Landscape Ecol (2021) 36:1647–1661
https://doi.org/10.1007/s10980-021-01254-2

RESEARCH ARTICLE

Comparison of methods for estimating omnidirectional landscape connectivity

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Received: 7 January 2021 / Accepted: 19 April 2021 / Published online: 30 April 2021

Abstract
Context Maintaining and improving ecological connectivity is an important component of wildlife conservation. Omnidirectional circuit theory algorithms model the flow of electric current across a resistance grid from all directions, making them particularly useful for modeling connectivity of multiple or widespread species, or when source and destination sites are not specified, such as in the case of continuously distributed species.
Objectives We compared three published omnidirectional connectivity methods—the point-based method, the wall-to-wall method, and the Omniscape method.
Methods We compared the three omnidirectional connectivity methods using ten simulated resistance grids, representing commonly encountered landscape features. We then used three Canada lynx (*Lynx canadensis*) snow-track datasets from Ontario, Canada to validate the ability of each method to detect landscape use.
Results Current density maps generated by all three methods were highly correlated for most simulated landscapes, with the exception of uniform resistance grids. In uniform grids, without landscape features to guide current, each method revealed unique node-placement biases. All three methods produced similar connectivity maps for lynx, showing higher current at lynx presence locations compared to absence locations. The main differences between methods were not in their output, but in their implementation and use of computational resources.
Conclusions Our findings suggest that all three currently published omnidirectional connectivity

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-021-01254-2.

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models produce similar current density maps and can accurately map landscape connectivity. We provide guidelines for selecting a method based on factors such as computational resources, study area, and project goals.

Keywords Circuitscape · Corridors · Current density · Landscape connectivity · *Lynx canadensis* · Omniscape

Introduction

In this time of unprecedented global change, landscape connectivity is predicted to continue its decline (Parks et al. 2020). Loss of landscape connectivity negatively affects movement of wildlife at multiple spatial and temporal scales (Tucker et al. 2018), from daily movements (Delciellos et al. 2017) and seasonal migration (Berger 2004; Seidler et al. 2015) of individuals, to gene flow (Crawford et al. 2016) and range shifts (Parmesan 2006; Moritz et al. 2008) of populations and species. Corridors are effective at promoting animal movement (Resasco 2019), and the creation of new corridors has been successfully implemented to improve movement and gene flow where barriers to movement exist (Ng et al. 2004; Soanes et al. 2018). Thus, the evaluation of existing or planned corridors for species of concern can help direct regional land management and conservation policies (Naidoo et al. 2018). Indeed, maintaining and improving ecological connectivity is an important component of wildlife conservation and management plans (Rudnick et al. 2012) and has become a global priority (Crooks and Sanjayan 2006; Hilty et al. 2020).

The accuracy and ease of modeling landscape connectivity across large spatial extents has expanded with the addition of new statistical tools. There are numerous methods for evaluating landscape connectivity, including least-cost path analysis (Adriaensen et al. 2003), resistant kernel models (Compton et al. 2007), and circuit-theory models (McRae and Beier 2007). Of these methods, circuit-theory based models have shown consistently high performance in estimating connectivity, and there has been a notable uptick in their use in connectivity modeling (see McClure et al. 2016; Laliberté and St-Laurent 2020; Zeller et al. 2020b; Fig. 1 in Hall et al. 2021). Circuit theory (McRae and Beier 2007) accounts for the possibility of multiple movement pathways across the landscape (McRae 2006), and is therefore widely used in modelling landscape connectivity (Dickson et al. 2019). Circuit theory uses the analogous properties of random walks across a surface of varied movement costs and electric current running through a circuit to generate maps of current density (Doyle and Snell 1984; McRae and Beier 2007). Current density is proportional to the probability of movement during a random walk (Doyle and Snell 1984). Consequently, the resulting current density map represents a prediction of functional connectivity, with high pixel values representing a high probability of use.

Recent adaptations to the circuit theory algorithm allow practitioners to model functional connectivity in all directions across an entire region (Koen et al. 2014; Pelletier et al. 2014; McRae et al. 2016). Traditional applications of circuit theory model connectivity between specific habitat patches in a pairwise fashion, which is appropriate for study designs with defined source and destination points, such as when estimating movement between habitat patches or gene flow between sample sites. When source and destination sites are not known, "omnidirectional" approaches are useful for producing regional-scale maps of connectivity (e.g. Anderson et al. 2012, 2019; Bowman and Cordes 2015; McRae et al. 2016; Pelletier et al. 2017), especially when mapping multispecies connectivity (Koen et al. 2014; Pelletier et al. 2014) or for evaluating connectivity of widespread species that may not be isolated to discrete habitat patches (e.g., Zeller et al. 2020a). Omnidirectional methods use the circuit theory algorithm to model the flow of electric current across the resistance grid from all directions, originating from the perimeter of the study area (Koen et al. 2014; Pelletier et al. 2014) or from all pixels within the map in a moving window approach (McRae et al. 2016). Omnidirectional connectivity methods have been applied to diverse tasks including identifying large-scale movement corridors (Aylward et al. 2020), understanding anthropogenic impacts on biodiversity (Correa Ayram et al. 2017) and endangered species (Ruiz-Lopez et al. 2016), evaluating genetic connectivity (Marrotte et al. 2017), and predicting the resilience of regional connectivity to landscape modification and climate change (McRae et al. 2016).

The advancement of tools and methods to estimate regional-scale connectivity means that practitioners have a variety of tools to choose from. Selecting the appropriate method can be a daunting task, as the pros and cons of each method might not be apparent and might even vary depending on the questions being asked and the idiosyncrasies of the regions being examined. While recent studies have compared circuit theory models to least-cost (McClure et al. 2016; Zeller et al. 2018; Laliberté and St-Laurent 2020) and other connectivity modeling approaches (Zeller et al. 2020b), there has been no comparison among the various omnidirectional circuit theory models. In this study, we sought to compare the three published methods commonly used to map omnidirectional landscape connectivity in Circuitscape: a point-based method (Koen et al. 2014), a wall-to-wall method (Pelletier et al. 2014), and a moving-window method (McRae et al. 2016). We used simple, simulated landscapes representing a variety of common landscape patterns to compare current density maps produced by the three methods. We then used all three methods to create connectivity maps for Canada lynx (*Lynx canadensis*) in Ontario, Canada, and validated each map with occupancy data of lynx at the southern edge of lynx distribution in Ontario to compare the ability of the three methods to predict corridors of high probability of use by individual lynx. Our analysis compares computation time, relative ease of implementation, and inherent biases of each method when mapping landscape connectivity in a variety of landscape configurations. We then provide guidance on the use and best practices of each method.

