



# Towards robust corridors: a validation framework to improve corridor modeling

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## Abstract

**Context** Ecological corridors are one of the most recommended ways to mitigate biodiversity loss. With growing recognition of corridor importance, corridor modeling lags others in the development of robust, quantitative validation methods.

**Objective** We propose a post-hoc corridor validation framework, considering the range of methods across data needs and statistical intensity. We demonstrate the importance of post-hoc corridor validation by testing several validation methods on different corridor model outputs.

**Methods** We used three different transformations on a Florida black bear (*Ursus americanus floridanus*) habitat suitability model to create different resistance grids, independent GPS collar data from a case study population, and Circuitscape to create corridor models. We used several validation methods, including a novel method, to compare resulting corridors.

**Results** Transformed resistance grids were all correlated, yet differing validation and resistance grids resulted in different recommended corridors. The use of one resistance surface and one validation type can result in the selection of inefficient or ineffective corridors. At a minimum, modelers should determine what proportion of an independent population falls within resulting corridors and should move towards more robust, documented methods as resources allow. The use of multiple validation methods can ensure greater confidence of modeling results.

**Conclusions** We encourage the use and further development of the framework presented here to

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Open Research: Generated datasets will be permanently archived in the Digital Repository for the University of Maryland (DRUM): <https://drum.lib.umd.edu/>.

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drive the corridor modeling field towards more effective corridor creation and improved conservation outcomes. If validation methods are not improved, the ecological and economic cost of poor corridor science will continue to increase with increasing biodiversity loss.

**Keywords** Black bear · Corridor · Circuit theory · Circuitscape · *Ursus americanus floridanus* · Validation

## Introduction

Ecological corridors are one of the most recommended ways to mitigate biodiversity loss in the face of a changing climate, and increased human landscape modification and connectivity planning is growing globally as a conservation strategy (Heller and Zavaleta 2009; Spear et al. 2010; Keeley et al. 2019). Corridors can be created for a number of conservation purposes—broad-scale ecological conservation, human recreation (Jongman et al. 2011), conservation of ecological zones along climate gradients (Beier and Brost 2010), conservation of specific species' habitat (structural connectivity), or conservation of animal movement routes (functional connectivity). Recent growth in global acknowledgement of connectivity as a necessary component of conservation and the adoption of connectivity plans at local, regional, and national levels has been accompanied by a growth in connectivity tools and methodological developments. Unfortunately, the selection of methods and tools used to identify corridors is more often driven by tool access than by the accuracy of results they produce (Dutta et al. 2022).

Corridors are considered more accurate when created using data reflective of the ecological or biological process being modeled (Elliot et al. 2014; Zeller et al. 2018). Although there is broad guidance for some decision points throughout the modeling process for specific taxa and conservation objectives (Adriaenssen et al. 2003; McRae and Beier 2007; Beier et al. 2008, 2011; Zeller et al. 2012; Cushman et al. 2013; Kumar et al. 2022), there remains little guidance on post-hoc corridor validation to ensure corridors are serving their intended purposes. For example, in the resistance surface corridor modeling paradigm, suitable habitat is first identified,

transformed to resistance representing the difficulty of moving across a landscape, and corridors between habitat patches are identified using a corridor model such as least-cost path or circuit theory. Resistance surfaces can be created from expert-based rankings, machine learning algorithms, or resource selection functions, the processes of which require multiple subjective decisions which can lead to the propagation of uncertainty throughout the process and into the final model results. However, resistance surfaces are usually created using global positioning systems (GPS), very high frequency (VHF), or other location data from animals utilizing their resident home ranges, not movement processes such as migration or dispersal. This can result in a mismatch between the data used in the corridor modeling process and the actual intent of the model (i.e. dispersal or migration). Making this potential mismatch even more glaring, Riordan-Short et al. (2023) found that validation of connectivity models was quite uncommon. In Riordan-Short et al.'s (2023) 2022 literature review, only 44% of studies included any validation effort, 31% only validated their input data, and just 18% validated the resulting corridor model outputs, with few utilizing independent validation data. Of the studies that validated their resulting corridor outputs, 36% found poor or inconclusive agreement between validation data and model outputs (Riordan-Short et al. 2023).

Rapid habitat loss and fragmentation coupled with climate change and limited financial resources of many natural resource agencies create an imperative to design and implement effective corridors. We suggest that high quality GPS data of dispersing or migratory animals should be used to identify and protect movement corridors, with subsequent validation determined using genetic data to measure gene flow between subpopulations. This “gold standard” process incorporating gene flow is rarely possible owing to low and short-term research budgets, poor project planning, the use of historical data, grant timelines, etc. (Cushman et al. 2013; Laliberté and St.-Laurant 2020).

In the absence of genetic data, there are several other options for corridor validation, though none are used regularly or in a standardized framework. For example, researchers have compared species presence and absence inside and outside corridors as a validation technique (Chardon et al. 2003; Quinby

2006; LaPoint et al. 2013). Some have gone beyond determining whether presence locations were within corridors and compared mean, maximum, and standard deviation of circuit theory corridors' current density (flow) at buffered species locations and at random locations using t-tests, with the expectation of higher values at species locations (Koen et al. 2014; Gantchoff and Belant 2017; Chege et al. 2021; Phillips et al. 2021). In the absence of direct field data, detection/non-detection gathered from local resident interviews has also been used (Zeller et al. 2011).

Broadly, these corridor validation methods can fit into four categories, ordered here from least data and statistically intensive to highly data intensive, providing modelers an array of options for validation:

1. Determining what percent of species locations lie within corridors using an overlay.
2. Testing the difference in modeled connectivity values at random and occurrence locations or within a buffered area around locations.
3. Identifying differences between connectivity surfaces and null models or using a step-selection function to ensure animals are selecting higher connectivity areas.
4. Validation of individual and population movement via camera trapping with individual identification and gene flow patterns on the landscape, respectively.

