The use of graph theory in the design of conservation area networks: Methods for maximizing network connectivity

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The use of graph theory in the design of conservation area networks: Methods for maximizing network connectivity

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Abstract

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Maintaining a viable conservation area network (CAN) often requires adding sites to increase connectivity. Graph-theoretic techniques are used to find such sites for CANs in the Eastern Himalayas, Ecuador, and Mexico. To identify sites connecting conservation areas, we score each external site based on: (i) the frequency with which an algorithm for prioritizing places based on biodiversity content selects the site and (ii) its distance from other sites. To identify the highest quality paths between the conservation areas, we rescore the external sites using: (i) the inverse distance to anthropogenically-transformed areas; (ii) distance to existing

conservation areas; and (iii) the physical length of the path. We report (i) the number of connected components (Mexico = 40, Ecuador = 20, Himalayas = 1), (ii) the number of edges that may be removed to fragment the network (Mexico = 0, Ecuador = 0, Himalayas = 14), and (iii) the number of minimum spanning trees, that is, the smallest sets of connections required to link all conservation areas (Mexico = 14, Ecuador = 183, Himalayas = 1). Paths connecting conservation areas contain 83 percent fewer sites than the conservation areas in Ecuador but 37 percent more sites in the Himalayas. Finally, we compare the connectivity of the existing national parks of Ecuador with that of a CAN selected by a biodiversity place-prioritization algorithm. Both networks have about the same number of connected components, but the national parks are more connected than the sites the algorithm selects insofar as fewer paths and less land are needed to link the former together (19 components; 26 paths; 2204 km.^{2}) than the latter (20 components; 122 paths; 13196 km.^{2}).

Table of Contents

List of Tables

List of Figures

I. INTRODUCTION

This thesis describes methods based on graph algorithms for optimizing the connectivity of conservation area networks (CANs), which are sets of sites administered so as to protect threatened features of biodiversity (Sarkar 2003). CANs include places where anthropogenic disturbance is mostly proscribed, such as national parks or reserves, as well as sites where it is regulated less closely, such as limited-harvesting areas. The networks in question may already exist or be a set of sites that has been proposed for protection. Planners may wish to increase the connectivity of a CAN so as to facilitate seasonal migration or permanent dispersal in the event that some sites in the network are destroyed. Conversely, network connectivity may need to be minimized so as to halt the spread of disease or invasive species. Only the former is discussed here.

In the analysis described below, CANs are modeled as graphs, discrete mathematical structures consisting of points ("vertices") connected by lines ("edges"). Previous research in landscape ecology that pertains to graph theory can be classified into 3 groups: (i) analyses of graph-like networks, (ii) studies of type (i) that explicitly use the term "graph", and (iii) studies of type (ii) that use graph algorithms to analyze ecological systems. Here, I will discuss the second and third type of study (though the landscape ecological literature contains thousands of works of type [i]). Graph theory has also been used extensively in phylogeny and epidemiologist. In landscape ecology, Fahrig, Lefkovitch and

Merriam (1983) used the term “graph” to describe a woodlot system in the St. Lawrence region in Ottawa, Canada, in which forest remnants (vertices) were connected by fencerows (edges). To determine the effect of connectivity on subpopulation viability, Fahrig *et al*. simulated the dispersal of mice (*Peromyscus leucopus*) and chipmunks (*Tamias striatus*) along the fencerows among 4 lots connected by 0 - 11 fencerows. Isolated populations were predicted to go extinct in 3 to 4 years whereas better-connected populations were predicted to survive up to 100 years. A surprising result was that there were arrangements of subpopulations connected by 2 or 3 edges only that were predicted to survive as long as the maximally-connected arrangement (6 edges). This work falls into category (ii) because no graph algorithms are used.

Cantwell and Forman (1993) analyzed aerial photographs of 25 landscapes ranging in area from 10 to 10 000 ha, treating circular shapes in the photographs as the vertices of a graph and straight lines connecting the vertices as edges. Under Cantwell and Forman’s approach, dissimilar structures within a landscape are treated as vertices (for example, fields, house clearings, and woods). Consequently, what constitutes a vertex differs between landscapes. After designating various elements of a landscape as vertices, Cantwell and Forman found the degree of each vertex, that is, the number of edges incident to the vertex. When the same landscape element was treated as a vertex in different landscapes, the average degree of the vertex differed between landscapes. In addition, Cantwell and Forman identified 7 common configurations of nodes and edges present in several landscapes. They argue that representing landscapes as graphs can be of use in the management of threatened species to the extent that habitat patches with few linkages to other sites face a greater extirpation risk than more extensively connected sites and may warrant more active management. Cantwell and Forman's paper includes more terminology from graph theory than Fahrig *et al*.'s, but they do not use any graph algorithms.

Keitt and collaborators modeled the habitat sites of the Mexican Spotted Owl (*Strix occidentalis lucida*) in 4 states in the southwestern United States as the vertices of graph (Keitt 2003; Keitt, Urban and Milne 1997; Urban and Keitt 2001). Keitt (1995) also mentioned graphs in the context of this system, but used an approach based on percolation theory rather than graph theory. Urban and Keitt used a graph algorithm, Prim's minimum spanning tree algorithm, and analyzed graph properties such as connected components and cut edges. They assigned edges to each pair of vertices such that the weight of the edge reflected the probability of dispersal from one of the vertices to another; this probability decreased with distance. Results indicated that an average dispersal distance of 45 km or greater was required to maintain the connectivity of the owl population. A similar approach was used to assess the extent to which a landscape in South Carolina was perceived as connected by the prothonotary warbler (*Protonotaria citrea*) and the American mink (*Mustela vison*); the graph-based model indicated that the area is 5 times more connected with respect to the migratory needs of the latter species than the former (Bunn, Urban and Keitt 2000). For both the southwestern landscape and the South Carolina one, the edges of the landscape quality graph represented potential corridors between habitat sites and the minimum spanning tree of the habitat sites of the target species was found.

Having mentioned previous uses of graph theory in landscape ecology, I will now discuss the biological importance of connectivity in order to provide a motivation for developing procedures to quantify connectivity (II.1). I will then present a GIS model for assessing connectivity called a “contiguity graph” (II.2-3). Each vertex of the contiguity graph corresponds to one cell in the study region. The next section (II.4.1) introduces the “landscape quality graph,” which models the landscape at a higher level of abstraction than the contiguity graph to the extent that each vertex of the former represents one conservation area (each conservation area may have more than one cell). Some properties of graphs useful for measuring connectivity in the context of place prioritization are then detailed (II.4.2). I then carry out a graph-based analysis of connectivity on data sets from India, Ecuador, and Mexico (II.5 and III). These data sets were used because they are all from developing countries where there are plans to augment or institute a CAN system so as to increase the amount of biodiversity under governmental protection. The final section identifies similarities among the landscape quality graphs in the 3 study regions and offers suggestions about the role of graph theory in landscape ecology.

