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The effect of cost surface parameterization on landscape resistance estimates

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Abstract

A cost or resistance surface is a representation of a landscape's permeability to animal movement or gene flow and is a tool for measuring functional connectivity in landscape ecology and genetics studies. Parameterizing cost surfaces by assigning weights to different landscape elements has been challenging however, because true costs are rarely known; thus, expert opinion is often used to derive relative weights. Assigning weights would be made easier if the sensitivity of different landscape resistance estimates to relative costs was known. We carried out a sensitivity analysis of three methods to parameterize a cost surface and two models of landscape permeability: least cost path and effective resistance. We found two qualitatively different responses to varying cost weights: linear and asymptotic changes. The most sensitive models (i.e. those leading to linear change) were accumulated least cost and effective resistance estimates on a surface coded as resistance (i.e. where high-quality elements were held constant at a low-value, and low-quality elements were varied at higher values). All other cost surface scenarios led to asymptotic change. Developing a cost surface that produces a linear response of landscape resistance estimates to cost weight variation will improve the accuracy of functional connectivity estimates, especially when cost weights are selected through statistical model fitting procedures. On the other hand, for studies where cost weights are unknown and model selection is not being used, methods where resistance estimates vary asymptotically with cost weights may be more appropriate, because of their relative insensitivity to parameterization.

Keywords: Circuitscape, connectivity, cost surface, gene flow, landscape ecology, landscape genetics

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Introduction

In recent decades, studies in landscape and metapopulation ecology have demonstrated that a population's extinction probability is affected by how well the population is connected through dispersal, migration and gene flow (Hanski 1991; O'Grady *et al.* 2006). Populations that are well connected should generally have a lowered extinction risk, because locally extinct habitats can be rescued through recolonization (Brown & Kodric-Brown 1977). The connectedness of populations is often referred to as landscape connectivity, which has been defined as the degree to which a landscape facilitates or impedes movement (Taylor *et al.* 1993). Given its conceptual link with extinction risk, landscape connectivity is considered an important aspect of landscape structure and one that is invoked as a conservation target for planning (Beier *et al.* 2008, 2009). Estimates of landscape connectivity are an essential aspect of landscape genetics, which attempts to predict gene flow across landscapes (Manel *et al.* 2003). Similarly, 'seascape' connectivity has been estimated in marine environments (e.g. Galindo *et al.* 2006; Hansen & Hemmer-Hansen 2007; White *et al.* 2010).

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Despite its perceived importance, measuring landscape connectivity is not straightforward, and there has been considerable debate about effective strategies for doing so (Tischendorf & Fahrig 2000, 2001; Moilanen & Hanski 2001; Goodwin 2003). Recent research efforts have begun to coalesce however, around the concept of a cost surface. Cost surfaces are also referred to in some applications as resistance surfaces. Cost or resistance surfaces are simply planar surfaces where cost weights are applied to different landscape elements reflecting their cost to movement or gene flow for the species in question. By definition, landscape connectivity is a species-specific concept (Taylor *et al.* 1993), so cost surfaces tend to be constructed on a species-specific basis.

Perhaps the most commonly used application of cost surfaces is to estimate least cost paths. Analysis of least cost paths involves identifying optimal routes between start and end points. Optimality is achieved by minimizing costs incurred across the route by choosing the least costly landscape elements to travel through (Adriaensen *et al.* 2003). Least cost paths have been used in studies of animal movement (e.g. Driezen *et al.* 2007), pollen and seed dispersal (e.g. Trenel *et al.* 2008), gene flow (e.g. Cushman *et al.* 2006) and for purposes of landscape planning to identify optimal routes for conservation (e.g. Beier *et al.* 2008; Chetkiewicz & Boyce 2009).

One drawback of the least cost path approach is that it assumes that individuals have optimal knowledge of the landscape and will therefore use the optimal route. Interest in a method to identify wider swatches of habitat or multiple paths between points has motivated the application of circuit theory to landscape connectivity studies (McRae 2006). Circuit theory takes advantage of similarities between current travelling through an electrical circuit and random walks (Doyle & Snell 1984). Start and end points in circuit theory are analogous to nodes in an electrical network, and effective resistance is measured as the voltage induced by passing a one-amp current between the nodes (Chandra *et al.* 1997). In landscape connectivity applications of circuit theory, current travels through a raster surface where all landscape elements are converted to pixels and considered nodes, and all pairs of nodes are connected by resistors (McRae *et al.* 2008). The voltage can vary depending on the cost weights of the landscape elements, and so multiple paths of greater or lesser resistance are identified. Effective resistance also varies with the number of paths; as routes for current are added, resistance declines. Effective resistance has been shown to predict gene flow in several systems (McRae & Beier 2007; McRae *et al.* 2008; Lee-Yaw *et al.* 2009; Row *et al.* 2010; Garroway *et al.* 2011).