Herein, we propose treating these four categories of validation as a strategic validation framework. The use of at least one of these validation categories, depending on project resources, could improve on-the-ground conservation and result in differing corridors, as we show with example data. More specifically, we calculate and test corridors resulting from different resistance surfaces for the Florida black bear (*Ursus americanus floridanus*), a highly mobile large mammal inhabiting the increasingly fragmented landscape of the U.S. state of Florida (Fig. 1). We propose a novel validation technique (category 3 in the above list) and determine how corridor validation methods categories 1–3 could influence corridor selection for Florida black bears. Then, we illustrate the significant importance of an adaptive approach to corridor delineation, discuss the need for corridor validation, and add to the sparse corridor validation literature to improve creation of ecologically and economically

sound corridor models that largely remain only theoretical in nature (Laliberté and St.-Laurent 2020).

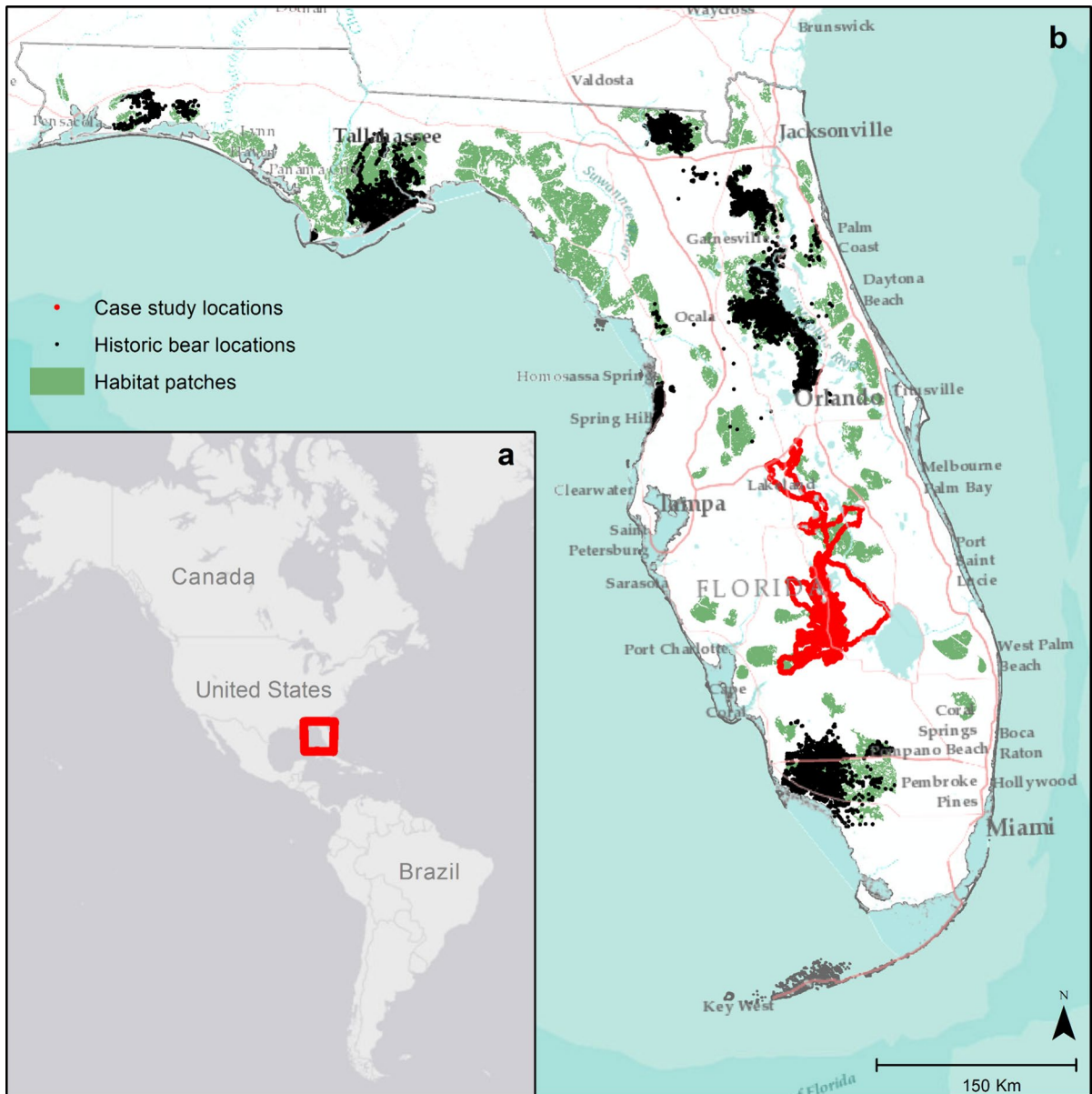
## Methods

### Study location

The state of Florida provides an ideal study area for corridor identification and validation of a wide-ranging species, the Florida black bear. Florida is a highly human-modified landscape with patches of natural lands throughout the state, many of which are high quality black bear habitat (Poor et al. 2020). The black bear in Florida has experienced significant habitat and genetic fragmentation caused by human land use changes since the early twentieth century (Dixon et al. 2007). Today, the statewide population is estimated to be >4000 bears (FFWCC 2019), but the statewide range is only about half of what it once was, distributed in seven distinct and still relatively functionally isolated subpopulations (Dixon et al. 2007; Scheik et al. 2023). Increased connectivity among these subpopulations is critical for the long-term genetic health of black bears and for the facilitation of dispersal in an increasingly human-modified landscape.