II. METHODS

1. The Biology of Connectivity

In the paper that introduced the term “connectivity” in landscape ecology, Merriam (1984) states that a landscape is connected if structures in the landscape that serve similar functions can be reached from one another. Later work by the same group (Taylor *et al.* 1993) equated connectivity with the extent to which the landscape helps or hinders animals’ search for resources (the requirement about functionally-similar structures was dropped). Analyses of landscape connectivity often draw a distinction between patches of suitable habitat and the “matrix” of inhospitable sites surrounding the habitat. This is simplistic to the extent that the matrix is heterogeneous and hospitable to varying degrees (Murphy and Lovett-Doust 2004). Connectivity can be divided into “structural connectivity,” which refers to features of a landscape independent of the properties of the organisms present and “functional” definitions of connectivity based on organisms’ behavior (Tischendorf and Fahrig 2000a). The total number of immigrants into all sites in the landscape (“dispersal success”) and the total distance between all pairs of patches (“search time”) have also been used to measure landscape connectivity (Tischendorf and Fahrig 2000b). Among the factors that reduce connectivity are habitat loss and habitat fragmentation. Definitions of fragmentation include increases in the number of habitat patches, decreases in the size of patches, and increases in the isolation of patches (Fahrig 2003). Over evolutionary time scales, fragmentation may hasten the extinction of species because it partitions populations into subgroups with decreased genetic variability and a diminished capacity to respond to environmental change (Stockwell, Hendry and Kinnison 2003). Over shorter time scales, species' persistence has been shown to depend on properties of the landscape related to connectivity. Nest success of the black-capped vireo (*Vireo atricapillus*), an endangered passerine that breeds in deciduous scrubland in central Texas, decreases with increasing fragmentation of scrubland sites due to increased brood parasitism by the brown-headed cowbird (Weinberg, Hayden and Cornelius 1998). The persistence of long-tailed tit (*Aegithalos caudatus*) populations in tree stands in central Sweden was found to depend on landscape parameters (the distance to the next patch and the proportion of suitable habitat in the landscape within 1 km of a given patch) and not on properties of each stand such as tree height or size (Jansson and Angelstam 1999). In plants, patch fragmentation decreases reproductive success because the probability of pollinator visits and the quality of pollen transfer decrease with inter-patch distance (Murphy and Lovett-Doust 2004); in this study, connectivity was considered beneficial for plant populations to the extent that there is higher quality pollen transfer in clumped populations than widely in dispersed populations. In these examples, fragmentation effects animal and plant populations adversely by reducing dispersal, but the effects of fragmentation *per se* are more controversial. Fragmentation may be beneficial for threatened species if habitat fragmentation divides a single population into groups able to survive independently. Under some scenarios, this reduces the probability that the species will be wiped out by a catastrophe.

2. Basic GIS Model

Each study region is divided into cells, the most basic units of the subsequent analysis. I stored each cell as an object with 5 data members (see below), though this is not essential for the GIS model. The set of all cells in the study area (hereafter, the set L), is partitioned into the set M of masked cells and the set A of all cells available for conservation planning. M is divided into the set R of extensively anthropogenically-transformed cells and the set $O = M - R$ of other cells inappropriate for conservation planning. A has subsets P, the set of cells that can potentially be included in a CAN, and B, the set of existing CAN cells, if the study region already has some conservation areas. The graph-based analysis described below requires the following data for each cell $a \in A$:

(i) a set, $Adj[a]$, consisting of the cell's neighbors, that is, those cells physically adjacent to a;

(ii) the longitude and latitude of the centroid of the cell (so that the results of the analysis can be displayed and further analyzed in a GIS software package);

(iii) a "contiguity" score, $contiguity[a]$. In the analysis described below, connectivity scores are rescaled such that $0 \le contiguity[a] \le 1$, where 0 is the best score in the ranking system and 1 the worst;

(iv) a "landscape quality" score, $landscape\_quality[a]$, rescaled such that $0 \le landscape\_quality[a] \le 1$, where 0 is the best score and 1 the worst.

(v) records of the probabilistic expectations of biodiversity surrogates present in the cell (these data are needed for the prioritization of cells based on biodiversity content).

In the examples presented here, all cells $a \in A$ were grid squares, but other cell shapes can be used as long as $Adj[a]$ can be determined. Cells shaped like natural features of the landscape such as watersheds (Bojórquez-Tapia *et al.* 2004) or administrative units like census plots (Rodrigues, Gregory and Gaston 2000) are often used in the design of CANs.

3. CONTIGUITY GRAPH

A place-prioritization algorithm is used to select S_i, the set of cells in network i, from A such that each biodiversity surrogate present in A satisfies a targeted level of representation (the Expected Surrogate Set Covering Problem [ESSCP]) (Sarkar *et al.* 2004). The set $T_i = P - S_i$ contains all potential CAN cells not included in the $i-$th solution to the ESSCP. When the study region already contains conservation areas, the cells in B are used to initialize the algorithm (unless otherwise specified); if so, $S_i \subseteq A$. Otherwise, $S_i \subseteq P$. In the examples below, the cells in S_i are selected so as provide a solution for the ESSCP using the ResNet software package, which implements an iterative rarity- and complementarity-based heuristic algorithm (Garson *et al*. 2002). The set $CA_i = \{CA_i^1, CA_i^2, \ldots, CA_i^n\}$ of conservation areas is a *partition* (Harary, Norman, and Cartwright 1965) of S_i such that each subset $CA_i^j \in CA_i$ contains the cells in 1 conservation area, $CA_i^j \cap CA_i^k = \emptyset, 1 \leq j \leq n, 1 \leq k \leq n$, and $\bigcup_{j=1}^{n} CA_i^j = CA_i$.

Next, a mapping $g : S_i \rightarrow V_c$ assigns each cell $s \in S_i$ to a vertex v of a directed, weighted "contiguity" graph $G_c = (V_c, E_c)$. The purpose for constructing the contiguity graph is to find the shortest path between pairs of cells in separate conservation areas. Each such path becomes an edge of the landscape quality graph, which represents the study region at a higher level of abstraction than the contiguity graph (see below). The function used to assign weights to the edges of the landscape quality graph need not be the same as the function g used to assign weights to the edges of the contiguity graph.

g is bijective since each $s \in S_i$ is mapped to a distinct $v \in V_c$ (injective) and for each $v \in V_c$, $g^{-1}(v) \in S_i$ (surjective). The edge set E_c contains an ordered pair $e = (u,v)$ if for a given pair of vertices $u,v \in V_c$, $g^{-1}(v) \in Adj[g^{-1}(u)]$. A mapping $w_c : E_c \to \mathbf{R}$ assigns weights to each $e \in E_c$ such that $w_c(u,v) = \begin{cases} contiguity[g^{-1}(v)] & g^{-1}(v) \in T_i \\ 0 & g^{-1}(v) \in S_i \end{cases}$; that is, edges pointing to vertices that represent cells in conservation areas have weight 0 whereas the weight of an edge pointing to a vertex that represents a cell outside of a conservation area is the contiguity score of the cell to which the edge points. The relation vRz ("are mutually reachable", $v, z \in V_C$) is an equivalence relation on $V_{sc} \subseteq V_C$, a strongly connected component of G_L, but the relation w_c is not an equivalence relation on V_C because w_c is not symmetric ($w_c(u,v) \neq w_c(v,u)$ if $u \in S_i$ but $v \in T_i$). (A strongly connected component of a digraph is the analogue of a connected component in an undirected graph). w_c is not injective because 2 edges $e, e' \in E_C$ may have the same weight and it is not surjective because the set of edge weights does not exhaust the real numbers (by assumption, $|E_C| < \infty$).

4. GRAPH ALGORITHMS

4.1 Construction of the landscape quality graph

We now construct a "landscape quality graph," G_L in order to represent the landscape at a higher level of abstraction than G_c. First, we find the shortest path between each pair of elements of CA_i using Dijkstra's algorithm for the single source shortest path problem on G_c (Cormen *et al*. 2001). Dijkstra's algorithm was used rather than the Bellman-Ford algorithm for the single-source shortest path problem because the former has a faster asymptotic running time and no negative weights were present in the graph. Given a "source" vertex s, the algorithm finds the length $\delta(s,v)$ of a shortest path from s to v for each $v \in V_c - \{s\}$ through a sequence of relaxations. A path p_i from vertex v_i to vertex v_j is a sequence of vertices $< v_i, v_1, v_2, \ldots, v_j >$ such that there is an edge (v_i, v_{i+1}) from each vertex to its successor in the sequence. A "shortest" path is minimal with respect to the summed weight of its edges (but not necessarily the number of edges). The implementation of the algorithm also kept track of the sequence of vertices in the shortest path (Siek, Lee, and Lumsdaine 2001). In each call to Dijkstra's algorithm, the source vertex was some $v \in V_c$ such that $g^{-1}(v)$ was the cell in its conservation area closest to the centroid of the conservation area found using the *XTools* 3.1 extension of the ArcMap 8.1 GIS software package (ESRI 2001).

