Quantifying and Validating Habitat Connectivity Across Greater Los Angeles

Clients: City of Los Angeles & The Nature Conservancy

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I. Abstract

Habitat connectivity is an essential condition for long-term species persistence because it maintains natural movement dynamics, reduces potential inbreeding, and allows recolonization of uninhabited, but suitable habitat. The City of Los Angeles and The Nature Conservancy (TNC) are currently involved in multiple local and regional efforts to incorporate connectivity into urban biodiversity conservation planning efforts. However, quantifications of connectivity are still only available for a handful of species or rest on a singular assessment of habitat quality, making spatial prioritization for all species difficult. Our project, which is a collaboration with the City of Los Angeles and TNC, accomplished three primary goals: 1) generation of current flow connectivity surfaces for 1,017 species, using the spatial modeling frameworks of Omniscape, 2) validation of the connectivity surfaces using both community science data from iNaturalist and field observations generated in our study, and 3) production of combined connectivity surfaces across functional groups of species to generate “heatmaps” of connectivity. Our study is the first of this magnitude to quantify species-specific connectivity surfaces that can be utilized in conservation planning to preserve overall connectivity across Los Angeles’ fragmented urban landscape, and help minimize the risk of local species extinction and maximize the potential to maintain high levels of urban biodiversity.

II. Introduction

Rapid urbanization across the globe occurs at the expense of wildlands as the development of infrastructure degrades and fragments natural landscapes (Datry et al., 2017). Habitat connectivity, defined as the degree to which a heterogeneous landscape impedes or facilitates the natural movement of organisms among suitable patches of habitat, is an important consideration in conservation planning addressing fragmented landscapes (Liu et al., 2018). Human-made barriers, such as roads, buildings, or fences, as well as natural barriers, such as rivers or mountains, can significantly reduce connectivity at the landscape level. Habitat is an area with a sufficient distribution of resources and environmental conditions a species needs to thrive (Dennis et al., 2003), and is species-specific. As a result, fragmented landscapes have contrasting effects across species, as some key areas or features of a landscape required by one species may not be required by others (Elmqvist et al., 2016). Even partially complete landscapes can be highly fragmented for certain species and less for others (Elmqvist et al., 2016).

One example of a landscape fragmented through rapid urbanization is the Los Angeles metropolitan area (hereafter, "LA"). LA is situated within the California Floristic Province, a biodiversity hotspot recognized for its high species richness and number of endemic species (Ethington et al., 2020). As LA was rapidly urbanized into one of the world's largest metropolitan regions, the extent of its native coastal sage scrub, chaparral, oak woodlands, wetlands, and various other natural communities were reduced by development (Ethington et al., 2020). This resulted in dramatically less natural area for LA's almost 1400 terrestrial species, to inhabit (Beninde et al., 2023). As species are limited in movement across the divided patches of suitable habitat, smaller and more isolated populations are subject to inbreeding, loss of genetic diversity, and even local extinction (Elmqvist et al., 2016; McKinney, 2006). Quantifying patterns of habitat connectivity on a species-by-species basis is integral to preserving and enhancing important corridors connecting patches of suitable habitat which can help promote population health and persistence of biodiversity on urban landscapes.

The City of Los Angeles is working to protect urban biodiversity and increase sustainability of the city in the face of climate change and urbanization with legislation such as the Biodiversity Motion (2017) (LA Sanitation & Environment, 2022b) which seeks to address biodiversity loss more holistically and LA's Green New Deal achieve "no-net loss" of biodiversity (Garcetti, 2019). The City is tracking progress on this target through the Los Angeles City Biodiversity Index. Assessments using this index will track LA's progress towards achieving no-net biodiversity loss and highlight areas requiring greater conservation attention and more detailed conservation planning (LA Sanitation & Environment, 2020).

In alignment with LA's goal to address biodiversity loss more holistically and bolster our understanding of habitat connectivity in LA, we modeled the habitat connectivity for 1,017 species across a 7,705 km² study extent encompassing LA. We used species-specific habitat suitability models generated in a previous study (Beninde et al., 2023) as the foundation of our analyses. Prior connectivity assessments within this landscape have been based on measures of broadly-defined landscape features, such as natural areas and hypothesized movement barriers, without considering interspecific variation in habitat associations. Our project took a novel approach to habitat connectivity by utilizing individual habitat suitability models to generate connectivity surfaces for each species. This method provided a more detailed species-by-species understanding of the relationship between regional biodiversity and the landscape. To validate our habitat connectivity models, we completed standardized surveys for 18 different species at randomized sites throughout the study area and used generalized linear models to examine if habitat suitability and connectivity values of the survey site significantly predicted species presence and abundance. We also used iNaturalist observations to validate our models for over 900 species using random forest models. Our connectivity surfaces and inferences will be used by The City of Los Angeles and The Nature Conservancy to better inform conservation planning on this complex landscape.

III. Research Questions

To quantify the connectivity of remaining habitats in LA, we have proposed three research questions:

1. What are suitable approaches to modeling habitat connectivity across a diverse array of plant, animal, and fungal species?
2. Can we validate habitat connectivity models with field data and iNaturalist data, and are these models useful for informing conservation management?
3. What are crucial conservation tactics to promote connectivity for LA's Biodiversity?

IV. Methods

4.1 - Study Extent

Our team developed individual connectivity models for 1,017 study species within a 7,705 km^2 extent of the greater Los Angeles metropolitan area. The study extent includes the City of Los Angeles and significant segments of Los Angeles, Long Beach, and Anaheim Metropolitan Statistical Areas, as well as parts of neighboring Ventura County to the west of LA, parts of western Riverside and San Bernardino Counties to the east, and some of Orange County top the south (Figure 1) (Beninde et al., 2023). Approximately 65% of the study area, which is dominated by developed urban land uses, can be classified as urban using the U.S. Census Bureau delineation (U.S. Census Bureau, Population Division, 2018). We classified large expanses of undisturbed vegetation with relatively minor developments as wildlands. These areas total about 35% of the area. This study's extent is unique in that it centers on extensive and densely populated urban areas interspersed with protected wildland areas. The urban-wildland interface captured in the sharp transition from the drastically different physical environments of the urban areas and adjacent wildlands will capture unique patterns of species distribution and, consequently, connectivity (Beninde et al., 2023).

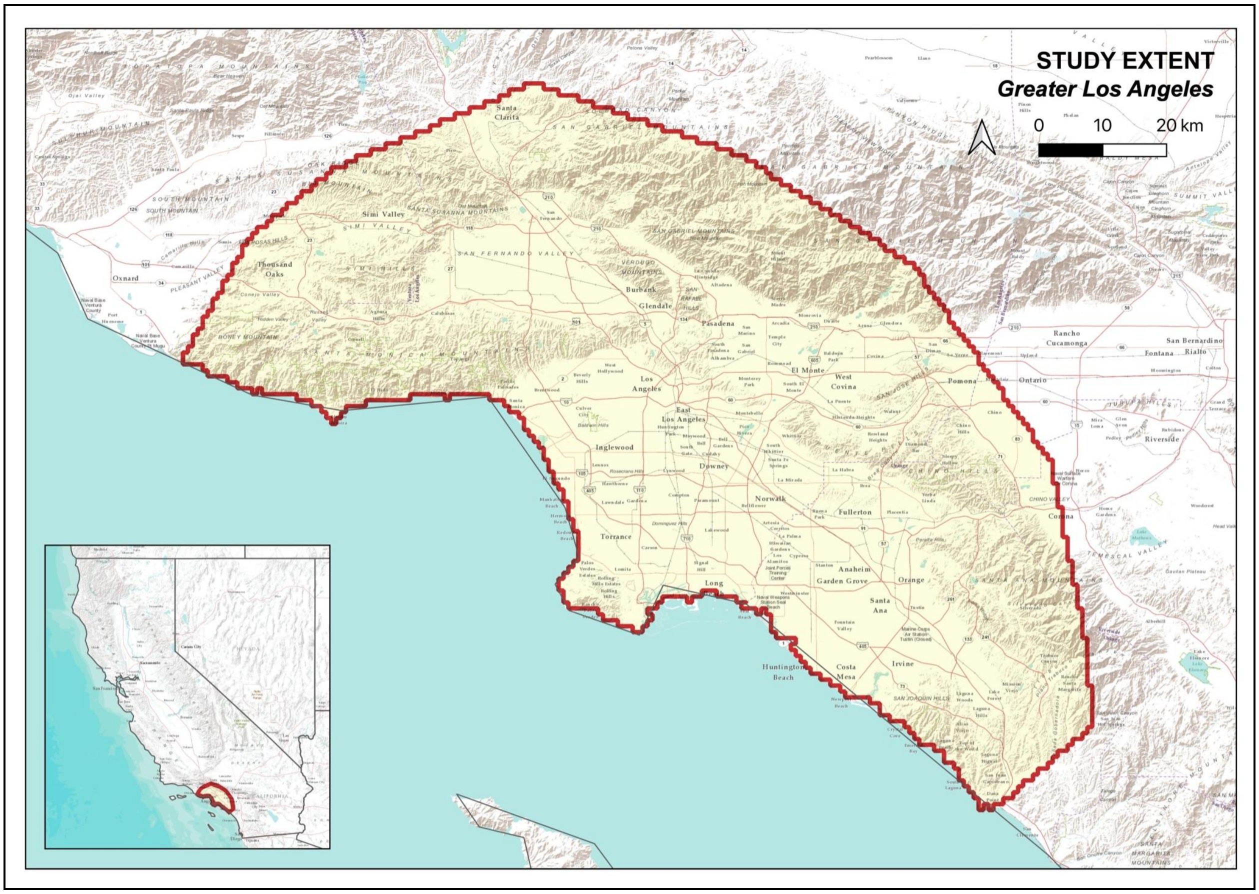

Figure 2. Study Extent. The region of Greater Los Angeles selected for this study is outlined in red. The 7,705 km² area includes the metropolitan center of Los Angeles and edges of its surrounding natural areas. Expert opinion and literature review guided selection of the study area.

4.2 - Connectivity Modeling

We used the moving window analysis in *Omniscape v0.5.8* to quantify current flow, also known as movement potential, across the study extent (Landau et al., 2021; Landau et al., 2022; see section "Circuitscape/Omniscape" and "Supplementary Figure 1" in the Appendix). We ran *Omniscape* in Julia, where we wrote a loop to autonomously cycle through, apply set inputs and parameters, and output current flow surfaces for each species.