Least cost paths and effective resistance are conceptually linked through the concept of redundancy. Recall that effective resistance is derived from circuit theory, where some wired routes in an electrical network may be redundant. McRae *et al.* (2008) introduced the redundancy ratio as the ratio of the least cost path to effective resistance. As paths are added, effective resistance declines, and redundancy is increased. A landscape with high redundancy would be highly connected with many possible routes. Conversely, a landscape with no redundancy would have only a single route that would be equivalent to the least cost path.

A major challenge in employing cost surfaces to estimates of least cost path or circuit-based resistance is parameterizing the surface by applying cost weights to different landscape elements. Parameterization is challenging because the true costs of movement are rarely known. There have been two main approaches to this problem: using empirical data and using expert opinion (Spear *et al.* 2010). Use of empirical data has most often involved studying rates of movement over relatively small areas (e.g. telemetry studies; O'Brien *et al.* 2006; Driezen *et al.* 2007). The relevance of such studies to larger scale landscape questions or assessments of gene flow is unknown (Spear *et al.* 2010). Genetic data may also be used to parameterize a cost surface (Epps *et al.* 2007; Garroway *et al.* 2011). Most often, expert opinion is used to estimate weights for cost surfaces in landscape ecology studies (Ray *et al.* 2002; Broquet *et al.* 2006; Spear *et al.* 2010).

Parameterizing cost surfaces would be more straightforward if their sensitivity to relative cost weights was known. As an extreme example, a surface that was insensitive to cost weights would be robust to errors in costs arising from expert opinion or extrapolations of empirical data. The influence of cost weights on resistance estimates can be assessed by conducting a sensitivity analysis, where variation in a model output can be attributed to sources of variation in model inputs (Saltelli *et al.* 2008). For cost surfaces, we can systematically vary cost weights and assess the effects on least cost path or effective resistance estimates.

Only a handful of studies have undertaken sensitivity analyses of landscape resistance estimates to relative cost weights. For effective resistance, two studies have varied cost weights during model fitting procedures, and in both cases, variation in costs appeared to have little effect on models (Lee-Yaw *et al.* 2009; Row *et al.* 2010). Rayfield *et al.* (2010) reviewed ten studies that have varied cost weights in analyses of least cost paths, and in eight of these studies, authors concluded that least cost path estimates were sensitive to cost weights; the deviation between least cost path and Euclidean distance increased with an increase in the contrast between cost weights. The emphasis in all of these studies, however, has been model fitting rather than sensitivity analysis *per se*, where the variation in effective resistance or least cost path is attributed to variation in cost weights. Thus, it is difficult to distil generalities about the effects of cost weights from these published analyses. Two studies are particularly germane however, in showing that landscape resistance estimates are sensitive to iterative increases in cost weights (Gonzales & Gergel 2007) and landscape spatial structure (Gonzales & Gergel 2007; Rayfield *et al.* 2010). There are no studies that assess the relationship between least cost path or effective resistance estimates and relative cost weights over a wide range of weights.

We sought to test the sensitivity of two applications of cost surfaces to relative cost weights. Using two landscapes, we assessed variation in least cost paths and effective resistance as cost weights varied. Further, we measured effective resistance and least cost path using both resistance and conductance surfaces. A conductance surface is simply the inverse of a resistance surface, where high values indicate high quality rather than high cost (McRae *et al*. 2008). For all cost surfaces, we were interested in assessing the direction and magnitude of change in model output as model inputs were changed. Given the potential conservation implications of the redundancy concept, we were also interested in assessing variation in the ratio of least cost path to effective resistance as cost weights changed.

Materials and methods

We compared the sensitivity of least cost path and effective resistance to variation in cost weights using two landscapes in Ontario, Canada: one in the boreal forest (hereafter forested landscape) and one in the Lake Simcoe region (hereafter settled landscape) (Fig. 1). We selected these two landscapes to provide a contrast in landscape context for our sensitivity analyses.

Forested landscape cost surface

We generated a cost surface representing habitat quality for American marten (*Martes americana*) in the boreal forest of Ontario (Koen *et al*. 2010, 2012). We assessed habitat quality based on habitat suitability models for marten (Elkie *et al*. 1999, 2009; Naylor *et al*. 1999) using Forest Resource Inventory data. Our cost surface consisted of 1 777 353 cells with a pixel size of 0.25 km^2 and two categorical values (low and high habitat quality). The surface was 34% high-quality habitat and 66% low-quality habitat. We randomly selected 30 points to use as the start and end points for calculating pairwise estimates of effective resistance and least cost path. The mean (SD) Euclidean distance between these random points was 513 (313) km (range = 358–1305 km).