Dijkstra's algorithm was called $|CA_i| - 1$ times, so as to find a shortest path from each vertex $s_i \in SV$, the set of source vertices, to every vertex $v \in V_c - \{s_i\}$. The set SP of shortest paths was then searched for each path $p = < s^1, v_1^1, v_2^1, \ldots, v_{i-1}^1, v_i^1, v_1^2, v_2^2, \ldots, v_{i-1}^2, v_i^2, v_1^3, v_2^3, \ldots, v_{i-1}^3, v_i^3 >$ such that:

(i) for each vertex $v \in < s^1, v_1^1, v_2^1, \ldots, v_{i-1}^1, v_i^1 > \vee < v_1^3, v_2^3, \ldots, v_{i-1}^3, v_i^3 >$, $g^{-1}(v) \in S_i$;

(ii) for each vertex $v \in < v_1^2, v_2^2, \ldots, v_{i-1}^2, v_i^2 >$, $g^{-1}(v) \in T_i$;

(iii) $s^1, v_1^3 \in SV$.

All shortest paths $p \in SP$ begin with a vertex that corresponds to the centroid of a conservation area, but the set $SPR \subseteq SP$ of shortest paths satisfying (i) – (iii) excludes shortest paths ending with any vertex that does not correspond to the centroid of a conservation area (for example, shortest paths that end outside conservation areas). In addition, requirements (i) – (iii) eliminate shortest paths that cross through any conservation area other than the starting and ending conservation areas.

We now construct $G_L = (V_L, E_L)$, a condensation on G_c with respect to the partition CA_i. G_L is an undirected subgraph such that there is 1 vertex

$v \in V_c$ for each subset of CA_i (Harary, Norman, and Cartwright 1965). The label of the vertex is the same as the name of the subset. E_L has an edge (CA_i^j, CA_i^k) if SPR contains some shortest path $q =< s^1, v_1^1, v_2^1, \ldots, v_{i-1}^1, v_i^1, v_1^2, v_2^2, \ldots, v_{i-1}^2, v_i^2, v_1^3, v_2^3, \ldots, v_{i-1}^3, v_i^3 >$ such that $g^{-1}(s^1) \in CA_i^j$ and $g^{-1}(v_i^3) \in CA_i^k$. The weight assigned to (CA_i^j, CA_i^k) can be based on the contiguity scores of the cells that correspond to the vertices in q or based on other vertex or cell attributes (see below).

4.2. Analysis of the landscape quality model.

At this stage in the analysis, I identify the following properties of the landscape quality graph G_L:

4.2.1. The connected components of G_L: Connected components of G_L are equivalence classes of vertices under the "is reachable from" relation (Cormen *et al*. 2001). The set of connected components $V_{cc} = \{\{V_{1i}, \ldots, V_{1n}\}, \{V_{2i}, \ldots, V_{2n}\}, \ldots\}$ is a partition of V_L and $|V_{cc}| \geq 1$. If $M = \varnothing$ and $|SP| = |SPR|$, then $|V_{cc}| = 1$ (in this case G_L is said to be "connected"). If the antecedent is false, either because some cells in the study region are unavailable for conservation planning or some potential edges were dropped because they crossed through other conservation areas, the number of components will be strictly greater than 1. The connected components were identified using a depth-first search (Siek, Lee, and Lumsdaine 2001). A depth-first search was used to find the connected components instead of a disjoint-sets approach because the vertex set of the landscape quality graph does not change once the graph has been constructed (in this sense, the landscape quality graph is "static"). Were the landscape quality graph not static, the disjoint-sets method would be more suitable.

4.2.2. All minimum spanning trees (MSTs). A subgraph H of graph G "spans" G if $V_H = V_G$ (Gross and Yellen 1999). A spanning tree is a spanning subgraph that is acyclic and connected (that is, a tree). A MST is a spanning tree such that the summed edge weight is minimized. Prim's MST (Cormen *et al*. 2001, Lenguaer 1990) algorithm was implemented using a min-heap priority queue Q in which those vertices $v \in V_C$ not yet added to the MST ($v \in Q$) were sorted in non-decreasing order according to $landscape\_quality[v]$. I constructed all MSTs of each component of G_L using the following procedure: If during iteration i of Prim's algorithm, there was more than 1 vertex in the set MQ_i of vertices such that $landscape\_quality[v] = \min_{v \in Q}\{landscape\_quality[v]\}$ the incipient MST MST_i was copied, a vertex was removed from MQ_i and added to MST_i, and the execution of Prim's algorithm continued. The copy of MST_i was stored in the queue I_MST of incipient MSTs and MQ_i was stored in the queue MQ of priority queues. Upon completion of the first MST, another vertex was removed from MQ_i, added to the stored copy of MST_i, and Prim's algorithm proceeded. If at iteration $j > i$ of Prim's algorithm, $|MQ_j| > 1$, a copy of the incipient MST at iteration j, MST_j, was enqueued I_MST in and MQ_j was enqueued in MQ. The procedure terminated when $I\_MST = \emptyset$ and $MQ = \emptyset$.

The procedure was verified by finding all MSTs of the all of the complete graphs from K_2 to K_7. A complete graph $K_n(V,E)$ is an undirected graph such that for each $v \in V$, $Adj[v] = V - \{v\}$ and $|V| = n$. For each of the complete graphs, all edges were given the same weight so that each spanning tree was a MST. The number of distinct spanning trees found using the procedure described above for each $K_n, 2 \le n \le 7$ equaled the number of spanning trees predicted by Cayley's Theorem, which states that the number of spanning trees on $K_n = n^{n-2}$ if $n \ge 2$ (Gibbons 1985).

4.2.3. All minimum edge cut sets: An edge cut set E_{CS} of a connected graph $G = (V, E)$ is a subset of E such that the number of connected components of $G' = (V, E - E_{CS})$, $|G'| > 1$. A minimum edge cut set is a cut set such that $|E_{cs}|$ is as small as possible. Edge weights are not taken into account in defining E_{CS}. An algorithm for finding 1 minimum cut set (Matula 1987) was modified so as to find all such sets. Matula's algorithm constructs a partition S, T, U of V_L initialized as follows:

(i) $S \leftarrow \delta$, a vertex of minimum degree in V_L;

(ii) $T \leftarrow \forall v \in V_L$ such that $\exists s \in S$ such that $v \in Adj[v]$;

(iii) $U \leftarrow V - S - T$;

(iv) $A \leftarrow \{v\}, \overline{A} \leftarrow V - \{v\}$;

(v) $Min-cut\ set \leftarrow (A, \overline{A})$.

During subsequent iterations, Matula's algorithm finds a vertex v of minimum degree in U and a minimum cut $(B, \overline{B})$ such that $v \in \overline{B}$ and $S \subset B$. Then v is added to S, T is updated as per (ii), U is updated as per (iii), and $Min-cut\ set \leftarrow (B, \overline{B})$. Matula's algorithm terminates when $U = \varnothing$. The modification of Matula's algorithm is similar to the modification of Prim's algorithm described above. If the cardinality of the set MD_j of minimum degree vertices in $V - S$, $|V - S| > 1$ at some iteration $j \geq 0$ (iteration 0 is the initialization stage), copies of S_j, the set S at iteration j, T_j, the set T at iteration j, and U_j, the set U at iteration j are stored in queues. The algorithm then selects 1 vertex v_j from MD_j, enqueues $MD - \{v_j\}$ and proceeds as per Matula's algorithm. When the min-cut set constructed with v_j is completed, $MD - \{v_j\}$, S_j, T_j, and U_j are dequeued and a new minimum cut set is constructed with some vertex $v_k \in MD - \{v_j\}$.

