albuquerque FS, Bateman HL, Frazier AE, Larson KL (2025) Urbanization and climate drive long-term bird community trends across a desert city ecosystem. Ecol Appl 35(4):e70063. https://doi.org/10.1002/eap.70063

Henckel L, Bradter U, Jönsson M, Isaac NJB, Snäll T (2020) Assessing the usefulness of citizen science data for habitat suitability modelling: opportunistic reporting versus sampling based on a systematic protocol. Divers Distrib 26(10):1276–1290. https://doi.org/10.1111/ddi.13128

Hijmans RJ, Barbosa M, Bivand R, Brown A, Chirico M, Cordano E, Dyba K, Pebesma E, Rowlingson B, Sumner MD (2025a) terra: spatial data analysis (Version 1.8–50) [Computer software]. https://cran.r-project.org/web/packages/terra/index.html. Accessed May 2025

Hijmans RJ, Phillips S, Leathwick J, Elith J (2024) dismo: species distribution modeling (Version 1.3–16) [Computer software]. https://cran.r-project.org/web/packages/dismo/index.html. Accessed May 2025

Hijmans RJ, van Etten J, Sumner M, Cheng J, Baston D (2025b) raster: geographic data analysis and modeling (Version 3.6–3.2) [Computer software]. CRAN – the comprehensive R archive network. https://cran.r-project.org/web/packages/raster/index.html. Accessed May 2025

Huang Q, Swatantran A, Dubayah R, Goetz SJ (2014) The influence of vegetation height heterogeneity on forest and woodland bird species richness across the United States. PLoS One 9(8):e103236. https://doi.org/10.1371/journal.pone.0103236

Huntley B, Collingham YC, Green RE, Hilton GM, Rahbek C, Willis SG (2006) Potential impacts of climatic change upon geographical distributions of birds. Ibis 148(s1):8–28. https://doi.org/10.1111/j.1474-919X.2006.00523.x

Iglhaut J, Cabo C, Puliti S, Piermattei L, O'Connor J, Rosette J (2019) Structure from motion photogrammetry in forestry: a review. Curr Forestry Rep 5(3):155–168. https://doi.org/10.1007/s40725-019-00094-3

Kang W, Minor ES, Park C-R, Lee D (2015) Effects of habitat structure, human disturbance, and habitat connectivity on urban forest bird communities. Urban Ecosyst 18(3):857–870. https://doi.org/10.1007/s11252-014-0433-5

Kass JM, Muscarella R, Galante PJ, Bohl C, Buitrago-Pinilla GE, Boria RA, Soley-Guardia M, Anderson RP (2025) ENMeval: automated tuning and evaluations of ecological niche models (Version 2.0.5.2) [Computer software]. https://cran.r-project.org/web/packages/ENMeval/index.html. Accessed May 2025

Keeley ATH, Beier P, Keeley BW, Fagan ME (2017) Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. Landsc Urban Plann 161:90–102. https://doi.org/10.1016/j.landurbplan.2017.01.007

Koenig WD, Haydock J, Dugdale HL, Walters EL (2023) Territory inheritance and the evolution of cooperative breeding in the acorn woodpecker. Anim Behav 205:241–249. https://doi.org/10.1016/j.anbehav.2023.08.021

Koenig WD, Hooge PN, Stanback MT, Haydock J (2000) Natal dispersal in the cooperatively breeding acorn woodpecker. Condor: Ornithol Appl 102(3):492–502. https://doi.org/10.1093/condor/102.3.492

Koenig WD, Walters EL, Barve S (2019) Does helping-at-the-nest help? The case of the acorn woodpecker. Front Ecol Evol. https://doi.org/10.3389/fevo.2019.00272

Kreling SES, Gaynor KM, Coon CAC (2019) Roadkill distribution at the wildland-urban interface. J Wildl Manag 83(6):1427–1436. https://doi.org/10.1002/jwmg.21692

Landau V, Shah V, Anantharaman R, Hall K (2021) Omniscape.jl: software to compute omnidirectional landscape connectivity. J Open Source Softw 6(57):2829. https://doi.org/10.21105/joss.02829

LaPoint S, Balkenhol N, Hale J, Sadler J, van der Ree R (2015) Ecological connectivity research in urban areas. Funct Ecol 29(7):868–878. https://doi.org/10.1111/1365-2435.12489

