

The sensitivity of least-cost habitat graphs to relative cost surface values

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Received: 9 October 2008 / Accepted: 25 November 2009 / Published online: 10 December 2009
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Abstract Maintaining and restoring connectivity among high-quality habitat patches is recognized as an important goal for the conservation of animal populations. To provide an efficient measure of potential connectivity pathways in heterogeneous landscapes, least-cost route analysis has been combined with graph-theoretical techniques. In this study we use spatially explicit least-cost habitat graphs to examine how matrix quality and spatial configuration influence assessments of habitat connectivity. We generated artificial landscapes comprised of three landcover types ranked consistently from low to high quality: inhospitable matrix, hospitable matrix, and habitat. We controlled the area and degree of fragmentation of each landcover in a factorial experiment for a total of 20 combinations replicated 100 times. In each landscape we compared eight sets of relative landcover qualities (cost values of 1 for habitat, between 1.5 and 150 for hospitable matrix,

and 3–10,000 for inhospitable matrix). We found that the spatial location of least-cost routes was sensitive to differences in relative cost values assigned to landcover types and that the degree of sensitivity depended on the spatial structure of the landscape. Highest sensitivity was found in landscapes with fragmented habitat and between 20 and 50% hospitable matrix; sensitivity decreased as habitat fragmentation decreased and the amount of hospitable matrix increased. As a means of coping with this sensitivity, we propose identifying multiple low-cost routes between pairs of habitat patches that collectively delineate probable movement zones. These probable movement zones account for uncertainty in least-cost routes and may be more robust to variation in landcover cost values.

Keywords Habitat connectivity · Least-cost · Corridors · Habitat resistance · Fragmentation · Graph-theory · Effective distance · Dispersal · Habitat resistance · Fragmentation

Electronic supplementary material The online version of this article (doi:[10.1007/s10980-009-9436-7](https://doi.org/10.1007/s10980-009-9436-7)) contains supplementary material, which is available to authorized users.

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Introduction

Faced with the reality of ever increasing habitat fragmentation (Riitters et al. 2000; FAO 2006), wildlife conservation efforts have recently focused on protecting and restoring habitat connectivity (Crooks and Sanjayan 2006; Hilty et al. 2006). Habitat connectivity is a concept that describes the

potential for an animal to move among high-quality habitat patches as a function of both the spatial structure of the landscape and the movement behavior of the animal in response to that spatial structure (Taylor et al. 1993; With et al. 1997, 1999; Tischendorf and Fahrig 2000b; Goodwin and Fahrig 2002a, b; Brooks 2003; Fahrig 2007). Recent studies have emphasized the role that the spatial structure and quality of the intervening matrix between high-quality habitat patches has on habitat connectivity (Ricketts 2001; Tischendorf et al. 2003; Bowne and Bowers 2004; O'Brien et al. 2006). Ultimately, however, the animal's movement behavior will determine the extent to which inhospitable matrix structure inhibits movement among habitat fragments (D'Eon et al. 2002; Bélisle 2005). Conservation planners must therefore describe a landscape from an animal's perspective in order to understand, measure, and conserve functional habitat connectivity (Wiens 1989).

Animal perceptions of landscape spatial structure are thought to be primarily determined by the fitness consequences, such as mortality and reproductive success, experienced by individuals moving through different landcover types (With et al. 1997; Drielsma et al. 2007). Physical resistance (Stevens et al. 2004) and energetic expenditures are two mechanisms that may influence fitness in a given cover type (Graham 2001; Drielsma et al. 2007). A quantitative description of movement behavior within habitats involves assigning organism-specific "cost values" that reflect the quality of the habitat in terms of ecological costs incurred by an individual moving through them. These cost values are often a function of several environmental variables that are relevant for a particular species such as slope, elevation, water, vegetation cover type and structure, roads, and human settlements (Ferreras 2001; Clevenger et al. 2002; Schadt et al. 2002; Chardon et al. 2003; Verbeylen et al. 2003; Beazley et al. 2005; Cushman et al. 2006; Kautz et al. 2006; Rouget et al. 2006; Driezen et al. 2007; Epps et al. 2007; Gonzales and Gergel 2007; LaRue and Nielsen 2008; see Table 1).

Representing a landscape as a cost surface relevant to a particular species involves: (1) identifying the number of perceptible habitat types in the landscape; (2) ranking all habitat types according to their cost for movement; (3) quantifying the relative cost of landcover types by assigning numerical cost values

(note that cost values in some cells may need to be adjusted to account for additional elements such as slope or elevation). Ideally, cost values should be assessed based on field and experimental data; however, these data are difficult and time consuming to collect, and this has resulted in a large number of studies relying entirely or in large part on expert opinion (Clevenger et al. 2002; Schadt et al. 2002; Chardon et al. 2003; Verbeylen et al. 2003; Johnson and Gillingham 2004; O'Brien et al. 2006; Gonzales and Gergel 2007). Some studies use field data on occurrence patterns in order to delineate landcover preferences instead of landcover costs (but see Haddad and Tewksbury 2005). They employ well known methods such as compositional analysis (Aebischer et al. 1993), wherein vegetation cells are ranked according to species' habitat preferences using a measure of time spent in each landcover type relative to its availability in the landscape (Ferreras 2001; Graham 2001; Kautz et al. 2006; O'Brien et al. 2006). Resource selection indices are also used to quantify landcover preferences by relating environmental variables with occurrence data through regression models (Boyce and McDonald 1999; Ricketts 2001; Manly et al. 2002). The inverse (Ferreras 2001; Graham 2001; Schadt et al. 2002; Chetkiewicz et al. 2006; Gonzales and Gergel 2007; LaRue and Nielsen 2008) or odds ratio (O'Brien et al. 2006) of these measures of landcover preference can then be taken as approximations of landcover cost values.