### Pre-existing corridors

The Center for Landscape Conservation Planning at The University of Florida created the Florida Ecological Greenways Network to identify and prioritize functional connectivity across public and private lands for a host of species, including the Florida black bear (FEGN; Hctor et al. 2000; Hctor 2021). Several regional, state, and federal programs within Florida use the top three FEGN priority levels (levels 1–3) to guide conservation efforts and prioritize lands to conserve for wildlife, ecosystem services, and ecological resiliency (Hctor et al. 2015). Levels 1–3 of the FEGN cover approximately 17.7 million acres of Florida, with approximately half in conservation lands (Hctor et al. 2015). We provide a comparison of these broad corridors created with multiple conservation objectives in mind and the corridors that we created using single-species corridor modeling methods to demonstrate different corridor validation



**Fig. 1** Location of Florida, USA in the Western hemisphere (a) and location of Florida black bear (*Ursus americanus floridanus*) habitat patches, historic bear GPS locations, and case study bear locations within the state of Florida (b)

methods and their interpretation for management and conservation objectives.

#### Bear location data

We had historical data from 1978–2016, collected by various researchers using VHF and GPS collars, to create a habitat suitability model (see Poor

et al. 2020 for complete methods description). For the suitability model, we used adult bears and removed bears with <30 locations or <3 months of data within a 12-month window (Murrow and Clark 2012). We subsampled bear GPS locations to every 5 h to reduce spatial and temporal bias. We used independent GPS location data collected from 2004–2010 in the Highlands-Glades area (Fig. 1) to

validate the corridors we created. Again, we only included bears with locations across  $\geq 3$  months and with  $\geq 30$  locations and also removed 2D locations with PDOP  $> 5$  (Lewis et al. 2007), deployment locations, and mortality locations. After data filtering, there were 13 males, 17 females, and 113,079 total locations in our validation dataset. We note here that these data included locations from individuals utilizing their home range as well as during dispersal events.

#### Habitat suitability data and resistance preparation

We used the previously created statewide habitat suitability model as a resistance grid for corridor dispersal (Poor et al. 2020). Resistance surface creation is a critical yet oft-ignored part of corridor modeling. Most often, habitat suitability surfaces are inverted using a linear inverse transformation, with the assumption that suitability and resistance are linearly related while, in reality, species may be able to traverse more low-quality habitat during periods of movement than this transformation implies (Elliot et al. 2014; Keeley et al. 2016). This transformation is a critical decision point along the modeling pipeline which can impact resulting corridors. Black bears in particular are often seen in and seem willing to travel through suburban neighborhoods (FFWC, unpublished data). Consequently, we transformed the habitat suitability model with a negative exponential function using three different  $c$  scaling parameter values that allow more low- and medium-quality pixels to be classified as low resistance and easier to cross and may more accurately reflect the movements of a habitat generalist (Supplementary Figure S1; Trainor et al. 2013; Keeley et al. 2016; González-Saucedo et al. 2021; Belote et al. 2022). The negative exponential function is:

$$100 - 99 * ((1 - \exp(-c * h)) / (1 - \exp(-c))),$$

where  $h$  was the habitat suitability value (range = 0–100), and  $c$  was set to 0.25, 2, and 8, based on recommendations in Keeley et al. (2016).  $C=0.25$  is an approximate negative linear transformation of suitability, meaning resistance decreases at a constant rate as the suitability increases, while 2 and 8 are two increasingly nonlinear transformations. Higher  $c$

values reduce the resistance of less suitable values, approximating the use of moderate-quality habitat by dispersers.

Hard boundaries, such as coastlines, create areas of edge effects known to impact Circuitscape modeling results. To mitigate these edge effects from Circuitscape, we buffered the entire state of Florida by 50 km after transforming the resistance grid. Then, each cell in the buffered area was given a randomly selected value from the distribution of each transformed resistance surface (the ‘sandpaper’ method; *personal communication*, M. Clark, The Nature Conservancy). This random raster buffer minimized the effects that coastlines and jurisdictional boundaries had on the flow of current in our later modeling stages by assigning a neutral resistance to the buffered area, rather than a maximum resistance value as is common in circuit theory modeling (Belote et al. 2022). After modeling, we removed the buffered area.

#### Habitat patches

Because we were interested in dispersal and movement between occupied bear areas (i.e. locations identified by the state authorities as frequently used by black bears (FFWCC 2019), we identified suitable source habitat patches. We used Core Mapper in the Gnarly Landscape Utilities toolbox (Shirk and McRae 2013) to identify the habitat patches using a moving window of 4 km, minimum patch size of 50 km<sup>2</sup> (based on the average black bear home range; FFWC 2019), and a habitat suitability threshold of 0.53 based on the sensitivity and specificity threshold of the previously calculated habitat suitability model (Poor et al. 2020).

#### Corridors

Currently, least cost path and circuit theory modeling are two of the most used corridor identification methods. In least cost path applications, two or more habitat patches are identified and the path of least landscape resistance between the two patches is identified for a given focal individual or species (Adriaensen et al. 2003). This method assumes a priori knowledge of the landscape by the moving individual or species. Least cost path methods may not reflect exploratory or dispersal movements but may better reflect directed movements such



as migrations (Poor et al. 2012). In circuit theory modeling, current is injected into habitat patch cells in a raster and allowed to flow across the landscape (McRae and Beier 2007). One criticism of circuit theory is that this algorithm assumes random movement across a heterogeneous landscape (Kumar et al. 2022), whereas movement may actually be driven by individual choice or other inherent biophysical processes. While connectivity modeling may be moving beyond the resistance surface framework towards movement driven modeling (Kumar et al. 2022), resistance surface connectivity modeling does not require high quality GPS collar data and will likely persist as a commonly used modeling framework in conservation for the foreseeable future because of its ease of access and existing knowledge base.