Connectivity Model Inputs

The two inputs required by *Omniscape* are a resistance layer and a current source layer in the form of rasters of equal extent, resolution, and origin (Figure 3). We derived our current source and resistance layers from species-specific habitat suitability models generated by Beninde et al. (2023). These models were parameterized using iNaturalist occurrence data in generated combination with landscape and environmental variables in random forest models. All iNaturalist observations within the study extent were filtered to include only species data with at least 25 occurrence records. The 10 variables used included imperviousness, photosynthetic activity (NDVI), bioclimatic conditions (precipitation, mean temperature, minimum temperature, mean diurnal range), soil characteristics (bulk density, cation exchange capacity, climatic water deficit), and water cover. Using the original random forest models parameterized at a resolution of approximately 1 km (WGS84 / lat/long), we repredicted these models at a 270-m equal-area projection (NAD83 / California Albers) to achieve a finer scale understanding of suitability and connectivity within our study area. Though the freely available iNaturalist dataset used as input for the habitat suitability models included 6,082 species for greater Los Angeles, only those with at least 25 occurrence records were included in the final model generation. Of the consequent 1,017 species, 45.5% are plants, 27.45% are arthropods, 22.2% are vertebrates, 3.2% are fungi, and 1.3% are mollusks. All fully marine and aquatic species were excluded (Beninde et al., 2023).

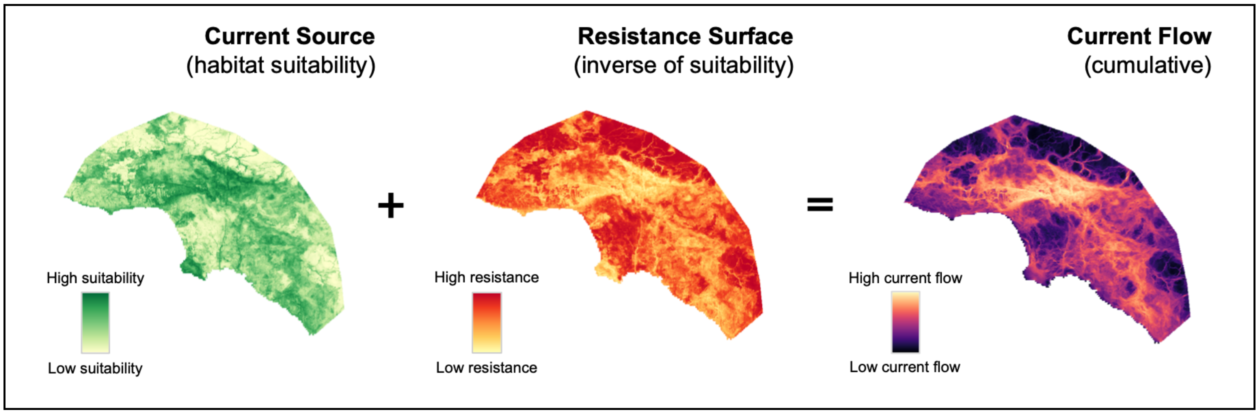

Figure 3. Inputs for generating connectivity surfaces. Data shown for the Western fence lizard (*Sceloporus occidentalis*).

Current Source - Habitat Suitability Models (HSMs)

We chose habitat suitability surfaces as our current source layer. Based on presence data habitat associations, these habitat suitability models predict how likely one is to find a species at a given location, with high suitability indicating the highest probability (Beninde et al., 2023). The habitat suitability rasters were used directly as the source input under the assumption that where there is a higher likelihood of a species in a given location, more species will likely originate from or travel to that location. As such, higher suitability areas will equally correspond to higher source weights.

To avoid edge effects which is necessary for connectivity modeling, the habitat suitability models were extended 25km beyond the study extent by using the predict function in R to apply random forest models, which include all of the suitability predictors, to a new raster stack (Koen et al., 2012). Holes in the input rasters were filled using the focal function in the raster R package (v. 3.6.20; Hijmans, 2023). To avoid dividing by zero when the inverse resistance layers were created, the new habitat suitability rasters were rescaled from 0-1 to 1-100 prior to input (Dutta et al., 2022; deRivera at el., 2022).

Resistance Surfaces

Direct measures of landscape connectivity for a large number of species over a heterogeneous landscape are not feasible to obtain due to the impracticality of quantifying individual species movements Instead, indirect assessments are achieved with spatial modeling (Braaker et al., 2015; Simpkins et al., 2019). As a result of the reliance of dispersal on landscape structure, resistance surfaces have become the basis of most such models (Tischendorf et al., 2000). Resistance surfaces are rasters that reflect the cost of movement through the landscape corresponding to each raster cell (Unnithan et al., 2022). Low resistance values are assigned to more permeable landscapes, whereas high resistance values are assigned to landscapes restricting or absolutely barring movement (Zeller et al., 2012). Differential propensity may depend on physiological costs or mortality associated with the specified environment or a species' willingness to cross that landscape (Diniz et al., 2019; Dutta et al., 2022). Parameterization of resistance surfaces is derived either by expert opinion or empirical data. Empirical data provide a more objective source and have both been more efficient and simple to use in parameterization and been shown to be more ecologically relevant when compared to expert-opinion approaches (Zeller et al., 2012). Basing parameterization values on biological data such as occurrence, movement paths, experimental movement behavior, or genetics can more effectively capture the functional response of a species to the environment variables (Braaker et al., 2015).

Derivation of resistance values from habitat suitability models has, as such, become a popular approach to creating resistance surfaces (Trainor et al., 2013). We converted habitat suitability layers to resistance layers by taking the inverse of the habitat suitability layers. Habitat suitability values can be converted into resistance values under the assumption that habitat quality has a direct relationship with species movement because organisms are more likely to move freely in a habitat suitable to them (Mateo-Sánchez et al., 2015). Thus, after habitat suitability is inversely transformed into a resistance surface using linear or negative exponential functions, the lowest resistance values will correspond to highest habitat suitability values (Zeller et al., 2012; Mateo-Sánchez et al., 2015).

Connectivity Model Parameters

Once these data layers are inputted into Ominscape*,* a set of code steps must also be parameterized to guide the analyses. Only a few of the calibrations to the run code have significant ecological implications, with the remaining code calibrations intended simply either to specify model outputs or to optimize computer modeling efficiency to reduce the run time (Brown et al., 2019). The "radius" parameter is an example of a parameter with significant ecological implications, while the "block_size" parameter optimizes modeling efficiency.

The "radius" parameter specifies in raster cells the size of the moving window. The moving window centers on each raster cell and measures its connectedness out to the set maximum distance specified as the radius (McRae et al., 2016). As the moving window size is ultimately representative of the enabled dispersal distance, individual species analyses typically set the radius dependent on the average movement of that species (Suraci et al., 2023). Several studies have discussed the independent and variable nature of species' dispersal distances, which may be greatly influenced by body size or functional group characteristics (Schloss et al., 2021; Cameron et al., 2022; Suraci et al., 2023). The method of choosing a moving window size based on an individual species' dispersal distance is not as applicable in studies assessing a large array of different species, so an alternative, more generalized moving window must be used to set the model for such a diverse grouping. As such, based on a study by deRivera et al. (2022), which took a similar species-by-species approach to modeling in southwestern Oregon, we set our radius at 1/8th of the study extent so that it is 25 km (93 raster cells). This encapsulates regional connectivity outside of the bounds of individual temporal or spatial daily ranges and movement rates (deRivera et al., 2022).

The "block_size" parameter coarsens the current source layer, reducing the number of source raster cells. We used a block size of 5, meaning that the current source layer was broken up into chunks of 25 raster cells (5x5 blocks) and only the centers of these blocks were considered as potential source raster cells. The center raster cells were assigned a new source weight equal to the sum of all 25 raster cells, ensuring that the total amount of current injected is the same as if all raster cells were considered source raster cells (Landau et al., 2022). The use of a block size greater than 1 was able to reduce our computation time from 5-15 hours per model to 10-30 minutes per model and had a negligible impact on the outputs.

Connectivity Surface Outputs

The Omniscape output options include the cumulative current flow map, the regional flow potential map, and the normalized current flow map (McRae et al., 2016). Cumulative current flow, which is the sum of all calculated current flow from the overlapping windows, is the default output of Omniscape. As the most basic output, high current flow values simply represent high movement potential on this raster map (LA Sanitation & Environment, 2020). Regional flow potential recalculates cumulative current flow under null conditions wherein the resistance layer values are all set to a constant of 1. This quantifies how much current flow would be anticipated across the landscape in the absence of all impermeable resistance, indicating movement potential between suitable areas without landscape barriers (LA Sanitation, 2020). The normalized current flow is calculated by dividing the cumulative current flow by the regional flow potential. As such, the raster can be classified into areas with more, equal, or less flow than would be expected on an unrestricted landscape (Schloss et al., 2021). This better reveals the structural mechanisms underlying current flow values and highlights the areas of concentrated and impeded current flow (McRae et al., 2016; Belote et al., 2022).

The two surfaces that are most frequently used in analyses are cumulative current flow and normalized current flow (McRae et al., 2016). Each surface has separate underlying assumptions and must be interpreted differently in regards to the information presented about connectivity. Cumulative current flow refers to the accumulated movement of organisms across the landscape. It represents the overall flow of individuals or populations through interconnected habitats. In this way it presents information about the relative degree of connectivity across the landscape.

On the normalized current flow surface, the normalized values represent the maximum possible movement that each habitat point contributes. Following McRae et al. (2016), the raster cells will be divided into four main classes: channeled, intensified, diffuse, and impeded (Table 1, Figure 5). Channeled areas have high concentrated movement potential with significantly more flow than anticipated. This describes areas where movement has been limited to a single linkage through an otherwise impermeable environment. Intensified areas also have more flow than expected but fewer movement constraints. This indicates that landscape permeability has been reduced by, e.g., land use, infrastructure, or water bodies and that relatively limited movement pathways exist. Diffuse areas have as much flow as anticipated. This is characteristic of large, relatively unrestricted habitat with few or no barriers to movement. Impeded areas have very limited or completely inhibited movement potential, which is expected in areas fragmented by human infrastructure or land uses (McRae et al., 2016; Schloss et al., 2021; Cameron et al., 2022)

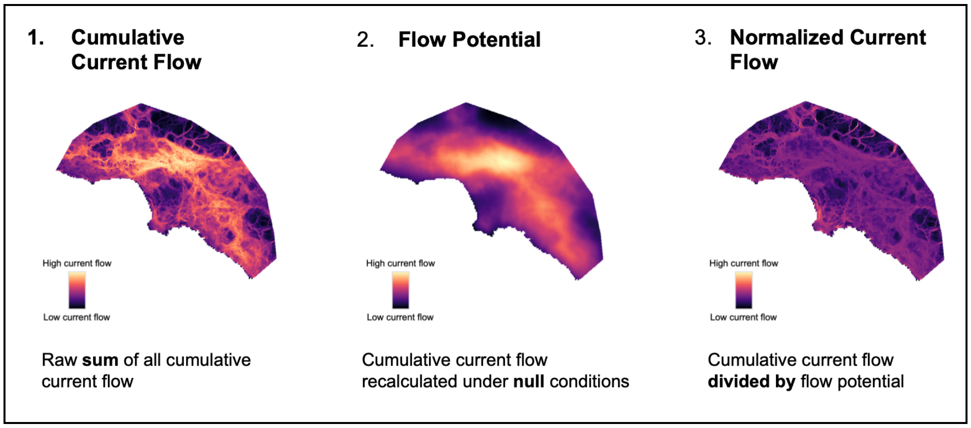

Figure 4. High movement potential, described as cumulative current flow, occurs between areas with high source weights i.e. high habitat suitability, and along paths of low resistance. Data shown for the western fence lizard (*Sceloporus occidentalis*).

