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CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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USING CIRCUIT THEORY TO MODEL CONNECTIVITY IN ECOLOGY, EVOLUTION, AND CONSERVATION

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Abstract. Connectivity among populations and habitats is important for a wide range of ecological processes. Understanding, preserving, and restoring connectivity in complex landscapes requires connectivity models and metrics that are reliable, efficient, and process based. We introduce a new class of ecological connectivity models based in electrical circuit theory. Although they have been applied in other disciplines, circuit-theoretic connectivity models are new to ecology. They offer distinct advantages over common analytic connectivity models, including a theoretical basis in random walk theory and an ability to evaluate contributions of multiple dispersal pathways. Resistance, current, and voltage calculated across graphs or raster grids can be related to ecological processes (such as individual movement and gene flow) that occur across large population networks or landscapes. Efficient algorithms can quickly solve networks with millions of nodes, or landscapes with millions of raster cells. Here we review basic circuit theory, discuss relationships between circuit and random walk theories, and describe applications in ecology, evolution, and conservation. We provide examples of how circuit models can be used to predict movement patterns and fates of random walkers in complex landscapes and to identify important habitat patches and movement corridors for conservation planning.

Key words: circuit theory; dispersal; effective distance; gene flow; graph theory; habitat fragmentation; isolation; landscape connectivity; metapopulation theory; reserve design.

INTRODUCTION

Connectivity among habitats and populations is considered a critical factor determining a wide range of ecological phenomena, including gene flow, metapopulation dynamics, demographic rescue, seed dispersal, infectious disease spread, range expansion, exotic invasion, population persistence, and maintenance of biodiversity (Kareiva and Wennergren 1995, Ricketts 2001, Moilanen and Nieminen 2002, Calabrese and Fagan 2004, Moilanen et al. 2005, Crooks and Sanjayan 2006, Damschen et al. 2006, Fagan and Calabrese 2006). Preserving and restoring connectivity has become a major conservation priority, and conservation organi-

zations are investing considerable resources to achieve these goals (Beier et al. 2006, Kareiva 2006).

Understanding broad-scale ecological processes that depend on connectivity, and making effective conservation planning decisions to conserve them, requires quantifying how connectivity is affected by landscape features. Thus, there is a need for efficient and reliable tools that relate landscape composition and pattern to connectivity for ecological processes. Many ways of predicting connectivity using landscape data have been developed (reviewed by Tischendorf and Fahrig 2000a, b, Moilanen and Nieminen 2002, Calabrese and Fagan 2004, Fagan and Calabrese 2006). Common approaches include the derivation of landscape pattern indices (e.g., Schumaker 1996), individual-based movement simulations (e.g., Schumaker 1998, Hargrove et al. 2005), and analytic measures of network connectivity, such as graph theory and least-cost path models (Keitt et al. 1997, Urban and Keitt 2001, Adriaensen et al. 2003, Minor and Urban 2007). The latter have gained increasing attention in recent years and are widely

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applied in connectivity modeling and in conservation planning.

We propose that connectivity models from electrical circuit theory can make a useful addition to the approaches available to ecologists and conservation planners. Circuit theory has been applied to connectivity analyses in chemical, neural, economic, and social networks, and has recently been used to model gene flow in heterogeneous landscapes (McRae 2006, McRae and Beier 2007). The same properties that make circuit theory useful in these fields hold promise for ecology and conservation as well. Because connectivity increases with multiple pathways in circuit networks, distance metrics based on electrical connectivity are applicable to processes that respond positively to increasing connections and redundancy. Additionally, previous work has shown that current, voltage, and resistance in electrical circuits all have precise relationships with random walks (Doyle and Snell 1984, Chandra et al. 1997). These relationships mean that circuit theory can be related to movement ecology via random-walk theory, providing concrete ecological interpretations of circuit-theoretic parameters and predictions. Finally, because algorithms to implement circuit models are well developed, they can be applied to large networks and raster grids.

Here we present several ways in which circuit theory can be used to model connectivity in ecology and conservation. We describe ecological applications of previously developed theory relating resistance, current, and voltage in electronic circuits to random walks on analogous graphs (Doyle and Snell 1984, Klein and Randic 1993, Chandra et al. 1997). This theory can be applied to predict movement patterns and probabilities of successful dispersal or mortality of random walkers moving across complex landscapes, to generate measures of connectivity or isolation of habitat patches, populations, or protected areas, and to identify important connective elements (e.g., corridors) for conservation planning. Our approach does not require new ways of representing landscape data; rather, it takes advantage of graph-theoretic data structures, which are already familiar to many ecologists, and can be applied in traditional graph-theoretic or raster GIS frameworks. Coupled with applications of circuit theory to predict equilibrium patterns of gene flow (McRae 2006, McRae and Beier 2007), these new applications comprise a modeling framework that integrates spatial aspects of ecology, evolution, and conservation.

BASIC CONCEPTS

Graph data structures and terminology

Connectivity models from circuit theory are applied to graphs (Harary 1969), so we will use the terminology of graph theory here (see Urban and Keitt 2001 for a review). Briefly, graphs are networks comprised of sets of nodes (connection points which represent, e.g., habitat patches, populations, or cells in a raster landscape) connected by edges (Fig. 1). Edges reflect functional

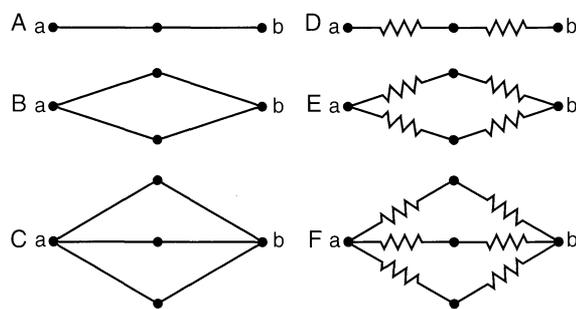


FIG. 1. Three graphs at left (A, B, C), with edge weights of 1. Traditional shortest path or geodesic distance, d , between nodes a and b is identical ($d=2$) all three cases. At right (D, E, F), edges have been replaced with unit resistors to create analogous circuits. Effective resistance, \hat{R} , measured between nodes a and b decreases from top to bottom ($\hat{R}=2, 1,$ and $2/3$, respectively), reflecting additional contributions from multiple pathways (figure modified from Klein and Randic [1993]).

connections, such as dispersal, between nodes. The weight of each edge typically corresponds to the strength of the connection (e.g., the ease of movement or number of dispersers exchanged) between the nodes it connects.