5. DATA SETS

5.1 Eastern Himalayas

The study area was the Eastern Himalayas ecoregion, which is the set of World Wildlife Fund ecoregions that intersect with the Eastern Himalayas region of India. Sites in the Eastern Himalayas lower than 400 m in elevation were excluded from the analysis. The remaining area of the ecoregion was divided into 1 395 0.2 ° x 0.2 ° cells. Associated with each cell were presence absence records for 32 abiotic parameters: mean annual temperature (divided into 10 equal interval classes), mean annual precipitation (divided into 10 equal interval classes), 4 soil types, the minimum temperature of the coldest period of the year (divided into 4 equal interval classes), and the maximum temperature of the warmest period (divided into 4 equal interval classes). These data were used as abiotic "surrogates" for biodiversity since data on the locations of rare or threatened species or habitat types were not available for the region (Sarkar et al., submitted). The ResNet software package constructed a CAN for these surrogates at a targeted 10 % level of representation for each. An adjacency preference was imposed so that cells would be selected in clusters. No masked cells or existing conservation areas were included in the analysis so that $|A| = |P| = |L| = 1395$.

The contiguity score of each cell equaled the frequency with which the cell was selected in 100 solutions generated by ResNet with the aforementioned target but without the adjacency preference. (Scores were rescaled so that cells selected frequently had lower scores than those rarely selected). Thus, the shortest path between each pair of conservation areas found during the contiguity establishment procedure was not necessarily the shortest with respect to physical distance. The sets of cells selected differed to some extent among solutions because each solution was generated from a different randomization of the input file. (The randomization shuffled the order of cells in the input list but did not change any attribute of a given cell.) The landscape quality score assigned to each cell equaled the minimum target level (20, 40, 60, 80 or 100 %) at which the cell was selected by ResNet (Figure 1).

5.2 ECUADOR

Continental Ecuador was divided into 61 554 2 km. x 2 km. cells (for details see Sarkar *et al*. 2004). 37727 cells were available for conservation planning after anthropogenically-transformed cells were removed. Hence $A \subset L$, $|A| = 37727$, and $|M| = 23\,927$. Associated with each $a \in A$ were the probabilistic expectations of 46 modeled vegetation classes, which served as biodiversity surrogates, and the minimum distance from the cell to an anthropogenically-transformed area. Two place-prioritization procedures were used. First, ResNet was initialized with the cells in the existing conservation areas. There are 10 303 such cells in 39 conservation areas comprising 14 percent of Ecuador's continental land area. The number of cells per conservation area ranged from 1 –2 769. Second, ResNet selected a conservation area network *ab initio* (without taking the existing conservation areas into account). In both cases, ResNet used a 10 % target for each surrogate and an adjacency preference. Each cell $t_i \in T_i$ was assigned the same contiguity score so that the shortest path between each pair of conservation areas contained as few cells as possible. This will be referred to as the "physical distance" contiguity model. The landscape quality score of each cell equaled the inverse distance from the cell to an anthropogenically-transformed area binned into 3 distance classes ("coarse-grained" landscape quality model) or 5 distance classes ("fine-grained" model).

5.3 MEXICO: TRANSVOLCANIC REGION

The transvolcanic belt of central Mexico was divided into 106 026 cells at a $0.01° \times 0.01°$ scale of longitude $\times$ latitude (Fuller, Mayfield, and Sarkar 2004). The average cell area was 1.163 $km.^2$ and the total cell area was 123 355 $km.^2$. Sites lacking primary or secondary vegetation were deemed anthropogenically transformed and unsuitable for conservation planning. Such cells amounted to 36.084 % of the area of the region ($|M| = 38274$). The existing CAN consists of 39 national parks with a total area of 9 179 $km.^2$ or 7.441 % of the area of the region. As in the previous examples, the place-prioritization algorithm selected cells so as to provide a 10 % representation of the modeled habitat sites of the biodiversity surrogates, 99 non-volant mammal species. Initialized with the existing CAN, ResNet selected an augmented CAN consisting of 10 620 cells with a total area of 12 390.697 $km.^2$ or 10.045 % of the area of the region. The landscape quality graphs were constructed by weighting edges based on (i) physical distance and (ii) solution frequency (see above). The plant distributions came from remotely-sensed data whereas the mammal distributions were models generated by GARP (Stockwell and Peters 1999).

III. RESULTS.

1. Eastern Himalayas

ResNet selected 15 conservation areas for the Eastern Himalayas comprising 134 cells. Hence $|S_i|$ = 134 and the landscape quality graph had 15 vertices (Figure 2). Of the 105 ($^{15}C_2$) possible edges between conservation areas in the landscape quality graph, the contiguity establishment procedure described above constructed only 39 edges. Since there were no cells blocking paths between pairs of conservation areas, this indicates that a substantial proportion of the possible edges (62.9 %) were dropped due to the requirement that no edge between conservation areas traverse an intermediate conservation area. Nevertheless, the 517 cells in the edges of the landscape quality graph took up such a large percentage of the area of the study region (37 %) that it would not be practical to add them all to the CAN. In contrast, the 14 edges of the MST comprised 97 cells (just 7% of the study region) but linked all of the conservation areas selected by ResNet (Figures 3 and 4). If planners wish to augment the connectivity of a CAN but budgetary or political constraints restrict the number of new cells that can be acquired, cells in the edges of the MST of the landscape quality graph are good candidates for addition to the network. The landscape quality graph had 1 connected component, which had only 1 minimum cut set consisting of a single edge, and 2 MSTs.

2. ECUADOR

The CAN selected *ab initio* consisted of 84 conservation areas with 3 753 cells, about 6 % of all the cells in Ecuador. The 122 edges in the landscape quality graph comprised on 3 299 cells, or an additional 5 % of the total cells (Figure 7). Unlike the Eastern Himalayas data set, in this example, a substantial proportion (39 %) of the cells in the study region belonged to the set *M* of masked cells. Thus, getting an upper bound on the number of possible edges in the landscape quality graph and assessing the extent to which potential edges were eliminated due to the requirement that edges not traverse intermediate conservation areas are less straightforward. The landscape quality graph had 20 connected components, 18 of which consisted of 3 conservation areas or fewer. For these components, identifying all minimum cut sets is trivial. Of the remaining components, 1 had 9 vertices and 3 minimum cut sets each consisting of 2 edges. The other had 51 vertices and 4 minimum cut sets consisting of 1 edge each. When the coarse-grained landscape quality model (Figure 5) was used to assign weights to the edges of the landscape quality graph, the 51 vertex component had 193 MSTs (Figures 8 and 9). Under the fine-grained model (Figure 6), this component had only 2 MSTs

The CAN selected by initializing the place-prioritization algorithm with Ecuador's existing conservation areas consisted 39 conservation areas made up

10 304 cells (Figures 10 and 11). The landscape quality graph had 26 edges made up of 551 cells (2 % of the total cells in Ecuador). There were 18 connected components, all but 1 of which had 3 or fewer vertices. The remaining component had 15 vertices and 4 minimum cut sets, each consisting of 1 edge.

3. MEXICO: TRANSVOLCANIC REGION

The landscape quality graph had 187 edges and 119 vertices. Each of the latter represents a contiguous clump of cells in the augmented CAN (Figure 13). For both models of landscape quality, 1 MST was found for each connected component of the landscape quality graph consisting of 2 or more conservation areas. The set of MSTs found when the edges of the landscape quality graph were weighted based on physical distance differs little from the set of MSTs found when edge weights were based on solution frequency (Figures 14 and 15). Two factors explain this similarity:

(i) Most cells had landscape quality scores of 0 under the solution frequency model. Repetitions of the place-prioritization procedure generate slightly different solutions because each run of the procedure uses a different randomization of the input set. In 100 runs of the place-prioritization procedure on the cells of the transvolcanic region with primary or secondary vegetation, a small proportion of the cells were selected often and most cells were never selected. As a result, the weights assigned to many edges under the solution frequency model were the same as the weights assigned under the physical distance model. (The physical distance model assigned the same weight to all edges of the graph.)