Methods

Simulated resistance grids

To evaluate the basic model behavior and any artifacts created by the three omnidirectional connectivity methods, we created ten different simple, conceptual resistance grids of features likely to be encountered in connectivity mapping or landscape genetic studies (Fig. 1). Of these grids, eight were binary grids with a value of 1 representing low resistance and a value of 10 representing high resistance to movement. These grids were meant to model common habitat features such as barriers, habitat patches, or urban areas (Fig. 1a–h). To mimic a more complex landscape, we also built a resistance grid with three costs: this grid contained five large, low cost (1) patches and fifty small patches of medium cost (3) interspersed within a high-cost (10) grid (Fig. 1i). Finally, we also created a uniform resistance grid (all cells had a value of 1) which allowed us to evaluate variation in current density due purely to differences in node placement, without effects of varying resistance values (Fig. 1j). The uniform surface also mimics a scenario that might be encountered when using a 'tiling' approach to map connectivity across large spatial extents (Pelletier et al. 2014; Koen et al. 2019). Tiling is a technique used to model connectivity, where smaller maps are stitched together to make a larger map, often to address computer processing limitations. Tiles can be square (Pelletier et al. 2014) or irregular (Bowman and Cordes 2015) in shape. Occasionally a tile is comprised of one land cover type with no variation in cost, and in studies with relatively small tiles and few cost values, this would be more likely to occur (Koen et al. 2019). For example, we can envision an analysis of global connectivity where some tiles might be composed entirely of ocean. While tiles will be recombined to examine connectivity across the entire landscape, it is still important to understand how the choice of method might impact the flow of current in any part of that landscape.

We manually created the simple resistance grids (Fig. 1a–h, j) in ArcGIS (ESRI 2020). The complex (three cost) resistance grid (Fig. 1i) was created in R version 3.6.6 (R Core Team 2020) using the landscapeR package v 1.2 (Masante 2017). All surfaces contained a 1000 $\times$ 1000 pixel core surrounded by a 500-pixel-wide buffer, for a total of 4,000,000 pixels. We used a large buffer (50% of the width of the core grid), that we removed before we interpreted the resulting connectivity maps, to ensure that we removed the bias in current density caused by the current sources around the edge of the resistance grids (Koen et al. 2010, 2014; Pelletier et al. 2014). These resistance grids were large enough to capture differences in the methods, yet small enough to run within hours to days, depending on method used, on a standard computer.

Omnidirectional Connectivity Methods

We modeled connectivity across each of the 10 simple resistance grids using each of the three published methods that use circuit theory to model