Circuit theory

In this paper, circuits are defined as networks of nodes connected by resistors (electrical components that conduct current) and are used to represent and analyze graphs (Fig. 1). The basic concepts of resistance, conductance, current, and voltage all apply, and their definitions and ecological interpretations are summarized in Table 1. Recall Ohm's law, which states that when a voltage V is applied across a resistor, the amount of current I that flows through the resistor depends on (1) the voltage applied and (2) the resistance R , such that $I = V/R$. The lower the resistance (or the higher the conductance, G , which is simply the reciprocal of resistance), the greater the current flow per unit voltage. Similarly, when a voltage is applied across two nodes in a resistive circuit (e.g., between nodes a and b in the circuits shown in Fig. 1), the total amount of current that flows across the circuit is determined by (1) the voltage applied and (2) the configuration and the resistances of the resistors the circuit contains. The effective resistance (\hat{R}) between the nodes is the resistance of a single resistor that would conduct the same amount of current per unit voltage applied between the nodes as would the circuit itself, i.e., $\hat{R} = V/I$.

In simple circuits, such as those shown in Fig. 1, effective resistance can be calculated using some basic rules. First, two resistors connected in series may be replaced by a single resistor with a resistance is that the sum of the two resistances. Thus, the effective resistance in the top circuit in Fig. 1D would be $\hat{R} = R_1 + R_2 = 2$ ohms. Conversely, connecting resistors in parallel decreases their effective resistance, such that they may be replaced by a single resistor whose conductance is

TABLE 1. Electrical terms and their ecological interpretations.

Electrical term (symbol, unit)	Ecological interpretation
Resistance (R , ohm), the opposition that a resistor offers to the flow of electrical current.	Opposition of a habitat type to movement of organisms, similar to ecological concepts of landscape resistance or friction. Graph edges or grid cells allowing less movement are assigned higher resistance.
Conductance (G , siemens), inverse of resistance and a measure of a resistor's ability to carry electrical current.	Analogous to habitat permeability. In random-walk applications, it is directly related to the likelihood of a walker choosing to move through a cell or along a graph edge relative to others available to it. In population genetic applications (see McRae 2006), it is a measure of migrants exchanged between neighboring populations.
Effective resistance (\hat{R} , ohm), the resistance to current flow between two nodes separated by a network of resistors.	Also known as the <i>resistance distance</i> , a measure of isolation between pairs of nodes on a graph or cells on a raster grid. Similar to ecological concept of effective distance, but it incorporates multiple pathways (Fig. 1D–F). It scales linearly with equilibrium genetic differentiation in population genetic applications.
Effective conductance (\hat{G} , siemens), inverse of effective resistance, a measure of a network's ability to carry current between two nodes.	A measure of connectivity between pairs of nodes on a graph or cells on a raster grid. It increases with additional available pathways and scales linearly with effective migration in population genetic applications.
Current (I , ampere), flow of charge through a node or resistor in a circuit.	Current through nodes or resistors can be used to predict expected net movement probabilities for random walkers moving through corresponding graph nodes or edges (Fig. 2).
Voltage (V , volt), the potential difference in electrical charge between two nodes in an electrical circuit. Related to current and resistance by $V = IR$.	Voltages can be used to predict the probability that random walkers leaving any point on a graph will reach a given destination (representing, e.g., successful dispersal) before another (representing, e.g., mortality; Fig. 3).

given by the sum of the conductances of the two resistors, that is, $\hat{G} = G_1 + G_2$. (In terms of resistance, these quantities are given by: $\hat{R} = R_1 R_2 / [R_1 + R_2]$.) Applying these equations to the circuits shown in Fig. 1, the effective resistance declines from the top to the bottom circuit.

Applying circuit theory to graphs involves preserving the same graph structure with interconnected nodes, but replacing graph edges with resistors, as in Fig. 1. The conductance of each resistor is typically a function of the corresponding edge weight or probability of movement between the pair of nodes it connects. The resistance of a resistor is the reciprocal of its conductance and can be thought of as representing isolation or movement cost between nodes.

INTERPRETATION OF RESISTANCE, CURRENT, AND VOLTAGE

Resistance and conductance

The simplest connectivity measure from circuit theory is the *resistance distance* (Klein and Randic 1993), a distance metric defined as the effective resistance between a pair of nodes when all graph edges are replaced by analogous resistors (as in Fig. 1D–F). A convenient property of the resistance distance is that it incorporates multiple pathways connecting nodes, with resistance distances measured between node pairs decreasing as more connections are added. Hence, the resistance distance does not reflect the distance traveled or movement cost accrued by a single individual. Rather, it incorporates both the minimum movement distance or cost and the availability of alternative pathways. As additional links are added, individuals do not necessarily travel shorter paths, but have more pathways available to them. For example, in the three

graphs in Fig. 1A–C, the minimum distance required to travel from node a to b (called geodesic distance in graph theory) is the same. However, the resistance distance decreases as more connections are added, reflecting increased flow capacities and levels of redundancy. In short, the resistance distance is small when two nodes are connected by many paths with low resistance (high conductance) edges and large when there are few paths with high resistance. Resistance distances can be calculated across irregular networks or with continuous landscape data, which are typically represented as discretized lattices or grids. On continuous surfaces, the resistance distance increases linearly with Euclidean distance in homogeneous one-dimensional habitats and with its log transformation in two-dimensional habitats, a property important for modeling gene flow (McRae 2006).

Resistance distances can also be related to random-walk times between nodes. For the theory and examples that follow, we assume that conductances are chosen so that the probability of moving from a node along any given edge is equal to the conductance assigned to the edge divided by the sum of the conductances of all edges connected to the node. For an organism moving through a habitat network (the main focus of this paper), this would correspond to a scenario where the individual chooses to move along an edge in proportion to the edge's conductance, a surrogate for habitat quality or (inverse) perceived risk, relative to the quality of all other choices of direction; this choice is then repeated at each subsequent step. For genes moving across a network of populations over many generations, this would correspond to a scenario where edge conductances correspond to per-generation migration rates (McRae 2006).

Chandra et al. (1997) showed that, when resistors are parameterized in this way, the resistance distance between a pair of nodes is precisely related to the *commute time* between the nodes, i.e., the expected time for a random walker to move from one node to the other and back again. The commute time between any pair of nodes u and v can be calculated using the following formula:

$$\text{Commute time} = \hat{R}_{uv} \sum_{x=1}^n \sum_{y=1}^n (1/R_{xy}) \quad (1)$$

where R_{xy} is the resistance of the resistor connecting nodes x and y and n is the number of nodes in the network. Note that Eq. 1 accommodates resistors connecting a node to itself, which would reflect a nonzero probability of staying at the node for any time step. Chandra et al. (1997) also provided formulas to calculate a commute *cost*, if there is a cost imposed for each step that is independent of the resistance (and thus independent of the behavior of a random walker). An interesting result of Eq. 1 is that if the goal is to minimize commute times between a pair of nodes, there is a penalty for adding connections which is offset by the degree to which the new connections help to lower effective resistance between the two nodes. Within a fixed network, commute times between different pairs of nodes will be directly proportional to the effective resistances measured between them. Another potentially useful way to apply resistance calculations across graphs is to compute upper and lower bounds for the *cover time*, or the expected number of steps of a random walk visiting all nodes in the graph (Chandra et al. 1997).