In this study, we chose Circuitscape, implemented in program Julia (Hall et al. 2021), as our corridor modeling platform because it is readily available, commonly used, and performs better than least-cost path methods when identifying destination-biased dispersal (i.e. patch-to-patch connectivity). We ran Circuitscape using the all-to-one option at 120 m resolution with eight neighbors. We tested our validation techniques on each of the three transformed outputs (resistance surfaces from  $c=0.25$ ,  $c=2$ , and  $c=8$  habitat suitability transformations). Circuitscape provides a continuous raster surface depicting unbounded current flow values. Higher values indicate higher current flow due to intensified or channelized current flow, i.e. corridors and pinch points (McRae et al. 2008; Dickson et al. 2018). In the Circuitscape context, low current values do not always indicate a lack of connectivity and may conversely indicate diffuse, widespread, non-channelized flow. To isolate ‘corridors’ from our Circuitscape output, we selected the top 10% of Circuitscape values from each output and converted these to polygons (Zeller et al. 2018).

We tested the three Circuitscape outputs with three different categories of validation, ranging from the least data-intensive (category 1) to a data-intensive method (category 3). We compared the validation results for each output to determine differences resulting from each transformation as well as how validation choice impacted corridor output.

Category 1 validation: proportion of occurrence points in corridors and FEGN

To determine the proportion of our validation dataset within our modeled corridors, we first used ArcMap 10.8.1 (Esri 2020) to identify bear locations overlapping corridors. We measured the efficiency of corridors to capture bear locations using number of locations/km<sup>2</sup>. We also calculated the percentage of bear locations falling within corridors. Then, to compare our single species corridor output with a multispecies corridor output, we compared the efficiency of the FEGN polygons (Priority 1 and Priority 1–3) and our modeled corridors.

Category 2 validation: current flow comparison at occurrence and random points

Next, we conducted multiple category 2 validations. We compared flow values at bear and random locations. We randomly selected 1000 bear locations from the validation population and created a 95% kernel density estimate (KDE) around the sampled population using the package *adehabitatHR* in R (Calenge 2006; R Core Team 2023). We then created 1000 random locations within the KDE. We sampled the Circuitscape outputs at both the randomly created and randomly selected bear locations and tested for differences in current flow values using a Welch’s two-sample t-test. Then, we identified the average hourly step length of bears using the *amt* package in R (Signer et al. 2019) and created buffers around the randomly selected bear locations and the random locations within the population’s 95% KDE using the step length (367.2 m) as the radius. We calculated the average current flow within each buffered area for each transformation output (C) and again tested for differences using Welch’s two sample test. Finally, we created 95% KDE home ranges for each individual bear and a matching number of random points within these home ranges. We buffered bear and random locations by the average hourly step length as the radius and extracted the average flow values within these circles for each location. We tested whether animals used areas of higher current flow by using a generalized linear mixed model (GLMM) with a logit link using package *lme4* (Bates et al. 2015). We set location type (bear or random) as the response

variable, mean current flow as the fixed effect, and individual as a random effect.

### Category 3 validation: step-selection and null model comparison

Category 3 validation methods moved beyond a simple comparison of animal and random locations. Because we had high-quality independent GPS data available, we used a novel method of validation by analyzing a step-selection function (SSF) using the Circuitscape current flow output surfaces as predictor variables to validate the corridors. Normally, step-selection functions allow integration of movement variables with landscape features, so a more accurate picture of habitat selection during dispersal can be obtained (Thurfjell et al. 2014). Used steps are contrasted with a random selection of steps to characterize ‘available’ habitat during an animal’s movement through the environment. These paths may inherently differ from landscape-scale corridors due to the differing scale of the underlying ecological processes (population-scale habitat selection vs. individual dispersal), but in the absence of population-wide high resolution GPS data, we posit these data provide a realistic alternate validation technique. Using a step-selection function in this framework allows for the comparison of current flow values at used steps with available steps originating from the same previous step location. While individuals are not ‘selecting’ current flow values while moving on the landscape, they are selecting for landscape features that may or may not facilitate movement. By proxy, our use of current flow as the predictor in a step-selection allows for the validation of the underlying habitat model, resistance surface, and corridor model parameters simultaneously. Until recently, the step-selection function modeling framework and computational restraints limited models to the individual scale (Muff et al. 2020).

