Landscape Ecol (2009) 24:253–266
DOI 10.1007/s10980-008-9303-y

RESEARCH ARTICLE

Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach

Naiara Pinto · Timothy H. Keitt

Received: 24 October 2007 / Accepted: 31 October 2008 / Published online: 29 November 2008

Abstract The impact of the landscape matrix on patterns of animal movement and population dynamics has been widely recognized by ecologists. However, few tools are available to model the matrix's influence on the length, relative quality, and redundancy of dispersal routes connecting habitat patches. Many GIS software packages can use land use/land cover maps to identify the route of least resistance between two points—the least-cost path. The limitation of this type of analysis is that only a single path is identified, even though alternative paths with comparable costs might exist. In this paper, we implemented two graph theory methods that extend the least-cost path approach: the Conditional Minimum Transit Cost (CMTC) tool and the Multiple Shortest Paths (MSPs) tool. Both methods enable the visualization of multiple dispersal routes that, together, are assumed to form a corridor. We show that corridors containing alternative dispersal routes emerge when favorable habitat is randomly distributed in space. As clusters of favorable habitat start forming, corridors become less redundant and dispersal bottlenecks become visible. Our approach is illustrated using data from a real landscape in the Brazilian Atlantic forest. We explored the effect of small, localized disturbance on dispersal routes linking conservation units. Simulated habitat destruction caused the appearance of alternative dispersal routes, or caused existing corridors to become narrower. These changes were observed even in the absence of significant differences in the length or cost of least-cost paths. Last, we discuss applications to animal movement studies and conservation initiatives.

Keywords Agroecosystems · Atlantic forest · Brazil · Functional connectivity · Corridors · Cost distance · Dispersal · Fragmentation · Graph theory · Matrix · Migration · Shortest path

Introduction

Animal movement can occur at a range of temporal scales, influencing foraging, migration, and gene flow (Crooks and Sanjayan 2006). The dispersal routes associated with these processes can be strongly constrained by the landscape matrix. Thus models specifying the effect of matrix heterogeneity on movement rates can more successfully predict patch occupancy (Ricketts 2001; Verbeylen et al. 2003), metapopulation dynamics (Vandermeer and Carvajal

N. Pinto (✉) · T. H. Keitt
Section of Integrative Biology, University of Texas,
Austin, TX 78712, USA
e-mail: Naiara.Pinto@jpl.nasa.gov

Present Address:
N. Pinto
Jet Propulsion Laboratory, 4800 Oak Grove Dr.,
Pasadena, CA 91109, USA

2001), genetic structure (Stevens et al. 2006), and persistence in fragmented landscapes (Laurance et al. 2002). The role of behavior and natural history in shaping species' responses to the matrix has recently motivated the concept of functional connectivity (Calabrese and Fagan 2004). While many connectivity studies have described the influence of different land cover types in channeling or repelling movement of particular species (e.g., Burel 1996; Lees and Peres 2008), few tools are available to integrate data on matrix heterogeneity and species' habitat preferences to model dispersal routes.

A challenge in modeling animal dispersal routes is that individuals rarely use a single optimum route (e.g., Driezen et al. 2007), and connectivity measures focusing on optimum routes fail to incorporate variation in individual behavior (Belisle 2005). In this paper, we model the location of multiple dispersal routes across a heterogeneous matrix. We employ a movement model that assumes successfully dispersing organisms are more likely to use the route of least resistance when moving between two points, or the least-cost path. Despite its simplifying assumptions, the least-cost path has been successfully used to predict patch occupancy (Chardon et al. 2003; Verbeylen et al. 2003) and inter-patch movement rates (Sutcliffe et al. 2003). The least-cost path is identified using a graph theory algorithm, Dijkstra's breadth-first search (Cormen et al. 2001). Many GIS software packages have functions to locate the least-cost path between two points. Although only one path is obtained, Dijkstra's algorithm can be easily modified to output multiple paths with similar costs. We describe this modification and its two outputs, the Conditional Minimum Transit Cost (CMTC) and the Multiple Shortest Paths (MSPs).

We propose that corridors are heterogeneous structures that may contain multiple dispersal routes. However, we do not advocate a method for designing corridors (including few or many dispersal routes), neither do we attempt to quantify corridors' role in conserving biodiversity. Rather, our goal is to integrate information on species' habitat preferences into regional-scale depictions of habitat connectivity. This paper has three parts. First, we applied our method to artificial landscapes in order to illustrate the effect of matrix heterogeneity on the cost and spatial distribution of dispersal routes. Second, we studied the effect of small, localized disturbance on large-scale dispersal routes. This was performed using data from the highly fragmented Brazilian Atlantic forest (Morellato and Haddad 2000). Last, we discussed how the approach proposed here can be refined and incorporated in animal movement studies and conservation initiatives.

Methods

The landscape graph

In this section, we describe the approach routinely employed to perform any type of distance calculations on grids. Most GIS software packages use graphs (Urban and Keitt 2001) to represent grid maps. Graphs are composed of vertices (V) placed on cell centers, and edges (E) that connect each vertex to its eight nearest neighbors (Fig. 1). Using this representation, we define two cost grids:

(a) Relative cost grid (Figs. 2a, 3a), also referred to as a friction layer (Verbeylen et al. 2003). Each vertex contains the relative cost to cross it in any direction.

(b) Cumulative cost grid (Figs. 2b, 3b). Consider a source (S) composed of one or more vertices. Each vertex in the cumulative cost grid contains the minimum cumulative cost to reach S. This is calculated in two steps: first, the cost to move between pairs of vertices is stored as edge weights. The weight *W* for an edge connecting vertices V1 and V2 is calculated as:

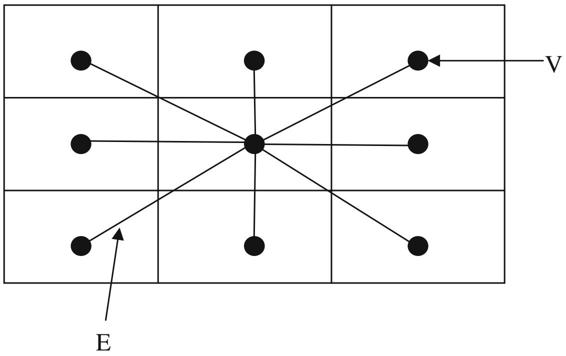


Fig. 1 The landscape graph. In most software packages, grid maps are internally represented as a graph. Vertices (V) are located in cell centers. Each vertex is connected to its eight nearest neighbors by an edge (E). Edge weights (not shown) hold information on the cost to move between pairs of vertices