The resulting cost surface can serve as the basis for analyzing habitat connectivity using a combination of least-cost route analysis and graph-theoretic techniques (Bunn et al. 2001; Chetkiewicz et al. 2006; O'Brien et al. 2006; Theobald 2006; Fall et al. 2007). Least-cost route analysis estimates efficient movement routes and costs between pairs of habitat patches based on the suitability of the intervening matrix (Adriaensen et al. 2003). Graph-theoretic techniques derive a holistic measures of habitat connectivity by using dispersal distance threshold as a surrogate of movement potential among all habitat patches in the landscape (Urban and Keitt 2001; Fall et al. 2007). By defining the links of a graph using least-cost routes, spatial information about the habitat patches and the surrounding matrix can be incorporated into graph-based measures of overall habitat graph connectivity. The habitat graph model scales

Table 1 Chronological and alphabetical presentation of connectivity studies using a cost surface to identify least-cost routes

No.	Study	Study species	Number of landcover types	Range of cost values	Response variable	Conclusion	Sensitivity detected?
1	Knappen et al. (1992)	Large and small mammals, birds, and butterflies in the Netherlands	9, 11, 6 and 13, respectively	1–21	Patch accessibility based on simulated dispersers	“It appeared that within the range of resistance values used (1–20), no alarming differences occurred between the accessibility patterns obtained.” p. 9	No
2	Graham (2001)	Keel-billed toucan (<i>Ramphastos sulfuratus</i>)	3	1–4	Number of transitions per day among forest remnants under constant energy constraints	Half as many transitions were predicted when a higher relative cost value was assigned to the least-preferred landcover type (pasture).	Yes
3	Schadt et al. (2002)	Eurasian Lynx (<i>Lynx lynx</i>)	3	1–1,000	Identification and location of least-cost routes	“Only when using very low cost values for matrix did the connections change, but these values can be assumed to be below a biologically realistic range.” p. 1479	Yes (only for very low cost values)
4	Chardon et al. (2003)	Speckled wood butterfly (<i>Pararge aegeria</i>)	6	1–100	Predict species' presence/absence in the proximity of source patches	“All resistance sets we explored had a significantly better fit to the data than Euclidean distance.” p. 570	Yes
5	Verbeylen et al. (2003)	Red squirrel (<i>Sciurus vulgaris</i>)	2 and 5	1–100,000	Predict species' presence/absence in the proximity of source patches	Prediction power varied among resistance sets. “the results of this study do show sensitivity to variation in these resistance values and allowed us to deduct a ‘most likely’ resistance set.” p. 801	Yes
6	Kautz et al. (2006)	Florida panther (<i>Puma concolor coryi</i>)	10 and 11	1–20	Locations of least-cost routes	“There were no discernable differences in the sensitivity analysis least-cost routes that were produced from versions of the cost surfaces that incorporated higher impedance scores for roads and water.” p. 126	No

Table 1 continued

No. Study	Study species	Number of landcover types	Range of cost values	Response variable	Conclusion	Sensitivity detected?
7 O'Brien et al. (2006)	Woodland caribou (<i>Rangifer tarandus caribou</i>)	6	1.7–3.5	Expected cluster size (ECS) of habitat patches in a network Threshold distances at which large increases in ECS occurred	“Hence, error in the cost values should only have a minor influence on the position of key thresholds at which large increases in ECS occur, while the structure of connected clusters will remain consistent.” p. 77	Yes (only at coarse spatial scales)
8 Driezen et al. (2007)	Hedgehogs (<i>Erinaceus europaeus</i>)	20	1–1,000	Cost and location of empirical versus least-cost routes (z-score)	“In our example with radiotracking data of hedgehogs, the average z-score of most resistance sets were negative and significantly different from zero, except for two sets (11 and 12) where this was also least expected.” p. 320	Yes
9 Epps et al. (2007)	Desert bighorn sheep (<i>Ovis canadensis nelsoni</i>)	3	1–100 (1,640 was applied to linear dispersal barriers)	Genetic distance and gene flow (population pairwise F_{ST} values), Number of migrants per generation (Nm), and migration rates (M)	“For... both measures of gene flow, best-fitting models resulted when sloped terrain had 1/20th to 1/10th the cost of movement across flat terrain (Fig. 2), with the slope weight of 0.10 most often favoured.” p. 719	Yes
10 Gonzales and Gergel (2007)	Eastern grey squirrel (<i>Sciurus carolinensis</i>)	18 (continuous landscape), 22 fragmented landscape)	0–160 (continuous landscape), 0–300 (fragmented landscape)	Distance and accumulated cost values of least-cost routes	“We also found that varying the absolute values, and thus range (the incremental increase) of friction values, however, produced greater variation than expected....Finally, our expectation that output from the nine scenarios at the contiguous site would be more similar to each other than outputs from the fragmented site was supported.” p. 1164	Yes

up from pairwise measures of effective distances between patches, which are typically generated by least-cost route algorithms, to consider the connectivity of the entire habitat graph. The graph theoretic approach also roots our measures of habitat connectivity in a conceptual model derived from metapopulation theory whereby the importance of each habitat patch in maintaining overall connectivity of the graph can be attributed to its topological position and source/sink characteristics (Urban et al. 2009).