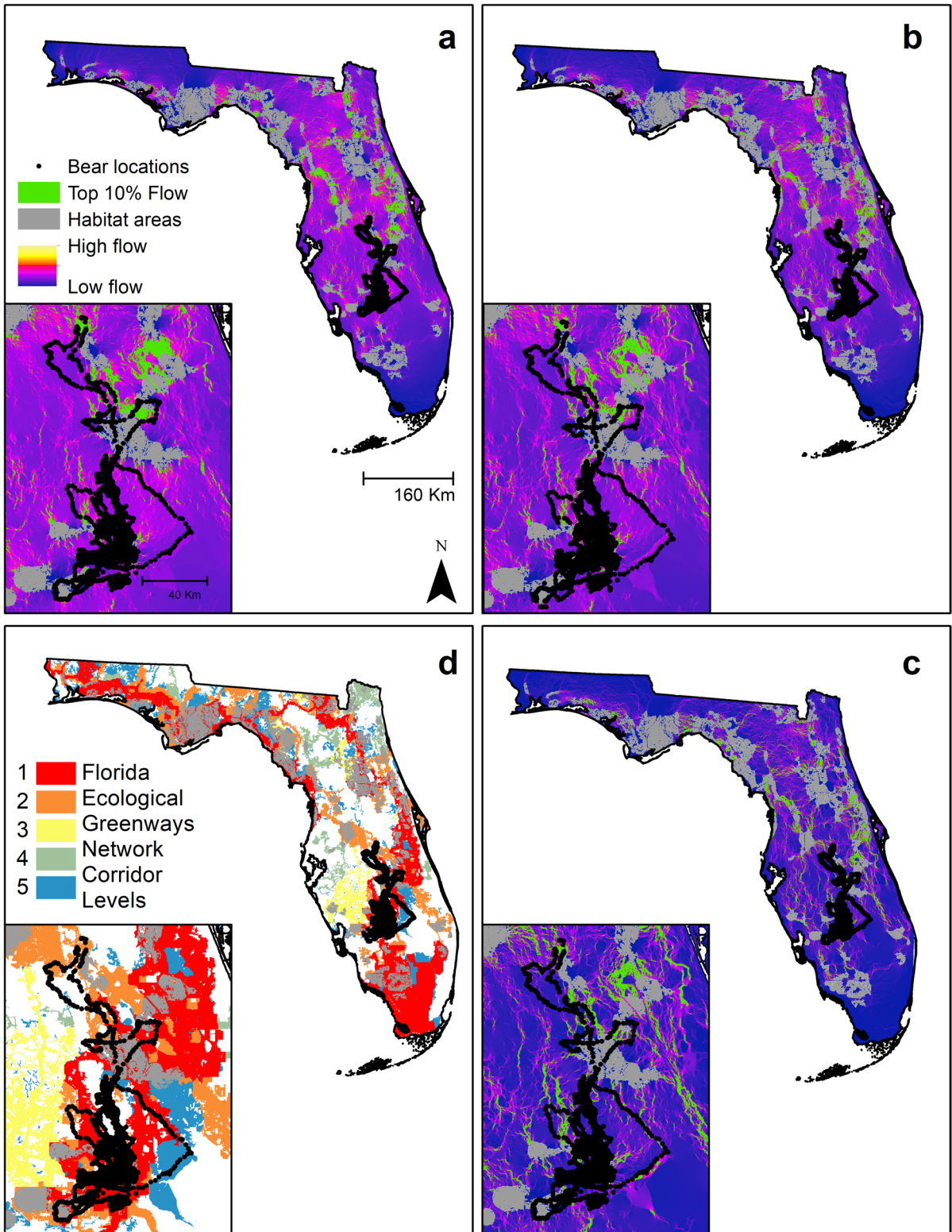
Conditional logistic regression models can approximate a Poisson model with stratum-specific fixed effects, thereby allowing for population-level step-selection modeling with individuals as random effects (Muff et al. 2020). Therefore, we created tracks in R package *amt* and resampled tracks to 10-min intervals (Signer et al. 2019). We generated 10 randomly available locations for each step and fit step lengths to a gamma distribution and turning angles to a von Mises

distribution (Avgar et al. 2016; Signer et al. 2019). We fit the SSF model with a random intercept and a large, fixed prior variance in R package *glmmTMB*, which is likelihood-equivalent to the more traditional SSF analysis using a conditional logistic regression but allows for efficient estimation of individual random effects (Muff et al. 2020). For each Circuitscape output, we used the value at the end of each observed and random step thereby relaxing the assumption that movement pathways between consecutive locations consisted of a straight line (Fortin et al. 2005). We used individual ID as a random effect and modeled Circuitscape outputs as fixed effects in three separate univariate models. We used AIC model selection to determine the best model fit across the three Circuitscape outputs.

Our final validation method and second category 3 validation was a comparison of empirical Circuitscape model outputs to a null model output. To determine whether our empirical models performed better than an isolation-by-distance model (i.e. where resistance is uniform across a landscape and distance is the main limiting factor in connectivity), we created a null Circuitscape model where resistance at all pixels = 1. We subtracted the null model output from each empirical model and calculated the mean and SE at each bear location within a corridor (Zeller et al. 2018). Positive values would indicate better performance of the empirical model than the null model, and vice versa. After removing bears that fell within identified habitat patch areas (resulting in 99,428 bear locations removed; 13,651 locations included in corridor comparison and validation), we standardized the empirical and null model outputs and identified the differences between them using paired t-tests in R.

## Results

The  $c = 8$  (C8) transformed resistance surface resulted in a higher average flow across the entire state and higher maximum flow areas where current was forced through highly unsuitable habitat at the high end of the resistance surface (Supplementary Table S1; Fig. 2). The  $c = 0.25$  (C025) transformation resulted in the lowest average current flow (Supplementary Table S1). As expected, all surfaces were highly correlated (Supplementary Table S2). Across all outputs, the C2 surface had 6292.1 km<sup>2</sup> of top 10% corridors,





◀**Fig. 2** Top 10% flow (green) and continuous Circuitscape model output (flow) for Florida black bears (*Ursus americanus floridanus*) using a  $c=0.25$  transformation (a),  $c=2$  transformation (b),  $c=8$  transformation (c), and Florida Ecological Greenways Network multispecies corridors (d), and case study black bear locations

the C8 surface had the most area within the top 10% corridors, 7816.9 km<sup>2</sup>, and the C025 top 10% corridors were 7424.5 km<sup>2</sup>. These corridors overlapped across more than half of their area, with 4536.6 km<sup>2</sup> of overlapping area

Category 1 validation: proportion of occurrence points in corridors

While the outputs initially appeared similar, there were stark differences. For the C025 surface, 42% of bear locations fell within corridors (Table 1; Fig. 2), while only 26% fell within corridors created using the C8 surface. However, the C8 corridors, which decreased the impact of highly human-modified areas on bear movements, included an entire corridor for one exploratory bear that was not included in the C025 corridors. Interestingly, C8 and C025 had more land area but C2 was the most efficient, as measured by bears/km<sup>2</sup> (Table 1). As expected, the least efficient black bear corridors were the multi-species FEGN level 1–3 corridors, with 93,470 km<sup>2</sup> and 1.11 bears/km<sup>2</sup>. Scaling the FEGN corridor area down to just include the top priority corridor area (level 1) increased efficiency slightly to 1.89 bears/km<sup>2</sup>.

