

# Restoring habitat corridors in fragmented landscapes using optimization and percolation models

Justin C. Williams<sup>a,\*</sup> and Stephanie A. Snyder<sup>b</sup>

<sup>a</sup> *Department of Geography and Environmental Engineering, Johns Hopkins University, 3400 North Charles Street, Baltimore, MD 21218, USA*  
E-mail: jcwjr@jhu.edu

<sup>b</sup> *U.S. Forest Service, North Central Research Station, 1992 Folwell Avenue, St. Paul, MN 55108, USA*  
E-mail: stephaniesnyder@fs.fed.us

Landscape fragmentation and habitat loss are significant threats to the conservation of biological diversity. Creating and restoring corridors between isolated habitat patches can help mitigate or reverse the impacts of fragmentation. It is important that restoration and protection efforts be undertaken in the most efficient and effective way possible because conservation budgets are often severely limited. We address the question of where restoration should take place to efficiently reconnect habitat with a landscape-spanning corridor. Building upon findings in percolation theory, we develop a shortest-path optimization methodology for assessing the minimum amount of restoration needed to establish such corridors. This methodology is applied to large numbers of simulated fragmented landscapes to generate mean and variance statistics for the amount of restoration needed. The results provide new information about the expected level of resources needed to realize different corridor configurations under different degrees of fragmentation and different characterizations of habitat connectivity (“neighbor rules”). These results are expected to be of interest to conservation planners and managers in the allocation of conservation resources to restoration projects.

**Keywords:** conservation planning, habitat fragmentation, landscape restoration, mathematical programming, percolation theory

## 1. Introduction

Landscape fragmentation and habitat loss resulting from human impacts are significant threats to the conservation of biological diversity [1,2]. Where restoration opportunities exist, restoring prior habitat connections and creating new corridors between isolated patches is one way to counter the effects of fragmentation [3]. Much of the focus in environmental restoration has been on specific approaches for restoring individual sites (e.g., abandoned mines, landfills, brownfields) or restoring particular types of ecosystems (e.g., tall grass prairies, wetlands), although a more general science of restoration ecology is now emerging [3,4]. The need for landscape-scale approaches to restoration, in addition to site-specific methods, has also been recognized [5]. The restorations of wetlands, forests, prairies, and other types of ecosystems are becoming an integral part of the conservation missions of government agencies and nongovernment organizations in the USA and other countries (e.g., U.S. Fish and Wildlife Service, The Nature Conservancy).

Because conservation resources are usually limited, it is imperative that restoration be undertaken in the most efficient and cost-effective way possible. In regions of competing land uses and multiple landowners, habitat may need to be selectively restored and reconnected without a wholesale expansion in the land area devoted to habitat [6]. In addition, in large, extensively fragmented landscapes, the number of possibilities for reconnecting habitat is like-

ly to be enormous. Hence, quantitative analytical approaches are needed to address the questions of where and how much to restore.

In recent years researchers have applied mathematical optimization techniques to a variety of decision problems in conservation planning. Optimization models have been formulated for problems of selecting and designing nature reserves (e.g., [7,8]; Williams et al., this volume) as well as for problems of forest harvesting and conservation (e.g., [9,10]) and the delineation of wildlife corridors [11,12]. However, applications of mathematical optimization for guiding habitat restoration analysis are only beginning to be used (e.g., [13]) and, to our knowledge, have not yet been applied at the landscape scale.

In this paper, we use the “shortest path” model from operations research to statistically evaluate the amount of restoration needed to reconnect a fragmented landscape. Specifically, we ask, “How does the minimum amount of restoration needed to reconnect opposite edges of a landscape with a habitat corridor change with the extent of fragmentation in the landscape?” We apply our methodology to simulated “neutral” landscapes, which have been studied extensively by landscape ecologists (as discussed below). We calculate the mean and standard deviation of the minimum amount of restoration needed under different levels of fragmentation and under different definitions of connectivity based on “neighbor rules.” The results provide an introduction and first step toward generating new policy-relevant information that is expected to be of interest to land managers and conservation planners. More broadly, the methodology is a conceptual

\* Corresponding author.

approach that can be used in a variety of different landscape contexts.

## 2. Background

### 2.1. Neutral landscape models

Habitat fragmentation at the landscape scale has been investigated in simulations using spatially explicit neutral models [14]. In such models, the landscape is treated as a large number ( $N$ ) of cells arranged in a rectangular lattice. The process used to generate the landscape is “neutral” in that it “produces an expected pattern [of fragmentation] in the absence of specific landscape processes” ([15], p. 19). In the simplest neutral models, the cells are either habitat or nonhabitat. Fragmentation is modeled by selecting some proportion  $P$  of cells to designate, at random, as habitat. Hence,  $PN$  of the cells are designated habitat and the remaining  $(1 - P)N$  cells are designated nonhabitat. Patterns of habitat generated by this process can be evaluated with respect to different spatial attributes, including connectivity, boundary length, and number of habitat clusters. These patterns can provide insight into the ecological implications of fragmentation in real landscapes and can serve as a baseline for statistical comparisons to patterns in real landscapes [16]. We chose to apply our analysis to neutral landscapes because they have been well studied by others, they are easily replicated and statistical results can be readily derived, and they serve as a simplest-case starting point on which to base analysis of more complex landscapes.

### 2.2. Percolating clusters

Of interest to us in the analysis of habitat fragmentation are the changes in habitat connectivity that result from different proportions of habitat  $P$  in the neutral landscape. To what extent are habitat connections lost as the landscape becomes increasingly fragmented? Habitat connectivity may be characterized as either *structural* or *functional* [17]. Structural connectivity implies physical contiguity, whereas functional connectivity is based on the behavioral responses of organisms to the landscape – the ability of an organism to move from one patch to another. One feature of fragmented landscapes that is important to both structural and functional connectivity is the “percolating cluster” [18].

A percolating cluster is an assemblage of connected habitat cells that extends from one edge of a landscape lattice (e.g., the north edge) to the opposite (south) edge (figure 1). In addition to providing a path between opposite edges, a percolating cluster also tends to have many intertwinning branches that spread out across the lattice. If a percolating cluster exists, it is theoretically possible for an organism to move from one edge of the lattice to the other along a path of habitat cells [16]. In neutral models, it is

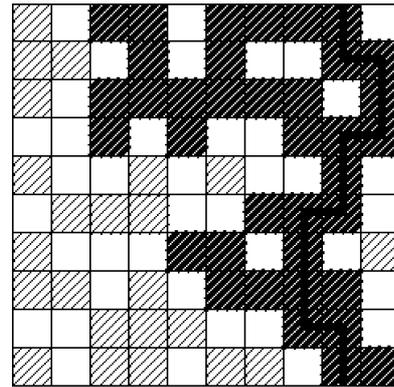


Figure 1. Percolating cluster. A  $10 \times 10$  lattice of 100 cells is shown. Sixty habitat cells (shaded) have been specified randomly ( $P = 0.60$ ). Dark-shaded cells belong to the percolating cluster, which connects the north and south edges (under the nearest neighbor rule). Light-shaded cells belong to smaller clusters or are isolated. A shortest path (“backbone”) through the percolating cluster is indicated.

usually assumed that organisms are restricted to using only habitat cells – and we make this assumption here as well.