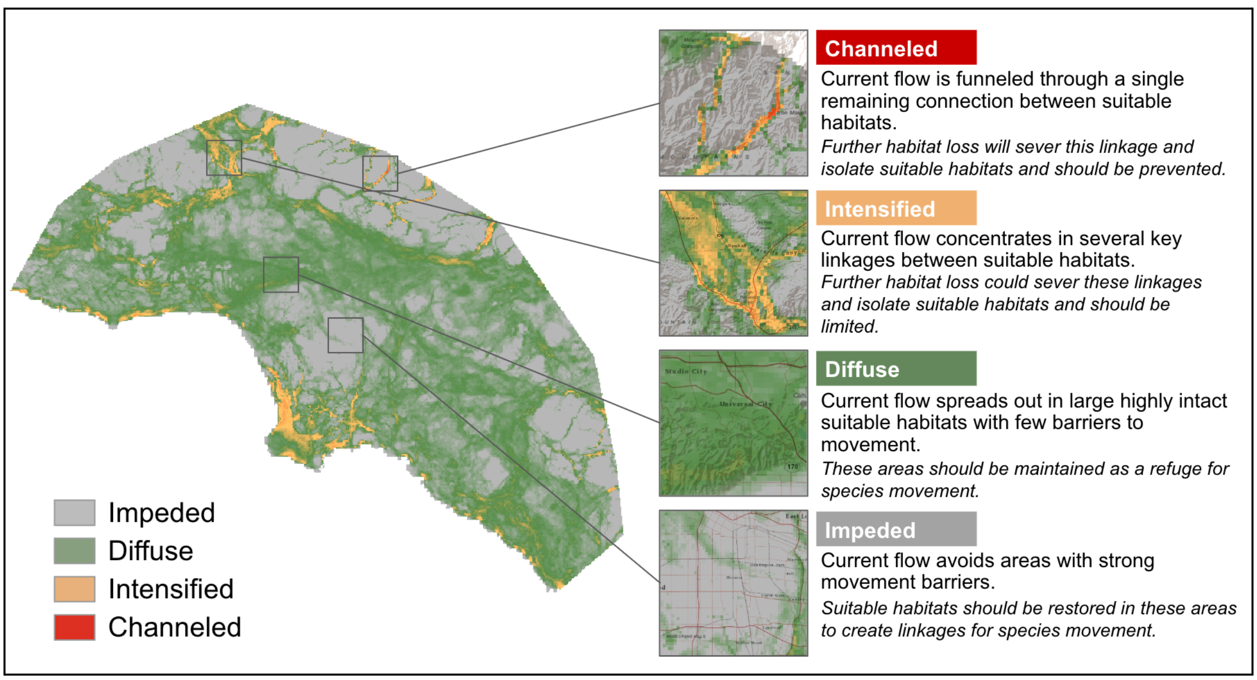

Figure 5. Description of classification classes for normalized current flow. Following the methodology of McRae et al. (2016), normalized current flow is divided into four main classes which better reveal the structural mechanisms underlying current flow. The classified normalized connectivity surface highlights areas of especially concentrated and especially impeded current flow. This information can be used to identify areas which might be prioritized for restoration or protection. Data shown for the western fence lizard (*Sceloporus occidentalis*).

Class	**Value**	**Definition**
Channeled	> 1.7	Significantly more flow than expected

Intensified	1.3 - 1.7	More flow than expected
Diffuse	0.7 - 1.3	As much flow as expected
Impeded	< 0.7	Less flow than expected

Table 1. Assignment of classification classes. Values are the quotient results of Omniscape dividing the cumulative current flow by null current flow potential to produce the normalized current flow. Values are the ratio of actual predicted current flow to the current flow expected on an unrestricted landscape.

4.3 - Model Validation

The purpose of validation is to provide a strong foundation that allows researchers to determine validity of results based on past and present real-world findings. For a connectivity model, validating predictions of movement potential across the landscape is critical to ensure sufficient representation of real-world patterns. The data used to specify actual population distributions should include data on species abundance across the landscape, movement patterns between habitats, or interpopulation genetic similarities. We approached model validation for our project with data from our own field studies and information we compiled from the public domain databases iNaturalist and Global Biodiversity Information Facility (GBIF). Similar to our field survey data, iNaturalist data records abundance and location of sampled species. For both our field data and iNaturalist data, we made the assumption that occurrences are positively influenced by habitat suitability and connectivity that we are testing in the statistical analyses. Location data will enable us to understand real-life species distributions which we can compare to presence and movement predicted by our models.

4.4 - Model Validation Using Field Surveys

Experimental Design Overview

We conducted fieldwork to validate the connectivity models by gathering abundance data for focal taxa in the following categories: reptiles, insects, birds, plants, and mammals. We ran generalized linear models using abundance data collected in the field to determine if our field sites' suitability and current flow values were significant predictors for abundances of our focal taxa.

Focal Taxa

We chose our focal taxa to be common species that are easily detected and identifiable in LA. This increases the likelihood of generating sufficient data for model validation. All of the species on the list below have wide ranges within our study area, are easily identified, and were expected to be present and observable within our study extent for the duration of the survey period.

Reptiles:

1. Western fence lizard (*Sceloporus occidentalis*)
2. Side-blotched lizard (*Uta stansburiana*)

Plants:

3. California bush sunflower (*Encelia californica*)
4. California poppy (*Eschscholzia californica*)
5. Black mustard (*Brassica nigra*)
6. Fennel (*Foeniculum vulgare*)

Mammals:

7. Ground squirrel (*Otospermophilus beecheyi)* (surveyed during the 20 min plant survey)

Butterflies:

8. Marine blue (*Leptotes marina*)
9. Fiery skipper (*Hylephila phyleus*)
10. Sara orangetip (*Anthocaris sara*)
11. Cabbage white (*Pieris rapae*)
12. Painted lady (*Vanessa cardui)*
13. West coast lady (*Vanessa annabella)*

Birds:

14. California towhee (*Melozone crissalis*)
15. California scrub jay (*Aphelocoma californica)*
16. Acorn woodpecker (*Melanerpes formicivorus*)
17. Dark-eyed junco (*Junco hyemalis)*
18. American crow *(Corvus brachyrhynchos)*

Site Selection

All focal taxa were searched for at all sites. To select sites, we first generated a single raster using the mean of suitability scores across the suitability surfaces of all focal taxa. We classified the suitability values categories of high, medium, and low using natural breaks in ArcGIS Pro (ArcGIS, 2010). We randomly generated coordinates for each category, with 30 sites each for low and medium suitability and 90 sites for high suitability, with the assumption that some randomly generated points would be unfeasible for field surveys. We then entered the generated coordinates into Google Maps and used Google Street View to manually determine the feasibility of each site as a field survey location, taking into account the feasibility of travel and accessibility. If the coordinates were unfeasible to get to (i.e., inaccessible from the road, on private property, etc.), we discarded the point. We surveyed 35 points total, including 24 high suitability sites, 7 medium sites, and 4 low sites.

Field Methodology

In order to conduct a field survey, certain weather parameters had to be met. We did not conduct surveys if it was raining, winds were greater than 15 km/hr, or it was less than 13℃. If it was between 14 and 17℃, we only surveyed if cloud cover was less than 40%. If it was greater than 17℃, we surveyed regardless.

We navigated to our sites using the randomly generated coordinates and got as close to the point as possible to begin our surveys. We stayed within 1km of the randomly generated point throughout the survey to control for the raster values for suitability and connectivity while also increasing probability of detection.

We conducted four 20-minute surveys at each of our sites, one for reptiles, butterflies, birds, and plants and the ground squirrel in the same category. Surveys were always conducted with two people for consistency of observation, and observed species were tallied. We walked within 1km of the site coordinate and searched areas that increased the likelihood of finding our focal taxa (i.e., travel to high places to find butterflies, tree areas for birds, and open areas with native plants for lizards). We paused the 20-minute timer when we spent greater than one minute identifying species. We recorded incidental observations of focal taxa not in the survey category, but we did not include it in the final analysis. We used binoculars for greater observation power, as well as butterfly nets and forceps for butterfly identification. We generated relative abundance for all animal species, and collected categorical data for plants. Our categorical data for plants ranged from 0-3, with 0 being no observations of the plant, 1 being a single patch or less of the plant (e.g., a single individual or multiple individuals adjacent to one another), 2 being multiple patches of the plant, and 3 being an abundance of the plant.

Generalized Linear Modeling

With our collected field work data, we used our abundance data for our focal taxa to run generalized linear models. We used the glm.nb function in the MASS package (Ripley, 2023) to run the negative binomial generalized linear models in R. We chose this method because we were dealing with noncontinuous data with non-negative values. We extracted values from our generated connectivity models for cumulative current flow and normalized current flow for all our field sites, as well as suitability values. First, we ran individual species models using cumulative current flow, normalized current flow, suitability, and temperature as predictors. We standardized all of the predictor variables using the scale function from the base R package to ensure our estimates were accurate. We only included temperature for our weather predictors, because when we included other measured weather factors, they were not significant predictors. We did not run models for species that were observed at less than 3 sites, which included the west coast lady, the marine blue, the variable checkerspot and the fiery skipper.

We also created a mixed generalized linear model with all of the species in one model with the field site as a random effect to account for duplication, and the same predictor variables as the individual species models. We used the glmmTMB function from the glmmTMB package (Brooks et al., 2023) to run mixed generalized linear models, and we defined the family as nbinom2(link = "log").