In this study, we addressed the difficulties and ensuing uncertainties that arise when deriving organism-specific descriptions of matrix structure. We examined the sensitivity of habitat connectivity assessments, based on least-cost links (Adriaensen et al. 2003) and graph-theoretic methods (Urban and Keitt 2001; Fall et al. 2007), to the way in which we quantify species-specific perceptions of matrix quality. We expected that the spatial location of least-cost links would depend on both the spatial pattern of the habitat and matrix landcover types as well as the relative cost values of each. Hence, we ran a factorial experiment to generate artificial landscape spatial patterns and corresponding cost surfaces with three factors controlling landscape spatial pattern and one factor controlling cost values. Comparing habitat connectivity measures among these artificial landscapes allowed us to systematically test the importance of each of the factors.

Methods

Generation of artificial landscape spatial patterns

We generated landscape spatial patterns in maps of 100×100 cells using three landcover types: habitat (H), hospitable matrix (HM), and inhospitable matrix (IM). The maps were generated based on a placement algorithm that arranged landcover types in fragmented and clumped configurations (Fahrig 1997, 1998; Tischendorf and Fahrig 2000a; Tischendorf 2001; Tischendorf et al. 2003; we follow the notation of Tischendorf and Fahrig (2000a, b) and Tischendorf et al. (2003) for consistency). The spatial pattern of each landcover type was controlled by two parameters: COV, which defined the proportion of that landcover type in the landscape; and FRAG, which defined the spatial arrangement of cells assigned to that landcover type. Defining these parameters for H

and HM constrains the placement of IM; hence the full landscape spatial pattern can be controlled by the following four spatial pattern parameters: H_COV, H_FRAG, HM_COV, and HM_FRAG.

The placement algorithm begins by assigning H to cells of the map. It repeats the following two steps until the number of cells that have been assigned is equal to the number of cells determined by H_COV: (1) the algorithm randomly selects an unassigned cell; and (2) it decides whether or not H will be assigned to this cell based on the assignment of its eight neighbor cells and the parameter H_FRAG. The decision to assign H to the selected cell is taken if it meets either of the following conditions: (1) the value of a random number between 0 and 1 is smaller than $(H_FRAG)^2$ or (2) one or more of the eight neighboring cells already has the assignment H. H_FRAG is squared in order to produce a linear relationship between H_FRAG and the number of patches comprised of cells assigned to H (Fig. 1a in Tischendorf and Fahrig 2000a). When H_FRAG is large, the random number will often be smaller than H_FRAG^2 and most of the cells will be assigned to H based on the first condition which will produce a random distribution of habitat. When H_FRAG is small, most of the cells will be assigned to H based on the second condition which will produce a more contiguous distribution of habitat with larger, less edgy patches. All groups of adjacent cells (based on eight neighbors) with value H are considered as habitat patches and paths are calculated based on all of these patches. The placement algorithm operates in an identical fashion to assign HM to cells and all remaining cells receive the assignment IM (see example landscapes in Fig. 1).

We defined the value of H_COV as 12% to represent the amount of habitat commonly targeted for protection in reserves in Canada (Pressey et al. 2003 and references therein). Evaluating the sensitivity of connectivity assessments, based on least-cost habitat graphs, in the context of a typical conservation scenario is consistent with the promotion of this habitat graph approach as a conservation planning tool for ecologists (Urban and Keitt 2001; Chetkiewicz et al. 2006; Urban et al. 2009). We manipulated the values of the three other parameters in a factorial experiment with 20 combinations of the three parameters (Table 2). We examined H_FRAG and HM_FRAG values of 0.05 and 0.5 because they

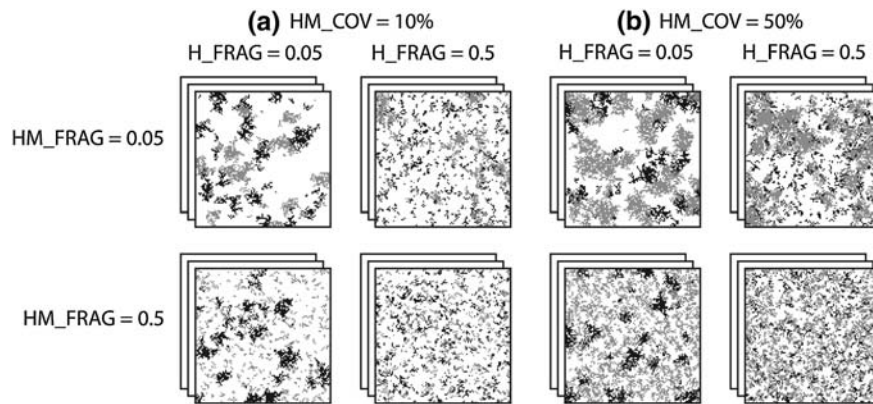


Fig. 1 Examples of the simulated landscapes at a resolution of 100×100 cells. Each landscape contains 12% habitat (*black squares*) and either **a** 10 or **b** 50% hospitable matrix landcover (HM_COV; *gray squares*). Habitat area is either aggregated