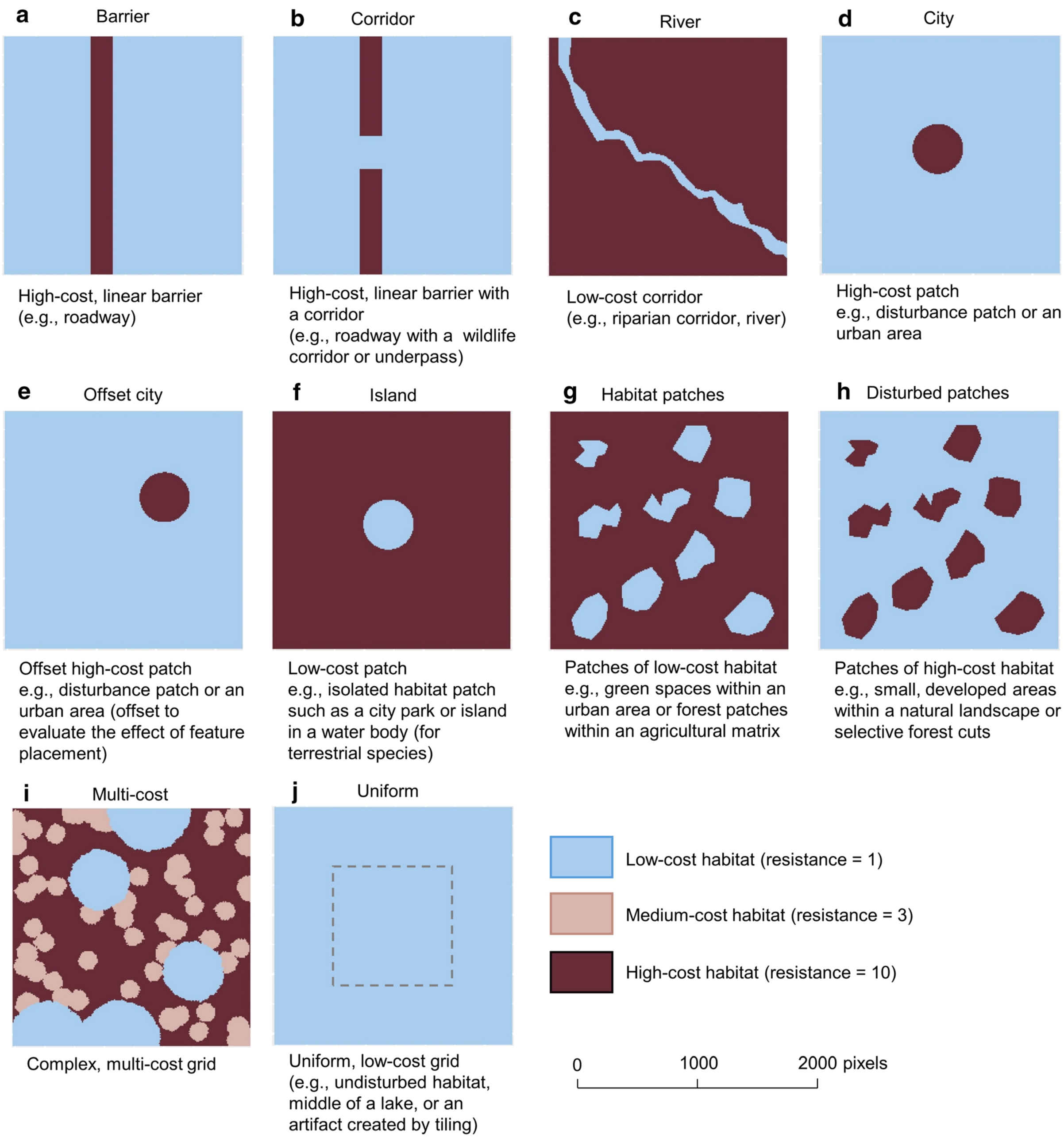

Fig. 1 Simulated resistance grids used to compare omnidirectional connectivity methods. Each grid had a 1000 pixel-wide core area with a 500 pixel-wide buffer (illustrated with a dashed line in panel j only), for a total of 4 million pixels

omnidirectional connectivity: a point-based method (Koen et al. 2014), a wall-to-wall method (Pelletier et al. 2014), and a moving-window method (McRae et al. 2016). We executed all three methods using Circuitscape software, which we implemented in Julia (Anantharaman et al. 2019; Hall et al. 2021; available at https://github.com/Circuitscape/Circuitscape.jl).

In point-based omnidirectional connectivity models (Fig. 2a, b), electrical current flows between nodes placed either randomly or at equal intervals along the outer edge of a buffered study region (Koen et al. 2014). In Circuitscape, pairwise current is then calculated between all nodes and averaged for a final composite score in each pixel. To evaluate

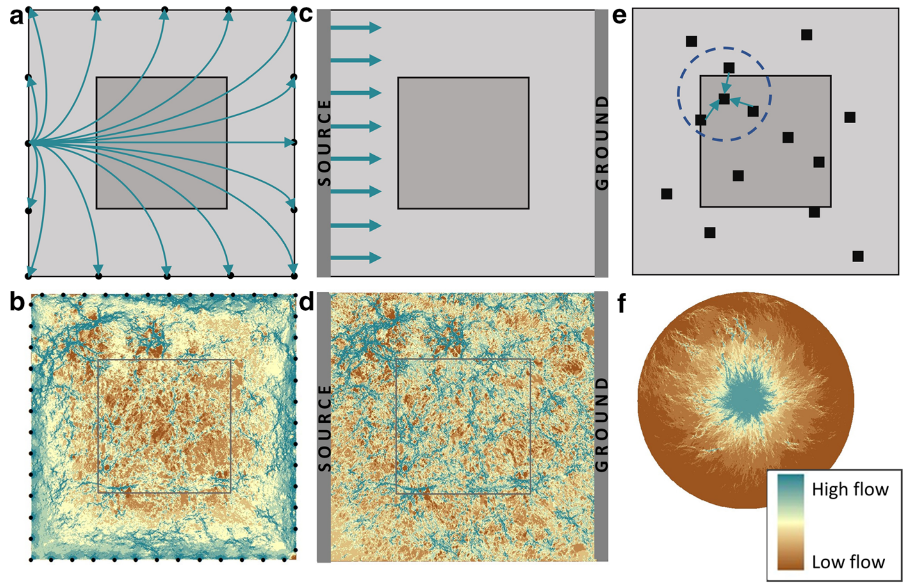

Fig. 2 Conceptual illustrations and example results of three omnidirectional, Circuitscape-based connectivity methods. Point-based omnidirectional connectivity **a**, **b** models current flow between pairwise sets of points at the edge of a study area. Wall-to-wall Circuitscape **c**, **d** models the flow of current from edge to edge between the four cardinal directions. Omniscape **e**, **f** models flow between source pixels, shown in black, within a user-defined search radius, represented with a dashed line. The circular search radii produced by omniscape (**f**) are then combined to form a cumulative current map similar to those produced by the other methods. The central square depicts the core area surrounded by a buffer

connectivity on our simulated resistance grids, we placed 50 nodes (Koen et al. 2014) at equal intervals along the edge of the buffer and evaluated the flow of current across the resistance grid between all combinations of nodes using pairwise modeling mode. The final output of Circuitscape was the cumulative current density map. The second method, wall-to-wall Circuitscape (Fig. 2c, d), models the flow of electrical current between thin, parallel source and ground strips placed on opposite sides of a buffered study region (Walpole et al. 2012; Pelletier et al. 2014; Anderson et al. 2016). The flow of current is modeled using advanced mode in Circuitscape across the region from north to south, south to north, east to west, and west to east. The resulting Circuitscape current maps in each of the four directions were averaged together for a final map of current density.

Finally, rather than placing source and ground nodes around the perimeter of the study area, Omniscape uses a moving window approach (Fig. 2e, f). Each cell in the resistance grid becomes the center of a moving window with a user-specified radius. Current moves from all surrounding pixels toward the central pixel and then is averaged across all moving windows to create the final cumulative current map (McRae et al. 2016). Omniscape allows the user to specify habitat types which will act as stronger sources of movement. In our analysis, we designated low-resistance cells (1 for the binary grids, and 1 and 3 in the case of the multi-cost grid) as sources. High-resistance cells (10) did not serve as sources of movement. In addition, the user must specify the radius across which current will move. For the simulated resistance grids, we tested three separate radius widths: 62 pixels, 125 pixels, and 500 pixels with a block size of approximately 1/10 of the search size (5, 11, and 49 respectively). We clipped the 500 pixel-wide buffer from each of the cumulative current density maps, leaving the 1000 $\times$ 1000 pixel core central study area for evaluation. We then used Z-scores to standardize the current values for each grid. We compared the methods quantitatively by comparing computation time and Pearson's correlations between current density maps, calculated in R (R Core Team 2020) using the *raster* package (Hijmans 2016). We also assessed visual patterns in current flow for each method and evaluated the applicability of the method to study areas which have an irregular shape or require tiling.