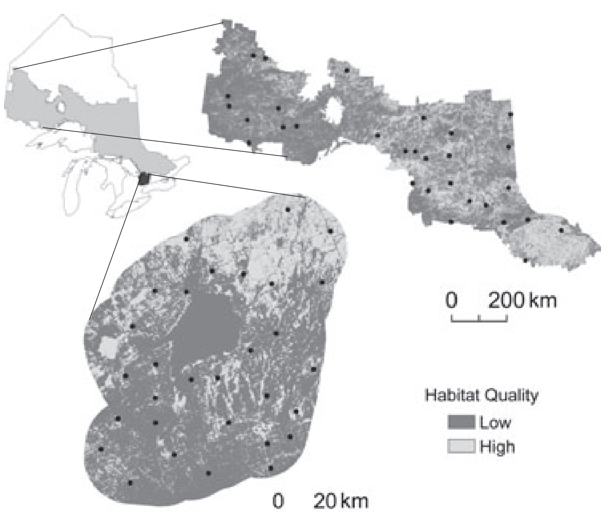

Fig. 1 Resistance surfaces used for sensitivity analysis. The cost surface for the forested landscape (upper right) represents marten habitat suitability in Ontario, Canada. The grid contains 1 777 353 cells with a pixel size of 0.25 km^2. The cost surface for the settled landscape in the Lake Simcoe region in Ontario (lower left) represents permeability of the landscape for animal movement and contains 1 512 036 cells with a pixel size of 0.01 km^2. Thirty random points on each cost surface indicate the start and end locations for least cost path and effective resistance estimation.

Settled landscape cost surface

We developed a cost surface for modelling wildlife corridors among protected natural areas in the Lake Simcoe watershed in Ontario. The surface included a buffered region (20 km buffer) around the watershed covering a total area of 10 986 km^2 and consisting of 1 512 036 cells, each 0.01 km^2 in size. The cost surface distinguished between land cover types that were considered to have high (31% of the surface) or low (69% of the surface) permeability to the movement of wildlife. Highly permeable landscape elements included natural land cover types (e.g. forests, wetlands, meadows) and unnatural yet permeable cover types (e.g. agricultural fields, golf courses, plantations, orchards, and tertiary and secondary roads). Landscape elements with low permeability included built-up urban areas, highways and large water bodies. Using the Ontario Land Cover Database (Ontario Ministry of Natural Resources 2004), a raster database identifying 28 vegetation and land cover types across Ontario, we aggregated landscape elements into the two permeability categories. Within the watershed, we generated 30 random points that represented the start and end points for pairwise comparisons of effective resistance and least cost path. The mean (SD) Euclidean distance between these points was 57 (24) km (range = 21–137 km).

Varying grid cell values

We undertook a sampling-based sensitivity analysis, where we varied input values (cost weights) and assessed the effects on model output. Within each of the scenarios, we varied the value we assigned to one of the two grid cell categories (i.e. high or low quality) so that its value was either doubled or halved for each iteration (Table 1). The position of high- and low-quality cells remained the same across all scenarios.

For each of our landscapes (forested and settled), we parameterized the cells using three different scenarios: resistance, resistance′ or conductance (Fig. 2).

Resistance surface. High cell values represented high cost. As we increased relative cell value contrast, we fixed the value of low-cost cells at 1 and increased the value of

Table 1 Cell values as relative cell contrast is increased, for three methods of cost surface parameterization*

Resistance		Resistance′		Conductance	
Good habitat	Poor habitat	Good habitat	Poor habitat	Good habitat	Poor habitat
1	2	0.5	1	2	1
1	4	0.25	1	4	1
1	8	0.125	1	8	1
1	16	0.0625	1	16	1
1	32	0.01325	1	32	1
1	64	0.01562	1	64	1
1	128	0.00781	1	128	1
1	256	0.00391	1	256	1
1	512	0.00195	1	512	1
1	1024	0.00098	1	1024	1

*Cost surfaces were parameterized as resistance (high cell values indicate high cost, and as contrast increases, high-cost values increase), resistance′ (high cell values indicate high cost, and as contrast increases, low-cost values decrease) and conductance (low cell values indicate high cost).

high-cost cells. Each iterative step represented a doubling of high-cost values.

Resistance′ surface. High cell values represented high cost. As we increased relative cell value contrast, we fixed the value of high-cost cells at 1 and decreased the value of low-cost cells. Each step represented a halving of low-cost values.

Conductance surface. High cell values represented high conductance (low cost). As we increased relative cell value contrast, we fixed the value of low conductance cells at 1 and increased the value of high conductance cells. Each step represented a doubling of high conductance values.

Least cost path and effective resistance

We estimated least cost path with the PATHMATRIX 1.1 (Ray 2005) extension for ARCVIEW 3.2 (Environmental Science Research Institute, Redlands, USA). We report least cost path as both the length, in kilometres, of the least cost path, and the accumulated cost distance of the least cost path, in cost units. We did not calculate least cost paths for the grids coded as conductance. We estimated effective resistance in ohms with the software CIRCUITSCAPE 3.5 (McRae & Shah 2009). We used the pairwise mode that connected eight neighbours. When we parameterized cost surfaces as a resistance or a resistance′ grid, we specified the habitat data in Circuitscape as resistance and connected the cells as an average resistance. When we parameterized cost surfaces as conductance, we specified habitat data in Circuitscape as conductance and connected the cells as an average conductance.