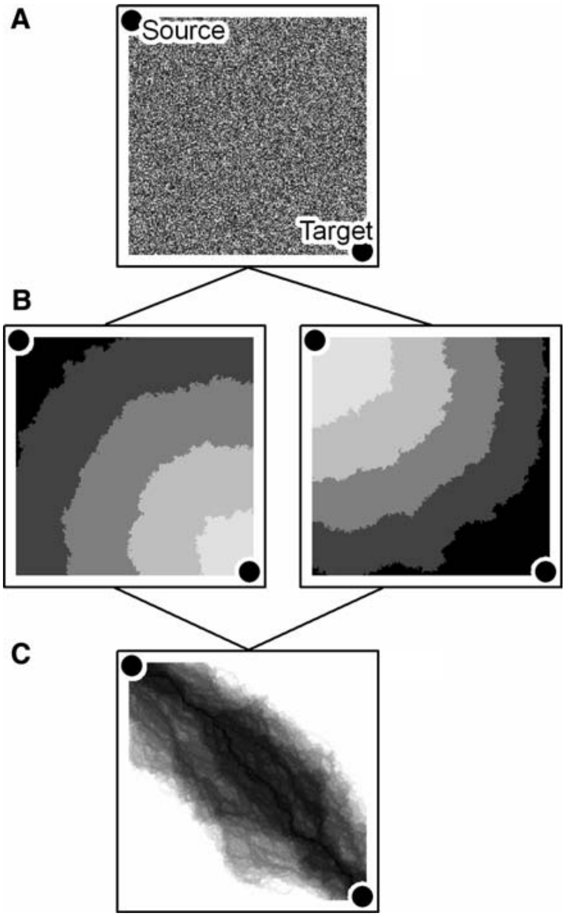


Fig. 2 Illustration of the procedure for calculating the CMTC. **a** Relative cost grid. **b** The cumulative cost grid for the target (*left*) and the source (*right*). Lighter shades indicate lower cumulative cost. **c** The two grids from (**b**) are added to produce the CMTC grid

$$W = [\text{Relative Cost (V1)} + \text{Relative Cost (V2)}]/2 \tag{1}$$

For diagonal edges, edge weights W' are calculated as:

$$W\prime = W \times \sqrt{2} \tag{2}$$

Second, Dijkstra's breadth-first search algorithm (Cormen et al. 2001) is used to calculate the least-cost path between S and each vertex in the graph. The minimum cumulative cost between S and a given vertex (V) is the sum of all edge weights in the least-cost path connecting S and V. To calculate the least-cost path between two habitat patches P1 and P2 we define all vertices in P1 as sources and all vertices in P2 as targets. The least-cost path between patches P1 and P2 will most likely link the two patches' most external vertices.

In the next two sections, we build on the above representation and describe two methods that extend Dijkstra's breadth-first search algorithm.

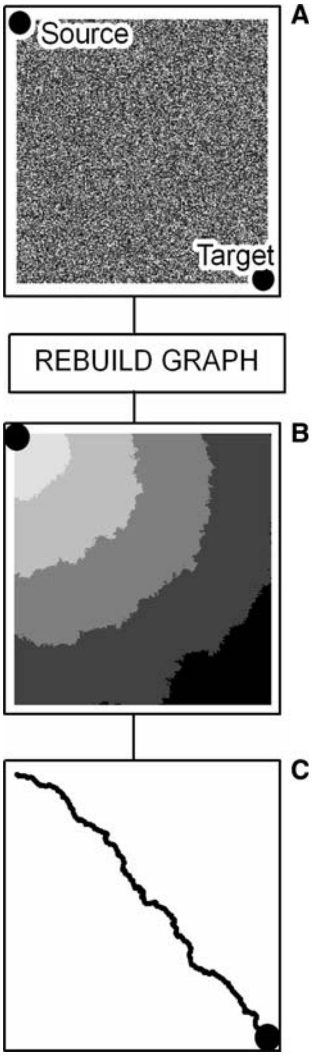


Fig. 3 Illustration of the procedure for locating MSPs. **a** Relative cost grid, **b** cumulative cost grid for the source. *Lighter shades* indicate lower cumulative cost. This was calculated after rebuilding the graph that represents the landscape, **c** with the cumulative cost grid, we trace the least-cost path between source and target, **b** and **c** are repeated 100 times to produce 100 least-cost paths

Conditional minimum transit cost (CMTC)

Consider a vertex (V) located between groups of source vertices (S) and target vertices (T). The Conditional Minimum Transit Cost (CMTC) for V is the cost-weighted distance to move from S to T, conditional on the route forming the shortest passage between S and T while passing through V. It is calculated as (Fig. 2):

$$\mathrm{CMTC}(\mathrm{V},\mathrm{S},\mathrm{T}) = \mathrm{Cumulative\,cost}(\mathrm{V},\mathrm{S}) + \mathrm{Cumulative\,cost}(\mathrm{V},\mathrm{T}) \qquad (3)$$

The final CMTC grid was obtained by masking out all cells with CMTC values larger than the minimum CMTC value plus 10% (Fig. 2c). The remaining values were then divided by the grid's maximum CMTC. According to Forman (1995), a corridor is "a narrow strip of land that differs from the matrix on either side". We assume that areas within the 10% threshold form corridors, but emphasize that our choice of corridor width was arbitrary.

Our analysis generates corridors that are highly heterogeneous. Visually inspecting the CMTC grid (Fig. 2c) enables identification of contiguous cells with low CMTC value. We refer to these cell groups as "dispersal routes", while recognizing that distinction between routes that are close together is arbitrary. The least-cost path is invariably located within one dispersal route.

In practice, obtaining a CMTC grid is straightforward with modules such as spatial analyst within ArcGIS (Esri, California). Some conservation biologists strongly advocate the CMTC approach for designing wildlife corridors (Majka et al. 2007). But to our knowledge, the relationship between matrix heterogeneity and the distribution of dispersal routes as predicted by the CMTC has not yet been explored.

Multiple shortest paths (MSPs)

We developed a stochastic version of Dijkstra's algorithm (Fig. 3) that outputs multiple realizations of the least-cost path, or Multiple Shortest Paths (MSPs). As described above, the least-cost path is obtained from a relative cost grid. Dijkstra's breadth-first search algorithm (Cormen et al. 2001) proceeds by iteratively marking vertices in the order of their cumulative distance from the source. At each step, the algorithm must identify the set of neighbors associated with the marked vertices. Standard algorithms use a static definition of the neighborhood, typically the nearest eight cells on a rectangular grid (Fig. 1). Our approach is to redefine the neighborhood as a stochastic function such that adjacency is non-deterministic and is instead determined randomly in proportion to edge weights. The algorithm proceeds as follows (Fig. 3):

1. Draw a number (U) between 0 and 1 from a random uniform distribution.
2. Delete edges in the graph. An edge with weight W connecting two adjacent vertices V1 and V2 is deleted if $W > U$. That is, connections with lower costs are more likely to be maintained.

A program implementing Dijktra's algorithm (with the above modification) was run 100 times in order to produce 100 MSPs for each study case (Fig. 3c shows one path). The cumulative cost associated with each path is a measure of effective distance and is calculated by adding the weights of all edges in the path. The programs used to obtain both CMTCs and MSPs were written in the Java programing language.