Application of connectivity models

We validated the three connectivity models in a real-world setting using occurrence data of Canada lynx from three independent, previously published snow-track datasets collected in Ontario, Canada (Walpole et al. 2012; Hornseth et al. 2014; Marrotte et al. 2020; Fig. 3). At the eastern edge of the study area, Walpole et al. (2012) snowshoed 56 1.5-km triangular transects during winters 2009 and 2010 and recorded lynx tracks observed (n = 12 transects contained lynx tracks). In our northernmost dataset, Hornseth et al. (2014) used 9320 km of routes surveyed by snow machine during January to March 2010; all lynx tracks encountered along these routes were recorded (n = 193 tracks), and an equal number of pseudo absences were generated for comparison (see Hornseth et al. 2014 for details). We used only data from the Chapleau and Mississagi study areas of the Hornseth et al. (2014) study, as the easternmost Temagami study area included data from Walpole et al. (2012). In the southern part of our study area, Marrotte et al. (2020) surveyed 35 routes by snow machine during winters 2016 to 2018 and recorded lynx tracks observed. The routes were 9 km in length, and encounters with lynx tracks were recorded (n = 16 routes contained lynx

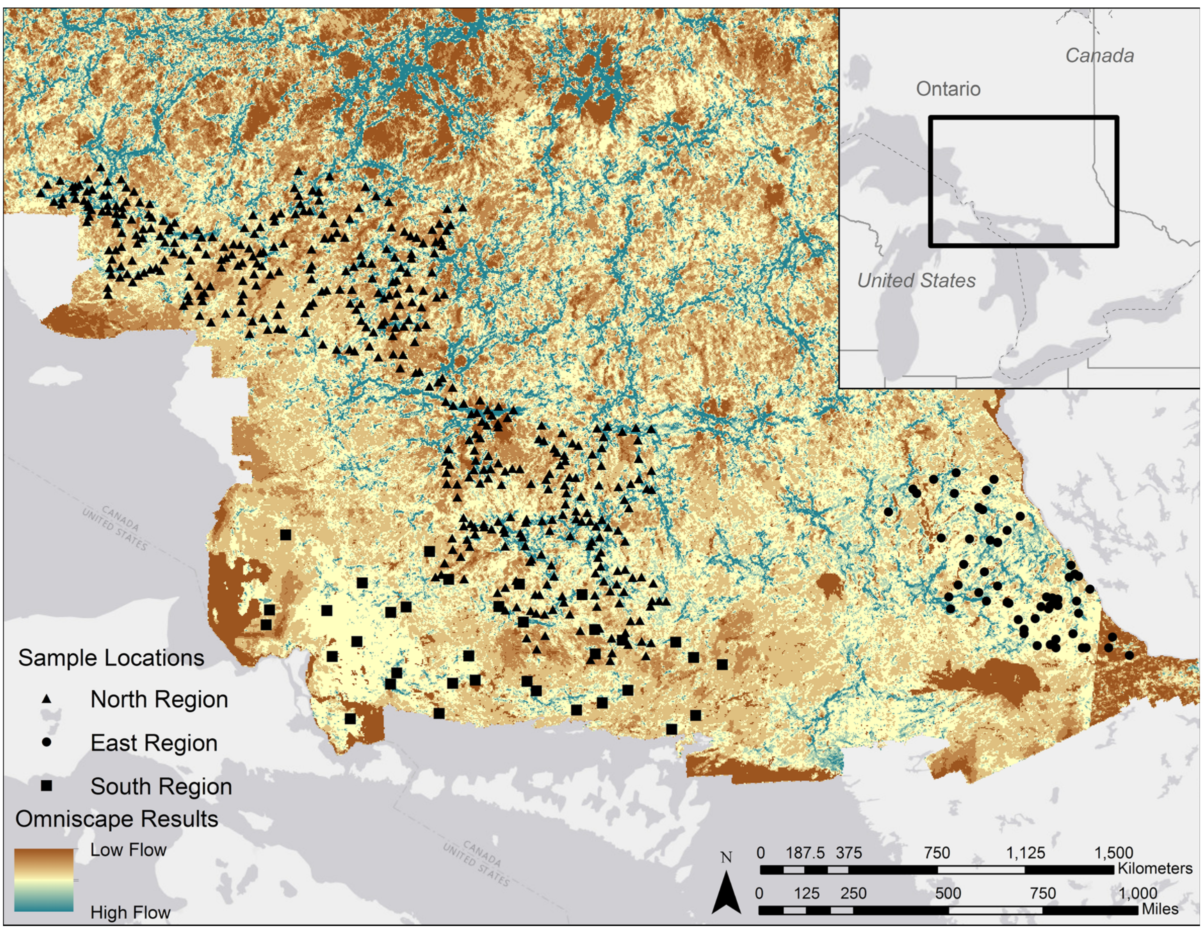

Fig. 3 A map of northern Ontario, Canada, showing the cumulative current map generated using Omniscape for Canada lynx (*Lynx canadensis*), and locations of lynx tracking sites for three previously-published snow-track datasets. Walpole et al. (2012) surveyed lynx tracks in the eastern portion of our study region; Hornseth et al. (2014) surveyed lynx tracks in the northern area of our study region; and Marrotte et al. (2020) surveyed lynx tracks in the southernmost portion of the study region

tracks). Because the three studies used different methods for estimating occupancy of lynx from snow tracks, we used binary data indicating whether tracks were detected on a transect or were not detected, without occupancy modeling. Hereafter, we refer to lynx data from the Walpole et al. (2012), Hornseth et al. (2014), and Marrotte et al. (2020) studies as data from the east, north, and south, respectively.