The likelihood that a percolating cluster exists depends on both the proportion of habitat  $P$  and the way in which connectivity between cells is defined (neighbor rules, discussed below). When connectivity is defined in terms of nearest neighbor cells (i.e., cells that share a common edge), the “critical threshold” value of  $P$  is 0.59275 in rectangular lattices [19]. For  $P$  slightly below this threshold a percolating cluster is unlikely to exist, but as  $P$  passes through the critical threshold the situation changes rapidly with a percolating cluster becoming very likely, even at one or two percentage points above the threshold. At the critical threshold – when approximately 59.3% of the cells are designated at random as habitat – the chance of a percolating cluster is about 50%.

The critical threshold also has implications for other aspects of landscape connectivity. At values of  $P$  greater than the threshold, the landscape is characterized by a few large habitat clusters, including a percolating cluster, which contains a majority of habitat cells. Below the critical threshold, the landscape is characterized by many small, disconnected habitat clusters [15]. At values of  $P$  near the critical threshold, the random conversion of a few habitat cells to nonhabitat may sever the percolating cluster and greatly reduce overall connectivity [16,20]. Hence, the critical threshold is a distinct transition point between a landscape that is largely connected and one that is largely disconnected.

### 2.3. Neighbor rules for connectivity

Whether or not an organism perceives a landscape as being connected depends on the scale at which fragmentation takes place relative to the movement capabilities of the organism [16,20]. Some organisms may be able to move across gaps in habitat that pose barriers to other organisms. To model scale phenomena, different neighbor

rules can be used to define or measure connectivity. Neighbor rules specify whether or not a connection exists between two cells, that is, whether or not a hypothetical organism could move directly from one cell to the other. In this paper, we consider three neighbor rules that have been used previously in neutral landscape models [14,20] (figure 2):

- (i) *Nearest-neighbor rule* (a cell is directly connected to each of its four edge-adjacent cells)
- (ii) *Next-nearest-neighbor rule* (a cell is directly connected to each of its eight edge- and corner-adjacent cells)
- (iii) *Third-nearest-neighbor rule* (a cell is directly connected to each of the 12 nearest cells)

An organism that perceives connectivity according to the nearest neighbor rule would be much more sensitive to, and restricted by, fragmentation than an organism governed by the third-nearest neighbor rule. The former organism would view a one-cell gap in habitat as a barrier to movement, but the latter organism would not. In the real world, the applicability of a particular neighbor rule to a particular species depends on the scale of the lattice (cell size) relative to the range of movement for the species [14,20]. If the cell size were relatively small so that an organism could “jump” across a one-cell gap, then the third-nearest neighbor rule would be appropriate, but if larger cells were used, the nearest neighbor rule might better represent that organism’s movement capability.

The critical thresholds for the formation of percolating clusters for the second- and third-nearest neighbor rules are about 0.407 and 0.292, respectively – much smaller than 0.593 for the nearest neighbor rule [18]. An organism operating under the third nearest neighbor rule would be expected to be able to traverse a (neutral) landscape in which only about 29.2% of the cells were habitat cells. Hence, landscapes remain functionally connected at much

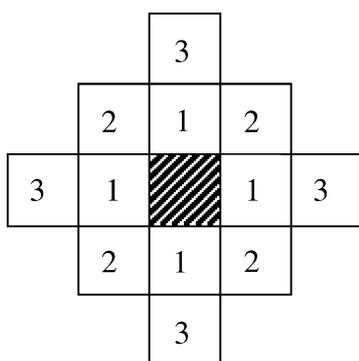


Figure 2. Neighbor rules. A direct connection exists between the center cell (shaded) and: cells labeled “1” under the nearest neighbor rule; cells labeled “1” and “2” under the next-nearest neighbor rule; and cells labeled “1,” “2,” and “3” under the third-nearest neighbor rule.

higher levels of fragmentation under the second- and third-nearest neighbor rules than under the nearest-neighbor rule.

### 3. Methods

#### 3.1. Connectivity and corridors

In large fragmented landscapes, many alternative patterns of restoration may be possible for reestablishing habitat connectivity. In this paper, we address the use of corridors to reconnect habitat. The pros and cons of habitat corridors have been debated extensively in the conservation literature [21–25]. Corridors provide species with access to needed resources and help species (re)colonize patches after local extinction. However, corridors may also promote the spread of diseases and exotic species, synchronize local population fluctuations [26], and function as bottlenecks that can be exploited by predators. Nevertheless, in a review of 32 published wildlife corridor studies, Beier and Noss [25] conclude that the evidence “generally supports the utility of corridors as a conservation tool” (p. 1,249).

The types of corridor configurations we consider are based on shortest paths, which are relevant for at least two reasons. The first is one of efficiency. From the perspective of a conservation planner, minimizing the amount of restoration needed to establish a connecting corridor is likely to be an important goal, which shortest paths can help achieve. The second reason is to promote ecological processes that involve the migration and dispersal of plants and animals. A shortest path is the most direct spatial connection between two patches that contain resources needed by an organism. Long, meandering corridors, in contrast, reduce the functional connectivity between patches, increasing the risk that an organism will fail to complete the interpatch journey [27,28]. Hence, we seek to systematically identify connecting corridors that require as little restoration as possible and that provide direct connections.

In a fragmented landscape, a corridor exists (by definition) if a percolating cluster is present and does not exist otherwise. If a percolation cluster exists, the connecting corridor may be a fairly straight line or may meander quite a bit, depending on the extent and pattern of fragmentation. In the case of meandering corridors, it may be possible to realize a shorter connection by restoring a few select cells from nonhabitat to habitat. If a percolating cluster does not yet exist but can be created, then corridors of differing length can potentially be realized, depending on which and how many cells are to be restored.

We consider two types of shortest-path habitat corridors, the “geometric shortest path” and the “least-restoration path.” For convenience, we concern ourselves with corridors that span the landscape in the north–south direction, although our analysis applies equally well to the east–west direction. Corridors that are required to connect

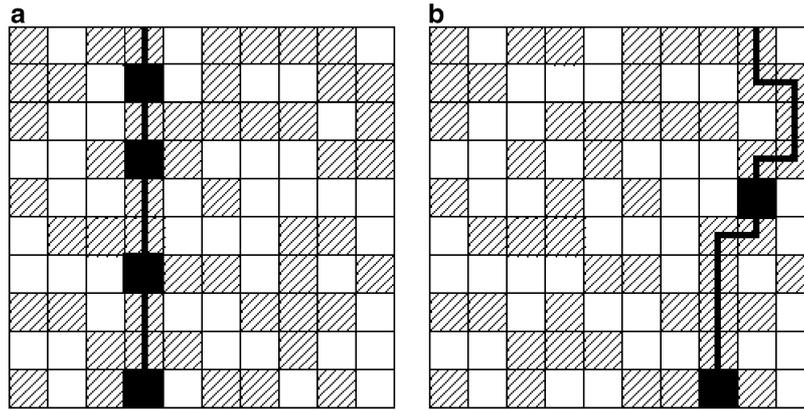


Figure 3. Habitat paths. Two identical  $10 \times 10$  landscapes are shown, each with 50 habitat cells (shaded),  $P = 0.50$ . A percolating cluster from north to south does not exist (under the nearest neighbor rule), but can be established by restoring nonhabitat cells. (a) A minimum of four nonhabitat cells need to be restored (black) to establish a geometric shortest habitat path; the length of this path is ten units. (b) A least-restoration habitat path from north to south can be established by restoring only two nonhabitat cells; the length of this path is 13 units.

both north–south and east–west edges simultaneously are beyond the scope of this paper. The percolation studies discussed above analyze connectivity along one directional axis but not both, so we have followed this precedent. We note that the problem of delineating corridors for both directional axes can be modeled as a “Steiner tree” problem in networks [29]. Sessions [11] and Williams [12] used Steiner tree models to optimize a system of corridors for linking several habitat patches or nature reserves.