(H_FRAG = 0.05) or more randomly distributed (H_FRAG = 0.5). Hospitable matrix area also either aggregated (HM_FRAG = 0.05) or more randomly distributed (HM_FRAG = 0.5) in both landscapes

Table 2 Parameters used to generate spatial patterns of landscapes and their factorial combinations

Factor/parameter name	Description	Parameter values	Number of levels
H_COV	Amount of habitat (percentage)	12%	1
H_FRAG	Fragmentation of habitat	0.05, 0.5	2
HM_COV	Amount of hospitable matrix	10, 20, 30, 50, 70%	5
HM_FRAG	Fragmentation of hospitable matrix	0.05, 0.5	2

Each cell in the artificial landscape was classified as habitat (H), hospitable matrix (HM), or inhospitable matrix (IM). The amount and fragmentation of inhospitable matrix was completely constrained by parameters for habitat and hospitable matrix. All factorial combinations result in 20 spatial patterns. Spatial patterns were generated using the (Fahrig 1997, 1998; Tischendorf and Fahrig 2000a; Tischendorf 2001; Tischendorf et al. 2003)

produced relatively extreme patterns of randomness and clumpiness, respectively for our 100×100 cell landscapes. We did not increase the parameters controlling the level of fragmentation, H_FRAG and HM_FRAG, beyond 0.5 to avoid having too many single cell patches. To keep this a controlled experiment, we have assumed that the cell size is the minimum habitat size required; filtering out small habitat patches would have compromised our ability to tie our results back to the H_COV and H_FRAG parameter values. We generated 100 replicates of each given combination of parameters for a total of 2,000 landscapes.

Cost values to quantify resistance to movement

Cost values were assigned to each of the three landcover types (H, HM, and IM) reflecting the ecological costs incurred by an individual of a

generic species dispersing through that cover type relative to the costs incurred by dispersing through the preferred habitat (H, which was always assigned a cost of 1). We performed a sensitivity analysis on these cost values to assess their effect on our measures of habitat connectivity using least-cost links and graph-theoretic connectivity analyses. The ranking of landcover types was preserved such that preferred habitat (H) was always least-resistant to movement, followed by the hospitable matrix (HM), followed by the inhospitable matrix (IM; Table 3). Cost values were chosen to capture the range presented in the connectivity literature, which reported using fractional, twofold, and orders of magnitude differences between landcover costs (Table 1). Emphasis was placed on the relative differences of the cost values in different landcover types rather than absolute values (Chardon et al. 2003). We compared eight sets of cost values (C1 to

C8) that systematically varied the relative cost between H and HM and between HM and IM. An illustration of the least-cost habitat graphs produced under different sets of cost values is provided in Fig. 2. We examined four relative cost differences between H and HM (1.5-, 2-, 5-, and 100-fold) and two relative cost differences between HM and IM (1.5- and 100-fold; Table 3).

Graph-theoretic representations of habitat connectivity using least-cost links

Graph-theoretic connectivity analyses summarize the spatial relationships between landscape elements. This is achieved by building a “graph” (Harary 1969) consisting of a set of “nodes” that represent preferred habitat patches and “links” that represent the potential movement of an organism among them (Keitt et al. 1997; Calabrese and Fagan 2004; Treml et al. 2008). When dealing with large landscapes that have many habitat patches and possible links, it is preferable to analyze a subset of all possible links that represents the connected core of the landscape for a given species (Keitt et al. 1997). The minimum planar graph is one such graph as it contains the subset of all possible links that includes the maximum number of non-crossing links that are of least weight (therefore loops are allowed; O’Brien et al. 2006; Theobald 2006). Least-cost routes are only delineated between topological neighbors (i.e., least-cost links) and will never cross habitat patches (see Fig. 2). The minimum planar graph allows for

computational efficiency while including alternate pathways to reflect important redundancy required for population resiliency which is not included in other graph types such as the minimum spanning tree (O’Brien et al. 2006; Fall et al. 2007). In the minimum planar graph, nodes are 2-dimensional habitat patches that are fixed in space and links connect patches from edge-to-edge rather than from centroid-to-centroid (Fall et al. 2007).

A benefit of the minimum planar graph is that it approximates the complete graph within a reasonable, bounded error (Keil and Gutwin 1992). Empirical testing on real landscapes suggests that the mean difference between paths in a complete graph and in the minimum planar graph (Euclidean or least-cost) is much lower than the maximum deviation (and with a space efficiency that can scale to large landscapes; Fall et al. 2007). Hence, while minimum planar graphs could represent an ecological assumption that organisms move through the graph by using stepping-stone paths through topological neighbors (Urban et al. 2009), this assumption is not necessary since they also approximate a complete graph.