We based our resistance grid on research from the region suggesting that Canada lynx prefer young coniferous forest (Walpole et al. 2012; Hornseth et al. 2014; Marrotte et al. 2020). We used the Forest Resource Inventory (FRI) data for the managed forest region of Ontario (45 million ha) to create two raster layers with 500 × 500 m (0.25 km^2) pixels: one that represented the proportion of early-successional forest (pre-sapling and sapling-stage forest) and one that represented the proportion of coniferous forest. We added an additional 100-km wide buffer (50% of the width of the study area) around the managed forest area to reduce bias in current density caused by the current sources (Koen et al. 2014; Pelletier et al. 2014). Because we did not have FRI data for the buffer, we populated the 0.25 km^2 pixels in the buffer with proportion values that were randomly assigned (Koen et al. 2010). We then added these two raster layers together such that high values represented high proportions of young, coniferous forest. We then converted this raster to a resistance grid by inverting it and rescaling it so that the costs ranged between 1 and 101, assuming an inverse linear relationship between proportion of young coniferous forest and probability of movement for lynx. In our model we assumed that the Great Lakes were a complete barrier for lynx movement (Fig. 3). The final resistance grid, with buffer, had 5,323,409 pixels.

We created three connectivity maps based on the resistance grid, using each of the three methods (point-based, wall-to-wall, and Omniscape). Our goal was to maintain consistency and comparability between methods while still using each method as intended by the developers. Therefore, we parameterized all settings as given by the original authors. As such, we used 50 evenly spaced nodes placed at the edge of the buffer around the entire area for the point-based method and divided the area into two 800 km-wide square tiles for the wall-to-wall method. For Omniscape, we set areas with high proportions (top 10%) of young coniferous forest as source habitat and used a radius of 125 km, approximating a lynx home range size (Koehler and Aubry 1994) and a block size of 12, approximately 1/10 of the search radius size. We ran all three methods using Circuitscape in Julia on the same server (2.40 Intel Xeon E5-2640 CPU v4 at 2400 Mhz with 20 cores server with 128 GB of system memory and solid state storage). We compared the three connectivity maps using Pearson's correlations, as above.

To evaluate how well the different connectivity models reflected movement behavior of Canada lynx, we converted each lynx dataset to a binary value (presence or absence of lynx tracks on a transect or route) for consistency across studies. Walpole et al. (2012) have previously demonstrated that occurrence of lynx can be used to model movement behavior. We used a Kruskal–Wallis analysis of variance to test for differences in mean and maximum current density and the standard deviation (SD) of current density between sample units (transects or routes) with and without lynx tracks. We made these comparisons among connectivity models separately for each of the three lynx study areas (north, south, and east). We expected that lynx tracks would be found more often in pixels with relatively high connectivity, compared to pixels where lynx tracks were not detected. We measured the connectivity at each location by calculating the mean, maximum, and standard deviation of current density within a circular buffer with a 3 km radius around each point location, or within buffered transect areas, depending on the study. The mean and maximum measured how much current flows through that location. Standard deviation is a measure of the amount of current change in a location, which creates a "pinch point" or an area where resistance funnels current into narrow corridors. We ranked the effect size (X^2) of the Kruskal–Wallis test by magnitude for each metric (mean, max, SD) across the connectivity models within each study area, and then aggregated the ranks across study areas.

Results

Simulated Resistance Grids

Overall, the current density maps generated from the three omnidirectional connectivity methods were similar after clipping the buffer from the study area

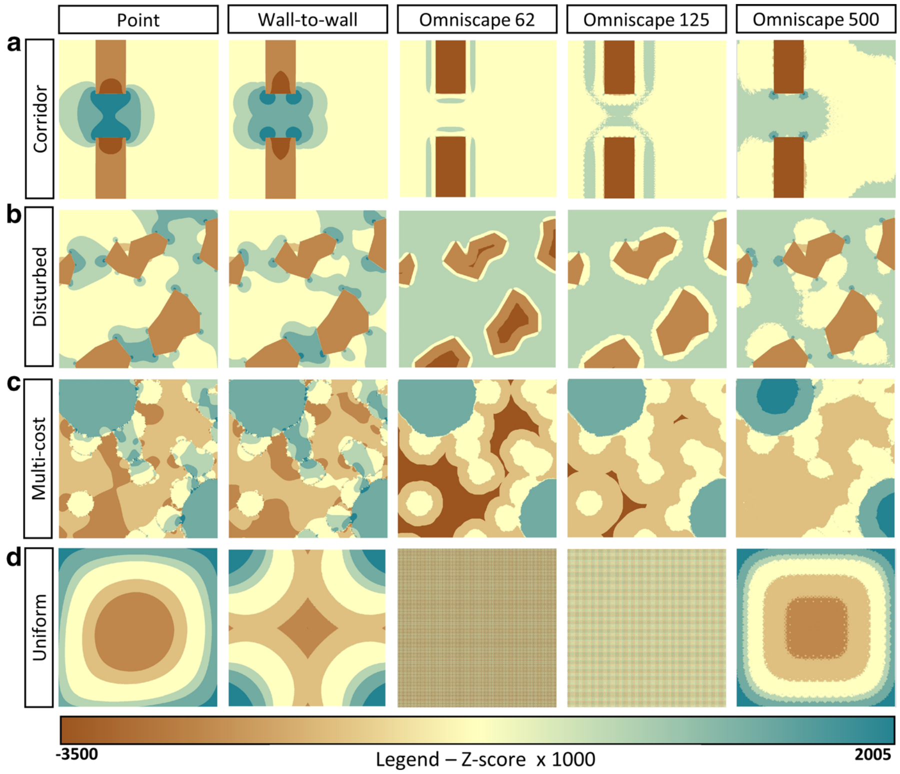

Fig. 4 Comparison of current density maps created from the three omnidirectional connectivity methods, with three different radii for Omniscape (62,125, and 500 pixels). We generated these maps from simulated binary resistance grids (**a** high-cost barrier with a corridor; **b** high-cost patches within a low-cost matrix; **c**; multi-cost; and d uniform), as shown in Fig. 1. In these images, we have removed the buffer and standardized current density values using Z-scores to facilitate comparison. Dark brown represents low current flow and dark blue represents high current flow

(Fig. 4a–c, Fig. S1). For the binary resistance grids, current density was highly correlated among the Omniscape methods (i.e., when different search areas were used; Pearson's correlations ranged from 0.907 to 0.996). Likewise, the wall-to-wall and point methods were highly correlated (Pearson's correlations ranged from 0.979 to 0.998; Fig. 5). For most grids, current density was also highly correlated between both the Omniscape and point-based and the Omniscape and wall-to-wall methods. However, for the barrier with a corridor (Fig. 4a) and for the multi-cost grid (Fig. 4c), Omniscape was not as highly correlated with either the wall-to-wall or point-based methods (Pearson's correlations: 0.740–0.789; Fig. 5). To examine this relationship more closely, we created scatterplots comparing current density between each pair of methods for the barrier with a corridor surface (results not shown). These plots suggested that correlations were weakest in areas of moderate current density, but that areas of low and high current density were in general agreement across methods. The regions of lower correlation appeared largely due to differences in node placement between the methods. Additionally, current density showed almost no correlation among most methods for the uniform grid (Pearson's correlations: − 0.14–0; Fig. 4d, Fig. 5), although the point-based method, wall-to-wall, and Omniscape with a 500 m radius were similar (Pearson's correlations: 0.765–0.925; Fig. 4d, Fig. 5).