3.2. Geometric shortest paths

In a lattice of size  $L \times L$  ( $= N$  cells), the shortest path from the north edge to the south edge is a straight line or column of  $L$  habitat cells,  $L$  units long. We call this a geometric shortest path (GSP) (figure 3a). Under the nearest neighbor rule, the GSP corridor that could be restored most efficiently would be the column containing a minimum number of nonhabitat cells. Such a column can be readily identified by inspection or by a simple automated search procedure. This approach may also be applied to the next-nearest-neighbor rule. When the third-nearest neighbor rule is used, a more complicated search procedure is needed because not all cells in a column need to be habitat for a GSP to exist; connectivity is maintained even if one-cell gaps of nonhabitat exist. The straight line implied by a GSP may not be a practical or desirable shape for a habitat corridor in some contexts. However, because the straight line represents one extreme of what can theoretically be achieved, it is useful in that it provides a baseline against which other configurations can be compared.

3.3. Least-restoration paths

If meandering paths are allowed, then reconnecting opposite edges of the landscape may be achievable with fewer restored cells than required by the GSP. A path that connects opposite edges with a minimum number of restored cells is referred to as a least-restoration path (LRP)

(figure 3b). The problem of finding an LRP can be stated as the “shortest path problem,” which is a well-known problem in network design (see, e.g., [30]). This problem is simply to find the shortest path between an origin node and a destination node ( $o$  and  $d$ ) in a network, where one can travel only along the nodes and arcs of the network (figure 4). The shortest path problem can be formulated as a zero–one linear programming model, which can be solved to optimality using commercially available linear programming software (one of the first such formulations appears in Dantzig [31]). Here we develop a version of the shortest-path model that finds LRPs on cellular lattices. The following notation is used.

- $J$  is the set of all cells (habitat and nonhabitat alike).
- $A_j$  is the set of cells  $i$  that are directly connected to cell  $j$  as determined by the specified neighbor rule.
- $X_{ij}$  is a zero–one decision variable; it is 1 if the least-

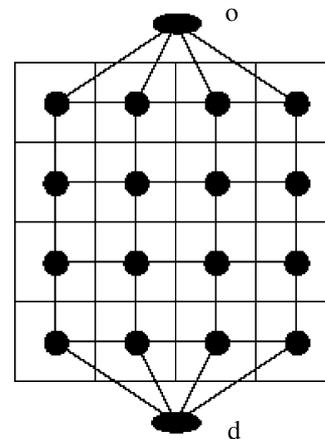


Figure 4. Node–arc network. A network of nodes and arcs is shown to be analogous to a cellular lattice. Cells are represented by nodes, and direct connections between cells are represented by arcs. The arcs shown follow the nearest neighbor rule. “Dummy” origin and destination nodes ( $o$  and  $d$ ) facilitate application of the shortest path model to the lattice.

restoration path includes a direct connection from cell  $i$  to cell  $j$ , that is, if it includes path segment  $(i, j)$ , and is 0 otherwise. Note that the  $X_{ij}$  variables are defined only for pairs of cells that are directly connected according to the specified neighbor rule.

$B_j$  is a zero-one parameter; it is 1 if cell  $j$  is currently nonhabitat, and 0 if cell  $j$  is currently habitat.

Least-restoration path model:

$$\text{Minimize: } \sum_{j \in J} B_j \sum_{i \in A_j} X_{ij} \quad (1)$$

$$\text{Subject to: } \sum_{j \in A_o} X_{oj} = 1 \quad (2)$$

$$\sum_{j \in A_j} X_{ij} - \sum_{k \in A_j} X_{jk} = 0, \quad \text{for all cells } j \quad (3)$$

$$\sum_{j \in A_d} X_{jd} = 1 \quad (4)$$

The objective (1) is to minimize the total number of restored cells needed in a corridor that connects opposite edges of the landscape. This is calculated by counting the number of nonhabitat cells  $j$  that are entered by the LRP. Constraint (2) requires that one path segment extending away from the origin cell  $o$  must be selected. Here, the origin is a “dummy” cell at the north edge of the lattice (figure 4). Constraint (3) requires that whenever the path enters a cell  $j$ , it must also leave the cell; this constraint is written for each cell  $j$  except  $o$  and  $d$ . Finally, constraint (4) requires that one selected path segment must enter the destination  $d$ , where  $d$  is a dummy cell at the south edge of the lattice. Dummy cells  $o$  and  $d$  have no restoration costs and are specified as being directly connected, respectively, to all cells at or near the north and south edges, depending on the neighbor rule used. We note that constraint (2) is redundant because it is implied by constraints (3) and (4).

In addition to linear programming methods, the shortest path problem can also be solved by any of several computationally efficient algorithms (see [32]). In this research, we have used a modified version of the basic shortest path algorithm presented by Hillier and Lieberman [30].

In identifying the LRP of a landscape, it may turn out that multiple LRPs of different lengths all require the same (minimum) number of restored cells. We would then be interested in the LRP having the shortest length, although more than one such LRP may exist. For example, in figure 3b, an LRP requires restoring two cells. A minimum-length LRP that can be realized by restoring two cells is 13 cells long, and there are three such paths. Other longer LRPs (14 or more cells long) can also be achieved by restoring two cells.

### 3.4. Corridor analysis

We evaluate both GSPs and LRPs as a mathematical means for efficiently reconnecting habitat in fragmented landscapes. We assess the differences in both the amount of restoration needed and path length between these two types of paths in  $48 \times 48$  cell landscape lattices ( $N = 2,304$  cells), under each of the three neighbor rules defined above (nearest neighbor, next-nearest neighbor, and third-nearest neighbor). For each neighbor rule, a range of habitat proportions (values of  $P$ ) was used to simulate different degrees of fragmentation. We used the critical threshold as a reference point and varied  $P$  in increments of plus or minus ten percentage points. For the nearest neighbor rule, habitat densities between 0.093 and 0.893 were simulated. The densities were 0.107 to 0.907 for the next-nearest neighbor rule and 0.092 to 0.692 for the third-nearest neighbor rule. Habitat densities of 0.792 and higher were not evaluated for the third-nearest neighbor rule because both GSPs and LRPs are virtually guaranteed to exist at the outset – no restoration is likely to be needed.