“Functional” or “effective” distance.—Used as an ecological distance metric, the resistance distance provides a conceptual complement to commonly used least-cost distances in two important ways. First, it integrates all possible pathways into distance calculations, whereas least-cost distances are measured along a single optimal pathway. Second, it offers a measure of isolation assuming a random walk, whereas least-cost distances presumably reflect the route of choice if a disperser has complete knowledge of the landscape it is traversing.

The resistance distance also provides a quantitative complement to least-cost distances. If only a single pathway between two nodes is available (e.g., in Fig. 1A or in any graph that is a tree), the resistance distance will equal the least-cost distance. On the other hand, when two identical and independent pathways connect a pair of nodes in parallel, the resistance distance will be half the least-cost distance. This suggests an interpretation of the resistance distance as an indicator of redundancy in connections relative to the least-cost distance:

$$\text{Redundancy} = (\text{least-cost distance})/(\hat{R}).$$

Thus, the two measures can be compared directly; their

ratio providing a rough measure of parallel pathways available to dispersers.

The relationship between resistance distances and commute times is one way to link circuit and ecological theories and is the basis of using resistance distances to predict patterns of gene flow and genetic structuring in heterogeneous landscapes (McRae 2006). Calculating commute times directly may provide valuable additional information because commute times take into account how efficiently a given landscape configuration will channel dispersal between source and destination nodes. Additional pathways that primarily result in increased wandering behavior rather than directed movement may reduce resistance distances but will increase commute times. Low commute times and low resistance distances between pairs of nodes indicate that dispersers will be efficiently directed between them.

Current

Currents in circuits can also be interpreted in terms of random walks on corresponding graphs. Consider again a graph in which the probability that a random walker will move from a node along any graph edge is proportional to its conductance. Doyle and Snell (1984) showed that when 1 A (ampere) of current is injected into one node (node a in Fig. 2A) and a second node (node e) is tied to ground, the current i_{xy} flowing through the resistor connecting any pair of nodes x and y is equivalent to the expected net number of times that a random walker, starting at a and walking until it reaches e, will move along that branch. Because we are tallying net passages through the branch, movements from x to y are counted as positive, whereas movements from y back to x are counted as negative.

Corridor identification and dispersal predictions.—By predicting net movement probabilities along branches or through nodes, current density can be used to identify landscape corridors or “pinch points,” i.e., features through which dispersers have a high likelihood (or necessity) of passing. High current through a node or branch indicates that removing or converting it will have a high impact on connectivity. In Fig. 2, all the current passes through node b; removing that node (or the link between nodes a and b) would completely disconnect nodes a and e, whereas removing node c, through which only half the current passes, would reduce redundancy but would still leave nodes a and e connected via the lower branch. In graph terminology, node b is a *cutnode*, and the resistor connected nodes a and b is a *cutlink*.

Voltage

Doyle and Snell (1984) also showed that voltage can be related to random walk probabilities. Consider a graph in which a voltage source set to 1 V is connected to one node (or to a set of nodes), and another node (or set of nodes) is connected to ground (Fig. 3). The voltage measured at any remaining node on the graph will equal the probability that a random walker, starting at that

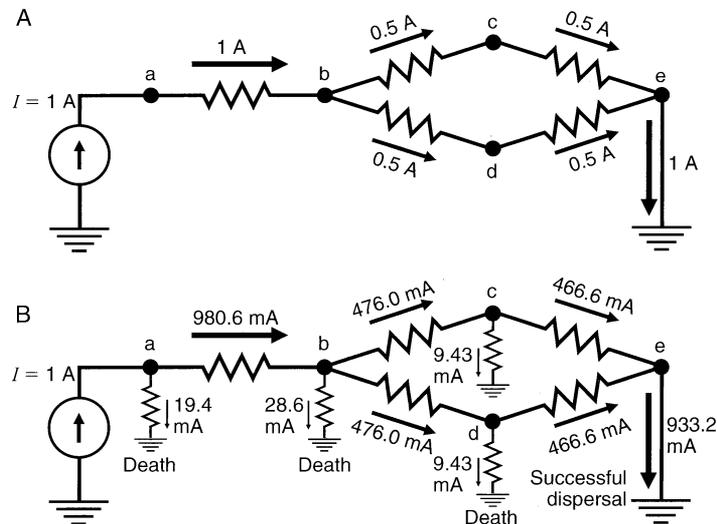


FIG. 2. (A) A simple circuit, with a 1-A (ampere) current source (I) placed at node a, and with node e tied to ground. Branch currents that would be observed with unit resistors are shown and reflect the net number of times that a random walker, starting at node a, is expected to pass along each branch before reaching node e. All random walkers must pass across the first branch, but half would be expected to take the upper pathway, and half the lower. Resistances connecting nodes were set to 1 ohm for this simple example; the methods we describe here can accommodate heterogeneous resistances with values from 0 to infinity. (B) The same circuit as in (A), but with ground resistors added to reflect a 1% probability of mortality as the random walker passes through each node. To achieve this, resistances to ground for nodes a–d were set to 99, 33, 49.5, and 49.5 ohms, respectively. Currents show the expected number of net movements along each branch, as well as the expected number of deaths at each node. For example, the proportion of dispersers leaving node a expected to successfully reach node e is 0.9332 (933.2 mA equivalent). Deaths at each node exceed 1% because nodes are visited multiple times by random walkers, with the highest numbers of deaths observed in nodes with the highest numbers of visits. Only one possible dispersal destination was included here, but the method can accommodate as many dispersal destinations as desired. Although we tied the destination node directly to ground, resistors could be added between destination nodes and ground, with their conductances set to reflect a finite probability that a walker would settle rather than continue walking once reaching a node.

node, will reach any of the nodes set to 1 V before reaching any node connected to ground. The most obvious application of this property is to predict the probability of successful dispersal via a random walk from any node on a graph. Suitable destination patches for dispersal can be set to 1 V, whereas mortality can be represented by resistors connected to ground, with their conductances reflecting probabilities of mortality (Fig. 3).