La Sorte FA, Aronson MFJ, Lepczyk CA, Horton KG (2020) Area is the primary correlate of annual and seasonal patterns of avian species richness in urban green spaces. Landsc Urban Plann 203:103892. https://doi.org/10.1016/j.landurbplan.2020.103892

Laszlo AM, Placyk JS, Williams LR, Williams MG, Banta JA (2022) A novel multivariate ecological approach to modeling freshwater mussel habitats verified by ground truthing. Hydrobiologia 849(14):3117–3133. https://doi.org/10.1007/s10750-022-04913-w

Lawrence B (2024) Lidar-based MaxEnt models to support conservation planning for endangered red-cockaded woodpeckers in urbanizing environments. Remote Sensing Applications: Society and Environment 34:101190. https://doi.org/10.1016/j.rsase.2024.101190

Lin Y, An W, Gan M, Shahtahmassebi A, Ye Z, Huang L, Zhu C, Huang L, Zhang J, Wang K (2021) Spatial grain effects of urban green space cover maps on assessing habitat fragmentation and connectivity. Land 10(10):1065. https://doi.org/10.3390/land10101065

Liu Z, Huang Q, Tang G (2021) Identification of urban flight corridors for migratory birds in the coastal regions of Shenzhen city based on three-dimensional landscapes. Landsc Ecol. https://doi.org/10.1007/s10980-020-01032-6

Lookingbill TR, Minor ES, Mullis CS, Nunez-Mir GC, Johnson P (2022) Connectivity in the urban landscape (2015–2020): who? Where? What? When? Why? and how? Curr Landsc Ecol Rep 7(1):1–14. https://doi.org/10.1007/s40823-021-00068-x

Los Angeles GeoHub (2017) Building footprints – City of Los Angeles. City of Los Angeles. https://geohub.lacity.org/datasets/813fcefde1f64b209103107b26a8909f_0/about. Accessed Oct 2024

Loss SR, Will T, Loss SS, Marra PP (2014) Bird–building collisions in the United States: estimates of annual mortality and species vulnerability. Condor 116(1):8–23. https://doi.org/10.1650/CONDOR-13-090.1

Lynch AJ (2019) Creating effective urban greenways and stepping-stones: four critical gaps in habitat connectivity planning research. J Plann Lit 34(2):131–155. https://doi.org/10.1177/0885412218798334

MacRoberts MH, MacRoberts BR (1976) Social organization and behavior of the Acorn Woodpecker in central coastal California. Ornithol Monogr 21:1–115

Manzoor SA, Griffiths G, Lukac M (2018) Species distribution model transferability and model grain size – finer may not always be better. Sci Rep 8(1):7168. https://doi.org/10.1038/s41598-018-25437-1

McCluskey EM, Kuzma FC, Enander HD, Cole-Wick A, Coury M, Cuthrell DL, Johnson C, Kelso M, Lee YM, Methner D, Rowe L, Swinehart A, Moore JA (2024) Assessing habitat connectivity of rare species to inform urban conservation planning. Ecol Evol 14(3):e11105. https://doi.org/10.1002/ece3.11105

McRae B, Popper K, Jones A, Schindel S, Buttrick K, Hall K, Unnasch RS, Platt J (2016) Conserving nature's stage: mapping omnidirectional connectivity for reslient terrestrial landscapes in the Pacific Northwest. The nature conservancy, pp 47. http://nature.org/resilienceNW. Accessed Jan 2023

Melin M, Mehtätalo L, Miettinen J, Tossavainen S, Packalen P (2016) Forest structure as a determinant of grouse brood occurrence – an analysis linking LiDAR data with presence/absence field data. For Ecol Manag Spec Sect: Drought US For: Impacts Potential Manag Responses 380:202–211. https://doi.org/10.1016/j.foreco.2016.09.007

Merow C, Smith MJ, Silander JA Jr (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36(10):1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

Merrick MJ, Koprowski JL, Wilcox C (2013) Into the third dimension: benefits of incorporating LiDAR data in wildlife habitat models. In: Gottfried, GJ, Ffolliott PF, Gebow BS, Eskew LG, Collins LC (eds) Merging science and management in a rapidly changing world: biodiversity and management of the Madrean archipelago III and 7th conference on research and resource management in the southwestern deserts; 2012 May 1–5; Tucson, AZ. Proceedings. RMRS-P-67, vol 67. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp 389–395. https://research.fs.usda.gov/treesearch/44465