For each combination of parameters (value of  $P$  and neighbor rule), 200 fragmented lattices were generated. In each lattice the locations of  $PN$  habitat cells were determined randomly (the actual number of habitat cells was the integer part of  $PN$ ). Specifically, the  $x$ - and  $y$ -axis coordinates of each habitat cell were determined by random numbers taken from a uniform distribution.

In each random lattice, we found both a GSP and an LRP by the methods described above. Solutions for the GSP problem indicate the minimum number of cells that would need to be restored to create a habitat column 48 units long that connects the north and south edges of the lattice. In contrast, solutions to the LRP problem indicate the minimum number of cells that would need to be restored to create any north-to-south habitat path – not necessarily a straight column, but likely a meandering path. As pointed out above, different LRPs may be possible, each requiring the same (minimum) number of restored cells. These alternate optima (if they exist) may have different total lengths, however, and our methodology selects the LRP having the shortest length.

For each set of 200 random lattices, the mean and standard deviation were calculated for (a) the number of restored cells needed in a GSP, (b) the number of restored cells needed in the LRP, and (c) the (minimum) length of the LRP. As well, in each case, the algorithm determined the number of lattices (out of 200) that initially contained a north-to-south path (i.e., a percolating cluster). Obviously, these lattices required no restoration to achieve an LRP.

Computing was done on a Dell Optiplex personal computer and the optimization algorithm was written in Visual Fortran 6.0. For each set of 200 simulations, computing times were about 1.75 h. In this amount of time the algorithm generated 200 random lattices and performed all optimization and statistical computations for both GSPs and LRPs.

Table 1  
Nearest neighbor rule, 48 × 48 grid (2,304 cells).

(1) <i>P</i>	(2) No. of rest cells GSP	(3) Length GSP	(4) No. of rest cells LRP	(5) Length LRP	(6) No. of percolating clusters
0.093 (214)	38.490 (1.245)	48.0	36.135 (1.165)	51.085 (2.181)	0
0.193 (444)	32.210 (1.366)	48.0	26.615 (1.489)	55.230 (3.289)	0
0.293 (675)	26.765 (1.497)	48.0	18.175 (1.362)	60.630 (4.422)	0
0.393 (905)	21.445 (1.529)	48.0	10.650 (1.535)	65.710 (6.077)	0
0.493 (1,135)	16.645 (1.634)	48.0	4.485 (1.149)	71.395 (8.604)	1
0.593* (1,366)	12.260 (1.242)	48.0	0.620 (0.660)	73.110 (10.704)	94
0.693 (1,596)	8.055 (1.101)	48.0	0 (0)	58.915 (2.700)	200
0.793 (1,827)	4.185 (1.091)	48.0	0 (0)	52.505 (1.170)	200
0.893 (2,057)	1.060 (0.645)	48.0	0 (0)	48.965 (0.569)	200

(1) *P*, the proportion of habitat cells in lattice (actual number of habitat cells); asterisk indicates critical threshold for a percolating cluster under the given neighbor rule.

(2) The mean minimum number of nonhabitat cells that would need to be restored to create a geometric shortest path (standard deviation).

(3) Length, in cell units, of the geometric shortest path.

(4) The mean minimum number of nonhabitat cells that would need to be restored to create a least-restoration path (standard deviation).

(5) The mean minimum length, in cell units, of the least-restoration path (standard deviation).

(6) The number of random realizations, out of 200, in which a percolating cluster appeared.

#### 4. Results

In this section we report the results of four sets of simulations (tables 1–4). In each of the first three sets, one of the three neighbor rules was applied to a range of habitat densities (*P*). In the fourth set, results for 48 × 48 lattices are compared to parallel results for 24 × 24 lattices.

##### 4.1. Nearest neighbor rule

For the nearest neighbor rule (table 1), as the proportion of habitat *P* increases from 0.093 to 0.893, the frequency with which a percolating clusters appears increases – not gradually, but with a sharp transition at the critical threshold (table 1, column 6). This is consistent with the results of other percolation experiments (e.g., [18]). At the critical threshold (*P* = 0.593), about half of the 200 random lattices (94 lattices) contain a percolating cluster,

as expected. At values of *P* below the critical threshold, none or very few of the landscapes contain a percolating cluster, and at values of *P* above the threshold, all or nearly all landscapes have a percolating cluster.

At the low habitat proportion of 0.093, on average 38 or 39 cells is the minimum number that would need to be restored to create a landscape-spanning GSP (table 1, column 2). Here, the lattice column with the largest amount of existing habitat has nine or ten habitat cells; the remaining cells would then need to be restored to complete the column. As the value of *P* is increased, the amount of restoration needed declines. At a habitat proportion of 0.893, only a single cell (1.060 cells), on average, would need to be restored. Some landscapes (about 19% of the landscapes; see Appendix) already contain a GSP at this habitat density. Overall, the number of cells to restore for a GSP declines from 48 to zero as the habitat proportion is increased from zero to one (figure 5). The variation (stan-

Table 2  
Next-nearest neighbor rule, 48 × 48 grid (2,304 cells).

(1) <i>P</i>	(2) No. of rest cells GSP	(3) Length GSP	(4) No. of rest cells LRP	(5) Length LRP	(6) No. of percolating clusters
0.107 (246)	37.475 (1.196)	48.0	22.225 (1.478)	58.424 (1.967)	0
0.207 (476)	31.535 (1.407)	48.0	12.050 (1.272)	60.597 (2.863)	0
0.307 (707)	26.100 (1.446)	48.0	4.770 (1.126)	65.100 (6.030)	0
0.407* (937)	20.790 (1.589)	48.0	0.615 (0.661)	66.663 (9.369)	97
0.507 (1,168)	16.030 (1.590)	48.0	0 (0)	56.429 (1.442)	200
0.607 (1,398)	11.600 (1.342)	48.0	0 (0)	52.831 (0.744)	200
0.707 (1,628)	7.305 (1.254)	48.0	0 (0)	50.920 (0.502)	200
0.807 (1,859)	3.530 (1.072)	48.0	0 (0)	49.359 (0.389)	200
0.907 (2,089)	0.705 (0.546)	48.0	0 (0)	48.284 (0.214)	200

(1) *P*, the proportion of habitat cells in lattice (actual number of habitat cells); asterisk indicates critical threshold for a percolating cluster under the given neighbor rule.

(2) The mean minimum number of nonhabitat cells that would need to be restored to create a geometric shortest path (standard deviation).

(3) Length, in cell units, of the geometric shortest path.

(4) The mean minimum number of nonhabitat cells that would need to be restored to create a least-restoration path (standard deviation).

(5) The mean minimum length, in cell units, of the least-restoration path (standard deviation).

(6) The number of random realizations, out of 200, in which a percolating cluster appeared.

Table 3  
Third-nearest-neighbor rule, 48 × 48 grid (2,304 cells).

