

Research paper

Assessing the performance of common landscape connectivity metrics using a virtual ecologist approach

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ABSTRACT

Due to increasing habitat fragmentation and concern about its ecological effects, there has been an upsurge in the use of landscape connectivity estimates in conservation planning. Measuring connectivity is challenging, resulting in a limited understanding of the efficacy of connectivity estimation techniques and the conditions under which they perform best. We evaluated the performance of four commonly used connectivity metrics – Euclidean distance; least-cost paths (LCP) length and cost; and circuit theory's resistance distance – over a variety of simulated landscapes. We developed an agent-based model simulating the dispersal of individuals with different behavioural traits across landscapes varying in their spatial structure. The outcomes of multiple dispersal attempts were used to obtain 'true' connectivity. These 'true' connectivity measures were then compared to estimates generated using the connectivity metrics, employing the simulated landscapes as cost-surfaces. The four metrics differed in the strength of their correlation with true connectivity; resistance distance showed the strongest correlation, closely followed by LCP cost, with Euclidean distance having the weakest. Landscape structure and species behavioural attributes only weakly predicted the performance of resistance distance, LCP cost and length estimates, with none predicting Euclidean distance's efficacy. Our results indicate that resistance distance and LCP cost produce the most accurate connectivity estimates, although their absolute performance under different conditions is difficult to predict. We emphasise the importance of testing connectivity estimates against patterns derived from independent data, such as those acquired from tracking studies. Our findings should help to inform a more refined implementation of connectivity metrics in conservation management.

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1. Introduction

As habitat fragmentation and land-use intensification continue, maintaining the ability for individuals to move among habitat patches and populations has become a major goal of many conservation plans (Fischer and Lindenmayer, 2007). Accordingly, measurements of 'landscape connectivity' often play a large role in land-use management schemes (Moilanen and Hanski, 2001; Moilanen and Nieminen, 2002). Landscape connectivity is a measure of the extent to which landscape structures and elements facilitate or impede movements among resources or habitat

patches (Taylor et al., 1993; Tischendorf and Fahrig, 2000). However, direct measures of landscape connectivity are difficult and costly to obtain (Kindlmann and Burel, 2008), and so most quantifications of connectivity are indirect.

Early efforts to estimate landscape connectivity used Euclidean distances between habitat patches (e.g. Green, 1994; Metzger and Décamps, 1997). However, because the dispersal capabilities of organisms are affected by landscape composition and configuration, and so vary across space, Euclidean distances often provide poor estimates of connectivity (Emel and Storfer, 2015; Vuilleumier and Fontanillas, 2007). Subsequently, connectivity has been estimated using various models which are underpinned by cost-surfaces. Cost-surfaces are raster depictions of landscapes in which the difficulty for individuals of some species of interest to traverse different features in the landscape is represented by a cost value (Douglas, 1994; Etherington, 2016). Connectivity tech-

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niques using cost-surfaces fall along a continuum of an individuals assumed familiarity with a landscape (Rayfield et al., 2011). At one extreme is least-cost path (LCP) modelling, which calculates a single route of maximum efficiency (i.e., ‘lowest cost’) between two points, assuming that an individual has complete and perfect knowledge of the composition and configuration of the landscape (Adriaensen et al., 2003; Douglas, 1994; Etherington, 2016). At the other extreme is circuit-theory, which assumes individuals move randomly through landscapes of which they have no prior knowledge, producing multiple pathways depicting the concentration of individuals’ flow between two points (McRae, 2006; McRae and Beier, 2007).

Given the proliferation of cost-surface derived connectivity models a number of studies have explored the factors that influence each model’s performance. Most of these studies examine the sensitivity of a single model (Rayfield et al., 2010), or compare the sensitivity of multiple models (Koen et al., 2012), to changes in cost-surface configuration (i.e. spatial structure) and/or composition (i.e. cost values). While such studies explain how connectivity models may react to changes in cost-surfaces they do not indicate how well each model captures the true connectivity of the underlying landscape. Recent studies have used tracking and genetic data to quantify the ability of connectivity models to capture this true landscape connectivity (McClure et al., 2016; Poor et al., 2012; Ruiz-González et al., 2014; Sawyer et al., 2011). The results of these studies have been mixed with regards to which model best represents landscape connectivity. However, these results highlight that the performance of connectivity models is context-dependent; for example, McClure et al. (2016) found that LCP was the best model for predicting the movements of migrating individuals but that circuit-theory was best for naïvely dispersing individuals. This context-dependence means that elucidating universal trends in model performance requires a large number of different contexts to be studied. However, due to the costs involved studies such as those mentioned above are rare and are often conducted only on a small number of species in a small number of landscapes, limiting the generalisability of their results (Spear et al., 2010).

Given the limited generalisability of current empirical studies, we adopted a ‘virtual ecologist’ approach in which we assessed the performance of multiple connectivity models (and their associated metrics) over a range of conditions via simulation (Zurell et al., 2010). We developed a spatially explicit agent-based model (ABM) that represented individuals dispersing through landscapes and from this we quantified simulated ‘true’ landscape connectivity. We then assessed model performance by comparing each connectivity model’s estimates of landscape connectivity to the simulated ‘true’ connectivity. Using this approach we aimed to: 1) determine the predictive performance of a suite of widely used connectivity estimation techniques; 2) examine to what extent predictive performance was dependent on landscape structure; and 3) explore how sensitive predictive performance was to organism behavioural traits. By using the ‘virtual ecologist’ approach to address these aims (Zurell et al., 2010), we were able to analyse each connectivity model over a large range of conditions so producing generalisable results.

2. Materials and methods

We used an ABM to simulate ‘true’ landscape connectivity values against which we evaluated the relative ability of four connectivity metrics (Euclidean distance; least-cost paths length; least-cost paths accumulated cost; and resistance distance) generated using three connectivity models (Euclidean distance; least-cost paths modelling; and circuit-theory) to accurately represent landscape connectivity. We ran our simulation over landscapes with a wide

range of compositions and configurations using simulated animal movements with varying behavioural characteristics. In this section, we first report on our ABM design (Section 2.1), then on the calculation of connectivity metrics (Section 2.2), and finally on the experimental design of our study (Section 2.3).

2.1. Agent-based model design

Our ABM used the open-source programming framework NetLogo v.5.1.0 (Wilensky, 1999) in conjunction with R v.3.2.3 (R Core Team, 2015), including the RNetlogo library v 1.4 (Thiele et al., 2012), and Python v.2.7.11 languages for the development of the connectivity models and assessment of their related metrics. The ABM description below follows the overview, design, concepts and details (ODD) protocol (Grimm et al., 2010). In Sections 2.1.1–2.1.3 we describe the surface level procedures of the model. The detailed formulaic descriptions of the sub-models underlying these procedures are given in Section 2.1.4.

2.1.1. Overview

2.1.1.1. Purpose. The purpose of our ABM was to generate ‘true’ connectivity values for a landscape, by virtue of the dispersal of naïve individuals from the centre of the landscape in search of habitat patches in which to settle; this represents, for example, the movements that occur after a translocation event. Our ABM did not, nor did it attempt to, perfectly emulate the observed movements of a specific taxa, but rather we sought to provide a simple representation of movement dynamics through spatially heterogeneous environments. Dispersal between habitat patches was selected as a movement type as it can be simulated with the fewest explicit assumptions, as opposed to movements such as migration that assume some degree of familiarity with a movement route. Additionally, because single dispersal events typically occur over relatively short time periods we did not represent energetic requirements. Mortality was not represented in the ABM because the data used to inform connectivity estimates are usually acquired from the individuals that survive a dispersal event; the agents in our model may be viewed as those surviving individuals.