We calculated redundancy as the least cost path divided by effective resistance, for both types of least cost path estimates (length and accumulated cost). We transformed redundancy estimates into standard scores (z-scores) so that we could compare trends in redundancy across landscapes (forested and settled) and across methods of resistance surface parameterization (resistance and resistance′). We calculated z-scores for each redundancy estimate (i.e. the mean across 30 pairs of start and end points) by subtracting mean redundancy (i.e. the mean across 10 contrast scenarios) and dividing by the standard deviation of mean redundancy.

Results

As the contrast between grid cell values of the cost surfaces increased, least cost path and effective resistance responded differently, and this depended on (i) how the cost surface was coded (resistance, resistance′ or conductance) and (ii) how least cost path was measured (as a length or an accumulation of cost values). Qualitatively, the responses to varying cost weights were independent of landscape, as trends were the same for our forested and settled landscapes (Figs 3 and 4).

When we coded our surface as resistance, our estimates of effective resistance increased linearly with increasing contrast between cell values (Fig. 3a). Our estimates of least cost path, measured as an accumulation of costs, also increased linearly with increasing cell value contrast (Fig. 4a). The length of the least cost path, however, increased to an asymptote as cell contrast increased (Fig. 4b).

When we coded our surface as resistance′, effective resistance decreased to an asymptote as cell contrast

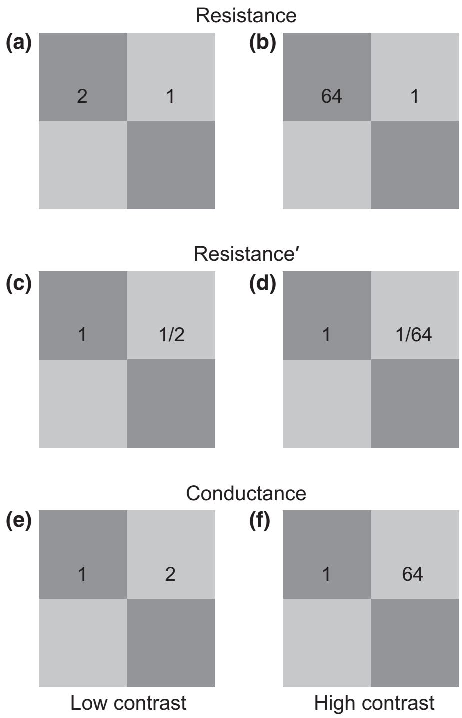

Fig. 2 An example of a grid coded as resistance, resistance′, or conductance. Light grey grid cells represent cells that are easy to move through (low cost), and dark grey cells represent costly cells to move through. Panels (a, c, e) are low-contrast grids, where the magnitude of the difference between low- and high-cost cells is 2. Panels (b, d, f) are high-contrast grids, where the magnitude of the difference between low- and high-cost cells is 64. All six panels are based on the same grid, but each are coded differently. Panels (a, b) are coded as resistance, where high-cost cells are assigned a high number. Panels (c, d) are also coded as resistance, except that as contrast increases, the low-cost cells become lower cost (resistance′). This is in contrast to panels (a, b), where the high-cost cells become higher cost as contrast increases. Finally, panels (e, f) are coded as conductance, where high-cost cells are given a low number indicating low conductance.

increased (Fig. 3b), similar to when the resistance surface was coded as conductance (Fig. 3c). The accumulated cost of the least cost path decreased to an asymptote as cell contrast increased (Fig. 4c), even though least cost path length actually increased (Fig. 4d).

The most sensitive cost surface parameterizations were those with linear responses to varying cost weights: surfaces coded as resistance and assessed for either effective resistance or accumulated least cost had the greatest proportional change in response to changing cost weights (Table 2). Parameterizations that led to asymptotic change were relatively insensitive at high-cost contrasts.

Redundancy ratios reflect the degree to which least cost path and effective resistance estimates convey the same information; when there are many pathways, redundancy ratios are high. When we coded the cost surface as resistance, redundancy ratios decreased with increasing grid cell contrast, regardless of whether least cost path was measured as a length or accumulated cost (Table 3, Fig. 5a,b). When we coded the cost surface as resistance′, however, patterns of redundancy ratios with increasing cell value contrast depended on whether least cost path was measured as a length or an accumulated cost. When least cost path was measured as a length, redundancy ratios increased as cell contrast increased (Table 3, Fig. 5c,d). Conversely, when least cost path was measured as an accumulated cost, redundancy ratios decreased with increasing cell value contrast (Table 3, Fig. 5c,d).

Discussion

Landscape geneticists and ecologists use cost surfaces to model gene flow or movement across space. Rarely, however, are the true costs known for different landscape elements. Instead, relative costs are estimated. We observed two qualitatively different kinds of responses of cost surface estimates to varying cost weights: either linear or asymptotic change. When cost surfaces were coded as resistance, mean effective resistance and accumulated cost of least cost paths increased linearly with relative cost weights. All other cost surface scenarios led to asymptotic change. The two linearly changing surfaces also had, on average, a greater proportional change in model output as a result of changes in model input (Table 2), indicating that these were the more sensitive surfaces.