4.5 - Model Validation Using iNaturalist

In addition to validation with field work, we also validated the connectivity surfaces using iNaturalist presence data. Using iNaturalist data allows us to validate a larger number of our species-specific connectivity surfaces. To do this, we used random forest classification tree modeling (Wiener, 2002). This allows us to compare the connectivity models created from older iNaturalist data during previous years (2000-2021), solidifying patterns simulated in our connectivity surfaces. This modeling shows us how important habitat suitability is in comparison to connectivity, and how well both are combined to predict new presence data and best inform conservation practices.

Data

We obtained research grade presence-only iNaturalist observations from GBIF from our study area seen January 1st, 2022 to the first day of field work March 18, 2023 to avoid any crossover of observations (iNaturalist Contributors, 2023). We then filtered the observations from GBIF, removing those with less than 1000 meters of location accuracy, less than 10 observations, and removing species without connectivity surfaces. Filtering the iNaturalist observations left us with 93,819 observations to validate the surfaces for 705 species.

Random Forest

The random forest classification algorithm is an ensemble or "forest" of classification trees, which is advantageous because it combines predictions from many different trees (Valavi et al., 2021). In our case, our model used a bagging method, where a generalized result is produced by combining different predictive models (Raj, 2021). To train the model, we used the filtered iNaturalist dataset obtained from GBIF and generated pseudo-absences to create a full dataset that can be used by random forest classification trees. Following the methods used in a previous suitability study Beninde et al. 2023, we generated these pseudo-absences because data for the species we created suitability models that includes both presences and absences was not available, similar to the methods used in Valavi et al., 2021. For predictors, we used the 270-meter resolution surfaces for cumulative current flow, normalized current flow, and habitat suitability. Using the randomForest function in the "randomForest" package (Liaw & Wiener, 2002), we set the model to run 1000 trees for each species and created a for loop to run 100 classifications per species. Using the same for loop, we populated a data frame for each species, compiled all the data frames into one table, and collapsed by species using the "collapse" function in the "collapse" package (Krantz et al., 2023). This final dataset included the mean and median from all 100 iterations of the following data: mean decrease accuracy scores, mean decrease gini scores, and out-of-bag (OOB) percent error values. Also included in the dataset are the correlation coefficients between habitat suitability and cumulative connectivity, habitat suitability and normalized connectivity, and normalized and cumulative connectivity.

Model Fit

We calculated the out-of-bag percent error (OOB) for each species in our dataset to determine fit for our random forest models. The OOB score is used in bagging algorithms similar to the one used to validate our connectivity models. The OOB score is the number of correctly predicted occurrences and non-occurrences found in the training dataset (Bhatia, 2019). The OOB score is found by comparing the occurrences in our dataset that were not included in the bagged data used in a specific tree in our random forest models. It allows the model to check itself to ensure it isn't over-fit, which can be an issue when variation is introduced to the model (Shukla, 2022). OOB is an ideal indicator of model fit for our application because it helps to train the model as it runs and the model continuously checks itself throughout its decision-making process by comparing its generated outputs with the training data. OOB allows us to see how well the habitat suitability surfaces generated with older iNaturalist data (January 1, 2000 to December 31, 2021) found in Beninde et al. (2023), that we used to create our connectivity surfaces, were able to predict species occurrences found in newer data. A lower OOB score indicates a higher accuracy of our predictor layers.

V. Results

Omniscape Outputs

We generated cumulative current flow, regional flow potential, and normalized current flow maps for all 1,017 species. We also created an average normalized current flow surface, which was a raster created by taking the mean of all 1,017 species-specific normalized current flow rasters. We used a similar process to create mean normalized current flow surfaces for native and nonnative species. The mean calculations were performed in R using the terra package (Robert and Hijmans, 2023).

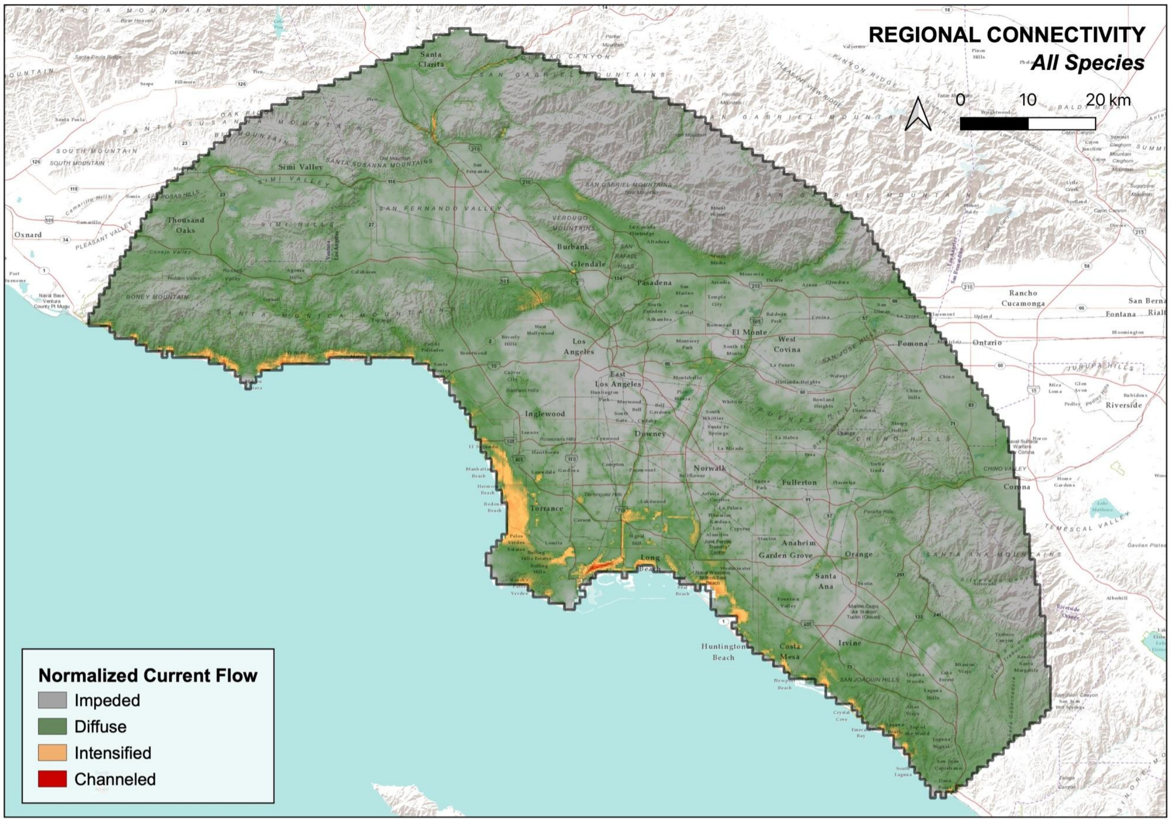

Figure 6. Mean normalized current flow surface for all 1,017 species.

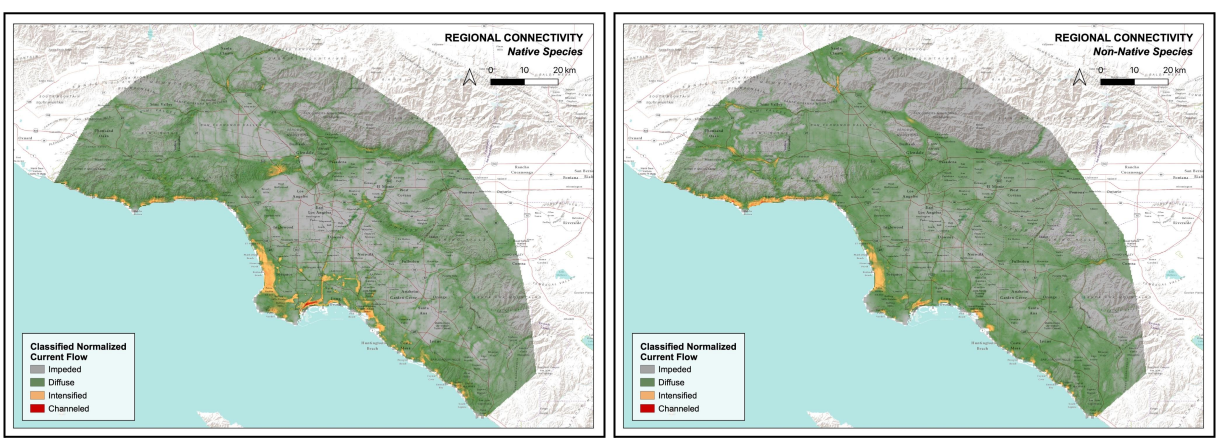

Figure 7. Native and non-native species normalized current flow surfaces. This is an average of the surface outputs for 688 native species and 288 non-native species. Some species are

excluded from these figures as they were unable to be classified as native or non-native species due to their migratory nature or the unknown nature of the species.

Model Validation using Field Work Data

For fieldwork model validation, we found that the abundance of California scrub jays, dark-eyed juncos, bush sunflowers, fennel, and the combined species had a significant positive relationship with the habitat suitability of survey sites. We observed that western fence lizard abundance increased when there was higher normalized current flow at a site, and we observed that the abundance of bush sunflowers decreased in areas with higher cumulative current flow and that black mustard increased in regions with higher cumulative current flow. We also observed that we recorded more acorn woodpeckers, dark-eyed juncos, common side-blotched lizards, Sara orange tips, and all species collectively when the temperature was higher (Table 2). The directionality of the estimates was generally positive with all four of the predictor variables as well. For the species that abundance values were not correlated with our generated connectivity and suitability values, it does not necessarily mean our models are inaccurate, or that habitat suitability and connectivity are not important to those species, but that we have not generated enough data to detect a relationship.