2.1.1.2. Entities, state variables, and scales. The spatial domain of the ABM was a 100×100 cell regular lattice (grid). Each cell in the lattice was classified into a landscape type and assigned a corresponding cost value that represented the difficulty of an agent traversing the cell (see “Landscape generation procedure”). As the model depicts a generic species with simplified movements that may occur over multiple scales, no explicit spatial scale was defined. While time-steps were not defined explicitly, each represented the period required for an agent to travel a distance equivalent to moving from the centre of one cell to the centre of one of its neighbours.

Each landscape had eight habitat patches arranged concentrically around the landscape’s midpoint, with orthogonal patches being slightly closer to the central cell than diagonal patches (Fig. 1). Simulation trials showed that using 16 or 32 patches did not result in qualitatively different outcomes (Supplementary Materials). A uniformly spaced concentric ring of habitat patches was selected as this minimised shadowing (i.e. habitat patches acting as barriers to habitat patches behind them), which frequently occurred when habitat patches were randomly located. Habitat patches were circular with a diameter of 10 cells and a cost value of one. The total number of agents reaching any part of each individual habitat patch was recorded.

The ABM contained one type of mobile agent. Agents were initially located at the centre of the landscape, facing a random direction. Each agent moved through the landscape until they reached one of the eight habitat patches, or left the simulation landscape (see “move procedure”). Model agents were characterised by

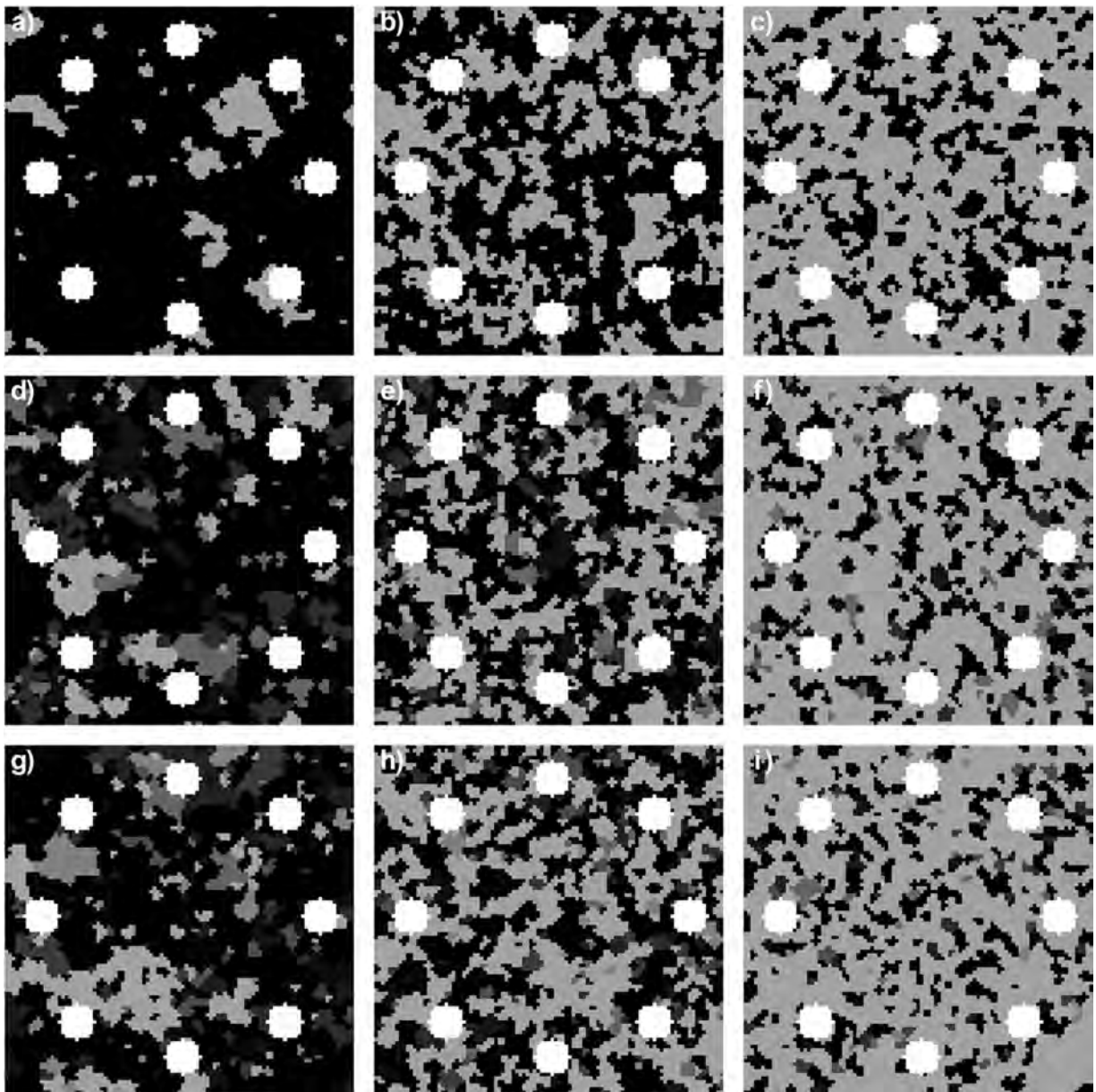


Fig. 1. Nine representative landscapes generated by the ABM under differing parameter settings. Costs are indicated along a continuum of dark (high) to light (low) greyscale shades. Habitat patches are denoted by white areas.

two state variables, which were determined prior to each run and together determined the agents' movement traits – '*directional bias*' and '*inquisitiveness*'. '*Directional bias*' determined how strongly an agent's direction of movement was auto-correlated between steps; empirical observations (Fahrig, 2007; Schultz and Crone, 2001) and theoretical studies (Zollner and Lima, 1999) suggest that dispersing animals tend to follow correlated paths. Decreasing the directional bias increases the influence of the cost-surface on an agent's movements, and so agents with low directional bias could be viewed as showing stronger habitat specialisation (i.e. habitat specialists) than those with high directional bias. '*Inquisitiveness*' was an integer ranging between one and eight that determined the number of neighbouring cells (in the adjacent Moore neighbourhood) which an agent could select from during the *move* procedure. When '*inquisitiveness*' was low the probability of selecting higher cost cells was increased as the total number of movement choices evaluated was reduced, therefore encouraging agents to explore cells beyond their optimal route. Low '*inquisitiveness*' values simu-

late species that may not be behaviourally averse to exploring costly areas. Agents also had a '*memory*' of the previous ten cells they had traversed, and this was used to limit repeated movements into the same cells. Agents did not interact with other agents in the model. A single model realisation continued until 250 agents reached one of the eight habitat patches.

2.1.1.3. Process overview and scheduling. At the start of each model realisation, all cells were allocated cost classes, representing cells with similar features (e.g. cover type or slope) and assigned corresponding cost values (*landscape generation* procedure). Next, 250 agents were generated in the central cell of the landscape and allowed to move (*move* procedure) once per time step until they reached a habitat patch, at which time the simulated 'true' connectivity between the central cell and the habitat patches was updated. The final simulated 'true' connectivity between the central cell and each habitat patch was recorded at the end of the simulation (i.e. after 250 agents had successfully dispersed to a habitat patch).

2.1.2. Design concepts

Agent movements were based on probabilistic rules that determined which one of the eight neighbouring cells an agent move to at each time step. Agents could ‘sense’ the cost values of the cells they were in as well as those of a random subset of their eight immediate neighbours, with the number of cells contained in the subset being equal to the ‘inquisitiveness’ value. ‘Inquisitiveness’ altered the probability of the agent selecting non-optimal cells (i.e. locally high cost cells) as the cells in the subset were selected independent of their cost value; this allowed agents to explore sub-optimal habitat areas, which may, for example, allow barriers to be crossed. Furthermore, agents stored a running list of the previous 10 cells that they had traversed (see Section 2.1.4.2 for a full explanation of the *move* procedure). Agents aimed to disperse in such a manner as to limit the cost of their movements given the local information they possessed.