(1) <i>P</i>	(2) No. of rest cells GSP	(3) Length GSP	(4) No. of rest cells LRP	(5) Length LRP	(6) No. of percolating clusters
0.092 (211)	16.670 (0.917)	48.0	13.015 (1.075)	52.388 (2.728)	0
0.192 (442)	12.525 (1.005)	48.0	5.015 (1.155)	59.493 (5.545)	0
0.292* (672)	8.815 (1.063)	48.0	0.460 (0.564)	64.122 (8.591)	115
0.392 (903)	5.720 (0.996)	48.0	0 (0)	52.472 (1.385)	200
0.492 (1,133)	3.535 (0.812)	48.0	0 (0)	49.781 (0.497)	200
0.592 (1,363)	1.525 (0.755)	48.0	0 (0)	48.651 (0.336)	200
0.692 (1,594)	0.350 (0.477)	48.0	0 (0)	48.145 (0.198)	200

- (1) *P*, the proportion of habitat cells in lattice (actual number of habitat cells); asterisk indicates critical threshold for a percolating cluster under the given neighbor rule.
- (2) The mean minimum number of nonhabitat cells that would need to be restored to create a geometric shortest path (standard deviation).
- (3) Length, in cell units, of the geometric shortest path.
- (4) The mean minimum number of nonhabitat cells that would need to be restored to create a least-restoration path (standard deviation).
- (5) The mean minimum length, in cell units, of the least-restoration path (standard deviation).
- (6) The number of random realizations, out of 200, in which a percolating cluster appeared.

standard deviation) in the number of restored cells is relatively small for each value of *P*, indicating that the mean is a reliable indicator of the amount of restoration needed to form a GSP.

At values of *P* below the critical threshold (0.593), percolating clusters are not likely to occur, so some cells would need to be restored to create an LRP. At *P* = 0.093, the average minimum number of cells that would need to be restored is about 36 (table 1, column 4). The average minimum length of the LRP is about 51 units (table 1, column 5). In comparison to the GSP, the LRP requires about two fewer restored cells but is three units longer at this value of *P*. As *P* increases, the number of restored cells needed declines with *P* until the critical threshold is reached. At the critical threshold, just over half a cell is needed on average to establish an LRP. At higher habitat densities, all lattices already contain a percolating cluster, so no cells would need to be restored to create an LRP. Here, too, the standard deviation in the number of restored

cells in the LRP is relatively small, suggesting that the mean is a reliable indicator for the amount of restoration needed.

For every value of *P* (except 0 and 1.0), the average minimum number of restored cells needed to create an LRP is less than the average minimum number needed to create a GSP (figure 5). This difference (table 1, column 2 minus column 4) is relatively small at very low and very high values of *P*, but grows as *P* approaches the critical threshold from either direction. The difference appears to be largest (about 12 cells) at or slightly below the critical threshold. At values of *P* less than the critical threshold, these differences occur because the LRP has more flexibility to exploit the existing pattern of habitat cells, whereas the GSP is constrained to be one of the lattice columns. At values of *P* greater than the critical threshold but less than 1.0, no restoration is needed for an LRP because it already exists (as part of the percolating cluster), whereas creating GSP tends to require some restoration.

Table 4  
Corridor restoration and length as a fraction of landscape width (nearest neighbor rule).

(1) <i>P</i>	(2) Rest GSP	(3) Rest LRP	(4) Length GSP	(5) Length LRP
0	1.0 (1.0)	1.0 (1.0)	1.0 (1.0)	1.0 (1.0)
0.093	0.802 (0.779)	0.753 (0.749)	1.0 (1.0)	1.064 (1.038)
0.193	0.671 (0.643)	0.554 (0.560)	1.0 (1.0)	1.151 (1.115)
0.293	0.558 (0.523)	0.379 (0.388)	1.0 (1.0)	1.263 (1.194)
0.393	0.447 (0.410)	0.222 (0.236)	1.0 (1.0)	1.369 (1.265)
0.493	0.347 (0.312)	0.093 (0.107)	1.0 (1.0)	1.487 (1.361)
0.593*	0.255 (0.220)	0.013 (0.022)	1.0 (1.0)	1.523 (1.383)
0.693	0.168 (0.136)	0 (0.001)	1.0 (1.0)	1.227 (1.203)
0.793	0.087 (0.063)	0 (0)	1.0 (1.0)	1.094 (1.076)
0.893	0.022 (0.006)	0 (0)	1.0 (1.0)	1.020 (1.006)
1.0	0 (0)	0 (0)	1.0 (1.0)	1.0 (1.0)

- (1) *P*, the proportion of habitat cells in lattice; asterisk indicates critical threshold for a percolating cluster under the nearest neighbor rule.
- (2) Ratio of the mean number of restored cells in the geometric shortest path to the landscape width, *L* = 48 (*L* = 24).
- (3) Ratio of the mean number of restored cells in the least-restoration path to the landscape width, *L* = 48 (*L* = 24).
- (4) Ratio of the length of a geometric shortest path to the landscape width, *L* = 48 (*L* = 24).
- (5) Ratio of the mean minimum length of the least-restoration path to the landscape width, *L* = 48 (*L* = 24).

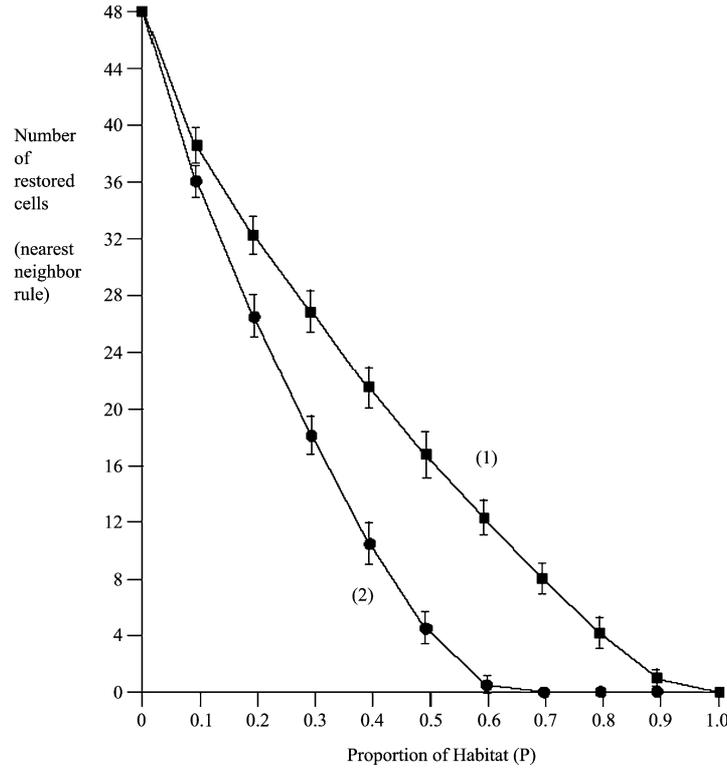


Figure 5. Under the nearest neighbor rule, the minimum number of restored cells needed is shown as a function of habitat proportion ( $P$ ) for the following cases. (1) Geometric shortest habitat path on a  $48 \times 48$  lattice, mean  $\pm$  one standard deviation; (2) least-restoration habitat path on a  $48 \times 48$  lattice, mean  $\pm$  one standard deviation.

On the other hand, for every value of  $P$  (except 0 and 1.0), the average length of the LRP is greater than the length of the GSP, which remains constant at 48 units. In exploiting the existing habitat pattern, the LRP will meander to some extent, depending on the value of  $P$  (table 1, column 5). At very low and very high habitat densities, the LRPs are nearly straight from north to south, close to the length and configuration of a GSP. At low densities, since many restored cells are needed anyway, the LRP tends to be straight minimize the number of restored cells. At high densities, nearly full columns of habitat cells already exist, so that the LRP and the GSP are nearly the same.