APPLYING CIRCUIT ANALYSES TO RASTER GRIDS

Predicting connectivity using circuit theory requires translating spatial data sets into a graph structure, but that doesn't mean that primary landscape data must be in a patch-based or network-style format. In fact, we envision most landscape applications operating on raster data, with a graph extracted from these data as is done for least-cost path analyses (Adriaensen et al. 2003). Since well-developed computer algorithms allow millions of cells to be processed, large raster landscapes can be accommodated.

Analyzing a raster grid involves first assigning resistances to different habitat types in the grid. Fig. 4 shows a simple example with three different habitat types: assigned unit, infinite, and zero resistance. The last is useful when practitioners wish to measure connectivity or identify important connective elements between areas (representing, for example, habitat

patches or reserves), rather than points on a landscape. To represent a grid as a circuit, cells with finite resistances are converted to nodes (gray), whereas cells with infinite resistance (i.e., those representing complete barriers, black) are dropped. Adjacent nodes are connected by resistors, with resistances reflecting a function (typically the mean) of the resistances of the cells they connect. Adjacent cells with zero resistance (open) are consolidated into a single node that is then connected by resistors to all nodes adjacent to the zero-resistance patch. Following this procedure, the 16-cell

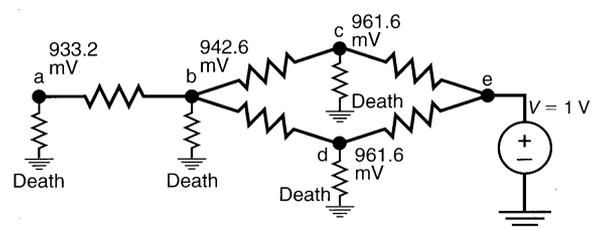


FIG. 3. The same circuit shown in Fig. 2B, but with a voltage source (V) of one volt at node e instead of a current source at node a. Node voltages reflect the probability that a random walker, starting at each node, will successfully reach node e. Consistent with the result from Fig. 2B, the probability of successful dispersal from node a to node e is 0.9332.

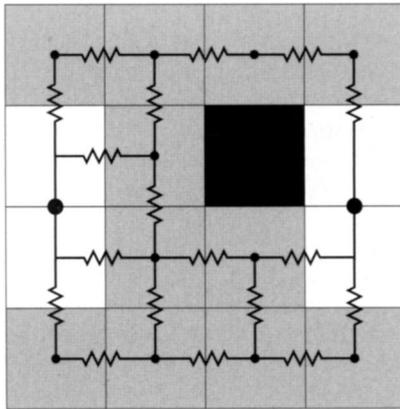


FIG. 4. A simple landscape represented as both a grid and a circuit. The landscape contains two contiguous patches of 0-resistance cells (open), dispersal habitat of finite resistance (gray), and one “barrier” cell with infinite resistance (black). Cells with finite resistance are replaced with nodes (small dots), and adjacent nodes are connected by resistors. Patches of cells with 0 resistance are each consolidated into a single node (large dots). Connections between diagonal neighbors and nonadjacent cells can also be incorporated, the latter representing “hops” over intervening cells. Current sources, voltage sources, and ground connections can be added as in Figs. 2 and 3.

grid in Fig. 4 is now represented as a circuit with 13 nodes and 18 resistors.

COMPUTATION

Although simple circuits can be solved by hand, *nodal analysis* is typically used to analyze larger circuits, such as those derived from raster grids (McRae 2006). Given a circuit with current or voltage sources, nodal analysis uses Kirchoff’s and Ohm’s laws in matrix form to solve for a vector, specifying voltages at each node; once these are known, Ohm’s law can be used to calculate currents passing through individual resistors or nodes. Effective resistance between a pair of nodes is given by the voltage between them when one is connected to a 1-A current source and the other is connected to ground (e.g., Fig. 2A). The method is described in standard circuit theory textbooks (e.g., Dorf and Svoboda 2003); an example of its use to calculate effective resistances is provided by McRae (2006).

Computer languages used for scientific computing such as Java, C, MATLAB, and Python include linear solver routines that can solve for effective resistances on graphs. Fast graph operations can be used to define connected components in a landscape and discard from a graph any components that are completely isolated. Very large graphs can be processed relatively easily and efficiently; we have solved for effective resistances, voltages, and current on landscapes containing over 1 million cells using Java (Sun Microsystems, Mountain View, California, USA), and up to 48 million cells using a parallel version of MATLAB (MathWorks, Natick, Massachusetts, USA) implemented using Star-P (Interactive Supercomputing, Waltham, Massachusetts, USA). Solving 1 million cells on a notebook computer

with a 2-GHz processor and 2 GB of RAM took us 16 minutes using Java and only 20 seconds using MATLAB. This calculation must be repeated for each configuration of current sources and grounds, but typical connectivity applications will require a small number of calculations (e.g., for each pair of populations or reserves between which connectivity is to be modeled). Calculations between multiple pairs can be sped up considerably using matrix preconditioning and/or parallel processing. Software implementing many of the algorithms in this manuscript is available (B. H. McRae, *unpublished data*).

EXAMPLE APPLICATIONS TO HETEROGENEOUS LANDSCAPES

Here we provide examples of the applications described above to predict connectivity and movement of random walkers across large raster grids. For the example analyses described next, we solved for effective resistances and node currents using code written in MATLAB R2007b. The example landscapes (i.e., resistance surfaces) were all created using ArcView GIS 3.2 (ESRI, Redlands, California, USA) and exported as ASCII raster grids, with cell values corresponding to resistances ranging from 0 to infinity (Fig. 5). For circuit analyses, cells with finite resistances were converted to nodes, whereas those with infinite resistances were dropped. Cells were connected to their eight neighbors such that the resistance between a pair of first-order neighbors was set to the mean of the two cells’ resistances, and the resistance between a pair of second-order (diagonal) neighbors was set to the mean resistance multiplied by the square root of 2 to reflect the

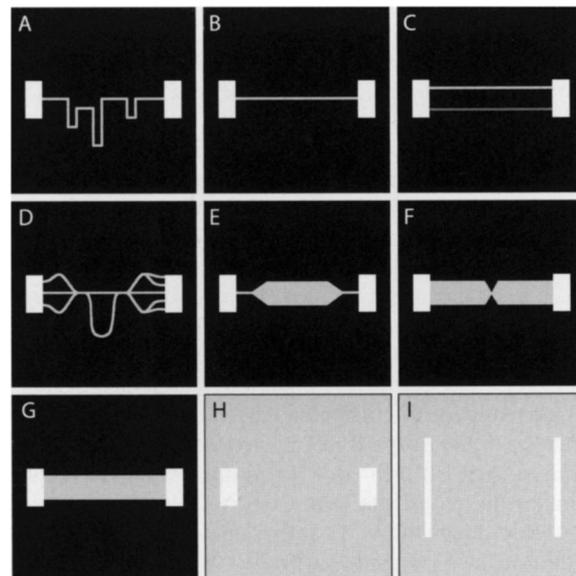


FIG. 5. Nine simple raster landscapes (A–I), consisting of 1000×1000 cells. Habitat patches (shown in white and assigned 0 resistance, or infinite conductance) are connected by different configurations of dispersal habitat (light gray, 10 ohms/cell; dark gray [lower corridor in panel C], 20 ohms/cell; black = infinite resistance or 0 conductance).