The distinction between linear and asymptotic changes is important for landscape geneticists, given their interest in parameterizing cost surfaces. Although costs should ideally be based on biological information, true costs of movement remain difficult to identify (Spear *et al.* 2010). Instead, cost surfaces tend to be incorporated into genetic studies in one of two ways. In the first method, users select a suite of cost surfaces that vary in the contrast of cost weights. Least cost path or effective resistance estimates are calculated for each cost surface, and the surface that correlates best with gene flow or movement is selected (e.g. Cushman *et al.* 2006; Pérez-Espona *et al.* 2008; Lee-Yaw *et al.* 2009). There is little to be gained however, from varying cost weights within the sill of an asymptote. We suggest instead that users of this model selection approach will have the best accuracy in parameterization by coding cost surfaces as resistance to vary linearly with changes in relative cost weights. We also recommend testing a wide range of costs; otherwise, one might underestimate costly landscape features when the contrast of cell weights is too narrow. This is especially the case when barriers are present in the landscape.

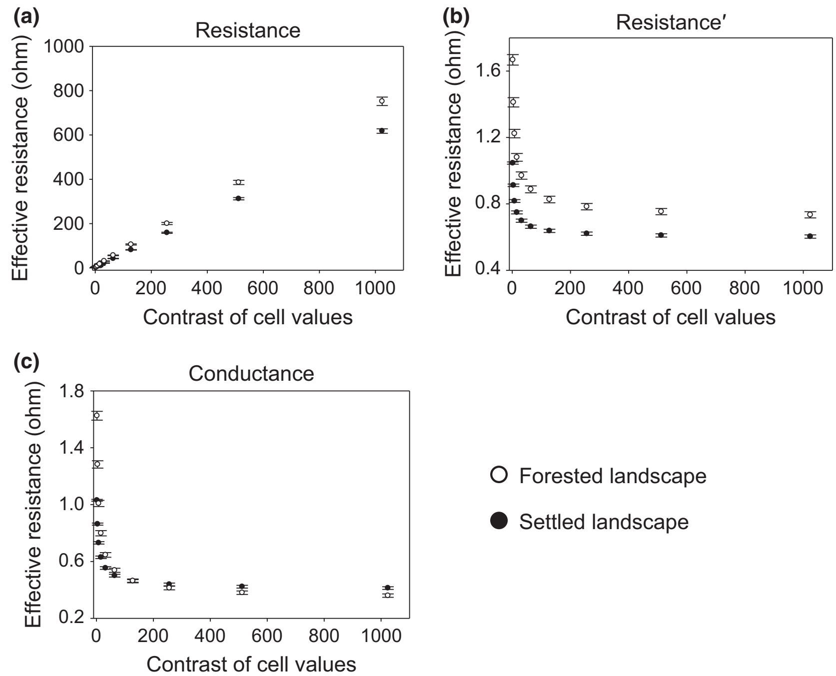

Fig. 3 The response of effective resistance estimates to increasing contrast of cost surface cell values. We coded cost surfaces as (a) resistance, (b) resistance′ or (c) conductance. We estimated mean (±SE) effective resistance for a forested and a settled landscape.

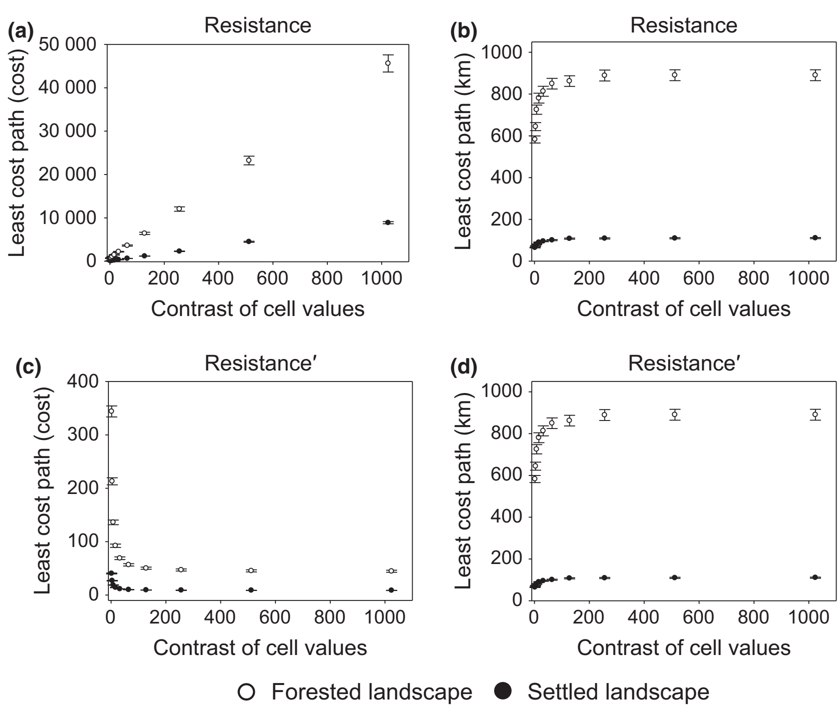

Fig. 4 The response of least cost path estimates to increasing contrast of cost surface cell values. Panels (a, b) are based on cost surfaces coded as resistance. Panels (c, d) are based on cost surfaces coded as resistance′. We measured least cost paths in panels (a, c) as the accumulated cost of the least cost path, in cost units. We measured least cost path in panels (b, d) as the length of the least cost path, measured in kilometres. We estimated mean (±SE) least cost paths for a forested and a settled landscape.