Stochasticity was incorporated into the model at two key stages: 1) the assignment of landscape types to cells in the *landscape generation* procedure, which determined landscape structure; and 2) during the *move* procedure, where the neighbouring cell an agent chose to move to was selected based on Bernoulli trials.

2.1.2.1. Observation. The ABM produced a single ‘true’ connectivity value for each of the eight habitat patches at the end of every model realisation. The simulated ‘true’ connectivity value of a particular habitat patch was calculated as the proportion of agents which entered that habitat patch over the sum of the agents which entered all eight patches. The ‘true’ connectivity values, for each of the eight patches, were used in all subsequent analysis to represent the true connectivity of the landscape (i.e. each landscape contained a sample of eight connectivity values, one for each habitat patch).

2.1.3. Initialisation

The ABM was initialised with 250 agents, located in the centre of the landscape and facing a randomly selected direction. The initial number of agents was selected based on a consistency analysis (Lorscheid et al., 2012; see Supplementary Materials). Agents began each model run with no list of previous cells traversed; this memory list was updated one cell at a time until 10 cells had been crossed. Additionally, all agents were initialised with the same pre-determined directional bias and inquisitiveness, with these values differing between model realisations and being determined using Latin Hypercube sampling (see Section 2.3.1)

2.1.4. Sub-models

2.1.4.1. Landscape generation. Grid cells in the simulated landscape were allocated to a cluster type using the random clusters nearest-neighbour neutral landscapes approach, as generated by the NLMpy Python package (Etherington et al., 2014a). The random clusters algorithm was based on the modified random clusters algorithm described by Saura and Martínez-Millán (2000); it generates a series of random clusters (collections of cells determined to be of the same group) while controlling both the proportion of the landscape in a cluster and the size of the individual clusters. Each cluster type was assigned a cost value, representing the cost of movement through cells of that type (Fig. 1). The composition and configuration of the landscape were determined by four parameters (see Table 1 for value ranges): 1) *maximum cost* determined the highest possible cost value in a landscape, with all landscapes having a minimum cost of one and intermediate values set at equal intervals depending on the number of landscape groups; 2) *matrix cluster size* determined the maximum allowable size of an individual cluster in the inter-patch matrix (the area between target patches), defined by fixing the proportion of cells selected to form clusters; 3) *number of landscape group types*, represented the total number

Table 1

Value ranges used in Latin Hypercube sampling for each model to determine parameter values.

Parameter	Value range
maximum cost	10–1000
number of landscape types	1–100
lowest cost amount	0.1–0.5
cluster size	0.2–0.5
inquisitiveness	1–8
directional bias	1–4

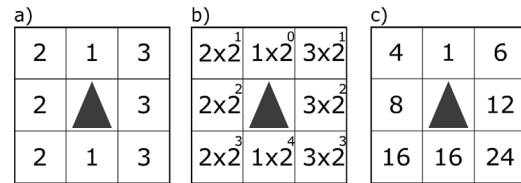


Fig. 2. Example of the calculation of perceived cost by an agent on a cost-surface following similar rules to that described in Palmer et al. (2011). Directional bias for the agent (the solid triangle) was set to 2 and inquisitiveness was set to 8 so that all cells were sampled. The agent is located in the central cell facing directly up. a) Represents the cost-surface with the values in the cells signifying the cost values. b) Denotes the calculation used by the agent for calculating perceived cost, decomposed into its component parts of cost value and directional bias weighting. The power the directional bias parameter is raised to increases from 0, if the direction of the cell was the same as the heading of the agent, to four if the cell’s direction was 180° different from that of the agent. c) The final perceived cost calculated by the agent. To allow for the simplest demonstration of how perceived costs were calculated it was assumed that this agent had an empty memory list during this step.

of cost classes in a landscape; and 4) *lowest cost matrix amount*, defined the proportion of cells in the inter-patch matrix assigned to the lowest cost class, with the remainder of the landscape being equally divided among the remaining cost classes. The value of the four parameters used during each model run was determined using Latin Hypercube sampling (Section 2.3.1)

2.1.4.2. Move. Our movement model was based on those described by Palmer et al. (2011) and Bender et al. (2003). These models were chosen as they reproduce realistic movement patterns (Fahrig, 2007) while being computationally simple and solely informed by a cost surface. During each time-step the agents evaluated whether any of their neighbouring eight cells (i.e. their Moore neighbourhood) were habitat patches; if any were, the agents immediately moved to the habitat patch and were deemed to have successfully dispersed. If none of the neighbouring cells were habitat patches the agent selected a random subset (of size equal to the agent’s *inquisitiveness* value) of its eight neighbouring cells. For each cell in that subset the agent calculated the perceived cost of moving into that cell as:

$$PC = C \times D \quad (1)$$

where: *PC* is the perceived cost of the cell, *C* is the cost value of the cell and *D* is the *directional bias* weighting.

Following Palmer et al. (2011), the directional bias weighting (*D*) was the agent’s *directional bias* parameter value raised to the power of zero in the direction of previous travel and to powers increasing from one to four as the angle of travel relative to the current heading increased from 45° to 180° (Fig. 2). To discourage agents from repeated movements to the same cells, all cells in an agent’s memory list had their perceived cost value set to the maximum cost value for the landscape prior to calculation of perceived cost.

Agents selected one of the cells in the chosen subset to move to by conducting sequential assessments using a modified version of the movement rules described by Bender et al. (2003). First, agents tested whether the perceived cost of a given member of the subset

was lower than the perceived cost of the current cell (as calculated from the previous step), if so the neighbouring cell was added to a list of potential movements. If a neighbouring cell had a higher perceived cost than the current cell, the agent tested whether the difference between the perceived costs was lower than a random deviate X , drawn from a uniform probability distribution:

$$X \sim U(1, \text{maximum cost value of landscape}) \quad (2)$$

If the difference was lower, the neighbouring cell was added to the list of possible movements. We allowed cells of higher perceived cost than the current cell to be selected both to ensure adequate dispersal across the landscape and to afford agents the chance to explore less ideal landscape types. If the difference between the perceived costs was greater than the random value, the neighbouring cell was rejected as a movement option. If no neighbouring cells were selected the agent repeated the procedure on a new randomly selected subset of its eight neighbouring cells until at least one cell was accepted as a valid movement choice. The agent then moved to the candidate cell in the subset with the lowest perceived cost. Agents that dispersed to the edge of the simulated landscape were removed from the simulation, having left the landscape, and a new agent was generated in the central cell in order to ensure equal sample sizes between model runs. In order to assess the sensitivity of our model to increases in perceptual range, the ABM was run over 200 landscapes with a perceptual range of two cells; this change had no qualitative effect on the results (see Supplementary materials).

2.2. Connectivity metrics calculation

Four commonly used connectivity metrics (Euclidean distance, LCP length, LCP accumulated cost, and resistance distance), generated from three connectivity models (Euclidean distance, LCP modelling, and circuit-theory), were calculated for comparison against the ‘true’ connectivity produced by the ABM (see Section 2.1.2.1). The landscapes and associated cost values created during the *Landscape generation* procedure (Section 2.1.4.1) were used as input cost-surfaces for each connectivity model. Connectivity estimates were generated between the central cell and the centre of each of the eight habitat patches for every landscape.

2.2.1. Euclidean distance

We used Pythagoras’ theorem to calculate the Euclidean distance from the central cell to each of the habitat patches.