Category 2 validation: current flow comparison at occurrence and random points

For the point comparisons, bear locations were at points with higher current flow than random locations across all model outputs ( $p < 2e-16$  in all cases; Table 2). Similarly, for the buffered points comparison, all bear locations were in areas with higher average flow values than random locations ( $p < 0.005$  in all cases; Table 2). When translating generalized linear mixed model results to probabilities from odds ratios, bear locations were 46, 35, and 14% more likely to be associated with higher flow values than random locations for the C025, C2, and C8 Circuitscape outputs, respectively (Table 3).

Category 3 validation: step-selection and null model comparison

All output grids had a significantly positive effect on bear step selection ( $p < 2e-16$ ), with a higher probability of bears selecting high-flow areas rather than low-flow areas. Across models, the C2 resistance grid was the best fit, with a 95% confidence interval near 1 (Table 4). No confidence intervals overlapped 0, indicating overall good model performance. In comparison with the null model, all empirical models were significantly different, with the C025 and C2 models performing significantly better than the null model (Table 5; Fig. 3).

## Discussion

We modeled corridors and tested three categories of corridor validation methods, categorized by data intensity, using a common corridor model. Our results highlight the subjectivity in corridor modeling and the importance of adequate corridor validation. Each of the three resistance surface transformations resulted in different spatial distributions of corridors, leaving the user to match management objectives with corridor distribution. Our results underscore the need for careful project planning to allow for corridor validation, and we establish a novel method for more efficient single-species corridor validation.

We demonstrate with sample data from Florida black bears that corridor selection varies with resistance transformation and validation category. Despite the high correlation among the three continuous flow outputs, little of the top 10% of the corridors across the resistance surfaces overlapped, indicating relatively low spatial concordance of the highest flow areas across resistance transformation outputs (Fig. 2). Though we did not have validation data available for the entire state of Florida, the variability seen in the Highlands-Glades population validation likely reflects broader patterns. To create corridors statewide, we recommend validating with independent data from within each ecoregion, especially given the unique biodiversity and landscape across the state.

Across all validation results, the C2 or C025 black bear models may be considered best in Florida. With category 1 validation, we found that the top 10% flow areas of the C2 surface were the most specific,

**Table 1** Percentage of bear locations, area covered, and bear location density (efficiency) from the sampled Highlands-Glades Florida black bear population across 5 defined corridors

Corridor	% of Bear Locs	Area (km <sup>2</sup> )	Bear Locs/km <sup>2</sup>
c=8	26	7817	3.57
c=2	38	6292	6.49
c=0.25	42	7425	6.08
FEGN Levels 1–3	96	93,470	1.11
Top FEGN (Priority 1 only)	78	44,533	1.89

Locations were quantified from the top 10% of the Circuitscape corridors across three different habitat suitability-resistance grid transformations and within Florida Ecological Greenways Network multispecies corridors and top priority areas

efficient use of space, including the greatest number of bear locations in the least amount of area (bears per km<sup>2</sup>). The C8 corridors identified areas used by a unique disperser but likely missed important common areas used by the entire population given the lack of efficiency of those corridors (Fig. 2). However, those corridors may provide insights for managers when they must prioritize unique genetic movements or conservation planning that aims to preserve connectivity rather than core habitat.

In category 2 validation, we found no distinguishing differences using the point comparison or buffered point comparison methods; in all cases, bear locations had significantly higher flow values than random locations, indicating all resistance surfaces resulted in high flow areas in bear usage areas. However, the GLMM results indicated the C025 resistance model (approximately a linear transformation of the habitat suitability model to resistance) resulted in a stronger association of bear locations and higher flow areas, while the C8 transformation resulted in

**Table 2** Average Circuitscape output flow values at 1000 Florida black bear and random point locations, and average Circuitscape flow values within buffered neighboring areas

C value	Point location Circuitscape flow value averages				Buffered point location Circuitscape flow value averages			
	Bear	Random	95% CI	t (p value)	Bear	Random	95% CI	t (p value)
0.25	1.30	0.98	−0.36 to −0.27	−13.01 (p<2.2e−16)	1.09	0.95	−0.19 to −0.09	5.50 (<0.005)
2	1.52	1.08	−0.51 to −0.37	−12.31 (p<2.2e−16)	1.25	1.04	−0.28 to −0.14	5.87 (<0.005)
8	2.37	1.48	−1.10 to −6.9	−8.48 (p<2.2e−16)	1.88	1.40	−0.64 to −0.31	5.55 (<0.005)

around bear and random locations from three resistance surfaces using c=0.25, c=2, and c=8 negative exponential resistance surface transformations

**Table 3** Generalized linear mixed model results from Florida black bear locations, where bear ID was a random effect and average Circuitscape model results (from a habitat model transformed using three different negative exponential c values) within a buffered area around bear locations were fixed effects

	Coefficient	SE	z	p	Variance	SD
c=0.25						
Intercept	−0.06	0.06	−1.01	0.32		
Flow value	0.38	0.03	11.85	<2.2e−16		
ID (random)					0.06	0.25
c=2						
Intercept	−0.02	0.06	−0.33	0.74		
Flow value	0.30	0.02	13.09	<2.2e−16		
ID (random)					0.07	0.26
c=8						
Intercept	0.1	0.06	1.66	0.09		
Flow value	0.13	0.01	13.31	<2.2e−16		
ID (random)					0.08	0.28

**Table 4** Mixed effects step-selection function output using resistance grids from three different negative exponential function transformations on a Florida black bear habitat suitability

model, with  $c=0.25$ ,  $c=2$ , and  $c=8$ . Population-level step-selections included individuals as random effects and 10 randomly available locations for each step

Model	Intercept	Coefficient	df	AICc	Delta AIC	Weight	95% CI
$c=2$	-2.786	0.09	3	742,004.7	0	1	0.081–0.994
$c=0.25$	-2.816	0.129	3	742,023.5	18.78	0	0.115–0.142
$c=8$	-2.711	0.026	3	742,126.8	122.12	0	0.023–0.295