Table 2 Proportional change in mean effective resistance and least cost path (LCP)* for each doubling or halving of cost weights

Cost surface†	Estimate	Change in cost weight per step	Forested Mean	Forested Range	Settled Mean	Settled Range
Resistance	Effective resistance	Doubled	0.83	0.69–0.95	0.88	0.74–0.98
	LCP (length)	Doubled	0.05	0.11–0.00	0.06	0.12–0.01
	LCP (cost)	Doubled	0.62	0.24–0.96	0.70	0.33–0.98
Resistance′	Effective resistance	Halved	−0.09	−0.15 to −0.03	−0.06	−0.13 to −0.01
	LCP (length)	Halved	0.05	0.11–0.00	0.06	0.12–0.01
	LCP (cost)	Halved	−0.19	−0.38 to −0.02	−0.15	−0.33 to −0.01
Conductance	Effective resistance	Doubled	−0.15	−0.21 to −0.05	−0.10	−0.16 to −0.02

*We calculated proportional change as $(B–A)/A$, where B is the value (e.g. effective resistance) at one contrast scenario, and A is the value at the previous (smaller) contrast. We then calculated mean proportional change across the 10 contrast scenarios (where each contrast scenario contained the mean estimate for the 30 random start and end points).
†We parameterized cost surfaces as resistance (high cell values indicate high cost, and as contrast increases, high-cost values increase), resistance′ (high cell values indicate high cost, and as contrast increases, low-cost values decrease) and conductance (low cell values indicate high cost).

Table 3 Redundancy ratio (least cost path*/effective resistance) as the contrast between cell values increased

	Forested landscape				Settled landscape			
	Resistance‡		Resistance′§		Resistance		Resistance′	
Cell contrast†	LCP length	LCP cost	LCP length	LCP cost	LCP length	LCP cost	LCP length	LCP cost
2	174.7	206.3	349.4	206.3	31.1	38.9	61.7	38.6
4	114.1	150.9	456.3	150.9	20.0	29.8	79.2	29.5
8	74.1	111.3	592.8	111.3	12.5	23.3	98.4	23.0
16	45.2	85.5	722.5	85.5	7.6	19.1	119.2	18.9
32	26.2	71.1	838.0	71.1	4.3	16.7	136.3	16.5
64	15.0	63.8	957.5	63.8	2.4	15.3	151.9	15.3
128	8.2	60.8	1043.2	60.8	1.3	14.7	168.7	14.7
256	4.4	60.0	1135.1	60.0	0.7	14.5	175.4	14.5
512	2.3	60.2	1181.6	60.2	0.4	14.4	179.7	14.4
1024	1.2	60.7	1212.7	60.7	0.2	14.4	182.9	14.4

*Least cost path (LCP) is measured as the length (km) or the accumulated cost (cost units).
†Grids are varied such that the location of each cell is constant but the values assigned to the cells vary.
‡Grid cells represent cost, with high values indicating higher cost. As contrast increases, high-cost values increase.
§Grid cells represent cost, with high values indicating higher cost. As contrast increases, low-cost values decrease.

In the second method, one cost surface is used, with a single parameterization based on expert opinion or empirical data (e.g. Ray *et al.* 2002; Broquet *et al.* 2006). For example, Row *et al.* (2010) and Koen *et al.* (2012) parameterized cost surfaces according to a resource selection function and a habitat suitability model, respectively, and made assumptions about how these values translated into costs of movement. An estimate of least cost path or effective resistance based on this cost surface is then correlated with gene flow estimates. Users taking this approach could minimize the risk of overestimating costs by using a cost surface that has an asymptotic response to varying cost weights and will thus be less sensitive to inaccurate parameterization when the true costs are unknown. As a general recommendation however, we prefer the former of these two approaches (i.e. using model selection and a surface that changes linearly with relative cost weights) because it allows the genetic or movement data to inform estimates of permeability to movement and puts less emphasis on the arbitrary assignment of cost weights based on expert opinion or habitat suitability data.