	Suitability		Normalized Current Flow		Cumulative Current Flow		Temperature ℃	
Species	Estimate	P-Value	Estimate	P-Value	Estimate	P-Value	Estimate	P-Value
California towhee	1.23	0.642	0.88	0.7	1.35	0.413	0.68	0.187
California scrub jay	**2.82**	**0.07**	0.57	0.34	1.26	0.616	0.84	0.575
American crow	1.37	0.372	1.35	0.344	0.77	0.368	1.07	0.756
Acorn woodpecker	0.59	0.733	0.91	0.857	4.85	0.289	**2.89**	**0.027**
Dark-eyed junco	**3.69**	**0.015**	0.79	0.664	0.78	0.508	**0.52**	**0.085**
Western fence lizard	1	0.998	**2.75**	**0.002**	1.44	0.306	0.94	0.767
Side blotched lizard	1.02	0.977	0.75	0.717	4.56	0.081	**0.26**	**0.06**
Sara orangetip	9.32	0.022	2.06	0.39	1.09	0.929	**0.17**	**0.078**
Cabbage white	3.9	0.214	0.69	0.73	0.64	0.578	0.99	0.984
Painted lady	0.31	0.355	2.14	0.491	2.48	0.309	**0.19**	**0.066**
California poppy	1.39	0.58	1.36	0.501	1.33	0.57	0.84	0.609
California bush sunflower	**0.75**	**0.007**	0.13	0.577	**-0.62**	**0.066**	-0.26	0.161
Fennel	**0.46**	**0.037**	-0.08	0.609	-0.17	0.427	-0.15	0.265
Black mustard	-0.21	0.564	0.01	0.961	**0.72**	**0.099**	-0.4	0.112
All species	**1.99**	**<0.001**	0.98	0.814	0.94	0.627	**0.85**	**0.056**
All animals	**1.81**	**0.001**	0.96	0.762	1.02	0.919	**0.85**	**0.095**

Table 2. **Results from field work model validation**. Slope estimate and P-values are reported for all 4 predictor variables and target species. Significant relationships (less than 0.1) are bolded.

Model Validation using iNaturalist

Our random forest models produced a dataset containing the importance scores and model fit scores to show us the significance of each predictor surface, connectivity and suitability and assess the ability of random forest to determine which predictors are important for occurrence at the species level.

	Correlation Coefficients			Mean Decrease Accuracy			Out-of-bag Error
Species	Suitability-Normalized	Suitability-Cumulative	Cumulative-Normalized	Suitability	Connectivity (norm.)	Connectivity (cumm.)	Percentage (%)
CA towhee	0.80	0.91	0.77	37.74	10.81	39.17	14.13
Scrub jay	0.78	0.91	0.72	40.49	3.50	32.49	16.52
Crow	0.81	0.92	0.79	53.47	22.42	29.48	17.26
Acorn woodpecker	0.75	0.94	0.69	29.65	20.75	21.11	9.39
Junco	0.73	0.93	0.65	26.79	19.47	17.12	10.33
Western fence lizard	0.82	0.91	0.79	48.52	22.88	32.57	13.23
Side blotched lizard	0.75	0.91	0.66	34.91	-1.28	29.75	16.03
Sara orangetip	0.70	0.91	0.64	25.71	4.96	29.31	15.47
Cabbage white	0.81	0.93	0.76	39.53	31.65	19.55	16.63
Painted lady	0.78	0.90	0.72	12.76	6.05	16.62	19.27
West coast lady	0.81	0.94	0.76	17.68	18.96	22.92	19.89
Marine blue	0.80	0.91	0.73	22.70	1.51	19.11	12.59
Fiery skipper	0.78	0.93	0.73	19.89	17.91	6.28	14.43
CA poppy	0.83	0.91	0.80	40.56	27.56	34.71	14.73
CA bushsunflower	0.83	0.90	0.83	76.39	17.23	26.55	12.91
Fennel	0.79	0.91	0.78	23.04	0.72	8.62	16.40
Ground squirrel	0.81	0.90	0.82	76.47	28.47	30.25	8.40
All species	0.79	0.92	0.74	34.36	14.07	24.09	14.95

Table 3. Results from iNaturalist model validation. Correlation coefficients, mean decrease accuracy scores, and out-of-bag error percentages are reported for each target species. Black mustard (*Brassica nigra*) was excluded due to an insufficient number of observations within the study extent on GBIF.

Averaged across all target species, we observed higher importance of habitat suitability when predicting occurrence compared to normalized and cumulative connectivity (Table 3). Among the connectivity surfaces, cumulative current flow had the highest importance when predicting occurrences on average. Notably, for the California towhee (Melozone crissalis) and three of our butterfly species, the sara orangetip (*Anthocaris sara*), painted lady (*Vanessa cardui)*, and west coast lady (*Vanessa annabella)*, importance was placed higher on their cumulative connectivity surface out of the three surfaces. Out-of-bag errors for all target species ranged from 8 to 20%. We observed the correlation between the habitat suitability and cumulative connectivity surfaces to be highest for all target species.

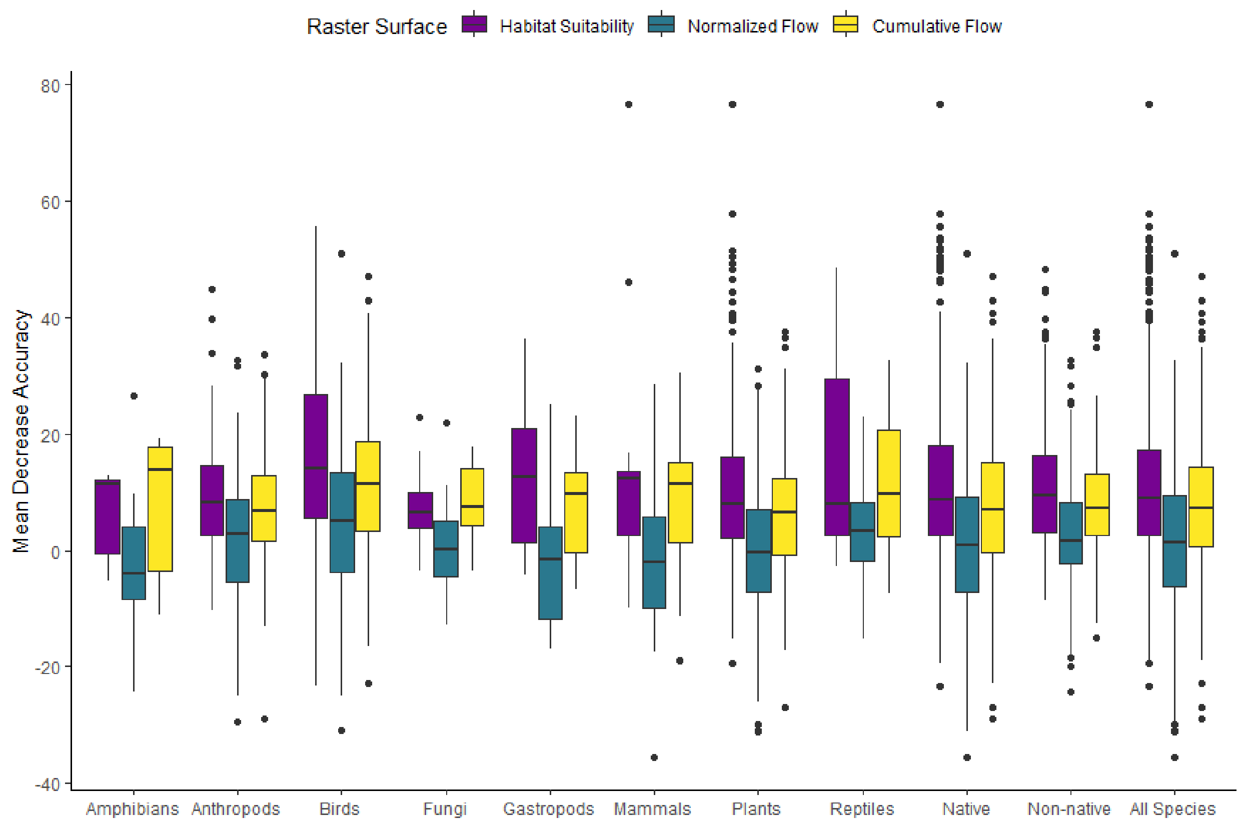

Figure 8. **Results from iNaturalist validation**. Mean decrease accuracy scores are reported for the habitat suitability, normalized current flow, and cumulative current flow for each functional group.

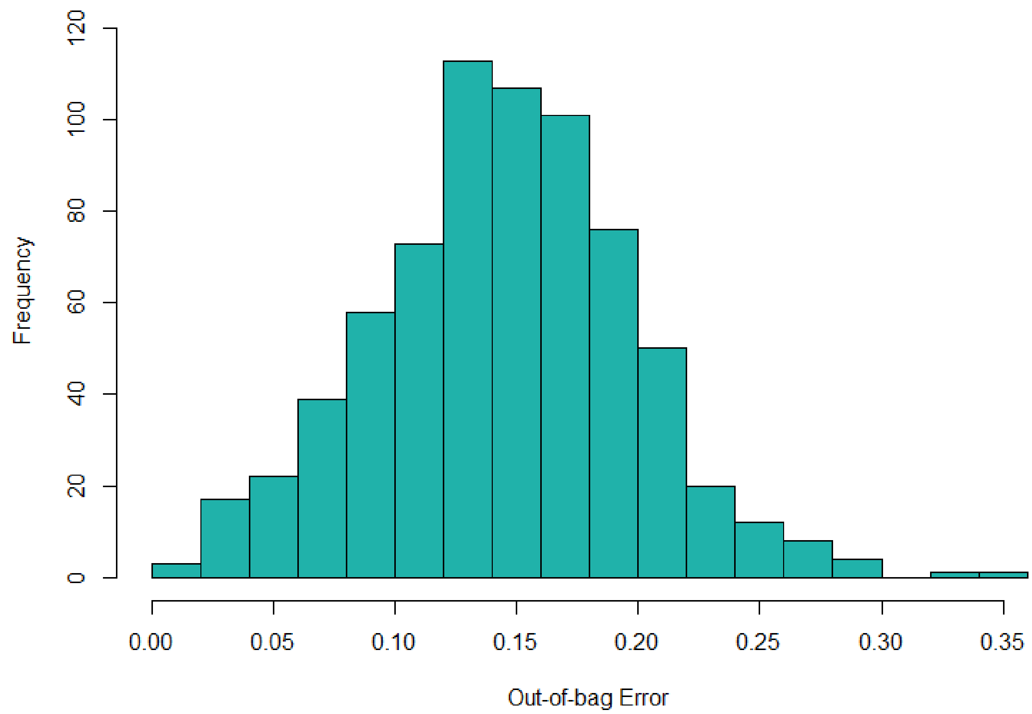

Figure 9. **Results from iNaturalist validation**. Histogram displaying the out-of-bag error proportions for all species is illustrated here.

Our analysis found that habitat suitability was more important for occurrence than connectivity across functional groups, with amphibians and reptiles notably receiving higher cumulative flow importance (Figure 8). Amongst the connectivity surfaces, we found that cumulative flow was more important for occurrence than normalized flow (Figure 8). To evaluate model fit, our random forest models completed out-of-bag error checks and the averaged OOB scores from our 100 iterations of our models across all species scores ranged from 1 to 35 percent (Figure 9). Across functional groups we saw ranges from 11 to 18 percent the average OOB score for all spec,ies was 15 percent (Figure 9).