2.2.2. Least-cost paths modelling

LCP modelling was used to develop two metrics, LCP accumulated cost and LCP length. LCPs were calculated using the Python package NetworkX (Hagberg et al., 2013). During LCP calculation the cost-surface raster was converted into a regular landscape graph, with the edge weights equal to the mean cost value of the two cells being connected multiplied by the distance between the cell centroids (Etherington, 2012). Dijkstra’s algorithm was then applied to the graph to create a Dijkstra tree (Dijkstra, 1959). The edges of the tree identified the shortest paths to each node and had as attributes the sum of the weighted edge values associated with the shortest paths. A Dijkstra tree’s shortest paths are equivalent to LCPs (Etherington, 2012). Using these shortest paths, LCP accumulated cost was calculated as the sum of the edge weights traversed between the start and finish vertices, i.e. the sum of the cost values accumulated when travelling along the LCP. LCP length was calculated as the number of cells crossed by the LCP between the central cell and a habitat patch, without taking the cost value of the cells traversed into account. While we chose the one-dimensional LCP length and cost metrics, other LCP-based metrics exist that can generate continuous surfaces (e.g. Compton et al., 2007). We evaluated

the one-dimensional metrics because they offer the most conservative single-value estimates of connectivity, as well as requiring the smallest amount of additional manipulation of the LCP algorithm that underpins all LCP-metrics.

2.2.3. Circuit-theory

Circuit-theory modelling was implemented using the ‘gdistance’ package v.1.9 in R (van Etten, 2014). The cost-surface raster was converted into a regular landscape graph with the nodes of the graph connected by resistors, with resistance equal to the cost of moving along the edge between two nodes, and the edge weights calculated in the same manner as those for the LCP models. Using this graph the resistance distance from the central node to each of the habitat patch nodes, defined as the effective resistance between a pair of nodes when all graph edges have been replaced by analogous resistors (Klein and Randić, 1993), was calculated following McRae (2006).

2.3. Simulation experiments and analysis

2.3.1. Experimental design

Model experiments were conducted to evaluate the performance (correlation between ‘true’ and estimated connectivity) of each connectivity metric under different landscape structures (as determined by *maximum cost*, *number of landscape types*, *lowest cost matrix amount*, and *cluster size*), and the two behavioural parameters (*inquisitiveness* and *directional bias*). Parameter values were chosen using Latin Hypercube sampling (McKay et al., 1979), with 200 points in the six-dimensional parameter space evaluated (Table 1). To evaluate the performance of each connectivity metric over a wide range of conditions we selected a large value range for each parameter. Each of the 200 parameter sets was repeated 50 times so creating 10000 unique landscapes, each with its own structure (see Supplementary Materials). For each simulation Spearman’s rank-order correlation between each of the four connectivity metrics and the simulated ‘true’ landscape connectivity was calculated. As the ABM simulated connectivity estimates in which high numerical values denoted high connectivity (the reverse of the four connectivity metrics), ‘true’ connectivity was multiplied by negative one prior to correlation to allow for an easier interpretation of results. We used Cohen’s d , the difference between group means over the pooled standard deviation (see Cohen, 1960), to quantify the effect size of the differences in correlations between the four metrics (Nakagawa and Cuthill, 2007).

2.3.2. Landscape structure statistics

In order to describe the landscape-level structure of the inter-patch matrix of each of the simulated landscapes five landscape metrics were calculated using FRAGSTATS v.4 (McGarigal et al., 2012). These landscape metrics were the five which captured the most variation in landscape structure out of an initial suite of 88 landscape metrics (see Supplementary Materials). Many of the original 88 landscape metrics were strongly collinear, with 72 metrics being discarded following the methods described by Riitters et al. (1995) and Dormann et al. (2013). To achieve this reduction, landscape metrics containing no useful information (e.g. unchanging values) were removed, and the remaining landscape metrics were then correlated with each other using Spearman’s rank-order correlation. Landscape metrics were grouped together such that each member had at least a Spearman’s $r_s > |0.7|$ to every other member. The most normally distributed landscape metric from each group was then selected. A principal components analysis (PCA) was then conducted on the remaining 16 landscape metrics (see Supplementary Materials), from which five components, explaining 95% of the total variance, were identified and the metric with the strongest loading for each component selected (see Supple-

mentary Materials). The five selected landscape metrics were; 1) modified Simpson's diversity index, a measure of the number of landscape group types in a landscape; 2) contagion, indicating the overall clumpiness of patches in a landscape; 3) perimeter-area ratio distribution standard deviation, representing the ratio of patch perimeter to patch area; 4) circumscribing circle range, a measure of the overall shape or roundness of patches in the landscape; and 5) area weighted mean Euclidean nearest-neighbour distance, measuring the isolation of landscape type patches (for a full description of these metrics see McGarigal et al. (2012)).

2.3.3. Landscape structure and agent behavioural trait analysis

Identifying whether any of the agents' behavioural traits or the characteristics of the cost-surface influenced the correlation between the connectivity metrics and the simulated 'true' connectivity would isolate conditions under which one connectivity metric may out-perform another. We used boosted regression tree (BRT) analysis (Elith et al., 2008) as implemented in the 'dismo' package v 1.4 in R v.3.2.3, to determine how, and to what extent, landscape structure and species behavioural parameters influenced the predictive performance of the four connectivity metrics. The predictors used in the BRT analysis were the five landscape structure metrics together with *lowest cost matrix amount*, *maximum cost*, *number of landscape types*, *directional bias* and *inquisitiveness*. We used a learning rate of 0.005 and a tree complexity of 5 to ensure that the BRT models produced a minimum of 1000 trees. BRTs provides a measure of the relative importance of each of the input parameters, based on the number of times a parameter is selected for splitting, weighted by the squared improvement to the model as a result of each split averaged over all trees (Elith et al., 2008; Friedman and Meulman, 2003). To generate confidence envelopes for the relative influence of each parameter 1000 BRTs were constructed each using 75% sub-samples of the full dataset, selected without replacement, as per Perry et al. (2012).

3. Results

3.1. Global trends

Our simulation analysis (Fig. 3) shows that when pooled across all parameter values each connectivity metric was, on average, positively correlated with simulated connectivity. The connectivity metric most strongly correlated with simulated 'true' connectivity was resistance distance ($r_s = 0.60 \pm 0.27$ [mean \pm 1 SD]), closely followed by LCP accumulated cost (0.54 ± 0.31). The similarity in these metrics' performance is highlighted by the small effect size (Cohen's $d = 0.22$; $CI = 0.19-0.25$), indicating a c. 92% overlap between the datasets. As the correlation with simulated connectivity for the two metrics declined, LCP accumulated cost declined more than resistance distance.

The mean correlation between LCP length and simulated 'true' connectivity (0.40 ± 0.33) was weaker than that of LCP accumulated cost or resistance distance, with these differences having a small to medium effect size for both LCP accumulated cost ($d = 0.42$; $CI = 0.40-0.45$) and resistance distance ($d = 0.66$; $CI = 0.63-0.69$), indicating a small, but likely practically meaningful, difference (Fig. 3). While LCP length occasionally produced stronger correlations than either LCP accumulated cost or resistance distance, correlations between LCP length and simulated 'true' connectivity were usually weaker. As with LCP accumulated cost, the rate at which the correlation between LCP length and simulated 'true' connectivity weakened was faster than for resistance distance.

Euclidean distance (0.14 ± 0.35) had the weakest mean correlation with simulated 'true' connectivity, and with a large effect size compared to even the next most poorly performing metric,

LCP length ($d = 0.81$; $CI = 0.76-0.86$). Euclidean distance rarely had stronger correlations with simulated 'true' connectivity than did LCP length and LCP accumulated cost, and never out-performed resistance distance.

The performance of all four connectivity metrics varied considerably across different model parameterisations, limiting confidence in any single metric's estimates for any one landscape (Fig. 3). The magnitude of this variability followed the same rank order as correlation strength, with resistance distance having the smallest variability, followed by LCP accumulated cost then LCP length and finally Euclidean distance.

3.2. Influence of landscape and behaviour

The fit (observed vs. predicted values) of the BRT models indicates that the predictors only weakly explain the variation displayed by Euclidean distance (Spearman's $r_s = 0.06$). This finding was supported with Euclidean distance deviance explained by the BRT model (0.02). The inability to predict this metric's performance arises simply because Euclidean distance disregards both landscape structure and species behaviour and so they are not informative predictors. Due to the BRT models' low explanatory power for Euclidean distance this metric was not considered further (see Supplementary Materials). The performance of LCP length (deviance explained = 0.17), LCP accumulated cost (0.21) and resistance distance (0.21), was better explained by the BRT models (Figs. 4 and 5), although the predictors did not fully explain the variability in the metrics' performances.