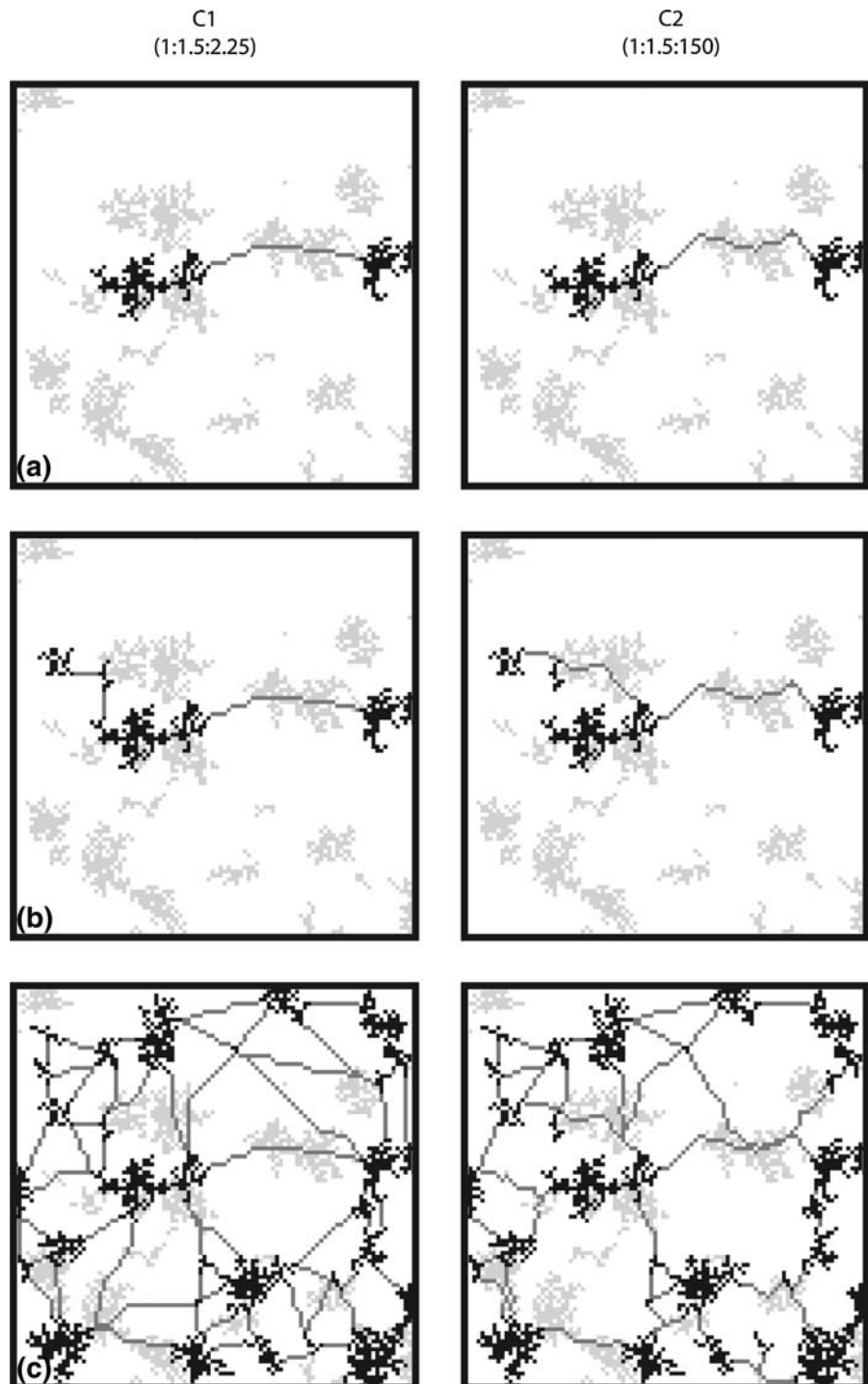
The potential for movement between a pair of high-quality habitat patches (graph link) is based on the assumed movement behavior of the organism. If one assumes the organism follows straight-line movement behavior then links that minimize the geographical (Euclidean) distance of the route traveled between habitat patches will be identified. However, if one assumes that the organism follows least-cost movement behavior then least-cost links that minimize the cumulative cost along the route will be identified (Halpin and Bunn 2000; O’Brien et al. 2006; Driezen et al. 2007). The length of both Euclidean and least-cost links can be measured in two ways: (1) the geographic length in metric distance units (e.g., meters or kilometers); or (2) the effective length as the cumulative sum of the cost values in cells traversed along the link multiplied by the length of the link segment crossing those cells.

In this study, we computed the minimum planar graph using Euclidean links for a given landscape. Then for each of the eight cost surfaces that corresponded to that landscape, we computed the least-cost links between all pairs of nodes that were present in the Euclidean minimum planar graph. This

Table 3 Sets of relative cost values used in factorial experiment

	Relative cost values		
	Habitat (H)	Hospitable matrix (HM)	Inhospitable matrix (IM)
C1	1	1.50	2.25
C2	1	1.50	150
C3	1	2	3
C4	1	2	200
C5	1	5	7.50
C6	1	5	500
C7	1	100	150
C8	1	100	10,000

Fig. 2 An illustration of **a** least-cost links, **b** paths, and **c** habitat graphs. A link is a route that directly connects two habitat patches (nodes). A path is route that indirectly connects habitat patches along a series of connected links and nodes in which no node is visited more than once. We used least-cost route analysis to identify least-cost links between habitat patches (nodes) to create least-cost habitat graphs. Least-cost habitat graphs contain 12% habitat (*black squares*), 10% hospitable matrix landcover cover (HM_COV; *light grey squares*) and the fragmentation parameter for both is 0.05 (H_FRAG, HM_FRAG). Habitat patches are connected by least-cost links (*dark gray*). The sets of cost values differ with respect to the relative costs between the matrix landcover types: C1—habitat = 1, hospitable matrix = 1.5, inhospitable matrix = 2.25; C2—habitat = 1, hospitable matrix = 1.5, inhospitable matrix = 150



produced an additional eight graphs that all had identical node and link sets; however, the length, the effective length, and the spatial location of the links could differ depending on the cost surface. In total,

for each of the 2,000 landscapes and eight sets of cost values, we produced 18,000 graphs (2,000 using Euclidean links and 16,000 using least-cost links). Results were analyzed using ANOVA (e.g., Li and

Reynolds 1994; Matter 2003; Hufkens et al. 2008) in order to examine main effects, two-way interactions, and higher order interactions among the four factors. No transformations of the data were required in order to meet the normality assumptions of ANOVA.