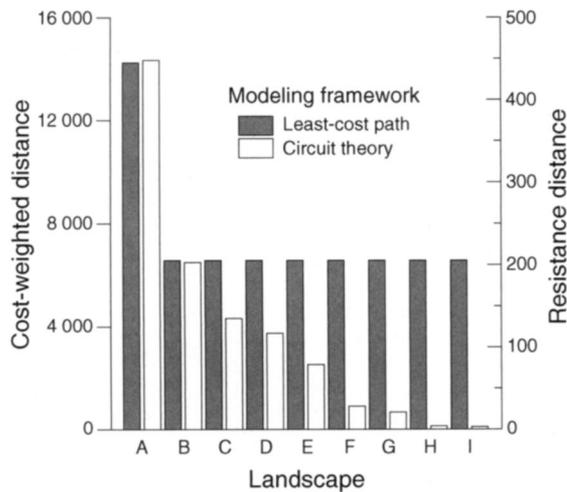


FIG. 6. Least-cost distances and resistance distances between habitat patches for the nine simple landscapes shown in Fig. 5. Least-cost distances decrease from (A) to (B) but are equivalent for all remaining maps. Effective resistances decrease not only from (A) to (B), but also from (B) to (I), reflecting the availability of more and wider pathways. Redundancy, defined here as the ratio of least-cost distance to effective resistance, would be roughly equal for cases (A) and (B) but would increase from (B) to (I). Cost-weighted distance (measured in cost units) were calculated using PATHMATRIX software. Resistance distances (measured in ohms) were calculated using Circuitscape software.

greater distance between cell centers. We converted individual cells to single nodes, except for cells in areas of zero resistance, i.e., open source/target patches; as in the simple landscape in Fig. 4, these cells were considered collectively and consolidated into a single node for the analyses. For all examples, we used the same resistance surfaces to calculate least-cost distances and map least-cost corridors using PATHMATRIX software (Ray 2005).

We started with nine simple landscapes (Fig. 5) meant to illustrate different properties of circuit models. The landscapes consisted of 1000×1000 cells each and contained two primary habitat patches, which were always the same distance from one another and always occupied the same total area. Least-cost and resistance distances calculated between habitat patches in the nine simple landscapes illustrate some advantages of the resistance distance (Fig. 6). Although least-cost distances correctly identify decreased isolation between habitat patches in landscape B relative to A, they were identical in landscapes B through I. Resistance distances show a similar decrease from landscape A to B, but they also decrease from B to I, reflecting the availability of additional, or wider, pathways. Note that between landscapes H and I, only the shape of the primary habitat patches has changed, and not their area or the distance separating them. Yet the resistance distance differs because the greater surface area of each habitat patch in landscape I acts as a “drift fence” to better intercept or release dispersers.

Commute times ranged from 1.2 million steps (landscapes B, C, and G) to 6.2 million steps (landscape A). They were intermediate for landscapes D, E, F, H, and I, which had commute times of 2.6, 3.0, 1.6, 2.7, and 2.0 million steps, respectively. Lower commute times reflect configurations in which dispersers are efficiently channeled between habitat patch pairs, minimizing wandering time.

These same simple landscapes also demonstrate how current maps (Fig. 7) can highlight connective elements in raster maps (Fig. 7) can highlight connective elements in raster maps. As the availability of multiple pathways increases, current density—indicating cells through which dispersers are likely to pass moving from one patch to the other—decreases. Pinch points are highlighted in landscapes D–F, and the “drift fence” effect resulting from the more linear shape of the habitat patches in landscape I is evident as well. Fig. 7J shows a least-cost path map for the “braided stream” corridor configuration. The technique identifies the route with the lowest cumulative cost, but gives no information about the contribution of alternative pathways. By contrast, the current map (Fig. 7D) clearly indicates the importance of different corridor segments, with current densities at their highest in the two critical linkages and at their lowest in segments that are most redundant.

We can now illustrate how these models can be used to analyze connectivity in more realistic landscapes. Fig. 8A shows a complex landscape, with patches of high-quality habitat, lower quality “matrix” habitat, corridors, and complete barriers. Fig. 8B shows cumulative travel cost mapped between two high-quality patches using standard least-cost path techniques. The map highlights the most efficient pathway between the two patches, as well as low-cost detours that do not actually contribute to connectivity, e.g., into habitat cul-de-sacs or along “corridors to nowhere.” By contrast, the current map between the same two habitat patches (Fig. 8C) highlights critical pinch points between the two patches. Habitat cul-de-sacs and corridors that do not contribute to connectivity have minimal current flow. The current map also indicates two broad routes linking the habitat patches, whereas only one is highlighted in the least-cost map. The current map thus gives important insight into the redundancy that would be lost if the second route were to be blocked.

Often it will be useful to summarize connectivity between many habitat patches or protected areas in a single map. Fig. 9A shows the result of adding 10 pairwise current maps calculated among all pairs of five habitat patches. These maps show which landscape elements are most important for overall connectivity among the five habitat patches, indicating the net number of times random walkers are expected to move through raster cells if one random walker moves from each patch to each other patch.

We could also extend the analyses of our raster maps in much the same way as the analyses in Fig. 2A were extended in Figs. 2B and 3. Ground resistors could be added to incorporate mortality or finite probabilities of