**Table 5** The mean and standard error (SE) and comparison (t) between the flow values from a null Circuitscape model where resistance=1 and each standardized empirical Circuitscape

model output (empirical model–null model) for three negative exponential functions at bear locations within modeled corridors

Output	Mean (95% CI)	SD	SE	t (p value)
$c=0.25$	8.16 (0.86–15.46)	3.65	0.012	65.31 (<2.2 e–16)
$c=2$	8.04 (-0.78–16.86)	4.41	0.014	39.47 (<2.2 e–16)
$c=8$	6.92 (-7.56–21.40)	7.24	0.023	-26.96 (<2.2 e–16)
Null model	7.54 (4.24–10.84)	1.65	0.005	

the weakest association. This was expected because the C025 transformation resulted in suitability values corresponding to higher resistance values, in turn resulting, on average, in higher flow values across larger areas (Supplementary Figure S1). The higher  $c$  value transformations (such as the C8 model) resulted in very high suitability values having very low resistance, resulting in increased channelization of flow (Fig. 2). Thus, the C8 output appears to have more channelization, where if bear locations fell outside of these 'corridors', it would result in a lower association between bear locations and high flow areas. If we were to use the category 2 validation method in isolation, we may determine that the C025 model had the best results, but when taken in context with the category 1 validation results of C2, the choice is not clear—the highest flow areas do not necessarily equate to more bears/km<sup>2</sup>.

Category 3 validation methods were inconsistent in identifying a top corridor model between C025 and C2. The novel use of a step-selection function to determine whether bears are selecting higher flow areas compared to available locations indicated the C2 model best represented bear corridors. However, when compared to the null model, C025 had the highest average, indicating higher flow than expected by an isolation-by-distance null model. This model was the only model where the confidence interval did not

overlap zero. The C8 model in both category 3 validation methods performed the worst and had lower flow than expected compared to the null model (Fig. 3). This was likely due to the transformation including more moderate suitability areas as low resistance areas. However, management objectives still must be considered given the unique output of C8.

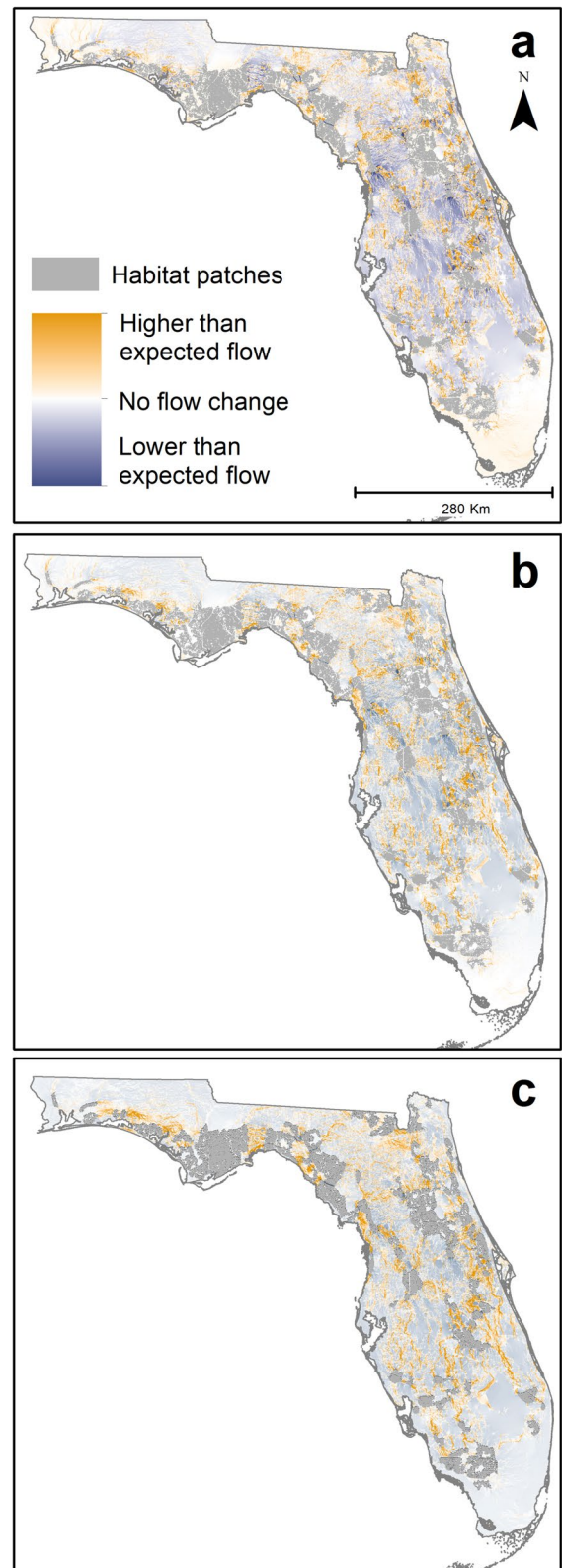
In this case study, the multispecies FEGN corridors were the least efficient in terms of solely identifying bear locations per km<sup>2</sup>, as could be expected from a multispecies corridor. From a broad ecological perspective, using the FEGN corridors as conservation guidance can help Florida meet multiple conservation objectives but do not provide conservation goals tailored specifically to black bears as do our corridor models, generated using only black bear occurrence data and habitat suitability. When interpreting our three models together, compared to FEGN, and considering the behavior of the underlying transformations, we suggest the C2 model performed the best for black bears specifically, as seen in the category 1 and 3 validation results. To more fully account for dispersal and exploratory movements of bears, a next step could be to prioritize Highlands-Glades corridor areas from the C2 model for specific conservation or management actions and incorporate those into the statewide conservation plan. In this and any study area, the selection of a final model should

**Fig. 3** Comparison of empirical Circuitscape Florida black bear corridor models with a null model, using resistance transformations where  $c=0.25$  (a),  $c=2$  (b), and  $c=8$  (c). Darker orange areas indicate higher than expected flow compared to the null model and darker blue areas indicate lower than expected flow

be informed by management and conservation goals and preferably by category 4 validation methods such as mark recapture/resight or gene flow analyses.