However, at middle values of  $P$  (as  $P$  approaches the critical threshold from either direction) the length of the LRP increases. The LRP appears to reach a maximum length at the critical threshold (figure 6). Here, the percolating cluster is sparse or may not quite exist, and although few or no restored cells are needed to form an LRP, the LRP is forced to meander quite a bit to realize this low level of needed restoration. At the critical threshold, the mean LRP length is about 73 units, 52% longer than the GSP.

The variation (standard deviation) in the length of the LRP follows an interesting pattern. At very low and very high values of  $P$ , the variation is relatively small, suggesting some level of uniformity among the 200 simulations. However, as  $P$  approaches the critical threshold

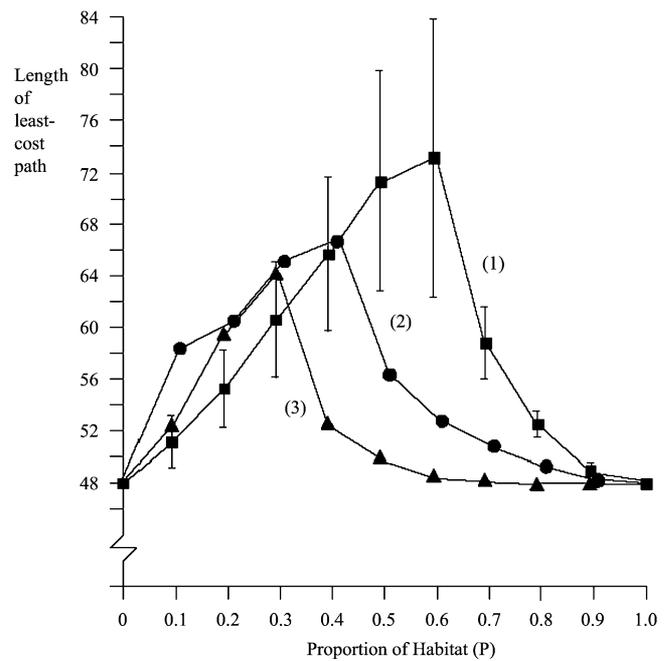


Figure 6. The length (in cell units) of the least-restoration habitat path is shown as a function of habitat proportion ( $P$ ) for the  $48 \times 48$  lattice. (1) Nearest neighbor rule, mean  $\pm$  one standard deviation; (2) next-nearest neighbor rule, mean only (maximum standard deviation = 9.369 for  $P = 0.407$ ); (3) third-nearest neighbor rule, mean only (maximum standard deviation = 8.591 for  $P = 0.292$ ).

from below, the standard deviation increases both absolutely and relative to the mean. The standard deviation appears to reach a maximum at the critical threshold, where it is nearly 15% of the mean, and then falls sharply once the critical threshold is surpassed (table 1, column 5, and figure 6). Hence, in lattices having a habitat proportion near or somewhat below the critical threshold, the reliability of the mean as an indicator declines, and the actual length of an LRP becomes more difficult to predict.

#### 4.2. Next-nearest-neighbor rule

Many of the results for the next-nearest-neighbor rule (table 2) parallel those of the nearest neighbor rule, although there are some interesting differences. The mean number of restored cells needed to create a GSP is the same under the two rules (slight differences in the values of column 2 of tables 1 and 2 result from slight differences in the respective values of  $P$ ). The connections that exist between diagonal cells under the next-nearest-neighbor rule provide no advantage in forming a GSP.

However, diagonal connections permit a sharp drop in the amount of restoration needed to form an LRP. The mean number of restored cells needed declines from about 36 cells to 10.65 cells as  $P$  increases from 0.093 to 0.393 under the nearest neighbor rule (table 1, column 4). The corresponding decline for the next-nearest neighbor rule is from about 22 cells to 0.6 cells for similar values of  $P$  (table 2, column 4) – a drop of 38% or more for each value of  $P$  relative to the nearest neighbor rule.

Under the next-nearest-neighbor rule, like the nearest neighbor rule, the mean length of the LRP appears to reach a maximum at the critical threshold ( $P = 0.407$ ). A comparison of LRP lengths for the two rules shows an interesting trend (column 5 in tables 1 and 2). At low habitat densities – at values of  $P$  equal to or less than about 0.4 – the LRP is somewhat longer under the next-nearest neighbor rule than under the nearest neighbor rule (figure 6). This occurs because, at low densities, a longer, meandering path requiring fewer restored cells is able to connect the north and south edges under the next-nearest neighbor rule. This same path, however, would not provide connectivity under the nearest neighbor rule. An LRP would require more restored cells under the nearest neighbor rule, but a shorter LRP would result. At larger values of  $P$ , however, the LRP becomes shorter under the next-nearest neighbor rule. The maximum LRP length is about 67 units (at  $P = 0.407$ ), 9% less than the maximum length of about 73 units (at  $P = 0.593$ ) under the nearest neighbor rule.

#### 4.3. Third-nearest neighbor rule

Under the third-nearest neighbor rule (table 3), in comparison to the other two rules, much less restoration is needed at each value of  $P$  to reestablish connectivity. GSPs under this rule require, on average, no more than

45% as many restored cells as under the nearest and next-nearest neighbor rules. Similarly, LRPs require, on average, no more than 36 and 49% as many restored cells as under the nearest neighbor rule and next-nearest-neighbor rule, respectively.

This reduction in restoration is expected, as organisms operating under this rule can traverse one-cell gaps in habitat. In fact, to minimize the amount of restoration needed, the algorithm tries to identify paths in which habitat cells are separated by nonhabitat gaps. At low values of  $P$ , the resulting habitat path is likely to resemble a series of “stepping stones.” Hence, under this neighbor rule, connectivity can be achieved with relatively few restored cells even at low habitat densities.

#### 4.4. Comparison to other lattice sizes

To give some indication of the effects of a change in landscape scale, we performed parallel experiments using  $24 \times 24$  (576-cell) lattices, and compared the results to those for the  $48 \times 48$  lattices. We found that for each value of  $P$  the mean number of restored cells scaled much more closely to  $L$ , the width of the landscape, than to  $N$ , the total area. Hence, a doubling of width (24 to 48) or fourfold increase in area resulted in roughly a doubling of the number of restored cells for both GSPs and LRPs (table 4). Similarly, the length of the LRP scaled more closely to  $L$  than to  $N$ , although this relationship became somewhat weaker as the critical threshold was approached from below. At the critical threshold, the length of the LRP was 52% longer than  $L$  in the  $48 \times 48$  lattice, but only 38% longer than  $L$  in the  $24 \times 24$  lattice (table 4). The  $24 \times 24$  lattice may also be interpreted as representing the  $48 \times 48$  landscape, but at a lower resolution (larger cell size). Under this interpretation, the fourfold increase in cell size of the  $24 \times 24$  lattice resulted in roughly a doubling of the amount of restoration needed.