Computationally, the wall-to-wall method had the fastest run time (10–11 min), whereas Omniscape took the longest to run (2–20 h; Table 1). The point-based method and the wall-to-wall method required less user input than the Omniscape method. Each method generated specific patterns in current density that result from node-placement, and these were most apparent in the uniform runs (Table 1; Fig. 4d). For instance, current tended to be higher at the edges, closer to where nodes were placed, in the point-based and wall-to-wall methods. When using Omniscape,

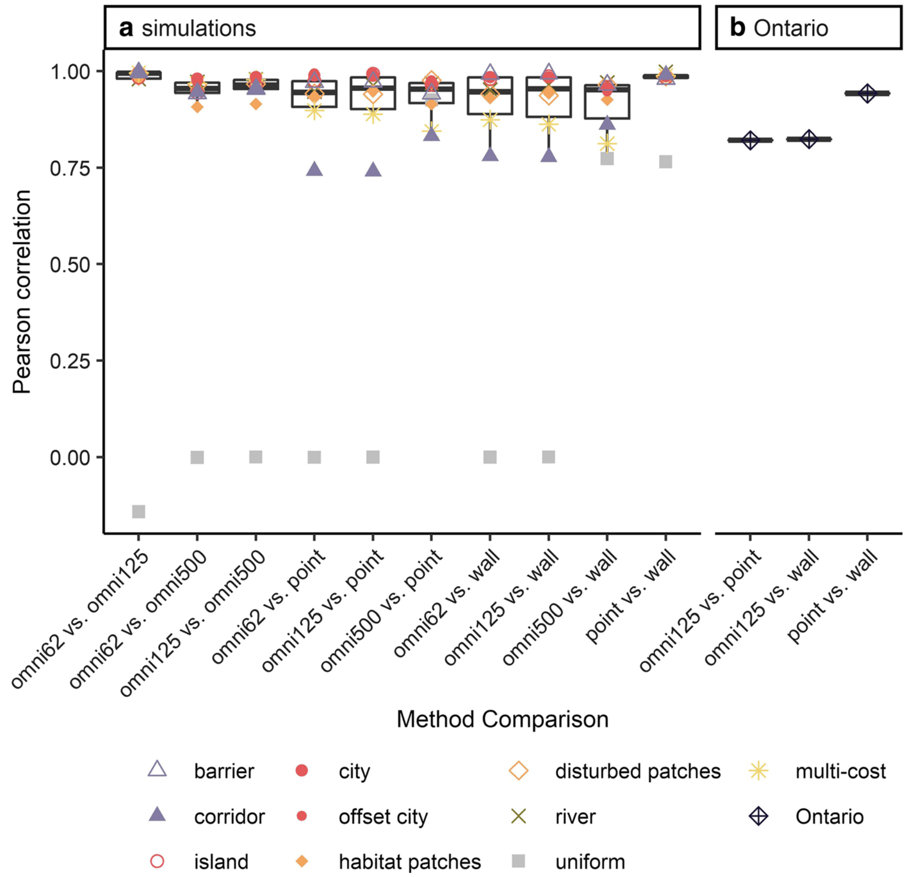

Fig. 5 Pearson's correlations comparing connectivity maps generated by the three omnidirectional methods for the simulated resistance grids (**a**) and the Ontario resistance grids (**b**). Methods are abbreviated as: point for point-based omnidirectional connectivity; Omni62, Omni125, and Omni500 for Omniscape using a 62-pixel, 125-pixel, and 500-pixel radius, respectively; and wall for the wall-to-wall method. See Fig. 1 for additional details on resistance grids

the smaller search radii produced a grid-like pattern, which was a result of the block size parameter coarsening the source's strength to save computational time.

Empirical Evaluation of Omnidirectional Connectivity Models

Mean and maximum current density and the standard deviation of current density were all higher where lynx tracks were present than where tracks were not detected, and this was true for all three connectivity models (Table 2). As expected, absolute current density values differed between the three connectivity models due to different implementations (e.g., the number of nodes varied across all methods). Our interests, however, were in comparing differences in effect size rather than absolute differences in current density across models. Generally, all three of the connectivity models performed similarly well in predicting the presence of lynx tracks. For example, ranking of effect sizes for mean current density from the Kruskal–Wallis analysis of variance demonstrated that each of the models had the largest effect size in one of the study areas (Table 2). Across regions, the average rank of the effect size of the mean current flow for all three methods was two. For the effect size of standard deviation, wall-to-wall ranked the best with an average rank of 1.3, followed by Omniscape and the point-based method, with average ranks of 2.2 and 2.5, respectively. Similarly, wall-to-wall had the highest average rank (1.3) for maximum current density, followed again by Omniscape (2) and the point-based method (2.7). All three current density maps were

Table 1 Qualitative comparison of omnidirectional connectivity methods

Method	Input needs	Avg. run time[a]	Qualitative assessment		
			Node-placement biases	Application to irregularly shaped study areas	Can be tiled for large study areas
Point-based	Resistance grid Coordinates of nodes around the edge of a buffer	5.87 h (1.02 SD)	Current may fade toward the center	Yes	Yes
Wall-to-wall	Resistance grid Tile size (for running large landscape)	11.19 min (0.27 SD)	Current may "bunch" around corners or circular objects	Must be tiled with buffer	Yes
Omniscape	Resistance grid Source layer (user designated) Search radius (user designated) Block size (to coarsen source strength to decrease processing time)	8.5 h (6.17 SD)[b]	Results may vary substantially depending on user-designated search radius; there may be artifacts of the block size in highly uniform landscapes	Yes	N/A[c]

[a]Each resistance grid was 4 million pixels, and each was run in Circuitscape in Julia on the same computer

[b]Computational time varied by the radius of the moving window. Average and standard deviations were 12.85 (7.33), 7.8 (4.73), and 5.04 (2.58) hours, for the 62 pixel, 125 pixel, and 500 pixel radii, respectively. Time decreased for larger radii due to use of a block size 1/10th the size of the search radius. See method for details

[c]Tiling is not necessary for Omniscape because it uses a moving window

highly correlated across the different methods (Pearson's correlations ranged from 0.821 to 0.942; Fig. 5).