Applications to artificial landscapes

We generated artificial landscapes with different degrees of spatial autocorrelation using the method of wavelet synthesis (Keitt 2000). We started with a grid containing values between 0 and 1, drawn from a random uniform distribution. Using this grid, each landscape was created in four steps: (a) apply the discrete Haar wavelet transform; (b) obtain wavelet coefficients; (c) multiply coefficients by 2 ^ ($L \times \beta$), where L is the coefficient level (higher levels representing low-frequency variation); (d) apply the inverse Haar wavelet transform on the modified coefficients; (e) map results to a random uniform distribution (min = 0; max = 1). The last step is taken to ensure that the distribution of quality values is consistent across all landscapes. The values of the parameter β were 0, 0.25, 0.50, 0.75, and 1. A β value of zero generates a white noise landscape with no spatial autocorrelation. Increasing β produces autocorrelated landscapes, where clusters of favorable habitat can be identified. Each artificial landscape represents one relative cost grid that served as input in calculations of CMTC and MSPs (Fig. 4a). We used ANOVA to test for differences among landscapes, in terms of

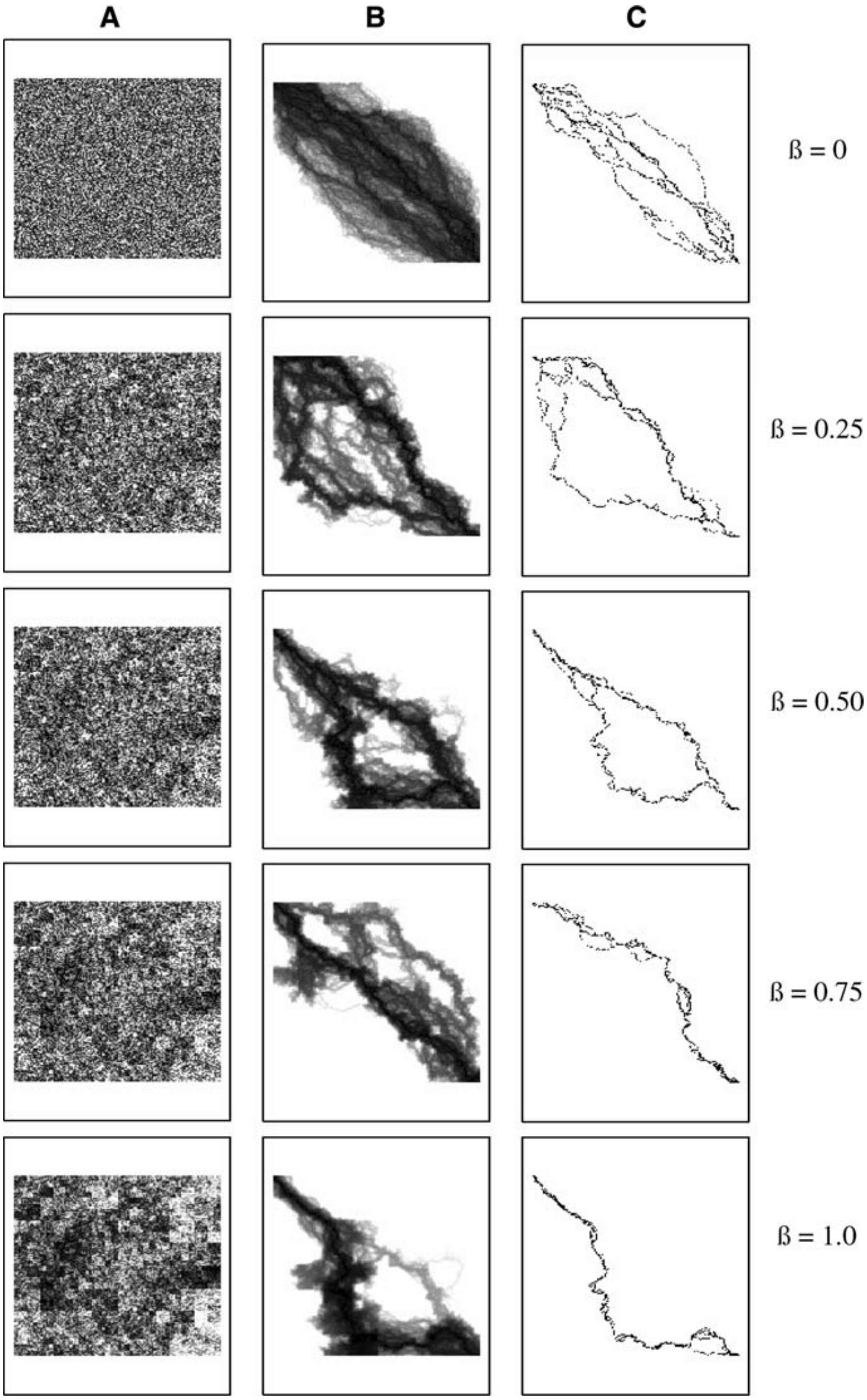


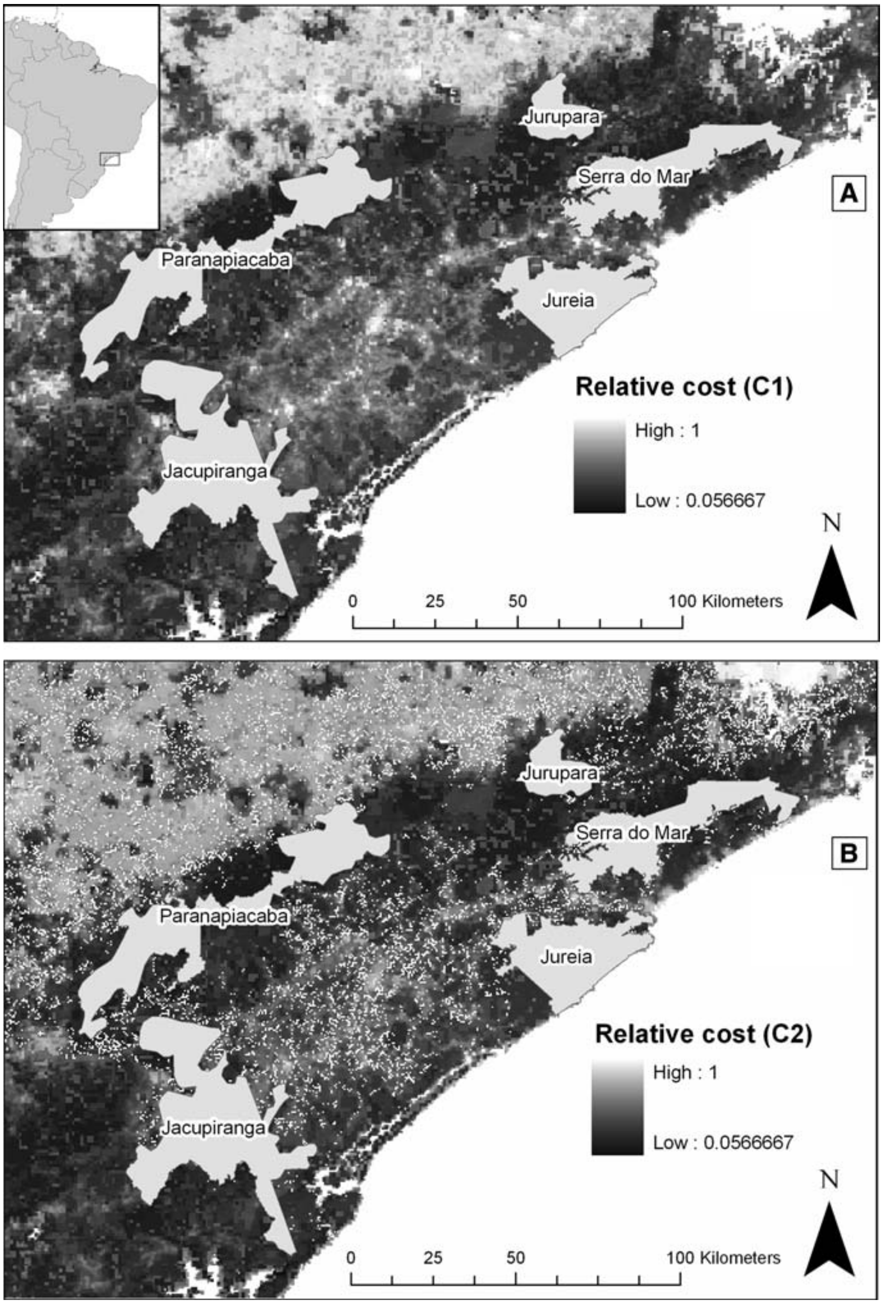
Fig. 4 Relative cost grids generated with the use of wavelet transforms (**a**), and the values of CMTC (**b**) and location of MSPs (**c**) for each landscape. A β value of 0 is a landscape with no spatial autocorrelation in habitat quality values, and landscapes become "patchier" as β values increase

cumulative costs associated with MSPs and mean CMTC. The generation of artificial landscapes and ANOVA tests were performed using the R programing language (R Core Development Team 2008).