Milanesi P, Holderegger R, Bollmann K, Gugerli F, Zellweger F (2017) Three-dimensional habitat structure and landscape genetics: a step forward in estimating functional connectivity. Ecology 98(2):393–402. https://doi.org/10.1002/ecy.1645

Nawrocki TW, Carlson ML, Osnas JLD, Trammell EJ, Witmer FDW (2020) Regional mapping of species-level continuous foliar cover: beyond categorical vegetation mapping. Ecol Appl 30(4):e02081. https://doi.org/10.1002/eap.2081

Pe'er G, Henle K, Dislich C, Frank K (2011) Breaking functional connectivity into components: a novel approach using an individual-based model, and first outcomes. PLoS One 6(8):e22355. https://doi.org/10.1371/journal.pone.0022355

Phillips P, Clark MM, Baral S, Koen EL, Bowman J (2021) Comparison of methods for estimating omnidirectional landscape connectivity. Landscape Ecol 36(6):1647–1661. https://doi.org/10.1007/s10980-021-01254-2

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Modell 190(3):231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31(2):161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol Appl 19(1):181–197. https://doi.org/10.1890/07-2153.1

Popescu VD, Kenyon M, Brown RK, Dyck MA, Prange S, Peterman WE, Dennison C (2021) Habitat connectivity and resource selection in an expanding bobcat (*Lynx rufus*) population. PeerJ 9:e12460. https://doi.org/10.7717/peerj.12460

Préau C, Dubos N, Lenormand M, Denelle P, Le Louarn M, Alleaume S, Luque S (2022) Dispersal-based species pools as sources of connectivity area mismatches. Landscape Ecol 37(3):729–743. https://doi.org/10.1007/s10980-021-01371-y

R Core Team (2024) R: a language and environment for statistical computing. R foundation for statistical computing (Version 4.4.3) [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Re AJ, Rogers AM, Possingham HP, Kark S (2025) Bird utilisation of vertical space in urban environments. Diversity 17(1):16. https://doi.org/10.3390/d17010016

Reynolds J, Ibáñez-Álamo JD, Sumasgutner P, Mainwaring MC (2019) Urbanisation and nest building in birds: a review of threats and opportunities. J Ornithol 160(3):841–860. https://doi.org/10.1007/s10336-019-01657-8

Richard Y, Armstrong DP (2010) Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data. J Appl Ecol 47(3):603–610. https://doi.org/10.1111/j.1365-2664.2010.01806.x

Robert K, Jones DOB, Roberts JM, Huvenne VAI (2016) Improving predictive mapping of deep-water habitats: considering multiple model outputs and ensemble techniques. Deep Sea Res Part I Oceanogr Res Pap 113:80–89. https://doi.org/10.1016/j.dsr.2016.04.008

Rogers ML (2022) Urban built form shapes avian richness in green spaces. Front Conserv Sci 3. https://www.frontiersin.org/articles/10.3389/fcosc.2022.768274

Rudnick DA, Ryan SJ, Beier P, Cushman SA, Dieffenbach F, Epps CW., Gerber LR, Hartter J, Jenness JS, Kintsch J, Merenlender AM, Perkl RM, Preziosi DV, Trombulak SC (2012) The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues in Ecology 16(Fall):1–20. https://research.fs.usda.gov/treesearch/42229

Saunders SP, Meehan TD, Michel NL, Bateman BL, DeLuca W, Deppe JL, Grand J, LeBaron GS, Taylor L, Westerkam H, Wu JX, Wilsey CB (2022) Unraveling a century of global change impacts on winter bird distributions in the eastern United States. Glob Change Biol 28(7):2221–2235. https://doi.org/10.1111/gcb.16063

Seavy NE, Viers JH, Wood JK (2009) Riparian bird response to vegetation structure: A multiscale analysis using LiDAR measurements of canopy height. Ecol Appl 19(7):1848–1857. https://doi.org/10.1890/08-1124.1

Shimazaki A, Yamaura Y, Senzaki M, Yabuhara Y, Akasaka T, Nakamura F (2016) Urban permeability for birds: an approach combining mobbing-call experiments and circuit theory. Urban Forestry Urban Greening 19:167–175. https://doi.org/10.1016/j.ufug.2016.06.024