Discussion

Our results demonstrated that the three Circuitscape omnidirectional connectivity methods—the point-based method, wall-to-wall connectivity, and Omniscape—generate similar connectivity maps. In general, there were high correlations between all pairs of maps in most situations. Therefore, findings from the three methods might be quite comparable, and decisions on which method to choose should be based on research design and computing limitations. We evaluated the similarity of these methods by generating current density maps across ten simulated landscapes using the point-based method, the wall-to-wall method, and the Omniscape method with three search radii. The point-based method and the wall-to-wall method were more similar to each other than to the Omniscape runs. Likewise, the three Omniscape versions (with different search radii) were more similar to each other than to the other methods. These patterns are reflective of the differences in current origin across the three methods; the point-based method and the wall-to-wall method both force current from the edges of the study area, whereas Omniscape generates current within the study area in a moving window approach. This pattern was upheld in current density maps of Ontario, which were generated from a resistance grid with more complexity and variability than any of our simulated grids. However, regardless of the differences in their underlying implementations, all three methods were remarkably similar across the simulated and real-world grids, with correlations in current density usually greater than 0.74.

The exception to the overall similarity in current density maps produced by the three methods was the uniform grid, where current density maps were less

Table 2 Average values for mean, standard deviation, and maximum current density (Amperes) for locations where Canada lynx (*Lynx canadensis*) tracks were either present (1) or absent (0) in three regions of Ontario, Canada

Region[a]	Mean of mean current density				Mean of SD of current density				Mean of max of current density			
Method[b]	P(1)	A(0)	X^2	Rank	P(1)	A(0)	X^2	Rank	P(1)	A(0)	X^2	Rank
North												
Point	− 2.5	− 182.3	48.2	1	641.8	499.8	23.4	3	2699.0	2667.4	0.5	2.5
Wall	3.8	− 160.0	32.7	2	691.4	547.1	24.1	2	2511.3	2394.1	2.2	1
Omni	138.9	18.1	20.6	3	727.7	590.2	24.8	1	2871.8	2881.8	0.5	2.5
East												
Point	− 166.7	− 346.6	3.2	2	224.6	100.8	5.2	2	171.2	− 206.9	4.7	2.5
Wall	− 39.3	− 289.9	2.9	3	253.0	116.9	5.3	1	319.0	− 133.6	5.1	1
Omni	254.5	11.7	4.3	1	263.7	140.0	4.8	3	631.0	206.3	4.7	2.5
South												
Point	− 242.5	− 274.9	0.4	3	236.9	186.9	1.7	2.5	861.8	584.5	0.7	3
Wall	− 280.5	− 393.0	3.9	1	249.0	192.3	1.9	1	607.0	315.0	2.2	2
Omni	− 41.3	− 121.1	1.3	2	286.6	217.6	1.7	2.5	1051.6	650.7	3.9	1

For mean current density, each of the models had the largest effect size in one of the study areas

For each region (north, east, and south), we ranked the effect size (X^2) of each measure from a Kruskal–Wallis analysis of variance within regions

[a]There were 244 absences and 200 presences in the North; 42 absences and 11 presences in the East; and 19 absences and 16 presences in the South

[b]For Omniscape, we used a search radius of 125 km

correlated. The patterning of current density values within a map varied based on the orientation of source nodes in the three methods, leading to relatively low correlation among methods. Without variation in resistance values in the map, current density variation is entirely due to difference in implementation, including node placement. This is most obvious when comparing the three Omniscape radii, where the block size parameter resulted in a grid-like pattern for the smaller radii. The largest radius of 500 m appears large enough to more closely approximate the other methods (i.e., wall-to-wall and point-based). The measure we used to compare current across maps, the Z-score, amplified these small differences in absolute current density values within a map. There was low variation in absolute current density values among pixels within a map arising from the uniform resistance grid, and this variation was much lower than variation in heterogeneous resistance grids. Therefore, when tiled together, artifactual variation on uniform tiles will likely be relatively small and unimportant after tiles are standardized and stitched back together (e.g., Koen et al. 2019). This finding may be particularly relevant for relatively homogenous landscapes, such as undisturbed natural habitat—in large, homogeneous areas, patterns in current density could be an artifact of the methodology and not the structure of the landscape per se. Pelletier et al. (2014) recommended using much larger buffers when current density values appear to be artifacts of the placement of the current source, and this may be one way to counter these effects. Alternatively, Koen et al. (2019) recommended using larger tiles to counter the effects of node placement for homogeneous resistance grids, because a larger tile is less likely to be homogeneous. This recommendation, however, may require the user to increase pixel resolution to balance the increase in pixel abundance relative to computational power, but in many cases this tradeoff does not reduce accuracy (e.g., Koen et al. 2019) and software advancements are continually increasing the number of pixels that can be computed (e.g., circuitscape.jl Anantharaman et al. 2019, utilized in this paper, and alternatives such as gflow Leonard et al. 2017).