Applications to real landscapes

We studied a real landscape (Fig. 5) that covers 111 km^2 of the Brazilian state of São Paulo (upper

Fig. 5 Study site in the Brazilian Atlantic forest, showing conservation units in Sao Paulo State. **a** Relative cost values for scenario C1. **b** Relative cost values for scenario C2 (after deletion of small forest fragments)



left coordinates: 23.60S, 49.00W; lower right coordinates: 25.40S, 46.20W). Remaining forests are part of the Atlantic forest biome (for a description, see Oliveira-Filho and Fontes 2000). Despite its location in highly industrialized São Paulo state, the study area still contains large forest tracts and rural properties. A recent vegetation map (Eva et al. 2002) estimates that 11.1% of the study area is devoted to intensive agriculture, 7% contains a mix of agriculture and degraded vegetation, 23% is a mix of agriculture and degraded forest, and 46% is covered with forest. Excluding São Paulo's metropolitan area, human populations per municipality range in size from 3,403 to 412,243 (mean = 60,410; IBGE 1991). Five conservation units are considered here: Pedro de Toledo Nucleus within Serra do Mar State Park (868 km^2), Juréia-Itatins Ecological Reserve (801 km^2), Jurupara State Park (259 km^2), Jacupiranga State Park (1,552 km^2), and the contiguous units Intervales State Park, Carlos Botelho State Park, Ecological Station Xitué, and Alto do Ribeira Touristic State Park (1,282 km^2), referred together here as "Paranapiacaba" due to their location along the Paranapiacaba Valley.

Our analyses consisted of modeling dispersal routes between all pairs of conservation units. We have built a relative cost map in an attempt to capture the habitat preferences of species that move in forested areas and suffer higher mortality when crossing disturbed habitat. In the discussion, we describe how more detailed models can be built and refined to reflect the habitat preferences of a particular species. Three land use/land cover maps were the main input for our analyses (Table 1).

1. The Modis continous fields, (Hansen et al. 2003) contains estimates of percent tree cover. Values were manipulated (Table 1) in order to obtain a grid with values ranging between 0 (=100% tree cover) and 1 (=no tree cover).
2. The human footprint map (Sanderson et al. 2002) is a global dataset with estimates of anthropogenic impact ranging from 0 (pristine land) to 100 (most disturbed land), normalized per ecosystem. These estimates were based on patterns of human population density, land use, and transportation networks. We divided original values by 100 (Table 1) to obtain a grid with values ranging from 0 (=pristine land) to 1 (=most disturbed land).
3. The South American vegetation map (SAVM; Eva et al. 2002) contains information on forest distribution, degree of forest disturbance, and mixture with agricultural lands. We assigned each class in the SAVM grid (Table 1) a relative cost value ranging from 0 (=closed or dense forest) to 1 (intensive land use or non-forested ecosystems).

The Footprint and SAVM grids were rescaled so as to bring their spatial resolution to 500 m. The first relative cost map (C1; Fig. 5a) was obtained by averaging the values in the three grids described above (Table 1). As a result, we obtained a grid where cell values ranged from 0.057 (minimum relative cost to cross) to 1 (maximum relative cost to cross).

The second cost map (C2; Fig. 5b) simulated the removal of small forest fragments from C1, which could result from clear cutting, selective logging, or road construction. Results do not necessarily reflect actual land cover changes taking place in the Atlantic forest, but they enable us to explore the effect of small, localized disturbance on regional connectivity patterns. The C2 map was built in three steps. First, we produced a binary map with areas classified as "forest" or "non-forest" based on the SAVM map. This binary map was eroded and dilated (Serra 1982) by 0.5 pixel, resulting on the deletion of fragments with area <5 ha and linear elements (such as riparian corridors) <500 m wide. Last, C2 was obtained by assigning the maximum relative cost (1) to the deleted cells. All other cells contained the same values as C1, and the range of relative cost values for the entire grid remained unchanged (0.057–1). It was assumed that individuals could not move through water, thus a cost value of positive infinity was assigned to cells representing water bodies in both C1 and C2 scenarios. Finally, we calculated the CMTC and MSPs for both C1 and C2 scenarios. All GIS layers were processed using programs written in Java

Table 1 Grids used to construct the relative cost maps used in the present study, their original spatial resolution (pixel size), period of data collection, and operations performed on original grid values

Layer	Resolution (m)	Years	Operations performed on the original raster values
South America vegetation map	1,000	1995–2000	0 = closed, dense, transitional forest 0.25 = open forest 0.5 = mosaic agriculture/degraded forest 0.75 = shrubland, savannah, grassland 1 = intensive agriculture, mosaic agriculture/degraded vegetation, desert, urban
Human footprint	1,000	1960–2001	Final value = (original value)/100
Modis continuous fields, % tree	500	2000–2001	Final value = (100 − original value)/100

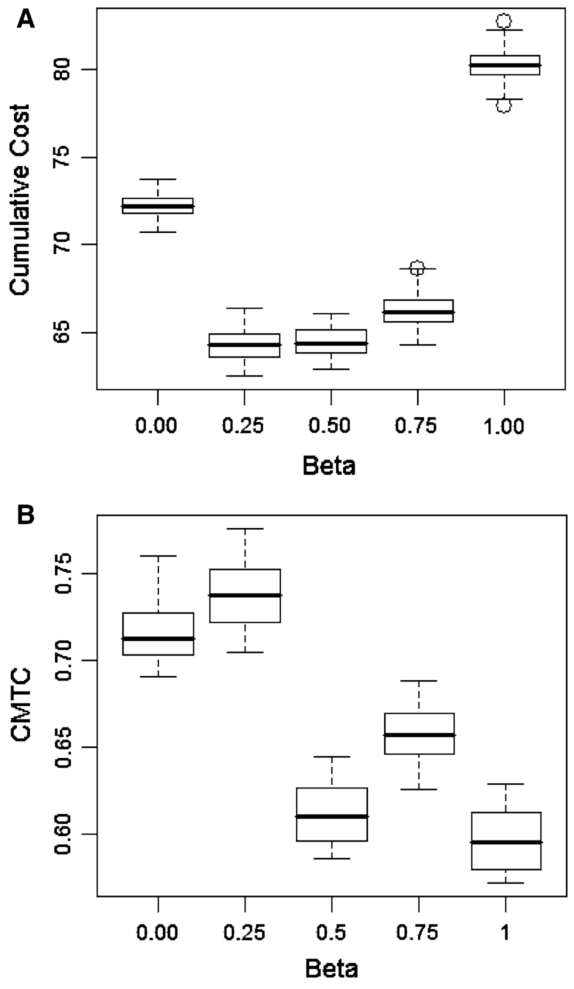


Fig. 6 The distribution of values of **a** Multiple Shortest Paths **b** and Conditional Minimum Transit Costs. A β value of 0 is a landscape with no spatial autocorrelation in habitat quality values, and landscapes become "patchier" as β values increase

programing language, and illustrations were produced in ArcMap (Esri, California).