## 5. Discussion

Previous studies in neutral landscape modeling have investigated the implications of landscape fragmentation on habitat connectivity and organism mobility. In this paper, we investigate implications of the reverse process, habitat restoration, for increasing connectivity by establishing corridors. Although we model fragmentation as a random process, we model corridor restoration as a deliberate decision-making process that can be “optimized” to minimize the amount of restoration or minimize corridor length. Our results may be used to predict the expected minimum amount of restoration needed to establish a connecting corridor in a simple fragmented landscape of rectangular cells.

The benefits of targeting restoration to minimize the amount of restoration needed can be large in comparison to restoration that is undertaken in an ad hoc or random

fashion. As an illustration, consider a  $48 \times 48$  lattice in which 50% of the cells are habitat cells ( $P = 0.5$ ) and the remaining cells are nonhabitat. Under the nearest neighbor rule, if nonhabitat cells were restored at random, about 230 cells (10% of the total lattice area) would need to be restored to realize a connecting path by establishing a percolating cluster. This is the number of cells needed to make  $P$  equal to 0.6, just above the critical threshold. In contrast, in the same landscape, it would be possible to establish a geometric shortest path by restoring only 16 or 17 cells. Furthermore, only four or five restored cells would be needed for a least-restoration path. This example indicates that shortest-path connections offer potential savings of more than 90% over ad hoc restoration. Although these results are based on simulated landscapes, they are suggestive of the efficiencies that may be realized if restoration efforts in real landscapes are carried out in a coordinated and systematic manner.

These results provide new information that should be useful to planners and decision makers for prioritizing conservation resources for real landscapes. For example, conservation funds might be directed toward fragmented landscapes in which  $P$  is below the critical threshold, as such landscapes are unlikely to have an existing connecting path. Furthermore, in allocating restoration funds to multiple landscapes, resources might be distributed to ensure that a connecting path is realized in a maximum number of landscapes. Of course, optimization procedures would need to be applied directly to the landscape(s) in question to identify specific restoration needs, but our research provides an advance estimate of what these needs are likely to be, given the level of fragmentation and the neighbor rule for connectivity.

The GSP and LRP corridors generated here are two of many possible corridor configurations. The two are likely to be very different, especially near the critical threshold where the LRP is likely to meander quite a bit. Conservation planners may then be interested in other corridors that represent a compromise between the two – corridors that are less expensive than the GSP but provide a more direct connection than the LRP. Compromise paths, which highlight efficient tradeoffs between the amount of restoration and directness, can be identified through multiobjective mathematical programming (e.g., [33]).

We have presented the methodology solely in terms where restoration should or could take place to realize efficient habitat corridors. However, conservation decisions are typically made within a dynamic context of shifting land uses and ownership patterns. Land that is presently suitable habitat may be at risk of development. Hence, decisions to restore degraded parcels may need to be made in tandem with decisions to preserve parcels that are at risk of losing their habitat values. Trade-offs may exist between restoration and preservation in that different corridor configuration may be possible, depending on the number of restored cells vs the number of preserved cells in the corridor. The analysis of such tradeoffs is another task for

multiobjective optimization and is suggested as an area for future research.

Corridors such as the GSP and LRP represent the minimum in resources that would be needed to establish a single path between one edge of the landscape and the other. Some (possibly many) habitat patches or clusters may remain unconnected to a GSP or LRP corridor, depending on the extent of fragmentation. In real landscapes, the GSP and LRP, as “minimalist” approaches, may not be optimal or even adequate once other restoration objectives are taken into account. Other possible objectives are to minimize the extent of habitat edge or maximize the total restored area. To meet such objectives, a more robust network of habitat with more extensive connectivity might be needed. Nevertheless, as efficient connections, GSPs and LRPs may represent a good first step in advance of more extensive restoration.

Our analysis is based on a number of simplifying assumptions: the landscape is modeled as a rectangular grid, habitat is a yes/no attribute, and fragmentation is a simple random process. Extensions of the research would involve relaxing these assumptions. First, although rectangular grids have advantages (they are commonly used and are compatible with raster GIS), the shortest-path methodology may be applied to other regular tessellations – triangles and hexagons – for which percolation thresholds have been derived (see, e.g., [18]). The results of a corridor restoration analysis applied to these tessellations are expected to differ from the rectangular grid results. Deriving statistical results for landscapes that have irregularly shaped parcels would be problematic, however, due to the difficulty of controlling for parcel area and adjacency.

Second, landscapes typically contain multiple types of habitat, rather than a single type. Our analysis, although presented in terms of a generic habitat type, is equally applicable to landscapes of multiple habitat types – we would only need to specify in advance the habitat type to which a nonhabitat cell would be restored (e.g., the prior habitat condition). A related issue is that of restoration cost. In the above analysis, we have considered the amount (area) of restoration needed rather than the cost of restoration. In heterogeneous landscapes, per-cell land acquisition costs and restoration costs are likely to be nonuniform, and the path of lowest cost (LCP) may therefore be different from the LRP. Land managers are likely to be interested in the LCP, but LCPs are unique to individual landscapes. Due to the many possible distributions of land costs, LCPs are unfortunately not nearly as amenable to statistical analysis as LRPs. However, in relatively homogeneous landscapes, per-cell costs may be fairly uniform, in which case the LRP would be a good surrogate for the LCP.

The third assumption to relax is that habitat fragmentation may need to be represented as a more complex process than the simple random process used here. Real fragmentation patterns and patterns of land use may exhibit

spatial correlation and hierarchical properties. These complicating factors have already been explored to some extent in the analysis of fragmentation (e.g., [34–36]), and this research could help guide the next steps of the analysis of restoration.

## 6. Summary and conclusions

In this paper we have developed a conceptual methodology for statistically quantifying the amount of restoration that would be needed to reconnect opposite edges of a simulated fragmented landscape. This method builds on prior results of percolation theory and neutral landscape modeling. Landscape parameters addressed here include landscape size (number of cells), level of fragmentation, and neighbor rule for connectivity. We use “shortest path” optimization models to identify the mean and variance of the minimum amount of restoration needed for each of two corridor types. The principal finding is that even extensively fragmented landscapes can be efficiently reconnected with a restored corridor, although the relationship between the level of fragmentation and amount of restoration needed is nonlinear. The information gained from this analysis is a first step toward developing a broader body of knowledge that is expected to be useful to planners and decision makers for allocating resources for the large-scale restoration of fragmented landscapes. Because simulated landscapes are approximations of real landscapes, these results should be viewed as approximate benchmarks with respect to applicability to real landscapes. Extensions of this research would build upon analytic methods presented here and elsewhere to better address the complexities of real landscapes.

## Acknowledgements

We thank two anonymous reviewers for their helpful comments on an earlier draft of this paper. This research was supported by a grant from the David and Lucile Packard Foundation, Interdisciplinary Science Program. We gratefully acknowledge their support.

## Appendix

Depending on the proportion of habitat ( $P$ ), a percolating cluster – and hence a least-restoration path – may exist in a fragmented landscape before restoration. Similarly, a geometric shortest path may already exist as well. The likelihood that a GSP exists can be readily derived for simple random landscapes for the nearest neighbor and next-nearest neighbor rules. (The expression of this likelihood for the third nearest neighbor rule is more complex and is beyond the scope of this paper.)