Contagion (that is, the overall clumpiness of patches in a landscape) had the greatest relative importance for all three connectivity metrics. As contagion increased the performance of all three metrics initially improved in their performance followed by a decline. This trend was strongest for LCP accumulated cost and effective resistance. *Maximum cost* had a high relative importance for all three connectivity metrics, with an increase in *maximum cost* associated with an increase in metric performance with this trend plateauing at higher costs. The modified Simpson's diversity index was also important for all three metrics with their performance increasing as the diversity index increased, though a drop off occurred towards the higher values. Interestingly, the two behavioural parameters, *directional bias* and *inquisitiveness*, had low relative importance for all three connectivity metrics. *Directional bias* had higher relative importance for LCP accumulated cost and resistance distance than LCP length, again highlighting the loss of information inherent in generating the LCP length metric. A final noteworthy point was the similarity in the shape of the partial dependency curves for LCP accumulated cost and resistance distance for each parameter (Fig. 5). No significant interactions between predictors were detected.

4. Discussion

4.1. Differences in predictive performance

Our assessment of four commonly used metrics of landscape connectivity (Zeller et al., 2012) suggests that their performance is likely to be highly context-dependent. However, it is also clear that incorporating the cost of landscape habitat types, as both the LCP metrics and resistance distance do, yields more accurate assessments of connectivity. This outcome is congruent with previous studies (Bender and Fahrig, 2005; Vuilleumier and Fontanillas, 2007). Of course, the incorporation of landscape habitat type costs into connectivity models can itself lead to uncertainty, with the methods used to generate cost estimates having variable degrees of reliability, especially when empirical data are scarce (Etherington

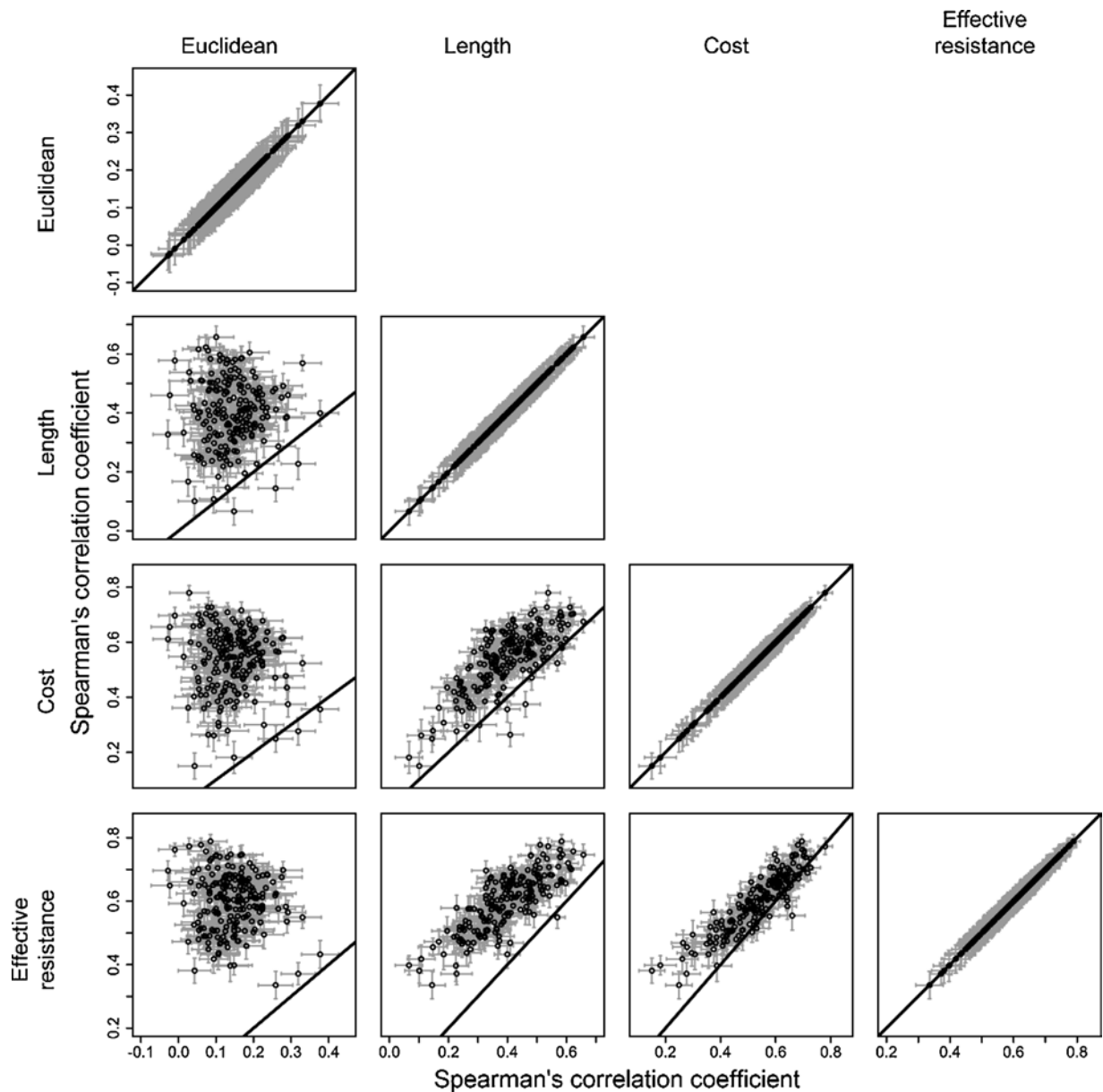


Fig. 3. Relative performance for each of the four investigated connectivity metrics: Euclidean distance ('Euclidean'), least-cost paths LCP length ('Length'), least-cost paths accumulated cost ('Cost'), and resistance distance ('Effective resistance'), for 10000 model runs. The performance value was the correlation between simulated 'true' connectivity generated by the ABM and estimated connectivity represented by each connectivity metrics. Each point indicates the intersection of performance for the metrics on either axis with each point representing the mean performance of the 50 model runs for each of the 200 different parameter settings for each pair of connectivity metrics. Error bars around points denote one standard error of the mean. Solid black lines indicate perfect fits (i.e., performance of the metric on the x-axis = performance of the metric of the y-axis).

et al., 2014b; Stevenson-Holt et al., 2014). Of the connectivity metrics we evaluated that incorporate cost, LCP length consistently performed poorly, especially compared with LCP accumulated cost, which uses the same algorithm. This poor performance is a consequence of LCP length not adequately considering variations in underlying costs (Etherington and Holland, 2013). The two metrics that fully incorporate landscape cost values, LCP accumulated cost and resistance distance, on average performed best, and there was only a small difference in their overall mean performance and responses to the various landscape and behavioural parameters analysed in BRT models. The similar predictive performance of LCP accumulated cost and resistance distance is consistent with the findings of McRae et al. (2008). The similarities between LCP accumulated cost and resistance distance suggest that the choice by researchers between the two metrics may not be critical in

many circumstances (at least for the production of summary metrics), allowing for the use of the model that best represents the movement ecology of the study species and the context they occur in; for example, resistance distance for species dispersing through unknown areas as it assumes ignorance of the underlying landscape (McClure et al., 2016).