Sillero N, Barbosa AM (2021) Common mistakes in ecological niche models. Int J Geogr Inf Sci 35(2):213–226. https://doi.org/10.1080/13658816.2020.1798968

Simons AL, Caldwell S, Fu M, Gallegos J, Gatheru M, Riccardelli L, Truong N, Viera V (2022) Constructing ecological indices for urban environments using species distribution models. Urban Ecosyst 25(6):1745–1764. https://doi.org/10.1007/s11252-022-01265-0

Skidmore AK, Coops NC, Neinavaz E, Ali A, Schaepman ME, Paganini M, Kissling WD, Vihervaara P, Darvishzadeh R, Feilhauer H, Fernandez M, Fernández N, Gorelick N, Geijzendorffer I, Heiden U, Heurich M, Hobern D, Holzwarth S, Muller-Karger FE,…, Wingate V (2021) Priority list of biodiversity metrics to observe from space. Nat Ecol Evol 5(7):7. https://doi.org/10.1038/s41559-021-01451-x

Sutherland GD, Harestad AS, Price K, Lertzman KP (2000) Scaling of natal dispersal distances in terrestrial birds and mammals. Conserv Ecol 4(1). https://www.jstor.org/stable/26271738. Accessed Feb 2026

Taylor PD, Fahrig L, With KA (2006) Landscape connectivity: a return to the basics. In: Crooks KR, Sanjayan M (eds) Connectivity conservation. Cambridge University Press, pp 29–43. https://doi.org/10.1017/CBO9780511754821.003

Tulloch AIT, Szabo JK (2012) A behavioural ecology approach to understand volunteer surveying for citizen science datasets. Emu Austral Ornithol 112(4):313–325. https://doi.org/10.1071/MU12009

U.S. Census Bureau (2021) 2020 decennial census: Los Angeles, California. https://data.census.gov/. Accessed May 2025

Venables WN, Ripley BD (2002) Modern Applied Statistics with S, Fourth edition. Springer, New York. ISBN 0-387-95457-0. https://www.stats.ox.ac.uk/pub/MASS4/. Accessed Feb 2025

Warren D, Dinnage R (2024) ENMTools: analysis of niche evolution using niche and distribution models (Version 1.12) [Computer software]. CRAN – the comprehensive R archive network. https://cran.r-project.org/web/packages/ENMTools/index.html. Accessed May 2025

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62(11):2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x

Warren DL, Seifert SN (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol Appl 21(2):335–342. https://doi.org/10.1890/10-1171.1

Warren PS, Katti M, Ermann M, Brazel A (2006) Urban bioacoustics: it's not just noise. Anim Behav 71(3):491–502. https://doi.org/10.1016/j.anbehav.2005.07.014

Wentz EA, York AM, Alberti M, Conrow L, Fischer H, Inostroza L, Jantz C, Pickett STA, Seto KC, Taubenböck H (2018) Six fundamental aspects for conceptualizing multidimensional urban form: a spatial mapping perspective. Landsc Urban Plann 179:55–62. https://doi.org/10.1016/j.landurbplan.2018.07.007

Yan X, Zhan Y, Yang W, Ross O, Liu Y, L Z, Lopez I, Perez I, Tao E, Vogel J, Cui D, Song L, Frazier AE (2025) Current and future habitat suitability for species of concern at the Jack and Laura Dangermond preserve. https://ecoevorxiv.org/repository/view/11124/. Accessed Feb 2026

Zeller KA, Jennings MK, Vickers TW, Ernest HB, Cushman SA, Boyce WM (2018) Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. Divers Distrib 24(7):868–879. https://doi.org/10.1111/ddi.12742

Zeller KA, McGarigal K, Cushman SA, Beier P, Vickers TW, Boyce WM (2016) Using step and path selection functions for estimating resistance to movement: pumas as a case study. Landsc Ecol 31(6):1319–1335. https://doi.org/10.1007/s10980-015-0301-6

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landsc Ecol 27(6):777–797. https://doi.org/10.1007/s10980-012-9737-0

Zhou Q, van den Bosch CCK, Chen J, Zhang W, Dong J (2021) Identification of ecological networks and nodes in Fujian province based on green and blue corridors. Sci Rep 11(1):20872. https://doi.org/10.1038/s41598-021-99416-4

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