Results

Artificial landscapes

The two graph theory approaches proposed here outlined the influence of matrix heterogeneity on dispersal routes. We detected a significant difference in mean cumulative costs associated with Multiple Shortest Paths (MSPs) among the five artificial landscapes (ANOVA, $F = 6{,}934.5$; $P < 0.001$). MSPs with lowest costs were observed when landscapes had intermediate patchiness (Fig. 6a; Tukey multiple comparisons of means, 95% family-wise confidence level, $P < 0.001$). We also observed significant differences in mean Conditional Minimum Transit Cost (CMTC) values (ANOVA, $F = 474{,}104$; $P < 0.001$). The most autocorrelated landscapes produced the lowest CMTC values (Fig. 6b; Tukey multiple comparisons of means, 95% family-wise confidence level; $P < 0.001$). In addition, we observed differences in the spatial distribution of dispersal routes. Landscapes with little autocorrelation in relative habitat quality produced redundant corridors with more alternative dispersal routes (Fig. 4; β closer to 0). As clusters of favorable habitat started to form, corridors became restricted to fewer routes (Fig. 4; β closer to 1). This was evidenced in the outputs of both the CMTC and MSPs calculations.

Real landscapes

We tested the influence of small, localized disturbance on corridors connecting five conservation units in the Brazilian Atlantic forest (Fig. 5). There were no significant differences in mean cumulative path costs calculated from MSPs, or in mean CMTC values (*t*-test, $P > 0.05$) between scenarios C1 and C2. But in most cases, simulated fragment removal influenced the spatial distribution of dispersal routes. Since small fragments were not homogeneously distributed in the study area, corridors obtained under scenario C1 were differentially affected by simulated fragment removal in scenario C2 (Table 2).

Table 2 Conservation units included in the present study

	Jacupiranga	Jurupará	Serra do Mar	Paranapiacaba
Juréia	72.321	35.391	6.905	3.993
	5	3.6	10.4	5.5
Jacupiranga		115.502	104.800	7.868
		4.0	5.0	21.0
Jurupará			7.263	43.739
			2.0	1.2
Serra do Mar				51.183
				2.3

Each unit in a pair can serve as a source or a target for dispersing organisms. The first line contains the straight-line distance between units (in kilometers), and the second line shows the percentage of 500-m^2 cells deleted from the corridor as a result of simulating fragment removal

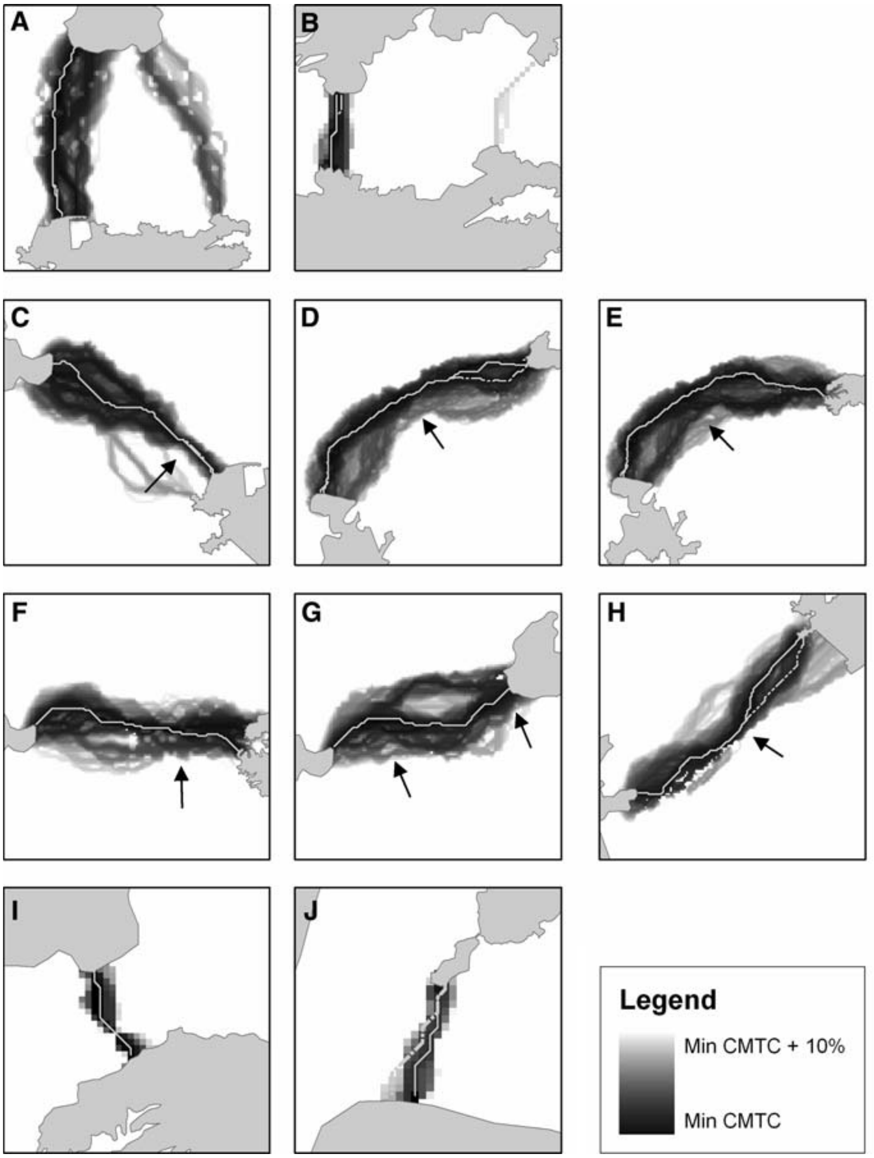


Fig. 7 CMTC grids for the corridor connecting conservation units in São Paulo, Brazil. The pairs are: **a** Jurupará–Juréia, **b** Juréia–Serra do Mar, **c** Juréia–Paranapiacaba, **d** Jacupiranga–Jurupará, **e** Jacupiranga–Serra do Mar, **f** Paranapiacaba–Serra do Mar, **g** Paranapiacaba–Jurupará, **h** Juréia–Jacupiranga, **i** Serra do Mar–Jurupará, **j** Paranapiacaba–Jacupiranga. *Gray lines* show the least-cost path. *Solid lines* represent least-cost paths obtained for scenarios C1 and C2, whereas *interrupted lines* represent sections of the least-cost path obtained for scenario C2 only. *Arrows* indicate potential dispersal bottlenecks

In most cases, the CMTC grid displayed more than one alternative route between conservation units, one of them being the least-cost path (Fig. 7a–h). When conservation units were close, the distance between them was small with respect to the variation in their shape. In this case, the CMTC grid produced narrow corridors, coinciding with the links representing the shortest Euclidian distance (Fig. 7b, i, j). When corridors contained alternative routes, these were rarely disjoint (Fig. 7a, b). The constriction zones where dispersal routes merged represented potential dispersal bottlenecks (Fig. 7c–h). In most cases, the location of the least-cost path did not change substantially as a result of small fragment removal (Fig. 7a–c; e–g; i, j). But in two cases, the least-cost path for scenario C2 was displaced to an alternative route located a few kilometers away from the least-cost path for scenario C1 (Fig. 7d, h).