The performance of all four connectivity metrics varied considerably even when landscape structure and agent behaviour remained constant (Fig. 3). Variability did decrease slightly as the performance of the connectivity metrics increased, with Euclidean distance having the largest variability and resistance distance the smallest. Such variation in performance may be exacerbated by the small empirical datasets that are typically used in assessments of landscape connectivity. The variability in predictive performance suggests that none of the methods we assessed consistently capture

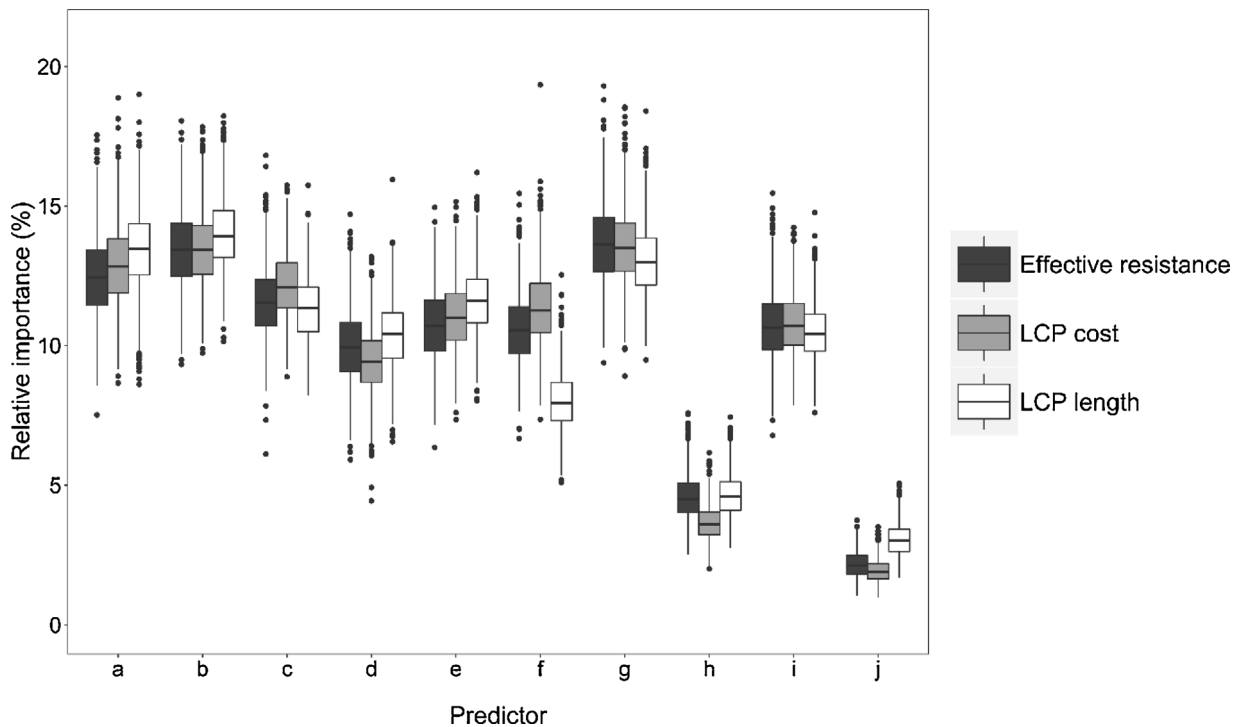


Fig. 4. Relative importance estimated from 1000 BRT resampled models for each of the ten landscape and behavioural parameters (a–j) of the three examined connectivity metrics. a) modified Simpson's diversity index, b) contagion, c) perimeter–area ration distribution standard deviation, d) circumscribing circle range, e) area weighted mean Euclidean nearest-neighbour distance, f) lowest cost matrix amount, g) maximum cost, h) number of landscape cost classes, i) directional bias, j) inquisitiveness. Horizontal black lines represent medians; boxes indicate 25th and 75th percentiles; whiskers denote 10th and 90th percentiles; black circles represent outliers.

the factors driving animal movements (even when these movements are simplified as in our ABM), thus occasionally producing large predictive errors that may be difficult to predict *a priori*. We suggest that, whenever possible, indirect estimates of landscape connectivity should be scrutinised against independently collected movement data and known behavioural patterns to evaluate the plausibility of the estimates (Grimm et al., 2005). It is clear, however, that the estimates produced by connectivity metrics will always contain an inherent level of uncertainty.

Our results corroborate Etherington and Holland's (2013) view that LCP length is not suitable as a landscape connectivity metric. Despite being underpinned by the same algorithm, LCP length consistently performed more poorly than LCP accumulated cost. Because the LCP model integrates distance travelled and traversal costs, the metric used to interpret these paths must also be based on a combination of these factors, i.e. LCP accumulated cost. While, on average, LCP length outperformed Euclidean distance, an argument can be made for the use of Euclidean distance over LCP length as an initial connectivity estimate. Euclidean distance is computationally cheap, does not require estimation of the underlying cost-surface and may produce acceptable estimates for landscapes that are homogeneous.

4.2. Effect of landscape structure and agent behaviour

Landscape structure and behavioural parameters only weakly explain the performance of the connectivity metrics; such low explanatory power likely arises from three main sources. First, the connectivity metrics, excluding Euclidean distance (which disregards landscape and behaviour), and the parameters used in the BRT models are an aggregated characterisation of landscape structure and animal movement behaviour, and discount the inherent stochasticity of fine-grained movements. This fine-grained stochasticity was inherent in the agents' movement rules and likely masked

the explanatory signal produced by the landscape structure and behavioural parameters. Second, and related to the previous point, the connectivity metrics we examined assume that an individual's movements are determined entirely by the cost-surface, which is unlikely as many factors not represented by the cost-surface (e.g. heterospecific interactions) also influence the movements of individuals. In our ABM we represent some of these effects in the stochastic nature of the movement process but in empirical studies they could be included (e.g. as spatial representations of predator densities) if adequate data were available. That an increase in maximum cost, which equates to increasing the influence the cost-surface has on an individual's movements, results in improved connectivity metric performance, highlights the importance of the assumption that the cost-surface alone controls movement. Finally, the connectivity metrics we evaluated rely on edges between different landscape categories (i.e., cells with different cost values) to generate changes in the directions of their paths with the areas between edges not adding additional information to the prediction. Dependence on patch edges for directional information may be realistic in some cases (St-Louis et al., 2014), but it is unlikely that such dependency is universal. These three factors combine to make it difficult to develop simple heuristics describing how a given connectivity metric will perform in a given landscape.

4.3. Limitations

Our ABM, as with all models, is a simplification of reality and we did not attempt to represent all the complexities of either landscape structure or organism behaviour. The movement decisions in the ABM from which movement trajectories and ultimately connectivity emerge are simplified, and are likely to be far more influenced by the underlying cost-surface than would normally be the case; this represents a best-case scenario for the connectivity metrics. As a result, we cannot conclude that any of the