Measuring the sensitivity of graphs with least-cost links

For each graph produced with least-cost links, we calculated a standardized measure of the spatial deviation of least-cost links attributable to the corresponding cost surface. This standardized measure, referred to as the total spatial deviation of links, was calculated as the difference between the geographic length of the least-cost link and the Euclidean link for each pair of connected patches, summed over all pairs of connected patches in the landscape graph. Large values indicate the presence of sinuous least-cost links that deviate from straight-line Euclidean links, whereas small values indicate that least-cost links closely follow the straight-line Euclidean links. The sinuosity of least-cost links will depend on both the spatial pattern of the habitat and matrix landcover types as well as the relative cost values assigned to each. This is why we ran a factorial experiment with three factors controlling landscape spatial pattern (degree of fragmentation of primary habitat, amount of hospitable matrix, and degree of fragmentation of

hospitable matrix) and one factor controlling cost values (set of relative cost values) to test which factors are most important in determining total spatial deviation of least-cost links (Table 2).

Results

The results of the four-factor ANOVA (Table 4) showed a significant three-way interaction between matrix composition (HM_COV), habitat fragmentation (H_FRAG), and the set of relative cost values assigned to different landcover types (COST). This significant interaction precluded any further significance testing for the two-way interactions or main effects; however, we were able to observe that the ANOVA clearly did not indicate significance for any two-way interactions including HM_FRAG or its main effect (Table 4).

The three-way interaction can be examined visually by plotting the interaction between two of the factors at each level of the third factor (Fig. 3, Appendix 1). In all of the two-way interaction plots the most striking result was the consistent differentiation between sets of cost values with odd numbers (C1, C3, C5, C7) versus even numbers (C2, C4, C6, C8). Cost sets with odd numbers had small differences between the relative costs of hospitable and inhospitable matrix landcover types, whereas even

Table 4 Effects of matrix composition (HM_COV), habitat fragmentation (H_FRAG), matrix fragmentation (HM_FRAG), and the relative cost values (COST) on the mean spatial deviation of least-cost links

Source	<i>df</i>	<i>F</i> -ratio	<i>P</i> value
HM_COV	4	12821.583	<0.001
H_FRAG	1	46350.009	<0.001
HM_FRAG	1	1.145	0.285
COST	7	14319.069	<0.001
HM_COV * H_FRAG	4	5616.703	<0.001
HM_COV * HM_FRAG	4	0.006	0.999
H_FRAG * HM_FRAG	1	1.265×10^{-5}	0.997
HM_COV * COST	28	2510.185	<0.001
H_FRAG * COST	7	6923.999	<0.001
HM_FRAG * COST	7	0.004	1.000
HM_COV * H_FRAG * HM_FRAG	4	9.306×10^{-6}	1.000
HM_COV * H_FRAG * COST	28	1135.699	<0.001
HM_COV * HM_FRAG * COST	28	2.652×10^{-5}	1.000
H_FRAG * HM_FRAG * COST	7	2.033×10^{-5}	1.000
HM_COV * H_FRAG * HM_FRAG * COST	28	4.076×10^{-5}	1.000
Residuals	15,840		

Presented are *F*-ratios and *P* values from the four-factor ANOVA

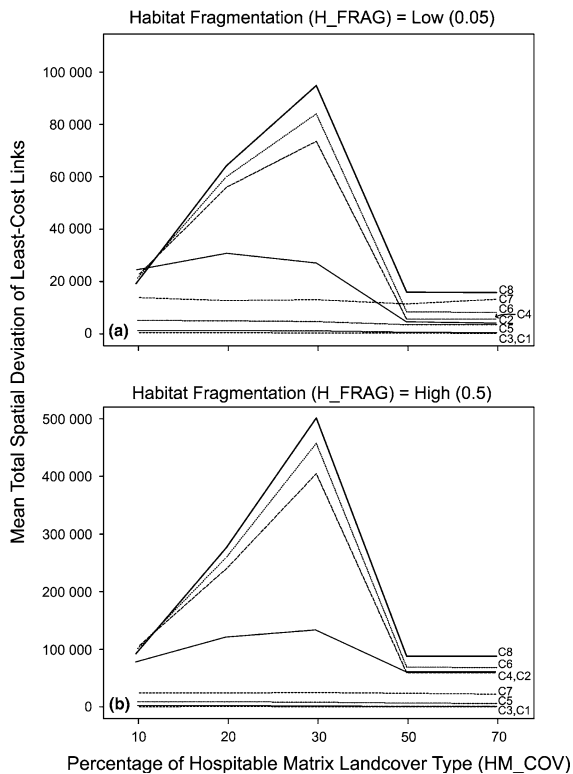


Fig. 3 Interaction plots for the percentage of hospitable matrix (HM_COV) versus the set of relative cost values (C1–C8) when habitat fragmentation is either **a** low (H_FRAG = 0.05) or **b** high (H_FRAG = 0.5). Mean values of the total spatial deviation of least-cost links is plotted for each of the cost sets at each level of HM_COV

numbered cost sets had large differences. This result is intuitive since larger differences between matrix landcover cost values would expectedly cause least-cost links to deviate more strongly from straight-line links. The difference in cost values between habitat and the matrix was evidently not important despite relative values that differed 100-fold. The interaction line for C2 lies between the odd and even numbered cost sets and shows dampened peaks consistent with the odd numbered cost sets.