We also identified the MSPs between pairs of conservation units. Compared to the CMTC calculation, this tool provided a better assessment of the impact of fragment removal on corridor redundancy. Examining the MSPs produced for the scenarios C1 and C2, we observed two trends. In some cases,

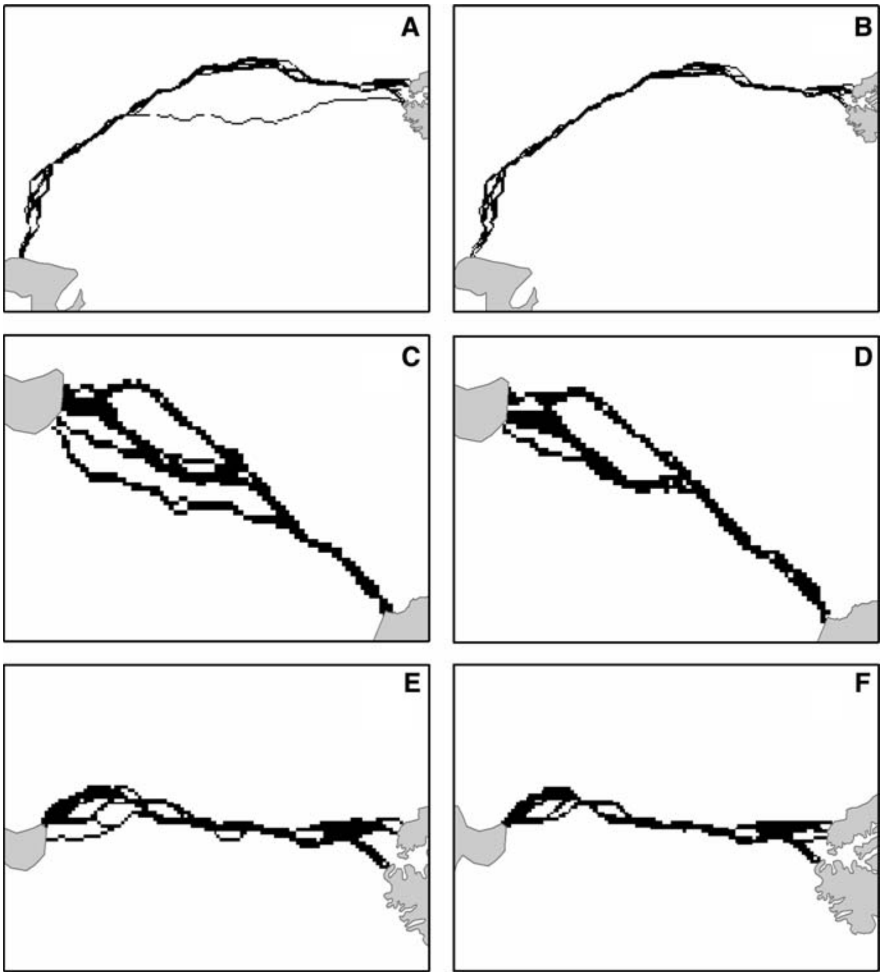


Fig. 8 Location of the first 100 least-cost paths connecting conservation units in São Paulo, Brazil. **a** Jacupiranga–Serra do Mar, scenario C1; **b** Jacupiranga–Serra do Mar, scenario C2; **c** Juréia–Paranapiacaba, scenario C1; **d** Juréia–Paranapiacaba, scenario C2; **e** Serra do Mar–Paranapiacaba, scenario C1; **f** Serra do Mar–Paranapiacaba, scenario C2

fragment removal led to the disappearance of external dispersal routes; corridors became narrower and less redundant (Fig. 8). In other cases, new, more external routes emerged after fragment removal (Fig. 9).

Discussion

Analyses of artificial landscapes show the influence of matrix heterogeneity on landscape connectivity. Redundant corridors with multiple alternative dispersal routes emerged in white noise landscapes, where favorable habitat is randomly distributed (Fig. 4, β closer to 0). As patches of favorable habitat started forming, corridors became narrower and less redundant (Fig. 4, β closer to 1). The cumulative cost of MSPs was on average lower in landscapes with intermediate degree of autocorrelation (Fig. 6a). This is because paths in white noise landscapes will often cross areas of high cost, whereas the presence of contiguous habitat patches in autocorrelated landscapes can lead to longer, more tortuous paths (Fig. 4c). The CMTC was on average lower in autocorrelated landscapes (Fig. 6b). This follows from our choice of CMTC value used to delimit corridors—under a 10% threshold, white noise landscapes produced wider corridors with higher CMTC values.

In addition to studying artificial landscapes, we illustrated our methods using data from a real landscape in the Brazilian Atlantic forest. In this region, a complex landscape matrix produced dispersal routes that were not apparent in land use/land cover maps (Fig. 7a–f, h–j), with the exception of the pair Paranapiacaba–Jurupará that is separated by an artificial dam (Fig. 7g). CMTC maps revealed highly heterogeneous corridors displaying bottlenecks to animal movement (indicated by arrows in Fig. 7c–h). Removing small fragments did not produce a significant increase in the mean cumulative cost of MSPs but led to changes in their spatial distribution (Figs. 8, 9). Our work illustrates two possible large-scale effects of small, localized disturbance on the landscape matrix. Narrower corridors were produced (Fig. 8), and the importance of external dispersal routes increased (Fig. 9). The latter case included the two pairs of conservation units with the largest amount of deleted habitat in the scenario C2 (Table 2; Fig. 9c–f).

Results of least-cost path analyses are strongly dependent on the selection of relative cost grids (Adriaensen et al. 2003; Rae et al. 2007). Our choice of relative cost grids (Table 1) was made as an attempt to approximate the habitat preferences of a forest specialist. Relative cost grids can be further refined and validated for a particular species using patch occupancy data (Verbeylen et al. 2003) or from ecological niche modeling and tools such as the Mahalonobis distance (Farber and Kadmon 2003). In addition to habitat preference estimates, an important issue is the time scale over which individuals are expected to disperse. Here, we were not concerned with the time interval or number of generations that individuals (or populations) took to move between source and target fragments (conservation units). More realistic models can be obtained by adjusting the maximum Euclidian distance allowed between source and target fragments so as to match the maximum distance that can be crossed by a species given a particular time interval (Keitt et al. 1997). The issue of time scale is related to the question of whether corridors should function as habitat or as