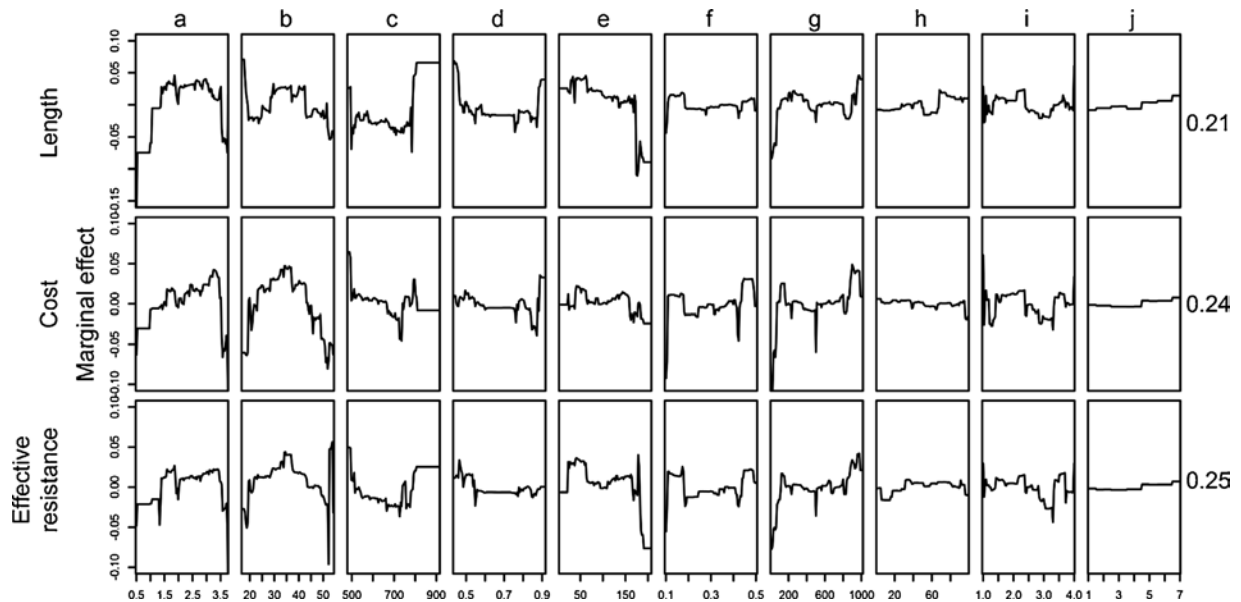


Fig. 5. Partial dependency curves generated by BRT analysis for the ten landscape and behavioural parameters (a–j) for each of the three examined connectivity metrics. a) modified Simpson's diversity index, b) contagion, c) perimeter-area ration distribution standard deviation, d) circumscribing circle range, e) area weighted mean Euclidean nearest-neighbour distance, f) lowest cost matrix amount, g) maximum cost, h) number of landscape cost classes, i) directional bias, j) inquisitiveness. Values to the right of the plots are Spearman's r_s indicating the fit of the BRT model for each connectivity metric.

connectivity metrics we evaluated will perform to similar levels in empirical studies as they did in our study. Nevertheless, with this caveat in mind those connectivity estimators that performed poorly in our simplified virtual system are unlikely to perform better in the face of additional complexity (Zurell et al., 2010). It is likely, therefore, that the qualitative trends we observed will hold for empirical studies. An additional simplifying assumption was that of a perfectly correct cost-surface, something not achievable empirically. We made this simplification in an effort to minimise any confounding factors that may have obscured the performance of the connectivity estimation techniques. It is clear, nevertheless, that the performance of the connectivity metrics depends on the accuracy and precision with which the cost-surface is calculated (Galpern and Manseau, 2013; Rayfield et al., 2010). Future work exploring how best to parameterise cost-surface representations of landscapes would be beneficial for improving understanding what levels of performance the various connectivity metrics might achieve (Bélisle and Desrochers, 2002; Simpkins et al., 2017).

We have evaluated four of the most commonly used connectivity estimation techniques, but this is not an exhaustive list of all such techniques available. For example, resistance kernels expand on basic LCPs by integrating LCPs with kernel estimators to develop estimates probability of movement for every point in a landscape (see Compton et al., 2007 for a detailed explanation). Further examination of such techniques is needed to understand how well they perform compared to the metrics we have tested. Additionally, a number of more *ad hoc* individual-based methods for calculating connectivity have emerged (e.g. Coulon et al., 2015; Kramer-Schadt et al., 2004). These individual-based methods tend to be developed on a case-by-case basis, with no method consistently adopted across multiple studies. Thus, while some of these techniques appear promising (Aben et al., 2014; Coulon et al., 2015), they are beyond the scope of our study. Additionally, our model assumed agents were dispersing through a landscape of which they have no prior knowledge as this was the type of movement that required the least assumptions. However, connectivity studies often consider organisms that do have some knowledge of their surroundings, such as migratory species or organisms mak-

ing fine-grained daily movements (e.g. Goodwin and Fahrig, 2002). An organism's knowledge of a landscape may influence the performance of the connectivity metrics, potentially favouring LCP cost, which assumes complete knowledge, as individuals become more familiar with a landscape (McClure et al., 2016). Representation of a perceptual range by, for example, individuals being able to see multiple cells in each direction can increase the performance of LCP models (Palmer et al., 2011). However, representing perceptual range requires a number of assumptions to be made, potentially limiting the generalisability of our findings. Additionally, due to the strong correlation in the performance of resistance distances and LCP costs (McRae et al., 2008), it is likely that any increase arising from the addition of further cognitive processes in the ABM would be seen in both metrics.

5. Conclusion

We have demonstrated that the predictive performance of four widely used connectivity metrics differs substantially, with resistance distance and LCP accumulated cost generating, on average, the most accurate estimates. However, estimates from all four connectivity metrics were highly variable even under similar conditions, meaning that single point-estimates of connectivity must be treated with caution. We suggest that indirect metric-based estimates of connectivity should be assessed against independently identified movement patterns whenever possible. Additionally, we determined that easily obtained measures of landscape structure and species behaviour only weakly account for the variation in the connectivity metrics' performance. Therefore, it is difficult to develop heuristics to predict the performance of any one connectivity estimate. We hope that by identifying general trends in the predictive performance of the investigated connectivity metrics, conservation managers may be better placed to understand the limitations of connectivity estimates and so develop more robust management plans.

Data accessibility

The NetLogo movement model used in this study is available at figshare, DOI [10.17608/k6.auckland.2008254](https://doi.org/10.17608/k6.auckland.2008254) from 15/06/2016 or from <https://figshare.com/s/a16baeb9fd36b5c08708>.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ecolmodel.2017.11.001>.