Let  $P$  also denote the (independent) probability that a cell is designated habitat. We wish to find the probability that at least one north–south column in the  $L \times L$  lattice contains

$L$  habitat cells. The probability that an individual column contains  $L$  habitat cells is  $P^L$ , and the probability that a column contains fewer than  $L$  habitat cells is  $1 - P^L$ . The probability that all  $L$  columns in the lattice contain fewer than  $L$  habitat cells is, then,  $(1 - P^L)^L$ . Finally, the probability that at least one column contains  $L$  habitat cells is the complement of this, or  $1 - (1 - P^L)^L$ . In a  $48 \times 48$  lattice, for example, this probability is only  $6.14 \times 10^{-10}$  at the critical threshold ( $P = 0.593$ ). Even at a very high habitat density of  $P = 0.893$ , the probability is only about 0.19. Hence, for densities at which percolating clusters (with meandering paths) are virtually guaranteed to exist, GSPs are unlikely.

## References

- [1] D.A. Saunders, R.J. Hobbs and C.R. Margules, Biological consequences of ecosystem fragmentation: a review, *Conserv. Biol.* 5 (1991) 18–32.
- [2] A.P. Dobson, A.D. Bradshaw and A.J.M. Baker, Hopes for the future: restoration ecology and conservation biology, *Science* 277 (1997) 515–522.
- [3] K.M. Urbanska, N.R. Webb and P.J. Edwards, *Restoration Ecology and Sustainable Development* (Cambridge University Press, UK, 1997).
- [4] J.J. Berger, ed., *Environmental Restoration* (Island Press, Washington, DC, 1990).
- [5] S.G. Whisenant, *Repairing Damaged Wildlands* (Cambridge University Press, UK, 1999).
- [6] A.H. Hampson and G.F. Peterken, Enhancing the biodiversity of Scotland’s forest resource through the development of a network of forest habitats, *Biodivers. Conserv.* 7 (1998) 179–192.
- [7] C.S. ReVelle, J.C. Williams and J.J. Boland, Counterpart models in facility location science and reserve selection science, *Environ. Model. Assess.* 7(2) (2002) 71–80.
- [8] A.S. Rodrigues and K.J. Gaston, Optimisation in reserves selection procedures – why not?, *Biol. Conserv.* 107 (2002) 123–129.
- [9] J. Hof, M. Bevers, L. Joyce and B. Kent, An integer programming approach for spatially and temporally optimizing wildlife populations, *For. Sci.* 40 (1994) 177–191.
- [10] S.A. Snyder, L.E. Tyrrell and R.G. Haight, An optimization approach to selecting research natural areas in national forests, *For. Sci.* 45 (1999) 458–469.
- [11] J. Sessions, Solving for habitat connections as a Steiner network problem, *For. Sci.* 38 (1992) 203–207.
- [12] J.C. Williams, Delineating protected wildlife corridors with multi-objective programming, *Environ. Model. Assess.* 3 (1998) 77–86.
- [13] J.L. Tucker, D.B. Rideout and R.B. Shaw, Using linear programming to optimize rehabilitation and restoration of injured land: an application to US army training sites, *J. Environ. Manag.* 52 (1998) 173–182.
- [14] K.A. With, The application of neutral landscape models in conservation biology, *Conserv. Biol.* 11 (1997) 1069–1080.
- [15] R.H. Gardner, B.T. Milne, M.G. Turner and R.V. O’Neill, Neutral models for the analysis of broad-scale landscape pattern, *Landsc. Ecol.* 1 (1987) 19–28.
- [16] K.A. With and T.O. Crist, Critical thresholds in species’ responses to landscape structure, *Ecology* 76 (1995) 2446–2459.
- [17] L. Tischendorf and L. Fahrig, On the usage and measurement of landscape connectivity, *Oikos* 90 (2000) 7–19.
- [18] R.E. Plotnick and R.H. Gardner, Lattices and landscapes, *Lect. Math. Life Sci.* 23 (1993) 129–157.

- [19] D. Stauffer and A. Aharony, *Introduction to Percolation Theory* (Taylor and Francis, Bristol, PA, 1994).
- [20] S.M. Pearson, M.G. Turner, R.H. Gardner and R.V. O'Neill, An organism-based perspective of habitat fragmentation, in: *Biodiversity in Managed Landscapes*, eds. R.C. Szaro and D.W. Johnston (Oxford University Press, New York, 1996) pp. 77–95
- [21] D. Simberloff and J. Cox, Consequences and costs of conservation corridors, *Conserv. Biol.* 1(1) (1987) 63–71.
- [22] R.F. Noss, Corridors in real landscapes: a reply to Simberloff and Cox, *Conserv. Biol.* 1(2) (1987) 159–164.
- [23] R.J. Hobbs, The role of corridors in conservation: solution or bandwagon?, *Trends Ecol. Evol.* 7(11) (1992) 389–392.
- [24] D. Simberloff, J.A. Farr, J. Cox and D.W. Mehlman, Movement corridors: conservation bargains or poor investments?, *Conserv. Biol.* 6(4) (1992) 493–504.
- [25] P. Beier and R.F. Noss, Do habitat corridors provide connectivity?, *Conserv. Biol.* 12(6) (1998) 1241–1252.
- [26] D.J.D. Earn, S.A. Levin and P. Rohani, Coherence and conservation, *Science* 290 (2000) 1360–1364.
- [27] M.E. Soule and M.E. Gilpin, The theory of wildlife corridor capability, in: *Nature Conservation 2: The Role of Corridors*, eds. D.A. Saunders and R.J. Hobbs (Surrey Beatty & Sons, New South Wales, 1991) pp. 3–8.
- [28] R.T.T. Forman, Landscape corridors: from theoretical foundations to public policy, in: *Nature Conservation 2: The Role of Corridors*, eds. D.A. Saunders and R.J. Hobbs (Surrey Beatty & Sons, New South Wales, 1991) pp. 71–84.
- [29] F.K. Hwang, D.S. Richards and P. Winter, *The Steiner Tree Problem* (North-Holland, Amsterdam, 1992).
- [30] F.S. Hillier and G.J. Lieberman, *Introduction to Operations Research* (McGraw-Hill, New York, 1986).
- [31] G.B. Dantzig, *Linear Programming and Extensions* (Princeton University Press, New Jersey, 1963).
- [32] G. Gallo and S. Pallottino, Shortest path algorithms, *Ann. Oper. Res.* 13 (1988) 3–79.
- [33] J. Cohon, *Multiobjective Programming and Planning* (Academic Press, New York, 1978).
- [34] R.V. O'Neill, R.H. Gardner and M.G. Turner, A hierarchical neutral model for landscape analysis, *Landsc. Ecol.* 7 (1992) 55–61.
- [35] R.H. Gardner, R.V. O'Neill and M.G. Turner, Ecological implications of landscape fragmentation, in: *Humans as Components of Ecosystems*, eds. M.J. McDonnell and S.T.A. Pickett (Springer-Verlag, New York, 1993) pp. 208–225.
- [36] K.A. With, R.H. Gardner and M.G. Turner, Landscape connectivity and population distributions in heterogeneous environments, *Oikos* 78 (1997) 151–169.