(ii) In addition, each pair of conservation areas in the landscape quality graph of the transvolcanic region is linked by a small number of edges so that the number of alternative paths between each pair is small. When the function used to assign weights to the edges of the landscape quality graph is changed from physical distance to solution frequency, in most cases, the shortest path between a given pair of conservation areas did not change with respect to which edges were included in the path. In addition, due to (i), the summed weight of the shortest path did not differ considerably between the landscape quality models for most pairs of conservation areas.

The landscape quality graph has 40 connected components ranging from 1 to 38 vertices each. There are 5 connected components with 3 or more vertices. The number of vertices per component is: 38, 15, 12, 8, and 4. The number of minimum cut sets is: 3, 2, 3, 3, and 1. The size of the minimum cut set does not depend on the number of vertices in the component to the extent that the minimum cut sets for all of these components consisted of a single edge. Nor does the number of minimum cut sets appear to depend on the number of vertices, insofar as the component with 8 vertices has as many minimum cut sets as the component with 38 vertices. For components consisting of 2 vertices, the minimum cut set is unique and consists of a single edge. Components consisting of a single vertex do not have a minimum cut.

IV. DISCUSSION.

The graph-based approach serves at least two purposes in landscape ecology. First, given an existing CAN, graph algorithms can be used to measure the extent to which the network is connected by determining the number of connected components, the cardinality of the minimum cut set, and other properties not discussed here. This allows the connectivity properties of CANs in different study regions to be compared. (van Langevelde and van der Knapp [1998] give techniques for rescaling graph properties in order to compare graphs whose vertex sets differ substantially in size.) Though the abiotic parameters, flora, and fauna of the Eastern Himalayas, Ecuador, and central Mexico differ in many respects, in the Eastern Himalayas CAN, the Ecuador CAN selected *ab initio*, and the CAN of the transvolcanic region, the landscape quality graph is sparse, that is, the number of edges is linear in the number of vertices ($\left| E_L \right| = O(V_L)$). The large difference in the number of connected components among the landscape quality graphs (Ecuador: 20; Eastern Himalayas: 1; Mexico: 40) results from the coarse-scale of the analysis of the Eastern Himalayas, which did not incorporate any data on land usage and divided into the landscape into cells too large to be practical for conservation planning. A finer-grained assessment would probably find that the number of connected components in the Eastern Himalayas landscape quality graph is proportional to the number of conservation areas (selected by ResNet).

Similarly, a preliminary analysis of the transvolcanic area of Mexico that did not distinguish between transformed and non-transformed areas found that the landscape quality graph had 1 connected component (data not shown).

Second, for both proposed and existing CANs, the graph-based approach can be used to recommend additional sites for inclusion in the network so as to increase the network's connectivity. Planners can augment CAN connectivity by preferentially acquiring cells (i) in the edge set E_L of the landscape quality graph (ii) or in the edge set of a minimum spanning tree (hereafter, E_{MST}). In the ResNet software package, if the adjacency preference is in effect, a place- prioritization algorithm evaluates the biodiversity contents of a cell before considering its spatial characteristics. The MARXAN software package, in contrast, minimizes a single objective function that is the sum of both the biodiversity attributes and the desired spatial attributes of sets of cells (Leslie *et al*. 2003). Membership in E_L or E_{MST} could be used as a tie-breaker in deciding whether to add a cell to a CAN as in ResNet or as a cell attribute on par with the cell's biodiversity contents as in MARXAN. It might be objected that the cells in E_L should not be added to a CAN because the edges of the landscape quality graph form long thin strips that could not, in practice, be managed as conservation areas. This can be remedied by initializing a place-prioritization algorithm with the cells in E_L or E_{MST}, which results in the selection of a set of cells (hereafter, the set ILQ) clumped between and around the edges of the landscape quality graph. The cells in ILQ have the desirable properties that (i) they link the conservation areas in the network together because they are clustered around the cells in E_L and (ii) it would be more practical to institute the cells in ILQ as conservation areas than the cells in E_L, because many of the subsets of ILQ form compact clusters with low perimeter area ratios (Figure 12).

Table 1: **Set notation used to describe** G_C and G_L.

Set	Description
L	All cells.
A	All cells available for conservation planning.
M	Masked cells.
R	Transformed cells.
O	Other masked cells.
B	Cells in an existing CAN used for initialization.
P	Cells available for inclusion in a CAN_i.
S_i	Cells selected in CAN_i.
T_i	Cells not selected in CAN_i.
CA_i	Partition of S_i with respect to conservation areas.
$G_c = (V_c, E_c)$	Contiguity graph.
V_c	Vertex set of the contiguity graph, G_c.
E_C	Edge set of the contiguity graph, G_c.
SP	All shortest paths between vertices in G_c.
SPR	Revised set of shortest paths between vertices in G_c.
$G_L = (V_L, E_L)$	Landscape quality graph.
V_L	Vertex set of the landscape quality graph, G_L.
E_L	Edge set of the landscape quality graph, G_L.
V_{CC}	The set of connected components of G_L. Each subset of V_{CC} contains the vertices in 1 connected component of G_L.
MQ	The set of priority queues used for finding all minimum spanning trees (MSTs).
I_MST	The set of incipient MSTs.
E_{CS}	A minimum cut set of G_L.
S	The set of minimum degree vertices of G_L.
T	The set of vertices adjacent to vertices in S.
U	The set of all vertices $v \in V_L$ not in S or T.
$(A, \overline{A})$	The minimum cut set of G_L.
S_j, T_j, U_j	The sets S, T, and U at iteration j of the min cut set algorithm.
E_{MST}	The edge set of a MST of G_L.
ILQ	The set of cells selected by a place-prioritization algorithm when the algorithm is initialized with E_L or E_{MST}.

Figure 1. **Landscape quality model for Eastern Himalayas data set**.

Large black circles represent cells selected by ResNet at low target levels. Small light gray circles represent cells selected by ResNet at higher target levels. Landscape quality scores are used to assign weights to the edges of the landscape quality graph.

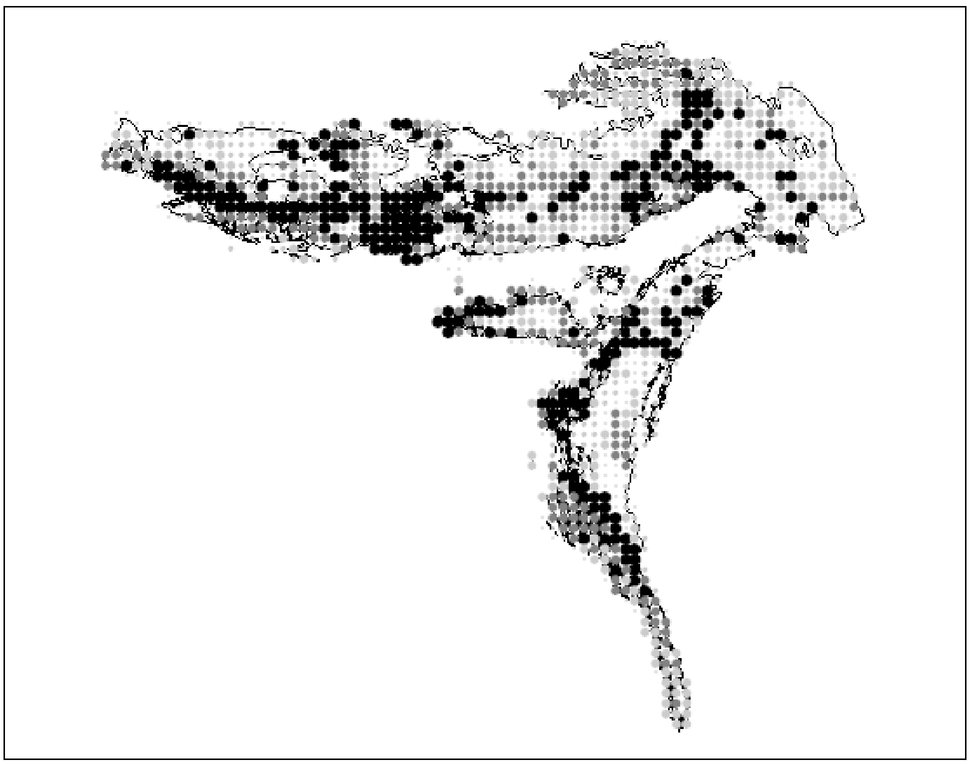


Figure 2. **Landscape quality graph for the Eastern Himalayas data set**

Black squares represent the cells in the conservation areas selected by ResNet. Such cells form the vertices of the landscape quality graph. Gray areas represent cells that can be used to link the conservation areas. Such cells form the edges of the landscape quality graph. Clusters of adjacent gray cells are sites where distinct edges overlap.