VI. Discussion

6.1 - Interpretation of Connectivity Modelling

In our combined connectivity surfaces based on our Omniscape outputs, we observe higher-than-expected flow in regions with highly suitable, fragmented habitat that are close to impermeable barriers such as mountains, development and the ocean. This phenomenon can be observed in more detail in Figure 10 and Figure 11. These results suggest that regions along the coast, such as the Palos Verdes Peninsula, and along the mountains, such as Santa Clarita, should be targets for conservation.

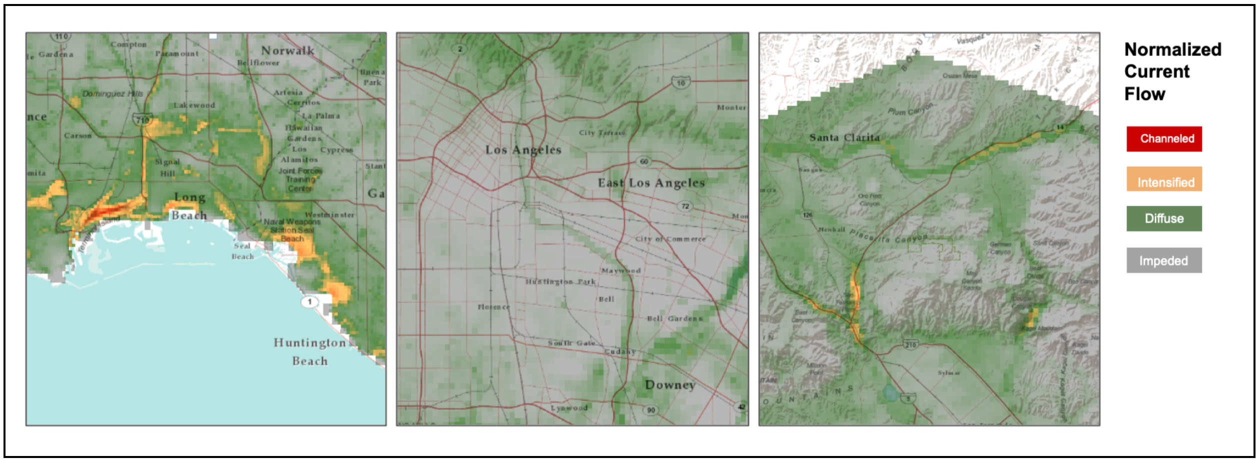

Figure 10. Influence of landscape structure on current flow for all species. a) Current is **channeled** and **intensified** in areas against the coastline as flow is restricted entirely across the neighboring water and the Palos Verdes development, b) current flow is **impeded** in urban areas where there are many barriers and few natural areas and, c) current is **intensified** between the more impermeable upper reaches of the mountain terrain where there is impeded flow and movement is directed into fewer paths.

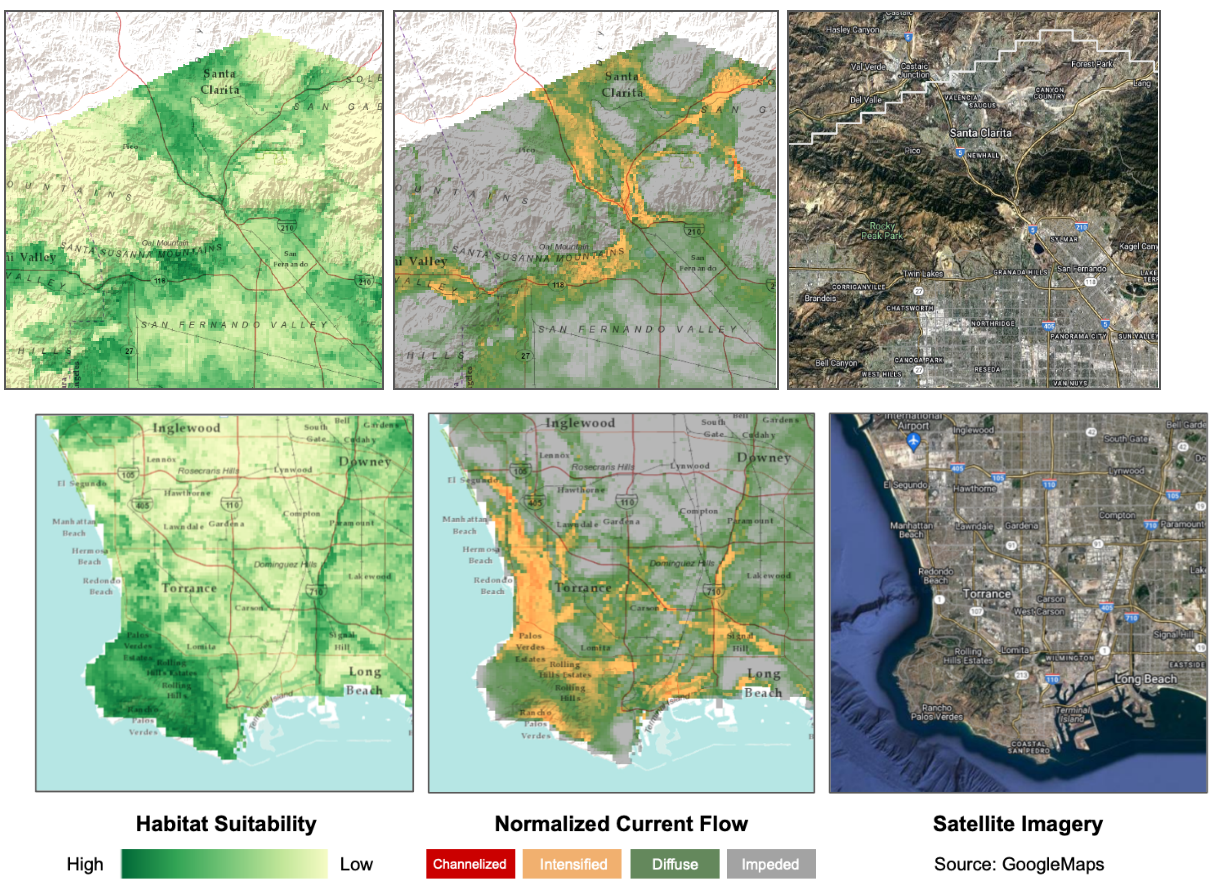

Figure 11. Examples of regions with high normalized current flow score. a) Santa Clarita, where current flow is **channeled** due to the low permeability of the surrounding mountain range

and development with a highly suitable landscape and, b) Torrance, where current flow is highly channeled due to development and lack of movement options due to the ocean boundary.

6.2 - Interpretation of Model Validation

Field Work Model Validation

The positive relationship between suitability and the abundance of species in our randomized sites across LA is in agreement with the literature. Suitability surfaces are generated using substrates that are desirable by certain species as well as observations of those species. Ecologically, it makes sense that we would observe a higher number of individuals in areas that are more suitable.

Further, we observed an increase in observations of western fence lizards in areas with higher normalized current flow. Increased current flow means that more species are predicted to be moving through an area, so it aligns with our finding that higher normalized current flow predicts more western fence lizards. For cumulative current flow, we found the expected increase in abundance for black mustard, but we found a decrease in California bush sunflower with an increase in cumulative current flow. A possible explanation for the decreases in bush sunflower despite the higher current flow for that species could be that other invasive species, such as black mustard, are outcompeting with the native species and decreasing their abundance.

Overall, our fieldwork demonstrated that our suitability models were effective at predicting an increase in abundance for species, and we had an interesting result with plant species in cumulative current flow.

iNaturalist Model Validation

The higher mean decrease accuracy values for the habitat suitability surfaces suggest that habitat suitability is more important to predict occurrences than current flow, which is similar to our fieldwork validation findings. Using pseudo-absences led us to predict higher error rates than the models actually had. In a habitat suitability study of estuarine predators with both presence and absence data, the study authors used OOB as one of their metrics determining model fit in predicting real absences. Their OOB scores ranged from 13 to 32 percent (Livernois et al., 2021). Our OOB scores across all functional groups were below 35 percent. As OOB scores approach zero, surfaces become more accurate in their predictions of new occurrences. Considering our use of pseudo-absences instead of true absences, our models are rigorous and highly accurate. When compared to the AUC used to evaluate the habitat suitability surfaces in Beninde et al. 2023, their models attained a mean score greater than 0.7, meaning the surfaces were highly accurate for predicting occurrences like the connectivity surfaces generated in ours. Greater accuracy allows for more confidence in the predicting power of both the connectivity and suitability surfaces, allowing accurate and targeted conservation plans for local species. Accuracy is also crucial when creating new conservation policies that require careful planning and public support. Future analyses should be conducted to cross-validate and explore the use and capabilities of the surfaces should in exploring the power of the combined suitability and connectivity surfaces as predictors for occurrence. A comparison of the absolute difference between mean decrease accuracy scores surfaces and their predictor's correlation coefficient can give us more insight into how we can provide better conservation efforts and further disentangle habitat suitability and connectivity.

6.3 - Case Studies

With the loss and modification of habitats due to urbanization, significant challenges have been posed to these native species. Our individually generated connectivity models can be used to inform conservation decisions for at-risk species that rely heavily on conservation or suitability.

Western Fence Lizard

The western fence lizard is a species that is impacted significantly by the connectivity of habitat as shown by our field work and iNaturalist validation. We can utilize our connectivity models to inform their conservation plan. In a recent study, the morphology and connectivity of western fence lizards in four populations across different levels of urbanization in Los Angeles was examined and found key differences in the behaviors of both areas between such substrates (Putman et al., 2019). Fence lizards utilize a variety of habitats available in Los Angeles, from rocky nodes to heavily urbanized areas where buildings and fences provide vertical habitats. As urbanization increased with each substrate, lizards exhibited reduced limb and toe lengths, as well as fewer dorsal scales in comparison to populations found in more naturally conserved areas (Putman et al., 2019). Along with this, these shifts were also found to be linked to the microhabitat use of each population to their local environmental factors. Furthermore, the decrease in dorsal scale counts suggests heightened vulnerability to evaporative water loss, possibly due to reduced natural water availability. While further research is needed to completely understand the specific factors driving these changes, the study underscores the value of studying the effect of urbanization gradients across local species. Western fence lizards, in particular, can help provide a better comprehension of urbanization responses, contributing to a broader understanding of how similar local groups may adapt to human-induced habitat transformations.