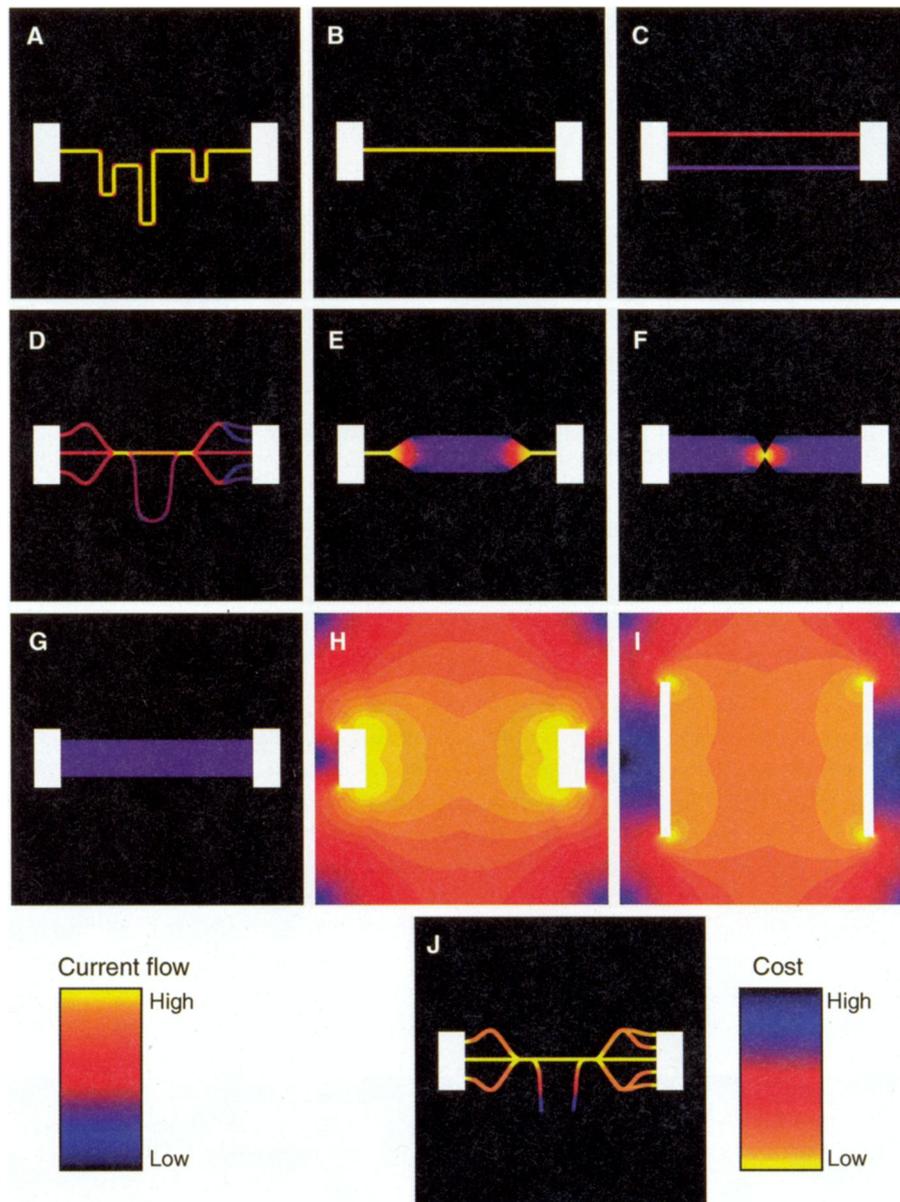


FIG. 7. Current flow through landscapes shown in Fig. 5 when 1 A (ampere) of current is injected into one habitat patch and the other is connected to ground. Current maps were log-transformed to facilitate display. Among the nine panels, three different quantitative scales are applied to the color schemes in order to most clearly illustrate differences in current densities. The three schemes are applied in panels (A)–(D), (E)–(G), and (H)–(I). Highest maximum current densities (indicating the greatest impact of habitat cell removal or conversion) are observed in (A), (B), and (D)–(E), where connectivity depends on single, narrow corridor segments. The lowest maximum current densities are observed in landscape (I), which provides the most redundancy and lowest effective resistance. This landscape also exhibits a drift-fence effect, in which the linear shapes of the habitat patches act to intercept dispersing individuals. (J) The least-cost path solution of the “braided stream” landscape shown in Fig. 5D. Whereas this technique highlights the most efficient travel path, it gives no indication of pinch points or effects of multiple parallel corridors.

settling once a disperser reaches a habitat patch or protected area. With multiple destination patches, a matrix of asymmetrical dispersal rates between all patch pairs could be generated. Or, target patches could be set to 1 V and probabilities of successful dispersal (or dispersal to one patch vs. others) from any point on the landscape could be mapped. Finally, additive maps (such as the one shown in Fig. 9A) could be adjusted to

give greater weight to important source or destination patches, with more current released or absorbed by larger or higher quality habitat patches.

Model sensitivity to landscape scale

Representing a landscape as a raster grid always involves choosing an appropriate scale of analysis (cell size and map extent). Because different species respond

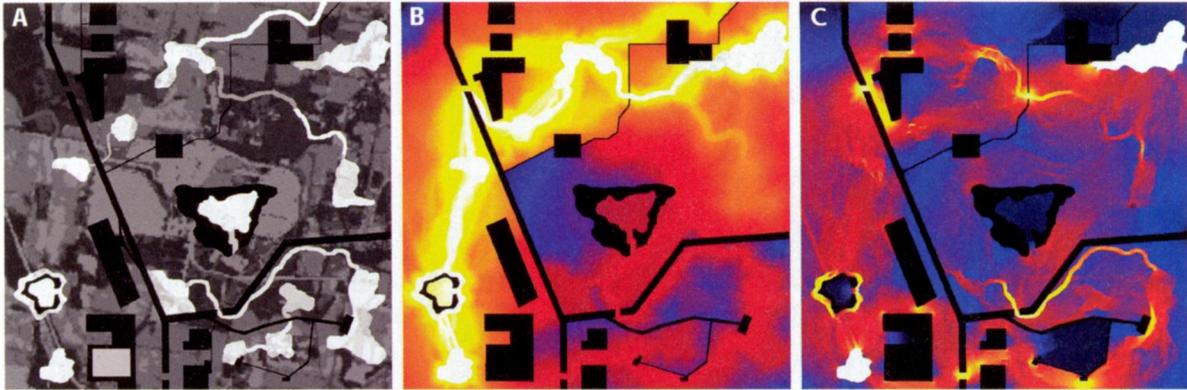


FIG. 8. Connective elements identified using least-cost path and circuit models in a complex landscape. (A) Map of the landscape, with resistances and costs for circuit and least-cost path analyses ranging from 1 (light gray) to 100 (dark gray) to infinite (black). (B) Results from least-cost modeling between habitat patches in lower left and upper right corners of the map. The value assigned to each cell indicates the cost accumulated moving along the most efficient possible route that passes through the cell from one habitat patch to the other; brighter areas indicate cells along the route of lowest cumulative cost. Some habitat cul-de-sacs are highlighted because the most efficient path connecting one patch to the other via the cul-de-sac has a low cost relative to most other features in the landscape. For the same reason, some "corridors to nowhere" are highlighted, such as the one leading off of the top of the map. (C) Current map between the same two habitat patches. Higher current densities indicate cells with higher net passage probabilities for random walkers moving from one patch to the other. The map highlights "pinch points," or critical habitat connections, between the two patches. Habitat cul-de-sacs have minimal current flow because they do not contribute new, independent pathways between habitat patches.