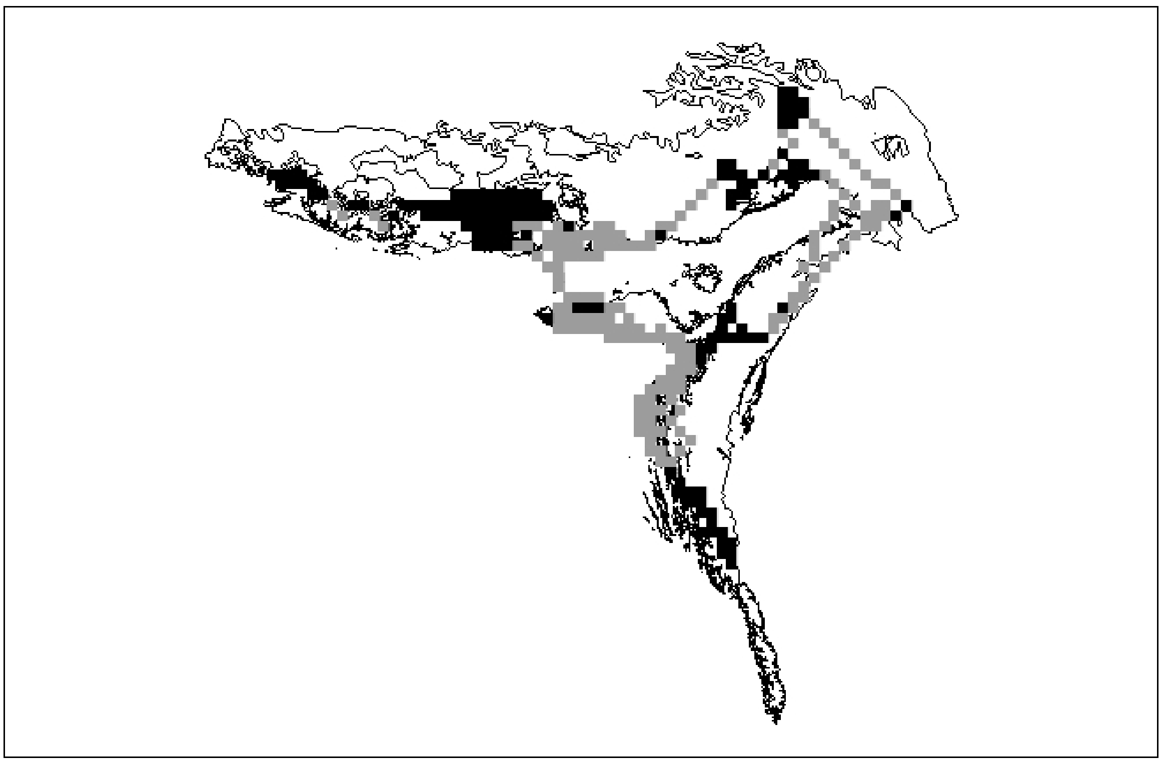


Figure 3. Minimum spanning tree (MST) of the Eastern Himalayas data set.

Overlapping white circles represent conservation areas. Black, gray, and light gray squares represent cells in the edges of the MST. Large black squares represent cells with good landscape quality scores. Small light gray squares represent cells with poor landscape quality scores.

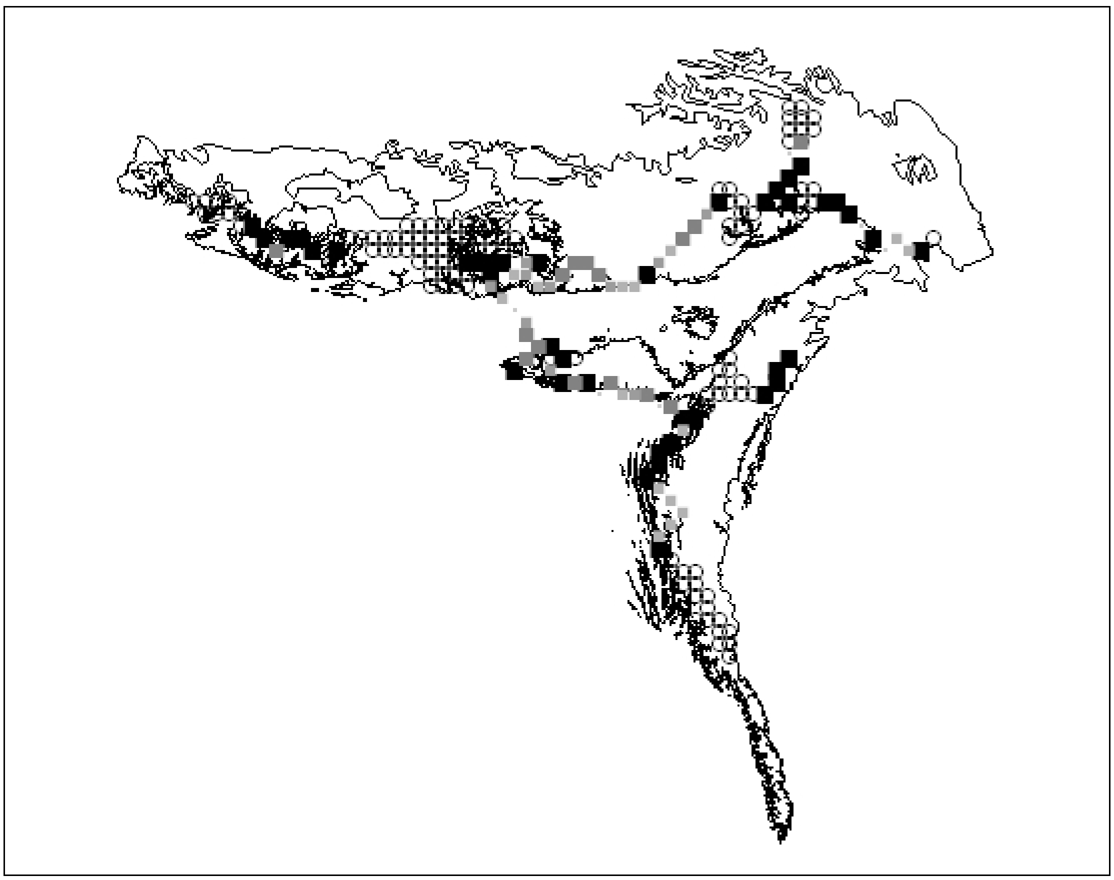


Figure 4. Abstract representation of the MST of the Eastern Himalayas data set.

White circles represent the 15 conservation areas selected by ResNet. Lines connecting the circles represent the edges of the MST. The values written outside the circles are the weights of the edges of the MST. Low edge weights represent edges made up of high-quality cells as scored by the landscape quality model.