It is worth considering how asymptotes are arrived at in cost surfaces. When our surfaces were coded as resistance, we only observed an asymptote in least cost path length. This is straightforward to interpret. At low

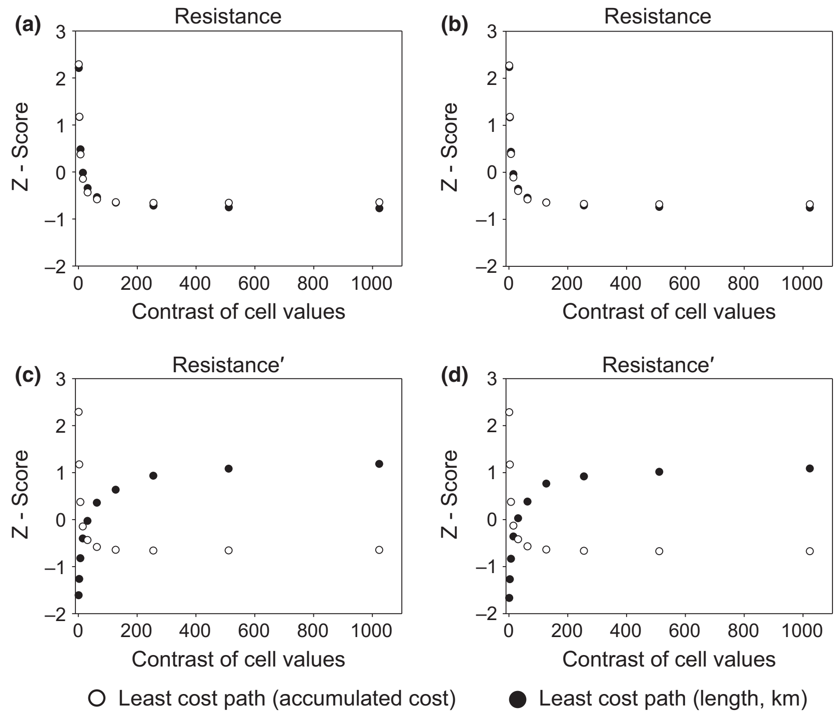

Fig. 5 Standardized (*z*-score) redundancy estimates (least cost path/effective resistance). *Z*-scores are for cost surfaces coded as resistance (panels a, b) or resistance′ (panels c, d). We estimated redundancy for a forested (panels a, c) and a settled (panels b, d) landscape.

contrast between cost weights, the least cost path approximates a straight line, but will shift to a longer path when cost weights along the shortest route are increased (e.g. Rayfield *et al.* 2010). Eventually though, an optimal path is arrived at that is relatively unchanging with cost weight. Accumulated cost will continue to increase along this path however, leading to the linear response we observed in the accumulated least cost metric. When we coded surfaces as resistance′, both effective resistance and accumulated cost of least cost paths declined to an asymptote. Such a procedure was used by Epps *et al.* (2007) and Pérez-Espona *et al.* (2008). In our resistance′ scenarios, low-quality elements were held constant at a relatively large number, so that eventually, at very low numbers, the high-quality elements made only a negligible contribution to the resistance estimate. Thus, at the asymptote, the resistance′ surface is largely a representation of only the costly elements. It is noteworthy that although accumulated least cost may decline to an asymptote in a resistance′ surface (Fig. 4c), least cost length still increased to an asymptote (Fig. 4d), giving the odd result that these two metrics (least cost path cost and length) vary in opposite directions with relative cost weights. It is also noteworthy that estimates of both effective resistance (Fig. 3a vs. b) and accumulated least cost path (Fig. 4a vs. c) differed in direction (linear increase or asymptotic decrease) when based on a resistance or a resistance′ surface, but estimates of least cost path length were insensitive to input surfaces, as least cost path length values were identical when based on a resistance or resistance′ surface (Fig. 4b,c).

In circuit theory, resistance and conductance are inverse measures (McRae *et al.* 2008). We found that whereas a resistance surface increases linearly with relative cost weights, a conductance surface decreases to an asymptote. To understand why this effect happens, it is important to realize how resistor values for the two surfaces are derived. The resistor is equivalent to an edge in the network, and in Circuitscape, it is calculated as the mean of node values for adjacent nodes (or as the product of the mean and the square root of two when the four diagonal neighbours are included) (McRae *et al.* 2008; McRae & Shah 2009). The resistor values for the resistance and conductance surfaces are true inverses. In simplified terms, where a resistor for a resistance surface is x, a resistor for a conductance surface is $1/x$. Thus, as relative cost weights increase, x increases, but $1/x$ decreases, becoming negligibly small and limiting effective resistance in a conductance surface to an asymptote. Much like the resistance′ surface, the asymptote in a conductance surface is largely a representation of the resistant elements.

A conductance surface can be made to vary in a positive, approximately linear fashion with varying cost weights however, by estimating effective conductance rather than effective resistance (Fig. 6a). Likewise, the positive linear change we observed in effective resistance as cost weights changed on the resistance-coded surfaces could be converted to decreasing asymptotic change by estimating effective conductance (Fig. 6b). Effective conductance, which is simply the inverse of effective resistance, is not offered as a standard output in Circuitscape, but it can be estimated by taking the inverse of each pairwise effective resistance estimate. For the purposes of model fitting, practitioners should be aware that many of the conclusions of our sensitivity analyses will apply in the inverse to surfaces measured as effective conductance. One exception is that a resistance′ surface will exhibit a positive asymptote rather than a linear increase when measured as effective conductance (Fig. 6c). This is because there is only negligible conductance in a surface coded this way when cell contrasts are high.