to landscape structure at different scales (Wiens 1985, Wiens and Milne 1989; Beier et al., *in press*), there will be no single correct approach to this. The extent of an analysis will obviously have important consequences, since map edges will constrain potential movement routes. Cell size is also important, but our analyses indicate that as long as it remains fine enough to capture relevant landscape elements, such as narrow corridors and barriers, there is considerable robustness in the technique to changes in cell size. Fig. 9B shows the same

landscape as in Fig. 9A, but analyzed using cell sizes that are an order of magnitude larger. Notably, current densities and resistance distances calculated among habitat patches are highly correlated between the two scales, a consistent result in our analyses in a wide range of natural and artificial landscapes. However, these analyses also show that it is particularly important to capture absolute barriers to movement that may not easily be detected at coarser cell sizes. Such barriers (such as the narrow roads in Fig. 9A) were automatically

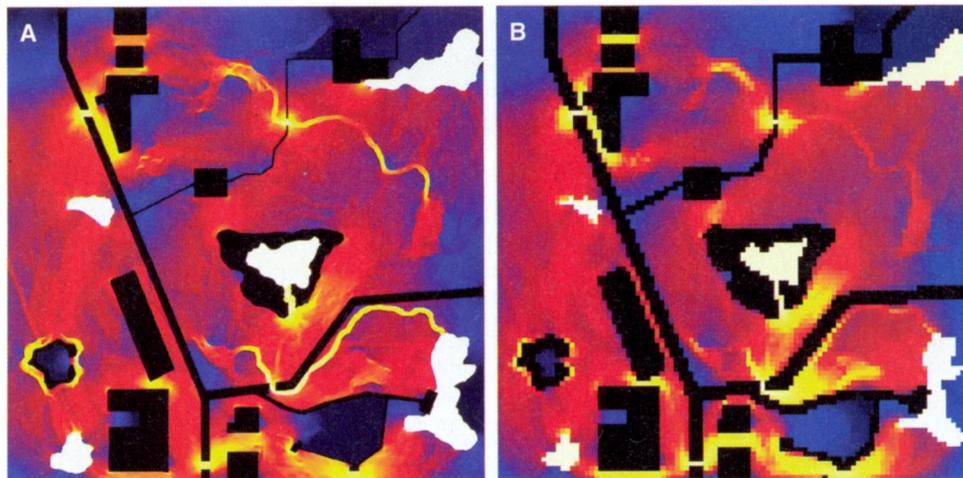


FIG. 9. Summed current from all pairwise current maps between five habitat patches, each shown in white. Calculations were performed (A) at the original 1000×1000 cell resolution and (B) at a reduced 100×100 cell resolution. To produce the coarser resolution habitat map, blocks of 10×10 cells were converted to single cells, with the resistance of each new cell set equal to the mean resistance of the 100 cells it contained. The current maps at the two resolutions identify the same pinch points and important corridors, and pairwise effective resistances measured between all habitat patch pairs at the two scales are highly correlated ($R^2 = 0.963$), illustrating the method's robustness to scale.



PLATE 1. Puma mother and kitten in Caspers Wilderness Park, Orange County, California. Circuit theory is being applied to inform efforts to conserve connectivity for pumas in the region. Photo credit: Donna Krucki.

incorporated into our analyses in Fig. 9B because we averaged resistances among consolidated cells, with infinite resistances “trumping” all others.

DISCUSSION

Although a wide variety of methods exists for predicting connectivity across landscapes, circuit-theoretic models provide some distinct advantages. First, the precise relationships between circuit theory and random walks lend theoretical justification to these models and mean that the metrics they generate can genuinely be considered to be process based. Second, these relationships also mean that circuit models will often be more straightforward to parameterize than other connectivity models because conductances and resistances assigned to edges or raster cells have clear interpretations in terms of movement probabilities. Third, unlike commonly applied least-cost path approaches, circuit methods incorporate multiple pathways, not only in generating metrics of connectivity and isolation, but also in identifying corridors and other important landscape elements connecting habitat patches or protected areas. An advantage of this property is that when dispersal pathways are lost, the predicted importance of remaining pathways increases. Finally, circuit models have an intuitive appeal in that the idea of using resistance and current to model connectivity across landscapes is readily understood by both practitioners and nonscientists. In effect, we find that the method objectively identifies important connective elements similar to those

identified by the human eye, replicating expert opinion but removing potential sources of bias once relative resistance values and scales of analysis have been defined.

Niches for circuit models

We envision several roles for circuit theory in evolution, ecology, and conservation. Circuit theory has already been shown to be useful for predicting patterns of gene flow in heterogeneous landscapes, particularly when data on absolute population sizes and migration rates are lacking, but relative population densities or permeabilities to movement are hypothesized for different landscape features (McRae 2006, McRae and Beier 2007). As discussed in the section below, the theory underlying gene flow modeling is similar to that described here, but relates resistance distances to random walks of genes over multiple generations rather than to random walks of individuals within single lifetimes.

In ecology, circuit models can be used as simple movement models, e.g., when data or time required for simulations are lacking or when the comparison of simple and complex model predictions is desirable. An example application would be to predict dispersal rates between populations based on simple landscape data in order to parameterize metapopulation models. Additionally, just as it can be used to predict gene flow, circuit theory may be useful in modeling other emergent

processes that depend on dispersal. Some ecological phenomena, e.g., community similarity and diversity, may respond to dispersal not of one species, but of several species with only somewhat similar dispersal abilities or habitat requirements. Here, simulations may be prohibitive or inappropriate because of the large number of species involved. However, analytic approaches like ours may be able to adequately capture these processes without imposing prohibitive data or computational requirements.

Measurements of resistance distances, commute times, and current densities have clear applications in conservation planning, such as corridor design or predicting the effects of different land use practices on connectivity. Circuit theory should provide an especially powerful tool for designing robust reserve networks, i.e., those that still provide for connectivity in the face of uncertainty in species distribution data and/or future habitat loss (Moilanen et al. 2006a, O'Hanley et al. 2007; Pinto and Keitt, *in press*). Importantly, circuit methods can be applied to the same resistance surfaces that are commonly employed in least-cost path analyses, and with little added computational expense.

In this paper, we limited our examples of circuit-based analyses to accessible interpretations of resistance, voltage, and current. However, there should be a large number of tools that could be derived from these basic properties. For example, metrics that combine predictions of efficient travel paths, pinch points, and mortality risks could allow practitioners to map landscape features that most effectively contribute to connectivity while minimizing mortality rates. Or, metrics derived from shortest path or least-cost distances, such as the Harary index (Ricotta et al. 2000, Jordán et al. 2003) or the integral index of connectivity (Pascual-Hortal and Saura 2006) could be modified by substituting resistance distances for least-cost distances in their calculation. Additionally, algorithms like edge and node thinning, used to evaluate impacts to connectivity of habitat loss in graph theory (Urban and Keitt 2001), can also be applied using circuit-based measures.