Validation of corridor work has increased in recent years, but validation of outputs using independent data is still rare (Riordan-Short et al. 2023). Testing the sensitivity of differing modeling decisions and using multiple categories of validation should be considered a best practice of corridor modeling. As shown here, using a single transformation on the resistance surface can result in inefficient corridors. The use of category 1 and category 3 validation methods revealed different ‘best’ corridors in our example population. If both differing resistance surfaces and multiple validation techniques are not used, the modeler may conclude that one resistance surface has high efficiency and propose corridors that capture only movement patterns of a subset of individuals and likely miss out on greatest possible gene flow. On the other hand, identifying wide multispecies corridors, which include the greatest number of species locations, may be wise ecologically, but without dedicated funding, these types of corridors may not be realistically conserved in multi-use, developing landscapes. More specifically, underfunded multispecies corridors could end up with scattered parcels that serve none of the species it was designed to support.

By testing multiple resistance surfaces and employing multiple validation techniques, the modeler can better understand the impact of parameter choices on corridors and better match proposed corridors to the population’s movement as well as to management goals. At a minimum, we suggest that researchers should evaluate the percentage of animal locations within corridors (category 1 validation) and should incorporate multiple validation methods into their modeling workflow. As one works through the validation framework from category 1 to category 4 validation, cost and time increase. Ensuring or restoring gene flow across a region is often the motivating factor underlying connectivity research, so if category 4 validation is available, other categories of validation





may not be necessary. However, our results suggest the use of categories 1–3 in concert will likely lead to more informed decisions and possibly more effective corridors. We recognize that this proposed framework for validation is not an exhaustive list, but we present this framework as a first step in advancing and standardizing corridor validation. We encourage others to expand on this framework and to identify other robust validation methods, such as our novel usage of SSE.

The need for multiple validation methods springs from the variety of ways in which corridors can be modeled and the various decisions that are necessary during the modeling process. We selected some of the more common methods, and we recommend modelers carefully consider all options and choose the best option for their data, landscape, and management and/or conservation objectives. There is mounting evidence that linear inverse transformations often may not accurately reflect the response of some species to human modification (Trainor et al. 2013; Keeley et al. 2016; Belote et al. 2022). As such, more care should be taken to go beyond empirical habitat suitability surfaces and match resistance surfaces with dispersal processes on the ground. Keeley et al. (2016) identified a method to evaluate empirical corridors against random corridors and test which cost surface transformation performs the best. Because this is a relational comparison for this category of corridor modeling and there is no standard transformation, we deemed this comparison more relevant than comparisons between corridor modeling methods or differing corridor width tests, which are important considerations but have larger evidence bases from which to guide decisions (Poor et al. 2012; LaPoint et al. 2013; Cushman et al. 2013; McClure et al. 2016; Zeller et al. 2018; Lalechere and Berges 2021; Kumar and Cushman 2022). Methods choices may have an outsized impact on model results, and the implications of these choices should be better understood and documented by modelers and communicated to landscape and species managers. This will ensure robust, functional corridors based on specific management objectives, financial resources, and timelines.

## Conclusions

We have added novel information to the sparse corridor validation knowledge base. We recommend

researchers always undertake post-hoc corridor validation and strongly encourage the use of multiple validation techniques. Corridor ecology has been a slow-to-develop field, and modeling methods have lagged in their statistical robustness in comparison with other areas of ecology. Along with validation, there are other areas in need of improvement in corridor ecology. There is a recent push for more movement-driven or genetically informed resistance surfaces (Mateo-Sánchez et al. 2015; Naidoo et al. 2018; Zeller et al. 2018) and using methods beyond the typical landscape resistance approach (Kumar et al. 2022). Such information could remove some of the subjectivity in traditional corridor modeling and better capture the spatiotemporal variability inherent in animal movement processes. However, that is likely far in the future. We also see an opportunity for the growth and incorporation of traditional ecological knowledge informing corridor models, because local communities may be well-informed about movement pathways and have knowledge hard to gain from telemetry or genetic data alone (Shokirov and Backhaus 2019). Such traditional knowledge may help inform questions of spatiotemporal movement variability. Finally, on a much broader scale, an additional consideration gaining momentum is the development and incorporation of climate change into corridor planning (Anderson et al. 2023). Climate change will force changes to current-day corridors and will require revisiting previously designated corridors and reassessing their on-going functionality (Hannah 2011). We applaud the development of these efforts and encourage researchers to think creatively in interdisciplinary teams to further advance these needs. However, to best advance all methods, we must first fully understand the abilities and limitations of the existing corridor modeling and validation methods, as illustrated here.

As humans continue to fragment habitat and wildlife populations decline, connectivity modeling is necessarily a growing field where advancements are needed (Keeley et al. 2019). The importance of corridors and connectivity modeling has gained local and global recognition with the agreement of the Kunming-Montreal Global Biodiversity Framework in 2022. With this recognition, we expect more corridor plans to arise, giving greater need for robust methods across all aspects of corridor modeling. If methods are not robust, countries could fail to meet their

conservation goals and funding could be ill-spent, but most concerning is that we could jeopardize wildlife populations globally. Development and implementation of standardized, robust validation methods that test corridor efficiency and effectiveness are more important now than ever.

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#### Declarations

**Conflict of interest** The authors declare no competing interests.

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