The two-way interaction between HM_COV and COST displayed a similar pattern for both low and high levels of H_FRAG (Fig. 3); however, spatial deviation values were five times larger when H_FRAG was high (Fig. 3b) compared to when it was low (Fig. 3a). Cost value sets C1, C3, C5, C7 and sets C2, C4, C6, C8 differed in their response to increasing HM_COV for both levels of H_FRAG. Two thresholds of HM_COV are apparent in these

interaction plots. First, there is an abrupt change in the behavior of C2, C4, C6, and C8 when HM_COV equals 30%. Below this level of HM_COV the spatial deviation of links increases with increasing HM_COV and above this level of HM_COV the spatial deviation of links decreases or stays the same with increasing HM_COV. Second, when HM_COV is above 50% all cost value sets become consistent in their response to increasing HM_COV.

The two-way interaction between H_FRAG and COST also showed a difference between the responses of cost value sets C1, C3, C5, C7 and sets C2, C4, C6, C8 for all values of HM_COV (Appendix 1). As H_FRAG increased, the spatial deviation of least-cost links also increased; however, this increase was very slight for cost value sets C1, C3, C5, C7 and was dramatic for cost value sets C2, C4, C6, C8. Differences among cost sets were in general much larger when H_FRAG was high. The rate at which the spatial deviation of links in C2, C4, C6, and C8 increased in response to H_FRAG differed depending on the level of HM_COV. When HM_COV was 10%, their slopes were visibly not parallel, indicating that they had different responses to increasing H_FRAG. When HM_COV was higher than 10% their slopes were generally parallel with the exception of C2.

Discussion

Our study confirmed that connectivity assessments based on least-cost routes do reveal effects of landscapes on potential movement pathways of organisms. Of interest, however, was the question of how sensitive these connectivity assessments were to the parameterization of the cost surface. Only a handful of connectivity studies that assume least-cost movement behavior have performed sensitivity analyses on the landcover cost parameter and most of these sensitivity analyses are performed on a single landscape (Table 1). Although these studies employ a variety of connectivity measures and test for their sensitivity with varying degrees of rigor, the majority did reveal some effects of the cost values on their results. Our sensitivity analysis is not comprehensive but it is the most rigorous of its kind in terms of examining the interaction effects between landscape structure and cost surface parameterization on least-cost route analyses. We found that indeed there were

significant interactions; hence, the sensitivity of least-cost links to relative cost values changed depending on the level of habitat fragmentation and the amount of hospitable matrix. Gonzales and Gergel (2007) also found that the results of their least-cost route analyses differed in fragmented and continuous landscapes.

Our analyses clearly showed that the least-cost links were more sensitive to the difference in cost values between hospitable and inhospitable matrix landcover types than between habitat and hospitable matrix landcover. We restricted our analyses to the extreme differences in relative cost values between matrix landcover types that had been reported in the literature (1.5- and 100-fold; Table 1) so that we could look at interactions among landscape structure and cost sensitivity. We acknowledge that more work needs to be undertaken to define a potential range of cost values that could produce consistent results in least-cost connectivity assessments in a variety of landscapes. Schadt et al. (2002) confirmed that their ability to classify connections among habitat patches in terms of exchange of animals and mortality risk was only sensitive to cost values when habitats within the matrix had “very low” values. In their study, they varied the cost of a hospitable matrix landcover type with relative cost values of 4, 7, 10, 20, 30, 100, and 500 while inhospitable matrix was assigned a constant cost of 1,000. Hospitable matrix cost values from 7 to 500 produced similar results and were deemed biologically plausible, but the smallest cost value of 4 changed their results and was dismissed as being below the biologically realistic range. Chardon et al. (2003) and Verbeylen et al. (2003) also found that models assuming least-cost movement fitted patch-occupancy data better than the models assuming Euclidean movement for a wide range of cost values. From this, they concluded that all chosen parameters and ratios were in the range appropriate for predicting the occurrence of their study species. However, they also found that the predictive power of their models were sensitive to the exact quantification of the cost surface. This supports the idea that a biologically realistic range of cost values may produce satisfactorily consistent results for coarse measures of connectivity, although some sets of cost values will improve accuracy of precise predictions. In light of these findings and given the extreme cost values assigned to matrix landcover types in our

study, we expected to observe some differences in the spatial locations of least-cost links. Indeed, least-cost links did follow larger spatial detours from straight-line links when the difference in cost values between matrix cover types was large (e.g., Fig. 2). The weaker effect of the difference between cost values assigned to habitat and hospitable matrix was unexpected as it has not been explicitly tested in previous least-cost route sensitivity studies. This result is not entirely surprising, however, given that our sensitivity analysis of least-cost routes was combined with a graph analysis approach. In the planar graph approach least-cost links did not cross nodes; hence, we would expect that multiplying all cost values except for the cost of habitat (which is fixed at 1) by a positive integer would result in the same spatial pattern of least-cost links, but the effective distance of links would be correspondingly larger. Therefore, we reiterate that the most important relative cost values are those between landcover types in the matrix when evaluating the sensitivity of least-cost routes implemented within a habitat graph modelling approach.