As with most of the simulated resistance grids, the current density maps for lynx in the managed forest area of Ontario were highly correlated between the three omnidirectional connectivity models. The increased complexity of the landscape did not reduce the similarity of the resulting maps produced by the three methods. All three methods performed well at estimating the use of the landscape by lynx, where we found higher current density in areas with lynx tracks compared to where lynx tracks were not detected. We parameterized our resistance grid so that areas with young coniferous forest had lower resistance to movement; therefore, our results align with previous studies of lynx movement and habitat use (e.g., Vashon et al. 2008; Mowat and Slough 2011). Across our three study regions, each omnidirectional map performed similarly, with the three methods ranking equally in their performance based on average current density. This means that for each of the three methods, there were similar differences in the mean current between lynx presence locations and lynx absence locations. However, the wall-to-wall method ranked higher for the effect size of the standard deviation and maximum current. Higher standard deviation at a single location of lynx presence suggests that lynx are using areas of high current relative to the lower-cost surrounding habitat (i.e. "pinch points"). Therefore, wall-to-wall may be more able to identify pinch-points in a landscape. However, our results overall suggest that all three methods can be applied to real-world scenarios to map landscape connectivity. For species with lower dispersal capacity than lynx, or for species with a patchier distribution, researchers may wish to test the impact of such parameters on the comparability of these three models. However, the similarity between models in the real-world landscape, coupled with our analysis of a variety of simplified landscapes, suggests that these models should produce similar results in a variety of situations.

Recommendations for choosing a method

We found that all three methods of estimating omnidirectional connectivity produced similar current density maps. Thus, researchers may want to consider other features, such as processing methods, run times, and unique characteristics of each method when applying omnidirectional connectivity models to their research. The choice of method will depend on the size and geographic layout of the study area, the time and computational power available, and the need for enhanced analytic capacities. Both the point-based analysis and Omniscape natively handle irregularly shaped resistance grids. For example, Bowman and Cordes (2015) used the point-based method to map connectivity across irregularly shaped watersheds, and McRae et al. (2016) used Omniscape to map connectivity across an irregularly shaped region. The wall-to-wall analysis requires a square or rectangular resistance grid and thus does not handle irregularly shaped grids as readily, although this problem can be circumvented by filling irregular edges with random pixel values (see Koen et al. 2010) to create a resistance grid with straight edges, as we did in this study. If the extent of the study area is large and has many millions of pixels, processing time will be a key consideration when choosing a method. The wall-to-wall analysis was designed to tile in a large landscape and is therefore ideal for large landscapes because of the computational efficiency of only running Circuitscape four times for each tile (versus the point-based method with run times that increase with the number of nodes). Omniscape, on the other hand, is natively designed to run continuously over the resistance grid, large or small, and does not require tiling. The trade-off is the time required for a large study area. Since Omniscape runs Circuitscape for each source or block in a landscape, it requires the most computing resources of the three methods. Until recently, Omniscape's processing time was prohibitively long in large landscapes, but recent advances in Omniscape, including its re-programing in Julia, have significantly increased its processing speed (Anantharaman et al. 2019; Landau et al. 2021).

It is important to scale the Omniscape search radius to the features of the landscape and the processes of interest. For example, if the goal is to identify movement corridors for dispersal or seasonal migration, a larger search radius will be required. Based on visual inspection of results from the simulated landscapes, when the search radius was small (62 cells or 125 cells), Omniscape failed to identify landscape pinch points (i.e., barrier with a corridor) or corridors (i.e., habitat patch or multi-cost) that were observed using the point-based and wall-to-wall methods. This was evident from the relatively low correlations between Omniscape methods and other methods for the multi-cost and barrier with corridor grids. With larger search windows, Omniscape current density maps will more closely resemble the point-based and wall-to-wall methods, but the tradeoff is longer processing time. In contrast, a smaller search window will be faster to run, but the resulting current density maps will be less similar to those of the other two methods. In particular, a small search area can lead to an overestimation of the importance of small habitat patches to regional connectivity, similar to the findings of Koen et al. (2019).

Omniscape additionally provides enhanced opportunities for the user to specify parameters relevant to the system and questions. This includes a conditional connectivity feature which allows the user to only connect matching source and ground pixels, which has been used to connect areas in climate connectivity scenarios (McRae et al. 2016; Landau et al. 2021). Omniscape can also be parameterized based on the study species with adjustments to the search radius or source habitat. Altering these parameters allows the user to incorporate more realistic movement and dispersal constraints, as compared to the other methods, which may incorrectly assume that an animal could theoretically move across the entire landscape. This feature may be irrelevant where multi-species connectivity maps are the goal, since parameters such as search radius tend to be species-specific considerations. However, for studies focused on one or a few species, the ability to mimic realistic conditions may be important. While the additional parameters have benefits of allowing users to tailor Omniscape for narrow applications, users should also be aware that more parameters can lead to greater uncertainty in models and consequently greater opportunities for error.

As a rule of thumb, for projects investigating multispecies connectivity in very large landscapes, especially when computational power is limited, the point-based or wall-to-wall methods may be most appropriate. In those cases, if the study area is also irregularly shaped, the point-based method is easier to implement. If tiling is necessary, the wall-to-wall method will yield faster results. Alternatively, Omniscape may be the best choice when a project focuses on one or a few species with habitat specialization or limited dispersal, especially if computational power is not limited. Additionally, Omniscape provides more opportunities to add additional parameters to connectivity models. Ultimately, we found that the three omnidirectional connectivity models yielded similar results, and the choice of which method to use is a matter of researcher discretion.

Acknowledgements We thank Megan Hornseth, Robby Marrotte, Aaron Walpole, and Lyle Walton for sharing lynx occurrence data. We also thank the participants of the Landscape Genetics Distributed Graduate Seminar of 2020 for their feedback in the early stages of this project. We also thank two reviewers for their thoughtful comments. Finally, we acknowledge Brad McRae, the developer of Circuitscape, for valuable conversations in the development and implementation of the wall-to-wall method implemented here.

Author contributions JB and EK conceived the study, and all authors contributed to the design. Resistance grids were created by MC and SB. Analyses were performed by MC, PP, and JB. The first draft of the manuscript was written by PP and MC and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding None.

Data availability The simulated resistance grids, Ontario resistance grid, and the source and ground points generated in this paper are available in the Dryad repository, https://doi.org/10.5061/dryad.80gb5mkqs. The.ini files associated with running each omnidirectional connectivity method in julia are included in the repository.

Code availability No custom code was generated as part of this study.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

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