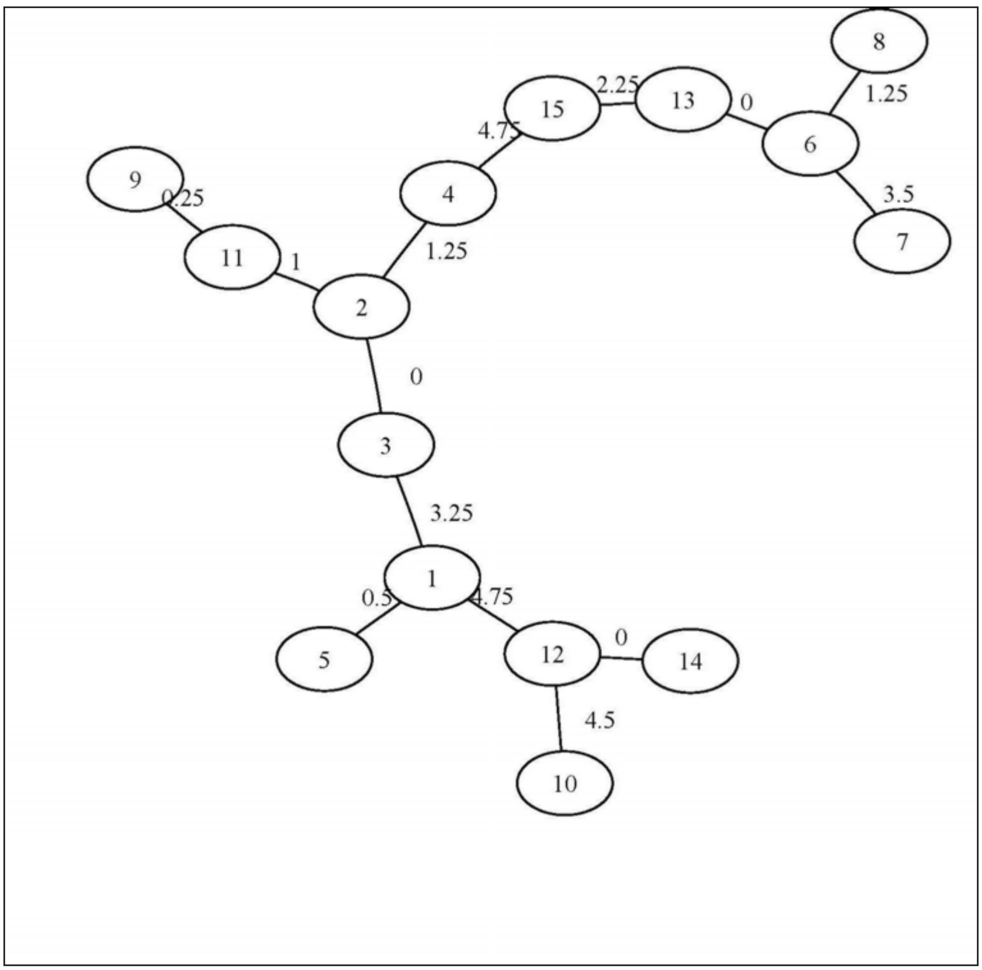


Figure 5. Coarse-grained landscape quality model of Ecuador.

Cells are colored based on their proximity to anthropogenically-transformed areas (binned into 3 distance classes). Black cells are furthest from transformed areas. Gray cells are closer to them and light gray cells are the closest to transformed areas. The coarse-grained landscape quality model gave the best scores to black cells are the poorest to light gray ones. This scoring system was used to assign weights to the edges of the landscape quality graph and its MSTs.

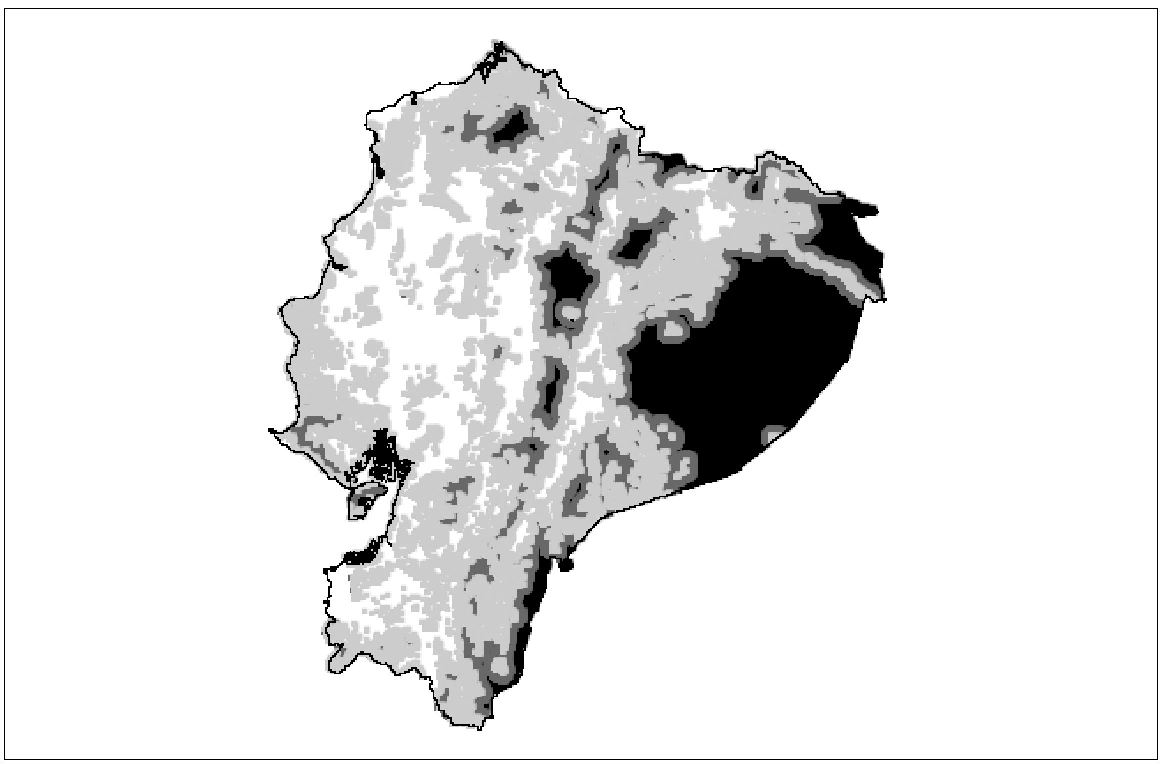


Figure 6. **Fine-grained landscape quality model of Ecuador**.

Cells are colored based on their proximity to anthropogenically-transformed areas (binned into 5 distance classes). Black cells are furthest from and light gray cells are closest to transformed areas. Black cells were assigned good (low) landscape quality scores and light gray cells poor (high) ones. In the landscape quality graph, edges of low weight made up of cells assigned low scores by the landscape quality model were preferentially included in an MST.