Our results also showed that the sensitivity of least-cost links to relative cost values was modified by the composition of the matrix. The spatial deviation of least-cost links from straight-line links peaked when the percentage of hospitable matrix in the landscape was 30%. For higher percentages of hospitable matrix, different sets of relative cost values produced more consistent least-cost links. Conversely, the degree of fragmentation of the matrix landcover types did not have an effect on the sensitivity of least-cost links to relative cost values. This result is consistent with results from empirical studies demonstrating that the effects of fragmentation are generally much weaker than the effects of habitat amount on various measures of species movement, distribution, and persistence (Fahrig 2003; and references therein). We set the amount of habitat in all of our simulated landscapes as 12% to reflect common conservation targets (Pressey et al. 2003) and found that for this proportion of habitat, the degree of fragmentation of the habitat did indeed affect the sensitivity of least-cost routes. In this respect, the least-cost habitat graph model is behaving consistently with the observation that the effects of fragmentation increase with decreasing habitat amount in the landscape (Andrén 1994, 1999) since

we have a low proportion of habitat in our landscapes. Indeed, the quality of landcover types has also been shown to modify the relationship between the size of habitat patches and population abundances (Mönkkönen and Reunanen 1999). The complex interaction among habitat fragmentation, amount of hospitable matrix, and relative cost values in our study further emphasize the importance of quantifying all three (pattern, amount, and quality) when making assessments of potential movement through heterogeneous landscapes.

Although a wide variety of values have been used to quantify habitat cost values for many different species in the connectivity literature (see Table 1), very few studies have empirically estimated relative cost values. There have been two studies, however, which have addressed this question with very different approaches (Ricketts 2001; Stevens et al. 2004). Stevens et al. (2004) conducted a manipulative, laboratory-based experiment to compare physical movement ability through five land cover types corresponding to sand, cement, field grass, and forest for *Bufo calamita*. They estimated cost values of 1, 1.5, 2, and 2.5 for these habitats, but these cost values only measure a single aspect of fitness, which limits their direct applicability to connectivity analyses. Ricketts (2001) used field surveys to estimate the difference between willow and conifer costs for six butterfly taxa. He found that the willow land cover had a cost value of 1.7, 0.9, 1.4, 2.0, and 1.1 for five of the six taxa studied relative to the meadow cost of 1. For four taxa, conifer cost was between 3 and 12 times higher than the willow cost. The small differences in landcover cost estimates from these studies raise questions about the large relative cost values that are generally assigned by expert opinion (see Table 1); however, it is important to note that the studies were all examining different species with different ecological sensitivities which could account for the drastically different cost values. Manipulative methods for the empirical estimation of landcover cost have also been suggested by Bélisle (2005), such as translocation and playback experiments, food titration experiments, and manipulating feeding and breeding site locations. These types of empirical efforts coupled with our work on the sensitivity of results to the cost values will be essential for the widespread acceptance of graph-theoretic connectivity

analyses that assume least-cost movement behavior as a tool to inform spatial planning decisions for conservation.

Conclusion

Despite their sensitivity to the parameterization of the cost surface, least-cost routes are increasingly being coupled with graph-theoretic techniques to assess connectivity in a diversity of applications. Easily accessible GIS software that allows least-cost routes to be computed rapidly has led to a proliferation in their use without examining key assumptions that may affect the ecological relevance of the conclusions based on their results (Gonzales and Gergel 2007). In our systematic study we considered how the interactions between quality, amount, and fragmentation of habitat and matrix cover types influence connectivity assessments that are based on least-cost routes and graph-theoretic analyses. We found that landscape structure affects how sensitive these connectivity assessments are to the quality (relative cost values) of landcover types, with the largest sensitivity occurring in fragmented landscapes. To overcome this sensitivity, we suggest identifying multiple low-cost paths between pairs of habitat patches that collectively delineate spatial zones (areas) accessible for probable movement within the intervening landscape (e.g., Sutherland et al. 2007). Pinto and Keitt (2009) have recently presented two methods for identifying multiple paths with similar costs, the Conditional Minimum Transit Cost method (see also Walker and Craighead 1997; Halpin and Bunn 2000; Theobald 2006) and the Multiple Shortest Path method. These spatial movement zones may be more robust to variation in cost values because the uncertainty in least-cost movement is incorporated into the delineation of the zones (Magle et al. 2009; Pinto and Keitt 2009). Additional spatial properties of these movement zones such as their geometry and area can provide additional information about the quality of connections between habitat patches (Theobald 2006; McRae et al. 2008). Coupled with graph-theoretic analyses, these multiple link movement zones will be particularly useful for guiding conservation planning decisions that must often be made quickly and with sparse data on disperser behavior.

Acknowledgments We would like to thank Josie Hughes for assistance with the implementation of the placement algorithm used to create simulated maps. We are also grateful to Stephen Smith who was invaluable with data management and information technology services. Many thanks are extended to the researchers in LE Lab and especially to Patrick James for helpful discussions and valuable comments on drafts. Funding was generously provided by NSERC as a CGS to BR and an NSERC Discovery Grant to MJF.

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