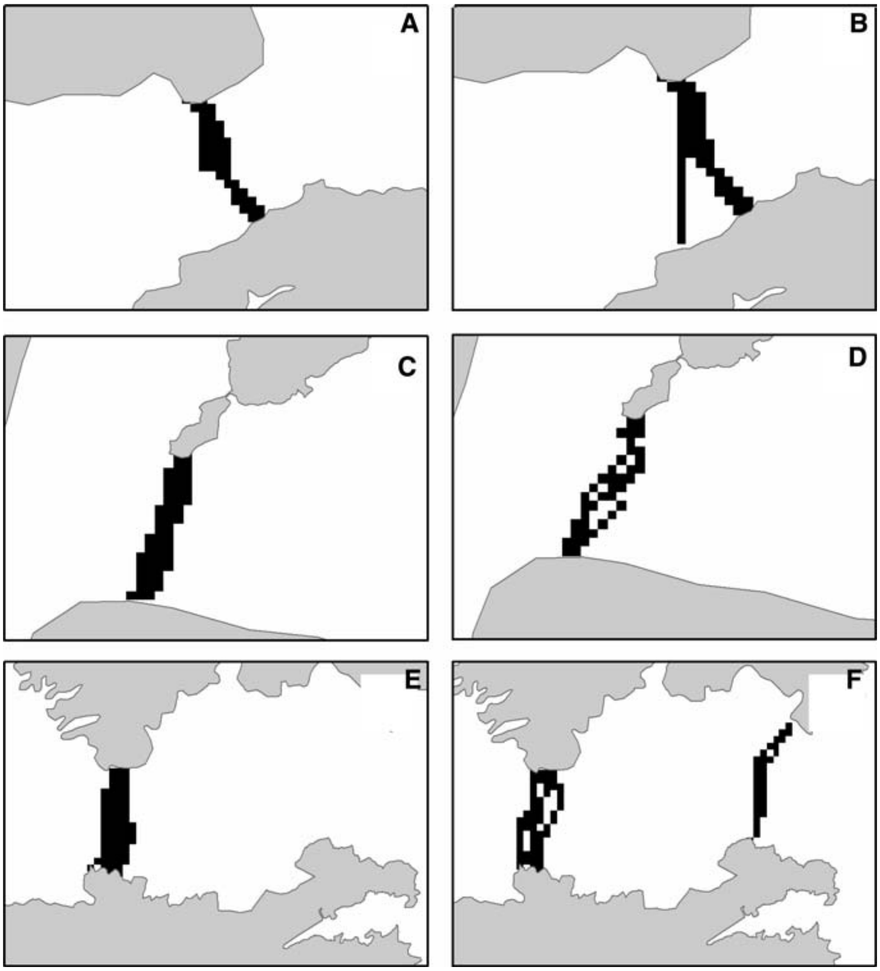


Fig. 9 Location of the first 100 least-cost paths connecting conservation units in São Paulo, Brazil. **a** Serra do Mar–Jurupara, scenario C1; **b** Serra do Mar–Jurupará, scenario C2; **c** Paranapiacaba–Jacupiranga, scenario C1; **d** Paranapiacaba–Jacupiranga, scenario C2; **e** Juréia–Serra do Mar, scenario C1; **f** Juréia–Serra do Mar, scenario C2

conduits (Hess and Fischer 2001)—i.e., individuals are expected to spend more time in habitat corridors. Corridor width can be adjusted by increasing the CMTC threshold to ensure that corridors contain minimum habitat requirements.

The ability to identify multiple dispersal routes can be desirable in conservation studies, for three main reasons. First, least-cost paths have been employed in the design of linked reserve systems (Hoctor et al. 2000; Schadt et al. 2002; Larkin et al. 2004). This approach, however, can lead to very narrow linkages (Alagador and Cerdeira 2007) that might not be located in land tracts available for purchase. Second, dispersal routes that appear similar may differ in terms of their conservation value. For example, field studies in Canada (Clevenger et al. 2001) show that drainage culverts can act as habitat linkages for several mammal species, but culverts near roads with higher traffic volume and noise levels are less commonly used. Third, the approach shown here enable the visualization of functionally unique landscape structures (Manning et al. 2006): narrow corridors or dispersal bottlenecks within corridors (e.g., Fig. 7).

Considerable attention has been given to quantifying the role played by agroecosystems in conservation (i.e., Bestelmeyer and Wiens 1996; Reitsma et al. 2001; Mas and Dietsch 2003). Agricultural lands can help support wild populations by providing critical habitat (Moguel and Toledo 1999) and influencing neighboring fragments, in which case potential outcomes depend on the spatial configuration and degree of mixture with pristine habitat (Perfecto and Vandermeer 2002; Perfecto et al. 2003; Tscharntke et al. 2005). Our study of the Brazilian Atlantic forest shows that private lands can collectively influence ecological processes occurring at large spatial scales and supports the assertion that small fragments can potentially shape regional patterns of gene flow (Bodin et al. 2005). This raises the necessity to view agricultural lands' contribution to biodiversity in a larger context.

Movement behavior is a key aspect in functional connectivity studies, but detailed data on animal movement remains hard to collect, especially for large spatial scales. In fact, the ability to produce accurate movement models has long been recognized as one of the main challenges of population biology studies (Turchin 1998). There is no consensus on the amount of biological detail that should be used in functional connectivity studies. It has been suggested that movement models ought to increase in complexity in order to capture the behavior of particular species (Goodwin 2003). At the same time, conservation biologists have raised the need for rigorous methods that predict the location of dispersal routes for many species (Boitani et al. 2007). Clearly a compromise is needed, which requires determining how much simplification can be made before losing predictive power (Baguette and Van Dyck 2007). Least-cost path predictions can be derived for many species, given the ever growing maps of habitat quality produced by ecological niche modeling. Also, rigorous protocols already exist to compare least-cost predictions with field data (Driezen et al. 2007).

Conclusions

In the present paper, we extended the graph theory algorithm that serves as the basis for least-cost path calculations. The two outputs are the Conditional Minimum Transit Cost (CMTC) and the Multiple Shortest Paths (MSPs). Our goal was to integrate information on habitat preferences to model dispersal patterns across a heterogeneous matrix. In addition to the path of least resistance between two points, the methods presented here outlined additional paths with similar length and relative cost. Results from artificial landscapes show that the location and relative cost of dispersal routes are strongly influenced by the spatial distribution of favorable habitat in the matrix. In addition, study of a real landscape shows that small, localized disturbance such as removal of small fragments can affect large-scale dispersal routes. Models producing multiple dispersal routes present a practical advantage over models assuming optimum behavior. Although the choice of number of dispersal routes or their location is application specific (and beyond the scope of this paper), our results suggest that the least-cost path is a flexible approach with a wide range of applications.

Acknowledgments The authors would like to thank Tania Peña-Baca, Courtney Abshire, Kathrine Behrman, Betsy Reardon, Jesse Lasky, Evan Economo, and three anonymous reviewers for comments on the manuscript.