Although we consider redundancy a useful concept from a conservation perspective, it is a rather new idea in that context (McRae *et al.* 2008), and we were unsure of how it would be affected by changing cost weights. We considered redundancy using both least cost path length and accumulated cost, and for surfaces coded both as resistance and resistance′. It was not clear from McRae *et al.* (2008) which least cost estimate (length or cost) should be considered in the numerator, but this turned out to be an unimportant distinction for surfaces coded as resistance. Regardless of the type of least cost estimate used, redundancy decreased to an asymptote as relative cost weights increased (Fig. 5a,b). Redundancy also changed asymptotically for resistance′ surfaces, but the direction of the change depended on whether the least cost length or accumulated cost was used in the numerator (Fig. 5c,d). Thus, we suggest that it may be best to apply the redundancy concept to surfaces coded as resistance and with high relative cost weights.

The qualitative responses that we observed to varying cost weights appeared to be somewhat independent of landscape structure, because both the settled and forested landscape exhibited nearly identical patterns (either linear or asymptotic change, depending on the scenario). Our two landscapes had similar proportions of good habitat however, and varying habitat amount should inversely affect the slope between accumulated least cost or effective resistance and relative cost weight, such that reducing habitat leads to a steeper slope. There are other situations, too, where least cost path or effective resistance estimates can depend on landscape structure. For example, Rayfield *et al.* (2010) used a factorial experiment to show that the spatial location of least cost routes was sensitive to both landscape fragmentation and matrix composition. Similarly, Gonzales & Gergel (2007) showed that cost surfaces were more sensitive to choice of cost weights in fragmented landscapes than in contiguous landscapes. On the other end of the spectrum, we can conceive of landscape configurations that would result in various cost surfaces being insensitive to changing cost

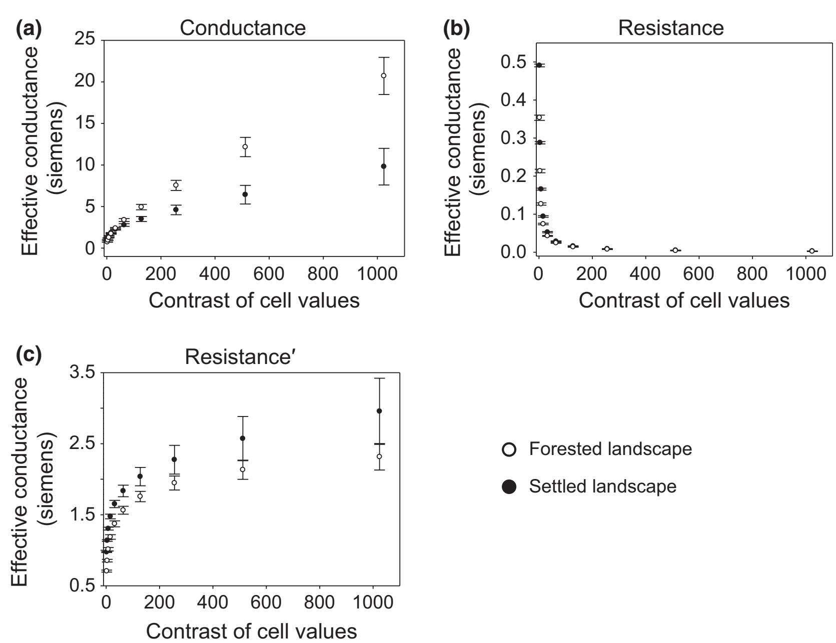

Fig. 6 The response of effective conductance estimates to increasing contrast of cost surface cell values. We coded cost surfaces as (a) conductance, (b) resistance or (c) resistance′. We estimated mean (±SE) effective conductance for a forested landscape and a settled landscape.

weights. For example, given two habitat qualities, the length and location of a least cost path would be independent of cost weights in a draughtboard (checkerboard) landscape configuration. Overall, however, the qualitative patterns that we observed should be relevant for most large, heterogeneous landscapes.

We have demonstrated that least cost path and effective resistance estimates are indeed sensitive to relative cost weights. In particular, we found that there are two qualitatively different responses to varying cost weights: linear and asymptotic changes. We recommend that researchers interested in cost surface parameterization using expert-based weights and statistical model fitting procedures code their surfaces as resistances (where high-quality elements are held constant at a low-value and low-quality elements are varied at higher values). This will produce a linear change in resistance estimates that will increase the likelihood of producing an accurate statistical model. The use of surfaces that change asymptotically with cost weights should be limited to only a few situations, including those where cost weights are not being varied or where cost weights are not being selected using statistical procedures. The asymptotic surfaces include those coded as resistance′ (where low-quality elements are held constant at a high value and high-quality elements are varied at lower values), least cost path length, and conductance surfaces used for estimating effective resistance with circuit theory. A conductance surface could be made to change linearly with relative cost weights however, if the output was measured in effective conductance. Users should consider the sensitivity of least cost path and effective resistance to cost weight contrast when choosing a cost surface.

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Data accessibility

Landscape grids are available in the Dryad repository: doi:10.5061/dryad.6b678210.