A note about ecological vs. evolutionary applications

It is important to be aware of subtle differences in assumptions behind applications of circuit theory to different processes. So far we have identified two distinct frameworks, one which models gene flow across population networks and the other focused on individual movement across habitat networks. The former assumes nodes (or cells) represent subpopulations (or occupied habitat for continuously distributed populations), with resistors representing numbers of migrants exchanged between adjacent nodes per generation (McRae 2006). By contrast, applications focused on individual movement will typically be implemented at finer temporal and spatial scales, with nodes (cells) mapped at the scale at which individual movement

decisions are made. Thus, the two will often be applied at different scales and with (at least somewhat) different habitat models. Similarly, predictions from the two frameworks must also be interpreted differently. For example, in applications where nodes or cells represent occupied habitat exchanging migrants, a decrease in the resistance distance between two nodes corresponds to a proportional increase in gene flow predicted between them; however, when nodes represent dispersal habitat rather than subpopulations, a decrease in the resistance distance corresponds only to an increase in available dispersal pathways, and not necessarily a commensurate increase in individual movement rates or gene flow. It does, however, indicate that there will be more pathways available to dispersers, and presumably greater robustness of the network to future habitat loss. Conservation applications may be implemented using either framework, but it is important to specify the process being modeled.

Model parameterization

A critical and challenging step in applying circuit models to landscape data will be assigning relative movement, mortality, and/or settlement probabilities to different land cover classes. Many of the same strategies for parameterizing least-cost path models using expert opinion, literature review or data on species occurrences, animal movement paths, or interpatch movement rates (reviewed by Beier et al., *in press*) will be useful in circuit modeling, particularly when viewed in light of the concrete interpretations of resistances in terms of random walk probabilities outlined here. Practitioners should also consider approaches taken to parameterize other models that consider habitat heterogeneity, such as diffusion and simulation models (e.g., Dunning et al. 1995, Schumaker 1996, Ovaskainen 2004; Arellano et al., *in press*; Ovaskainen et al., *in press*).

Connections between resistance distances and gene flow (McRae 2006, McRae and Beier 2007) should facilitate the use of genetic data to estimate relative resistances of different habitats. Still, because assumptions differ between evolutionary and ecological applications of circuit theory (as discussed here), using data from one to parameterize the other must be done with care.

Regardless of the method used to assign them, there will always be uncertainty in resistance values. We encourage uncertainty analyses to address how decisions at each modeling step affect results; Beier et al. (*in press*) reviewed strategies for conducting uncertainty analysis in least-cost path modeling, and these should be equally applicable to circuit theory. Additionally, for corridor and reserve designs, uncertainty in landscape resistances could be incorporated in much the same way as proposed by Moilanen et al. (2006b), with penalties that reflect modeled error incorporated into landscape resistance input maps.

Limitations and alternatives

As with other methods for describing connectivity in complex landscapes, there are limitations to our approach that should be considered when deciding if it is appropriate for a given problem. First, because resistors are isotropic, i.e., their resistance to current flow is the same in both directions, the methods described here cannot accommodate movement that is biased in one direction (as in directed graphs). This will limit applications in some systems, e.g., marine environments, where directional currents play a large role in determining dispersal rates. Second, circuit models are restricted to Markovian random walks, i.e., random walks in which each step is independent of previous moves. Random walkers thus have no “memory,” and our framework cannot incorporate correlated random walks, changes in movement behavior with time, or mortality rates that increase with an organism’s age. Even when the assumption of constant mortality with time is reasonable, incorporating mortality into circuit models must be done with care. Because they have no memory or long distance perception, random walkers can retrace their steps over and over, inflating mortality rates because travel time and exposure to mortality risks are increased (Fig. 2B).

Several other connectivity modeling frameworks provide complements to ours. The conceptually and computationally simplest are based on Euclidean distances, and can be quickly calculated on grids with millions of cells (e.g., Moilanen et al. 2005, Moilanen and Wintle 2007). Least-cost path models have been applied for over a decade in connectivity analyses and have proven useful in conservation planning efforts (e.g., Beier et al. 2006, Rouget et al. 2006). Although they do not have the theoretical foundation in random walk theory that circuit models do, their intuitive appeal and ability to identify efficient movement pathways make them useful counterparts to the applications we have described here. Recently, variants on these approaches have been developed that identify and rank the importance of multiple pathways across landscapes (Theobald 2006; Pinto and Keitt, *in press*).

More sophisticated analytical and simulation models can be used to derive results similar to those produced by circuit theory, with some advantages. Markov chain models use the same data structures as those described here, but can accommodate directionality in movement along edges, providing more flexibility for modeling, e.g., effects of directed dispersal, prevailing winds, or ocean currents. Still, although Markov chain models have been available for decades, ecologists and conservationists have been slow to adopt them, whereas simpler, more intuitive least-cost path models have been widely employed. Spatially structured diffusion models (Ovaskainen 2004) are promising because they also integrate over all movement paths and can approximate correlated random walks in their long-term behavior, but their mathematical formulation can be quite

challenging. Of course, individual-based movement simulations (e.g., Schumaker 1998, Hargrove et al. 2005) offer much more flexibility than analytic models, can incorporate subtle effects of dispersal behavior and other aspects of life history, and can simulate transient effects of landscape characteristics that evolve over time. However, the data and computational requirements of such models will likely continue to limit their use in many applications (Minor and Urban 2007). Our hope is that circuit models will fill a niche between simpler Euclidean or least-cost path analyses and more powerful analytic and simulation approaches.

Future prospects

Our focus has been on measuring connectivity in heterogeneous landscapes using models from circuit theory. Even in this context, there remain many exciting applications to explore. Nonequilibrium circuit analyses may be applicable to ecological problems (McRae and Beier 2007), and nonlinear circuit elements show promise as well (for example, diodes would allow incorporation of movement probabilities with directional bias). Additionally, analytical techniques developed to minimize effective resistances across networks (Ghosh et al. 2006) may be useful in designing optimal networks for connectivity conservation. More broadly, circuit theory will likely benefit other areas of ecology that deal with networks, such as the analysis of community interactions, food web structure, exotic invasion, or disease transmission. In the meantime, circuit models are being actively applied to conservation planning for species of concern in rapidly developing landscapes, including pumas (*Puma concolor*; see Plate 1) in southern California.

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