References

Adriaensen F, Chardon P, de Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of "least-cost" modeling as a functional landscape model. Landsc Urban Plan 64:233–247. doi:10.1016/S0169-2046(02)00242-6

Alagador D, Cerdeira JO (2007) Designing spatially-explicit reserve networks in the presence of mandatory sites. Biol Conserv 137:254–262

Baguette M, Van Dyck H (2007) Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. Landscape Ecol 22:1117–1129. doi:10.1007/s10980-007-9108-4

Belisle M (2005) Measuring landscape connectivity: the challenge of behavioral landscape ecology. Ecology 86:1988–1995. doi:10.1890/04-0923

Bestelmeyer BT, Wiens JA (1996) The effects of land use on the structure of ground-foraging ant communities in the Argentinian Chaco. Ecol Appl 6:1225–1240. doi:10.2307/2269603

Bodin O, Tengo M, Norman A, Lundberg J, Elmqvist T (2005) The value of small size: loss of forest patches and ecological thresholds in southern Madagascar. Ecol Appl 16:440–451. doi:10.1890/1051-0761(2006)016[0440:TVOSSL]2.0.CO;2

Boitani L, Falcucci A, Maiorano L, Rondinini C (2007) Ecological networks as conceptual frameworks or operational tools in conservation. Conserv Biol 21:1414–1422

Burel F (1996) Hedgerows and their role in agricultural landscapes. Rev Plant Sci 15:169–190. doi:10.1080/713608130

Calabrese JM, Fagan WF (2004) A comparison-shopper's guide to connectivity metrics. Front Ecol Environ 2:529–536

Chardon JP, Adriaensen F, Matthysen E (2003) Incorporating landscape elements into a connectivity measure: a case study for the Speckled wood butterfly (*Parge aegeria* L.). Landscape Ecol 18:561–573. doi:10.1023/A:1026062530600

Clevenger AP, Chruszcz B, Gunson K (2001) Drainage culverts as habitat linkages and factors affecting passage by mammals. J Appl Ecol 38:1340–1349. doi:10.1046/j.0021-8901.2001.00678.x

Cormen TH, Leiserson CE, Rivest RL, Stein C (2001) Introduction to algorithms. MIT Press, Cambridge

Crooks KR, Sanjayan M (2006) Connectivity conservation. Cambridge University Press, Cambridge

Driezen K, Adriaesen F, Rondinini C, Doncaster CP, Matthysen E (2007) Evaluating least-cost model predictions with empirical dispersal data: a case-study using radiotracking data of hedgehogs (*Erinaceus europaeus*). Ecol Model 209:314–322. doi:10.1016/j.ecolmodel.2007.07.002

Eva HD, Miranda EE, Bella CM, Gond V, Huber O, Jones S, Sgrenzaroli M, Fritz S (2002) A land cover map of South America. EUR 20159, European Commission, Joint Research Center

Farber O, Kadmon R (2003) Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. Ecol Model 160:115–130. doi:10.1016/S0304-3800(02)00327-7

Forman RTT (1995) Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge

Goodwin BJ (2003) Is landscape connectivity a dependent of independent variable? Landscape Ecol 18:687–699. doi:10.1023/B:LAND.0000004184.03500.a8

Hansen MR, De Fries R, Townshend JR, Carroll M, Dimiceli C, Sohlberg R (2003) Vegetation continuous fields, MOD44B, 2001 percent tree cover, collection 3. University of Maryland, College Park

Hess GR, Fischer RA (2001) Communicating clearly about corridors. Landsc Urban Plan 55:195–208. doi:10.1016/S0169-2046(01)00155-4

Hoctor TS, Carr MH, Zwick PD (2000) Identifying a linked reserve system using a regional landscape approach: the Florida ecological network. Conserv Biol 14:984–1000. doi:10.1046/j.1523-1739.2000.99075.x

IBGE (1991) Census of Brazilian municipalities. http://www.ibge.gov.br

Keitt TH (2000) Spectral representation of neutral landscapes. Landscape Ecol 15:479–493. doi:10.1023/A:1008193015770

Keitt TH, Urban DL, Milne BL (1997) Detecting critical scales in fragmented landscapes. Conserv Ecol [online] 1:4. http://www.consecol.org/vol1/iss1/art4

Larkin JL, Maehr DS, Hoctor TS, Orlando MA, Whitney K (2004) Landscape linkage and conservation planning for the black bear in west-central Florida. Anim Conserv 7:23–34. doi:10.1017/S1367943003001100

Laurance WF, Lovejoy HL, Vasconcelos EM, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem decay of forest fragments: a 22-year investigation. Conserv Biol 16:605–618. doi:10.1046/j.1523-1739.2002.01025.x

Lees AC, Peres CA (2008) Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. Conserv Biol 22:439–449

Majka D, Jennes J, Beier P (2007) CorridorDesigner: ArcGIS tools for designing and evaluating corridors. http://corridordesign.org

Manning AD, Fischer J, Lindenmayer DB (2006) Scattered trees as keystone structures—implications for conservation. Biol Conserv 132:311–321. doi:10.1016/j.biocon.2006.04.023

Mas AH, Dietsch TV (2003) An index of management intensity for coffee agroecosystems to evaluate butterfly species richness. Ecol Appl 13:1491–1501. doi:10.1890/01-5229

Moguel P, Toledo VM (1999) Biodiversity conservation in traditional coffee systems of Mexico. Conserv Biol 13:11–21. doi:10.1046/j.1523-1739.1999.97153.x

Morellato LPC, Haddad CFB (2000) Introduction: the Brazilian Atlantic forest. Biotropica 32:786–792

Oliveira-Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. Biotropica 32:793–810

Perfecto I, Vandermeer J (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. Conserv Biol 16:174–182. doi:10.1046/j.1523-1739.2002.99536.x

Perfecto I, Mas A, Diestsch T, Vandermeer J (2003) Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. Biodivers Conserv 12:1239–1252. doi:10.1023/A:1023039921916

Rae C, Rothley K, Dragicevic S (2007) Implications of error and uncertainty for an environmental planning scenario: a sensitivity analysis of GIS-based variables in a reserve design exercise. Landsc Urban Plan 79:210–217. doi:10.1016/j.landurbplan.2006.01.001

Reitsma R, Parrish JD, McLarney W (2001) The role of cacao plantations in maintaining forest avian diversity in southeastern Costa Rica. Agrofor Syst 53:185–193. doi:10.1023/A:1013328621106

Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. Am Nat 158:87–99. doi:10.1086/320863

Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. Bioscience 52:891–904. doi:10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2

Schadt S, Knauer F, Kaczensky P, Revilla E, Wiegand T, Trepl L (2002) Rule-based assessment of suitable habitat and patch connectivity for Eurasian Lynx in Germany. Ecol Appl 12:1469–1483. doi:10.1890/1051-0761(2002)012[1469:RBAOSH]2.0.CO;2

Serra J (1982) Image analysis and mathematical morphology. Academic Press, London

Stevens VM, Verkenne C, Vandewoestijne S, Wesselingh RA, Baguette M (2006) Gene flow and functional connectivity in the Natterjack toad (*Bufo calamita*). Mol Ecol 15:2333–2344. doi:10.1111/j.1365-294X.2006.02936.x

Sutcliffe OL, Bakkestuen V, Fry G, Stabbetorp OE (2003) Modelling the benefits of farmland restoration: methodology and application to butterfly movement. Landsc Urban Plan 63:15–31. doi:10.1016/S0169-2046(02)00153-6

Tscharntke T, Klein A, Kruess A, Steffan-Dwenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. Ecol Lett 8:857–874. doi:10.1111/j.1461-0248.2005.00782.x

Turchin P (1998) Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Massachusetts

Urban DL, Keitt TH (2001) Landscape connectivity: a graph theoretic perspective. Ecology 82:1205–1218

Vandermeer J, Carvajal R (2001) Metapopulation dynamics and the quality of the matrix. Am Nat 158:211–220. doi:10.1086/321318

Verbeylen G, De Bruyn L, Adriaesen F, Matthysen E (2003) Does matrix resistance influence red squirrel (*Sciurus vulgaris* L. 1758) distribution in an urban landscape? Landscape Ecol 18:791–805. doi:10.1023/B:LAND.0000014492.50765.05