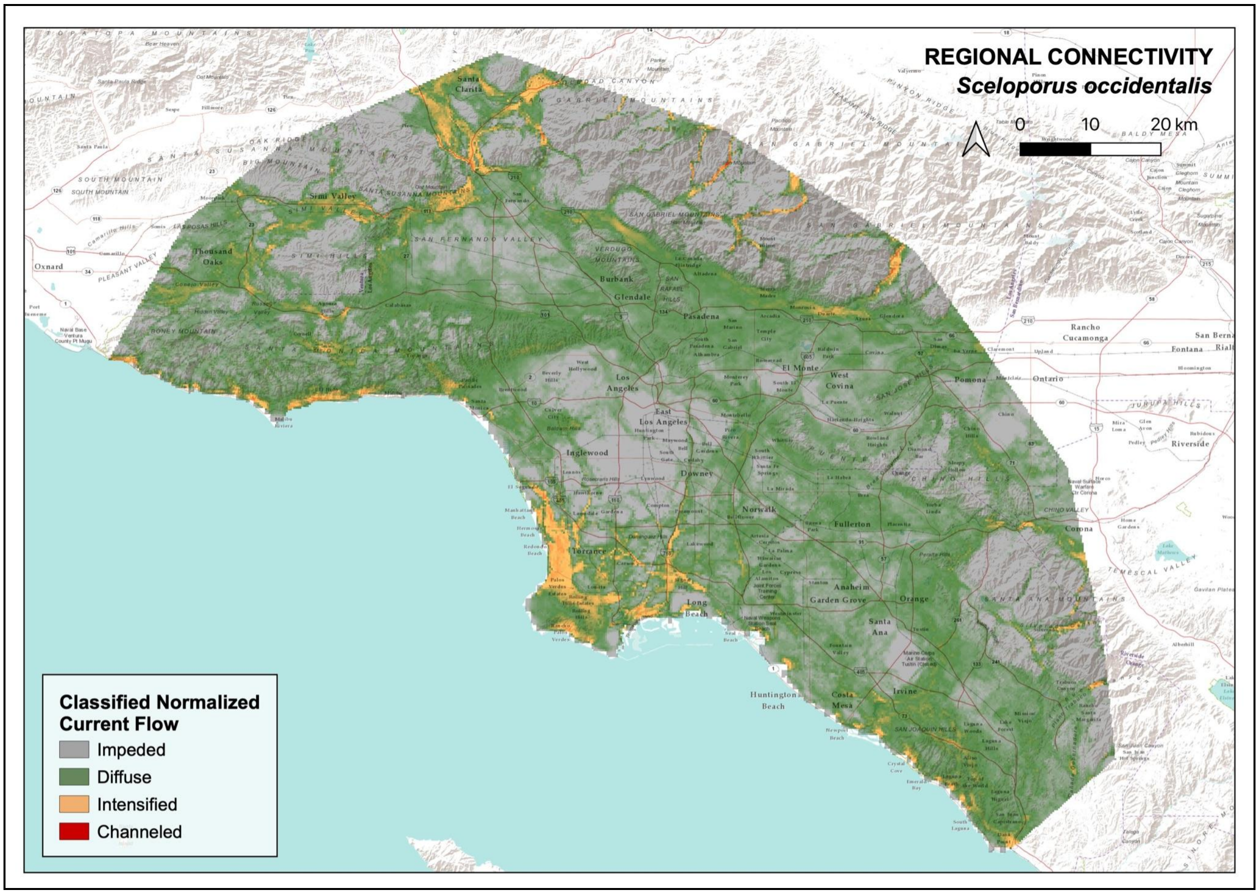

Figure 12. Regional connectivity for the western fence lizard (*Sceloporus occidentalis)* depicting areas with impeded, diffuse, intensified, and channeled current flow. Impeded areas have no available linkage for the species to utilize, which can affect genetic variation.

6.4 - Conservation Applications for the City of LA and The Nature Conservancy

LA City Biodiversity Index

As a first step in creating the LA City Biodiversity Index, Los Angeles Sanitation & Environment (LASAN) assessed LA's biodiversity through the Singapore Index (LA Sanitation & Environment, 2018). The National Parks Board of Singapore created the Singapore Index in 2008 as a tool that Singapore and other cities can use to regularly assess and quantify their conservation endeavors (Biological Diversity, n.d.). However, because Singapore and Los Angeles are very different in size, topography, vegetation, habitat fragmentation, and other factors, LASAN found that many adjustments to the original index had to be made to ensure a better fit for the broader Los Angeles area.

In 2022, LASAN published the LA Biodiversity Index Baseline Report. This report includes the completed LA City Biodiversity Index, created using the Singapore Index's components while adding new categories that better address issues specific to the Los Angeles area. The new LA City Biodiversity Index addresses connectivity in three separate categories instead of one to include regions that are not considered natural areas and identify differences between types of habitat connections (LA Sanitation & Environment, 2022a). These three categories are: "Connectivity of Natural Areas" (1.1D), "Connectivity of Urban Landscapes &

Open Space" (1.1E), and "Connectivity of Streams and Riparian Areas" (1.1F) (LA Sanitation & Environment, 2022a).

Possible Contributions to the LA City Biodiversity Index

Our models will most directly contribute to metric 1.1E of the LA Index (LA Sanitation & Environment, 2022a). Metric 1.1E evaluates connectivity between urban areas and open space through a current flow model generated in Omniscape to determine which urban areas see the most species movement and pinpoint patterns of where the weakest and strongest connective barriers are located (LA Sanitation & Environment, 2022a). This model was generated using a habitat quality map that served as a source layer and a resistance layer that represents the ability for species to move within a given landscape (Brown, 2019; LA Sanitation & Environment, 2022a). The resistance layer was made from merging the source layer with the Southern California Council of Governments (SCAG) 2008 Land Use layer (LA Sanitation & Environment, 2020; Brown, 2019).

For metric 1.1E, LA received a score of approximately 2 out of 5, where a score of 2 means that most urban corridors analyzed in the model are considered pinch-points (LA Sanitation & Environment, 2022a). Pinch-points are connectivity regions that are very narrow compared to the patches they connect, making them resemble a funnel or a bottleneck (Schuett-Hames, 2012). Because of how narrow these corridors are, pinch-points are susceptible to being easily cut off due to development, which could lead to habitat patch isolation (Schuett-Hames, 2012). The current model that metric 1.1E is based on excludes information on patterns between species and the types of corridors they are forced to travel through, which is important when trying to create species-specific conservation plans. Through our connectivity models that cover 1,017 species in Los Angeles, the City can gain information on which species populations in LA are moving through these compromised corridors and where to prioritize connectivity and species conservation efforts.

Habitat Restoration

To restore these degraded urban ecosystems, it is crucial to prioritize soil recovery and revegetation efforts that facilitate the establishment of native plant species, eventually lending to the recovery of other native taxa (Beltran et al., 2014). This is especially necessary in order to prevent the presence of an "extinction debt," a common phenomenon in urban areas where native species gradually go locally extinct over extended periods of distress even if they persist at first, a vulnerability that's becoming increasingly present as Los Angeles continues to further its urban development (Kuussaari et al., 2009). Survival of these different species without true recovery of their presence can effectively cause the consequences of habitat degradation and urbanization to be underestimated, furthering the rate at which local biodiversity could decline and emphasizing the need for proactive and collaborative recovery.

In the greater Los Angeles area, restoration of native vegetation has proven to be key in the recovery of various species. As an example, the California ground squirrel, a key ecosystem species in supporting other native taxa, faced threats from development and loss of native vegetation. Ground squirrels are considered ecosystem engineers, meaning their existing behaviors support the restoration of key habitat structures through activities such as vegetation clipping and burrowing, helping to create beneficial ecosystems for local species (Lenihan 2007). In Southern California however, population declines of important species like ground squirrels have risen due to changes in vegetation composition by invasive non-native species such as wild oat *Avena Fatua*, creating dense ground cover that lessens the ability of these squirrels to move and create the valuable structures necessary in fostering native biodiversity. In an effort to recover these habitats to historic conditions, researchers found an effective means of restoration was to not eradicate non-native vegetation, but could be achieved through managing a mixture of both pre-invasive and post-invasive conditions with reductions in invasive grasses as well as soil decompaction (Hennessy et al., 2016). As a result, increases in movement and burrowing from ground squirrels were found, helping to increase coverage of the species and stability of their population, as well helping to create valuable structures used by fellow native species such as . The hybrid approach here recognizes that complete eradication of all invasive species may not be feasible or realistic in many cases. By prioritizing areas for management and employing a combination of prevention, control, and restoration strategies, it is possible to achieve a more efficient and effective use of resources while still conserving native species and habitats. This approach promotes resilience and ecosystem health, allowing native species to persist and thrive in a changing environment.

Land Acquisition & Community Engagement

Along with approaching mindful habitat restoration, it’s important to note the value in community collaboration in proactive recovery. The Palos Verdes blue butterfly (*Glaucopsyche lygdamus palosverdesensis*), listed as endangered in 1980, was able to recover from the help of relevant and community driven collaboration that included the establishment of captive-rearing facilities and collaborative work among various partners, such as the U.S. Navy, local organizations, and government agencies, with habitat restoration efforts involving the removal of non-native vegetation and reintroduction of native plants (Weagley, 2009). Since then, restoration efforts along the coastal bluffs of Palos Verdes, have been mainly led by a coalition of residents, conservationists, government officials, and nonprofit organizations such as The Urban Wildlands Group, illustrating how instrumental community engagement can be in providing long term recovery to listed species. Involving residential communities in activities such as species tracking and vegetation restoration fosters a sense of ownership and empowers individuals to contribute actively to conservation efforts. This can include citizen science programs, where community members participate in monitoring native species populations, reporting sightings, and collecting data. Additionally, engaging communities in vegetation restoration projects, such as native plantings or invasive species removal, helps improve habitat quality and enhances community members' connection to their natural surroundings.

Furthermore, efforts to acquire private lands for conservation purposes can be successful, with the recent efforts in the Santa Monica Mountains serving as a prime example. While land acquisition for open space in the Santa Monica Mountains exceeded 5,000 acres per decade between 1960 and 2010, open space acquisitions since then have shown a decline during the most recent decade (2010-2020), suggesting a potential limit to the amount of land that can be feasibly acquired for conservation purposes (Cooper, 2022). Even with a lack of expansion available, government agencies should proactively seek partnerships with local community organizations to best understand how to manage and communicate best practices of existing land moving forward through formal agreements, joint planning committees, and regular meetings to discuss conservation priorities, share information, and coordinate efforts. Moreso, it’s essential to communicate the benefits of such collaboration, with these efforts helping to ensure the health and resilience of such ecosystems, which in turn may help provide benefits of improved water quality, pollination services, soil fertility, and natural pest control, which are valuable to both governmental agencies and residential communities. By collaborating closely and engaging residential communities, governmental agencies can leverage local knowledge, resources, and enthusiasm to achieve more successful and sustainable native species conservation outcomes.