References

- Aben, J., Strubbe, D., Adriaensen, F., Palmer, S.C.F., Travis, J.M.J., Lens, L., Matthysen, E., 2014. Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes. *J. Appl. Ecol.* 51, 693–702.
- Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., Matthysen, E., 2003. The application of least-cost modelling as a functional landscape model. *Landscape Urban Plann.* 64, 233–247.
- Bélisle, M., Desrochers, A., 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecol.* 17, 219–231.
- Bender, D.J., Fahrig, L., 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. *Ecology* 86, 1023–1033.
- Bender, D.J., Tischendorf, L., Fahrig, L., 2003. Using patch isolation metrics to predict animal movement in binary landscapes. *Landscape Ecol.* 18, 17–39.
- Cohen, J., 1960. A coefficient of agreement for nominal scales. *Educ. Psychol. Meas.* 20, 37–46.
- Compton, B.W., McGarigal, K., Cushman, S.A., Gamble, L.R., 2007. A resistant-kernel model of connectivity for amphibians that breed in vernal pools. *Conserv. Biol.* 21, 788–799.
- Coulon, A., Aben, J., Palmer, S.C.F., Stevens, V.M., Callens, T., Strubbe, D., Lens, L., Matthysen, E., Baguette, M., Travis, J.M.J., 2015. A stochastic movement simulator improves estimates of landscape connectivity. *Ecology* 96, 2203–2213.
- Dijkstra, E.W., 1959. A note on two problems in connexion with graphs. *Numer. Math.* 1, 269–271.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münckmüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46.
- Douglas, D.H., 1994. Least-cost path in GIS using an accumulated cost surface and slope-lines. *Cartographica* 31, 37–51.
- Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–813.
- Emel, S., Storfer, A., 2015. Landscape genetics and genetic structure of the southern torrent salamander, *Rhyacotriton variegatus*. *Conserv. Genet.* 16, 209–221.
- Etherington, T.R., Holland, P.E., 2013. Least-cost path length versus accumulated-cost as connectivity measures. *Landscape Ecol.* 28, 1223–1229.
- Etherington, T.R., Holland, E.P., O'Sullivan, D., 2014a. NLMpy: a python software package for the creation of neutral landscape models within a general numerical framework. *Methods Ecol. Evol.*
- Etherington, T.R., Perry, G.L.W., Cowan, P.E., Clout, M.N., 2014b. Quantifying the direct transfer costs of common brushtail possum dispersal using least-cost modelling: a combined cost-surface and accumulated-cost dispersal kernel approach. *PLoS One* 9, e88293.
- Etherington, T.R., 2012. Least-cost modelling on irregular landscape graphs. *Landscape Ecol.* 27, 957–968.
- Etherington, T.R., 2016. Least-cost modelling and landscape ecology: concepts, applications, and opportunities. *Curr. Landscape Ecol. Rep.* 1, 40–53.
- Fahrig, L., 2007. Non-optimal animal movement in human-altered landscapes. *Funct. Ecol.* 21, 1003–1015.
- Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecol. Biogeogr.* 16, 265–280.
- Friedman, J.H., Meulman, J.J., 2003. Multiple additive regression trees with application in epidemiology. *Stat. Med.* 22, 1365–1381.
- Galpern, P., Manseau, M., 2013. Finding the functional grain: comparing methods for scaling resistance surfaces. *Landscape Ecol.* 28, 1269–1281.
- Goodwin, B.J., Fahrig, L., 2002. How does landscape structure influence landscape connectivity? *Oikos* 99, 552–570.
- Green, D.G., 1994. Connectivity and complexity in landscapes and ecosystems. *Pac. Conserv. Biol.* 1, 194.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* 310, 987–991.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. *Ecol. Modell.* 221, 2760–2768.
- Hagberg, A., Schult, D., Swart, P., Conway, D., Séguin-Charbonneau, L., Ellison, C., Edwards, B., Torrents, J., 2013. Networkx. High Productivity Software for Complex Networks, Webová stránka <https://networkx.lanl.gov/wiki>.
- Kindlmann, P., Burel, F., 2008. Connectivity measures: a review. *Landscape Ecol.* 23, 879–890.
- Klein, D.J., Randić, M., 1993. Resistance distance. *J. Math. Chem.* 12, 81–95.
- Koen, E.L., Bowman, J., Walpole, A.A., 2012. The effect of cost surface parameterization on landscape resistance estimates. *Mol. Ecol. Resour.* 12, 686–696.
- Kramer-Schadt, S., Revilla, E., Wiegand, T., Breitenmoser, U.R.S., 2004. Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. *J. Appl. Ecol.* 41, 711–723.
- Lorscheid, I., Heine, B.-O., Meyer, M., 2012. Opening the black box of simulations: increased transparency and effective communication through the systematic design of experiments. *Comput. Math. Organ. Theory* 18, 22–62.
- McClure, M.L., Hansen, A.J., Inman, R.M., 2016. Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. *Landscape Ecol.* 1–14.
- McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. University of Massachusetts, Amherst.
- McKay, M.D., Beckman, R.J., Conover, W.J., 1979. Comparison of three methods for selecting values of input variables in the analysis of output from a computer code. *Technometrics* 21, 239–245.
- McRae, B.H., Beier, P., 2007. Circuit theory predicts gene flow in plant and animal populations. *Proc. Natl. Acad. Sci.* 104, 19885–19890.
- McRae, B.H., Dickson, B.G., Keitt, T.H., Shah, V.B., 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89, 2712–2724.
- McRae, B.H., 2006. Isolation by resistance. *Evolution* 60, 1551–1561.
- Metzger, J.-P., Décamps, H., 1997. The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. *Acta Oecol.* 18, 1–12.
- Moilanen, A., Hanski, I., 2001. On the use of connectivity measures in spatial ecology. *Oikos* 95, 147–151.
- Moilanen, A., Nieminen, M., 2002. Simple connectivity measures in spatial ecology. *Ecology* 83, 1131–1145.
- Nakagawa, S., Cuthill, I.C., 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev.* 82, 591–605.
- Palmer, S.C.F., Coulon, A., Travis, J.M.J., 2011. Introducing a stochastic movement simulator for estimating habitat connectivity. *Methods Ecol. Evol.* 2, 258–268.
- Perry, G.L.W., Wilmshurst, J.M., McGlone, M.S., Napier, A., 2012. Reconstructing spatial vulnerability to forest loss by fire in pre-historic New Zealand. *Global Ecol. Biogeogr.* 21, 1029–1041.
- Poor, E.E., Loucks, C., Jakes, A., Urban, D.L., 2012. Comparing habitat suitability and connectivity modeling methods for conserving pronghorn migrations. *PLoS One* 7, e49390.
- R Core Team, 2015. R: A Language and Environment for Statistical Computing. R foundation for statistical computing, Vienna, Austria.
- Rayfield, B., Fortin, M.-J., Fall, A., 2010. The sensitivity of least-cost habitat graphs to relative cost surface values. *Landscape Ecol.* 25, 519–532.
- Rayfield, B., Fortin, M.-J., Fall, A., 2011. Connectivity for conservation: a framework to classify network measures. *Ecology* 92, 847–858.
- Riitters, K.H., O'Neill, R.V., Hunsaker, C.T., Wickham, J.D., Yankee, D.H., Timmins, S.P., Jones, K.B., Jackson, B.L., 1995. A factor analysis of landscape pattern and structure metrics. *Landscape Ecol.* 10, 23–39.
- Ruiz-González, A., Gurrutxaga, M., Cushman, S.A., Madeira, M.J., Randi, E., Gómez-Moliner, B.J., 2014. Landscape genetics for the empirical assessment of resistance surfaces: the european pine marten (*Martes martes*) as a target-species of a regional ecological network. *PLoS One* 9.
- Saura, S., Martínez-Millán, J., 2000. Landscape patterns simulation with a modified random clusters method. *Landscape Ecol.* 15, 661–678.
- Sawyer, S.C., Epps, C.W., Brashares, J.S., 2011. Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? *J. Appl. Ecol.* 48, 668–678.
- Schultz, C.B., Crone, E.E., 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82, 1879–1892.
- Simpkins, C.E., Dennis, T.E., Etherington, T.R., Perry, G.L.W., 2017. Effects of uncertain cost-surface specification on landscape connectivity measures. *Ecol. Inf.* 38, 1–11.
- Spear, S.F., Balkenhol, N., Fortin, M.-J., McRae, B.H., Scribner, K.I.M., 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Mol. Ecol.* 19, 3576–3591.
- St-Louis, V., Forester, J.D., Pelletier, D., Bélisle, M., Desrochers, A., Rayfield, B., Wulder, M.A., Cardille, J.A., 2014. Circuit theory emphasizes the importance of edge-crossing decisions in dispersal-scale movements of a forest passerine. *Landscape Ecol.* 29, 831–841.

- Stevenson-Holt, C.D., Watts, K., Bellamy, C.C., Nevin, O.T., Ramsey, A.D., 2014. Defining landscape resistance values in least-cost connectivity models for the invasive grey squirrel: a comparison of approaches using expert-opinion and habitat suitability modelling. *PLoS One* 9.
- Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape structure. *Oikos* 68, 571–573.
- Thiele, J.C., Kurth, W., Grimm, V., 2012. *RNetlogo: an R package for running and exploring individual-based models implemented in Netlogo*. *Methods Ecol. Evol.* 3, 480–483.
- Tischendorf, L., Fahrig, L., 2000. On the usage and measurement of landscape connectivity. *Oikos* 90, 7–19.
- Vuilleumier, S., Fontanillas, P., 2007. Landscape structure affects dispersal in the greater white-toothed shrew: inference between genetic and simulated ecological distances. *Ecol. Modell.* 201, 369–376.
- Wilensky, U., 1999. *NetLogo*. Evanston, Center for Connected Learning and Computer-Based Modeling, Northwestern University.
- Zeller, K., McGarigal, K., Whiteley, A., 2012. Estimating landscape resistance to movement: a review. *Landscape Ecol.* 27, 777–797.
- Zollner, P.A., Lima, S.L., 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80, 1019–1030.
- Zurell, D., Berger, U., Cabral, J.S., Jeltsch, F., Meynard, C.N., Münkemüller, T., Nehrbaas, N., Pagel, J., Reineking, B., Schröder, B., Grimm, V., 2010. The virtual ecologist approach: simulating data and observers. *Oikos* 119, 622–635.
- van Etten, J., 2014. *R package gdistance: distances and routes on geographical grids*. *J. Stat. Softw.* 23.