VII. Conclusion

As urban landscapes continue to increase around the world to accommodate a growing human population, so does the need for available habitat for the species of these areas. Maintaining habitat connectivity is crucial in ensuring the survival of species across the planet, and maintaining this biodiversity is an instrumental part of human health, as well. Our hope is that our work sets the precedent for further studies in urban areas across the globe, exemplifying a way to collect concrete information and use it to create a more suitable landscape for humans and animal species alike. Revealing which natural areas throughout Los Angeles are most in need of connection can inform city officials on the most efficient way to protect the greatest number of species, and this will help the general public have a better idea of what they can do to improve habitat conditions on their own property. Modeling habitat connectivity in urban areas is a critical step in turning real-world data into usable guiding information to aid in conservation efforts wherever these methods are applied, and Los Angeles is just one example of an area where this information can lead to change for the better.

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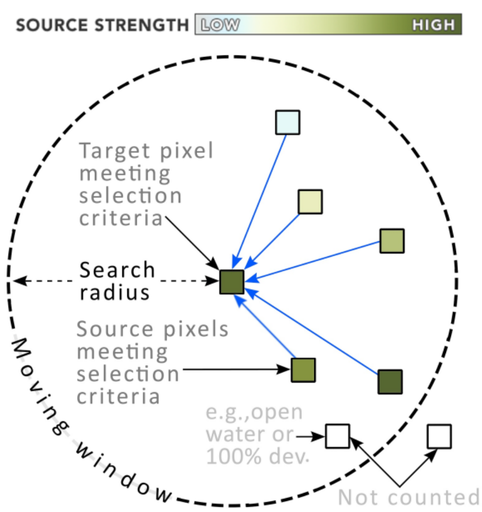
X. Appendix

Circuit Theory

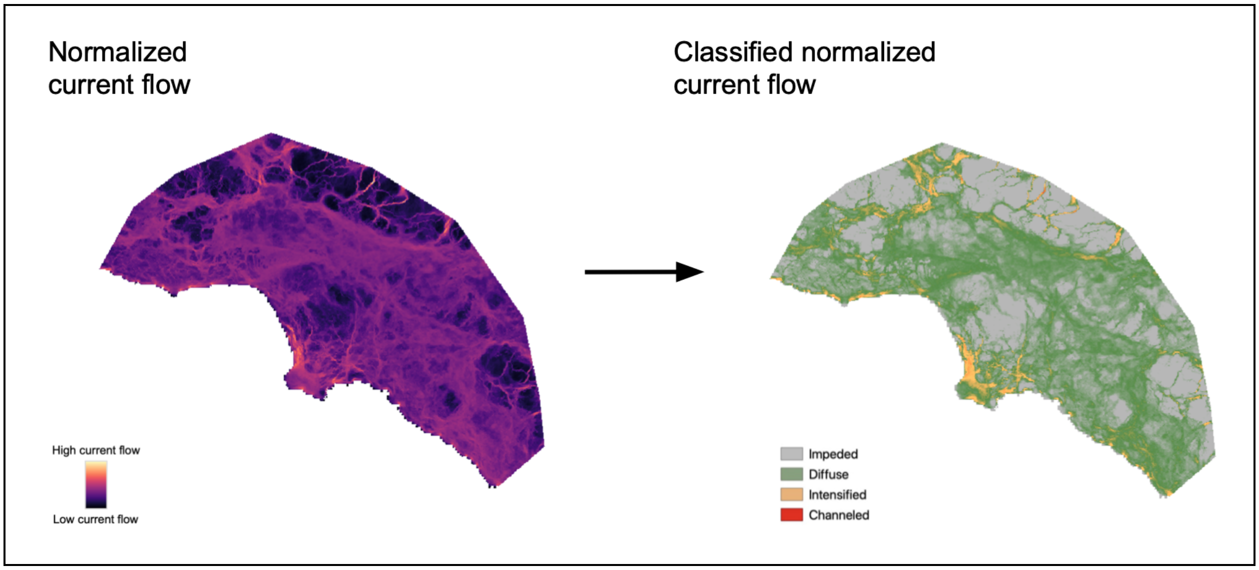
The connectivity modeling approaches built on the input of these resistance surfaces include least-cost models (LC) and circuit-theory based models (CT) (Diniz et al., 2019). In these approaches, the resistance surface is transformed into a weighted lattice graph in which nodes representing cells of habitat patches are connected by edges denoting the probability of movement between the locations (Diniz et al., 2019). The edges are weighted according to Euclidean distance (the measured distance between two points) and resistance values from neighboring cells (Diniz et al., 2019). An algorithm is used to determine a route trajectory that combines an array of edges to achieve the lowest accumulated cost-distance between nodes (Diniz et al., 2019). The required inputs of least-cost path models are the resistance surface and the predefined source and destination (SD) coordinates which serve as the nodes (Diniz et al., 2019). The assumptions behind classic LCP models reduce its application to animal movement across a diverse landscape because it is unrealistic to surmise that the animal has a clear destination and an innate knowledge of the cheapest of likely many travel routes (Braaker et al., 2015; Diniz et al., 2019; Unnithan et al., 2022). LCP may then be appropriate for regularly migrating species that have extensive knowledge of the available routes, but not for more naively dispersing individuals (Simpkins et al., 2019). In a CT model, the same graph theory process described with LC modeling applies but the edges are instead replaced by resistors (Diniz et al., 2019). As such, the landscape is transformed into a circuit board wherein each raster cell becomes a resistor with source locations denoted as nodes from which electric current originates, relative resistance values described by corresponding resistor strength, and animal movement simulated as current flow across the circuit (Dickson et al., 2018; Unnithan et al., 2022). CT models have particular ecological significance because they closely parallel random walk theory. In the same way that current flows across multiple resistors in a circuit, an individual has the potential to pursue “random walks” across all routes in any direction (Braaker et al., 2015; Antharaman et al., 2020). Recent adaptations have also taken on an omnidirectional approach which uses the resistance surface to calculate a continuous, wall-to-wall assessment across the landscape extent in any direction (McClure et al., 2017). Current densities are ultimately produced for every raster cell where higher current values indicate higher net movement probability through that location (Antharaman et al., 2020; Unnithan et al., 2022). Increasing the number of potential paths by reducing surrounding resistance to current will decrease the current flow through any single path. In this way, pinch points can be highlighted as dense areas of high current where few alternative pathways exist (Braaker et al., 2015). This random movement approach is beneficial as compared to LCPs because it makes no assumption of prior landscape knowledge (Simpkins et al., 2019). However, there is no clear consensus on whether resistance kernels or circuit theory have the more accurate predictive ability (Unnithan et al., 2022).

Circuitscape/Omniscape

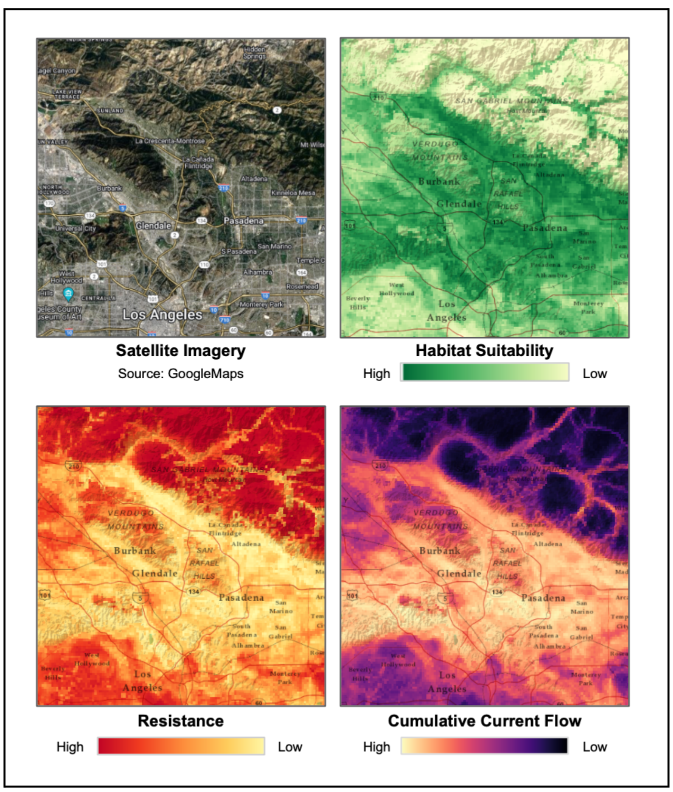
Circuitscape, which is based on electric circuit theory, is the most cited landscape connectivity tool worldwide (McRae et al., 2008; Antharaman et al., 2020). *Omniscape* is a recent extension of *Circuitscape* which makes use of a moving window function to map wall-to-wall instead of pairwise connectivity (Brown et al., 2019; Landau et al., 2021). As such, instead of the specific SD points required by prior versions of *Circuitscape*, *Omniscape* parameterizes its omnidirectional analysis using two raster surfaces: the resistance layer and source layer. The resistance layer represents how conducive to movement the landscape is. Movement-permeable areas are given low resistances, and areas that act as barriers to movement are given high resistances. The source layer weights the variation in importance for different points of potential dispersal origin to describe the probability that a species would move to or from a given cell (Brown et al., 2019). Using a source raster to continuously quantify origin and destination potential across the landscape removes the bias introduced by arbitrarily selecting core points and allows all areas to comprehensively contribute to connectivity (McRae et al., 2016; LA Sanitation, 2018). The moving window highlights an area of specified distance around each raster cell to test subsequent current flow density from that point through surrounding cells within that extent. A smaller window would assess more local connectivity, whereas a larger window would test connectivity over a greater distance (Brown, 2019). All iterative window analyses are summed together to produce a map of cumulative current flow representing movement potential across the landscape. The newer Julia package, *Circuitscape/Omniscape.jl*, provides more computational power and efficiency to this process enabling much larger and more finely-scaled analyses to be conducted with greater speed (Antharaman et al., 2020).



Supplemental Figure 1. Omniscape Moving Window. A diagram of one moving window iteration for the Omniscape algorithm (Landau et al., 2021)



Supplemental Figure 2. The classification of normalized current flow. Following the methodology of McRae et al. (2016), normalized current flow is divided into four main classes which better reveal the structural mechanisms underlying current flow.Data shown for the Western fence lizard (*Sceloporus occidentalis*).



Supplemental Figure 3. Cumulative current flow inputs. Each image is zoomed in to better visualize patterns within each input.