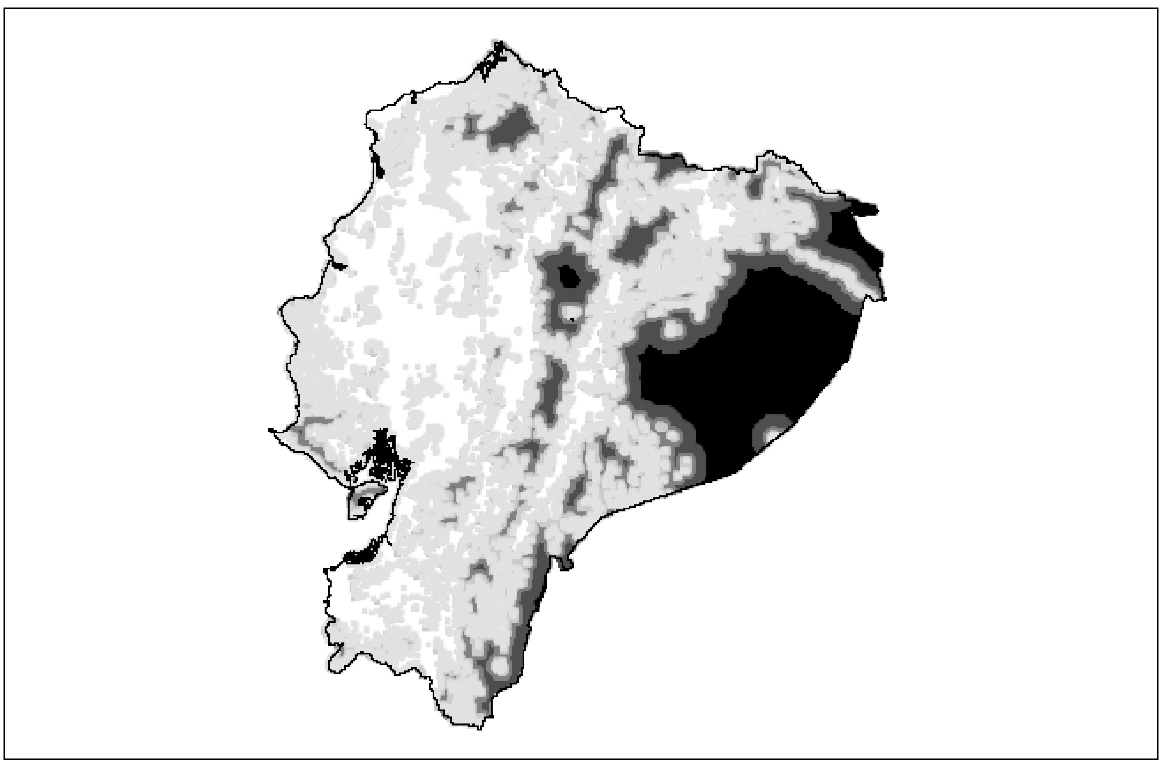


Figure 7. **Landscape quality graph of the Ecuador CAN** (**selected** *ab initio*).

Areas in dark gray represent conservation areas selected by ResNet when the place-prioritization algorithm was not initialized with the existing conservation areas. The thick black lines are the edges of the landscape quality graph. Transformed areas are white and areas available for conservation planning are in light gray.

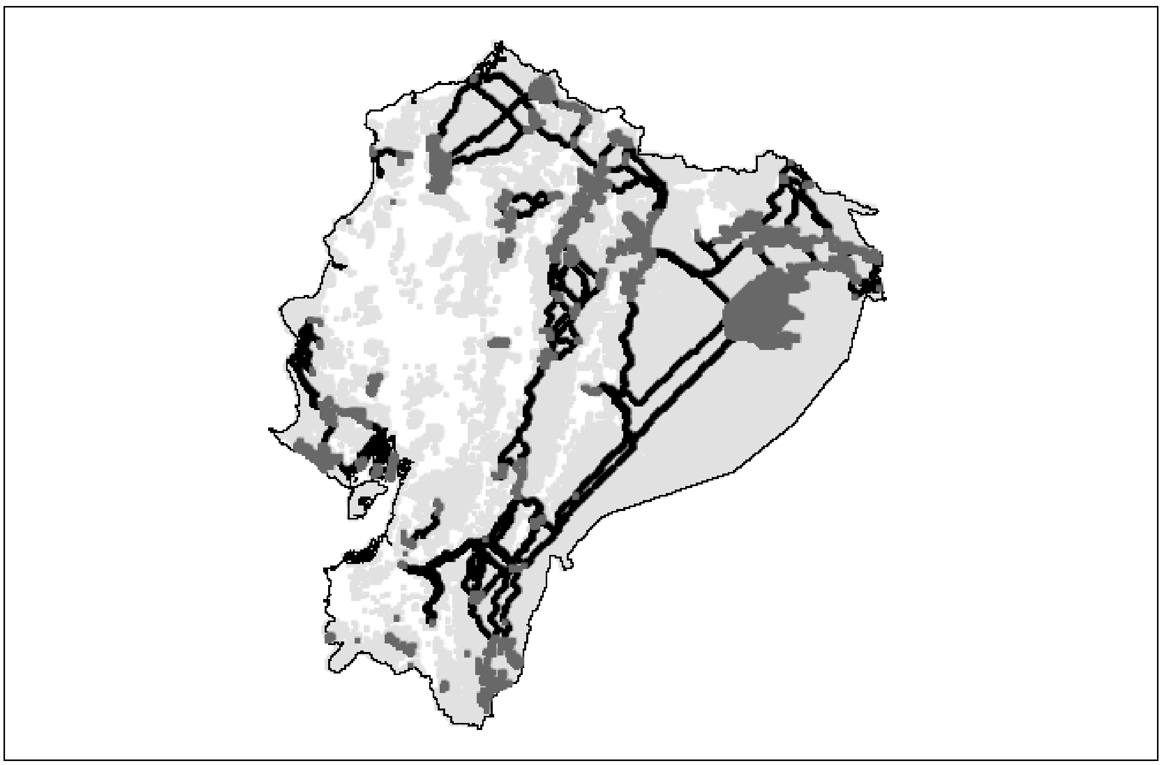


Figure 8. A MST of the Ecuador CAN (coarse-grained landscape quality model).

Thick black lines are the edges of the MST of the largest component of the Ecuador landscape quality graph. Dark gray areas are the conservation areas in the CAN selected *ab initio*.

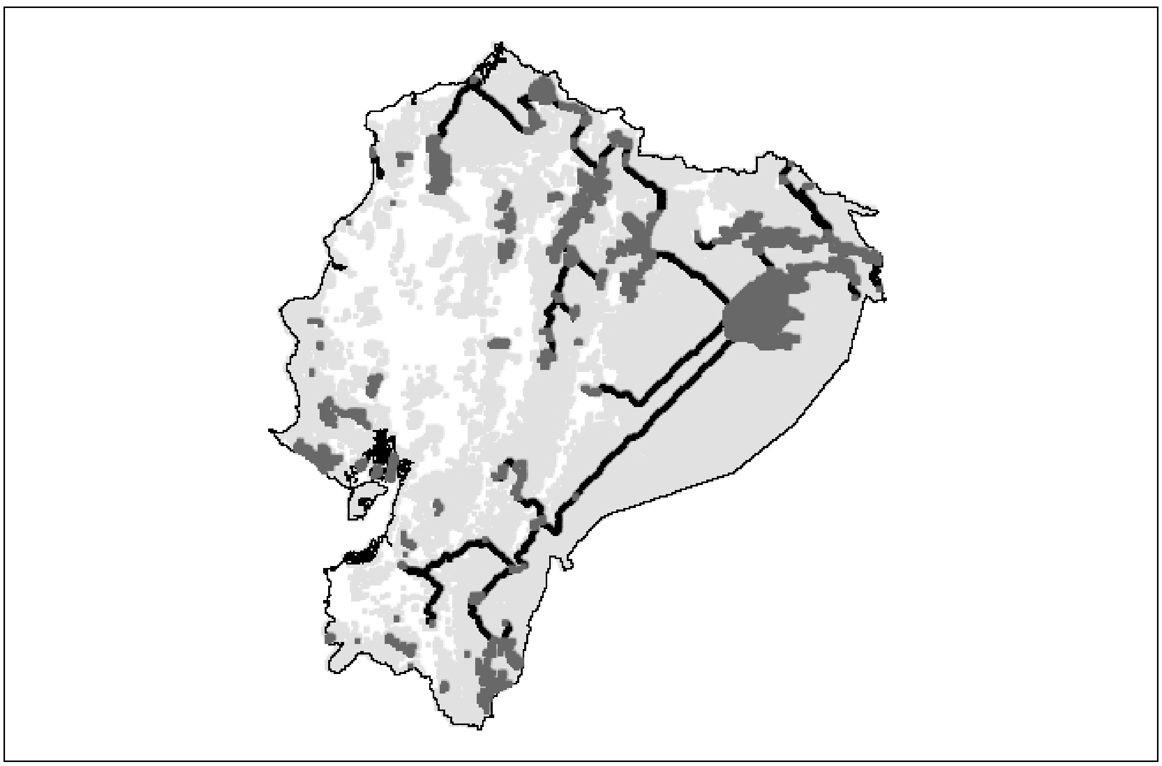
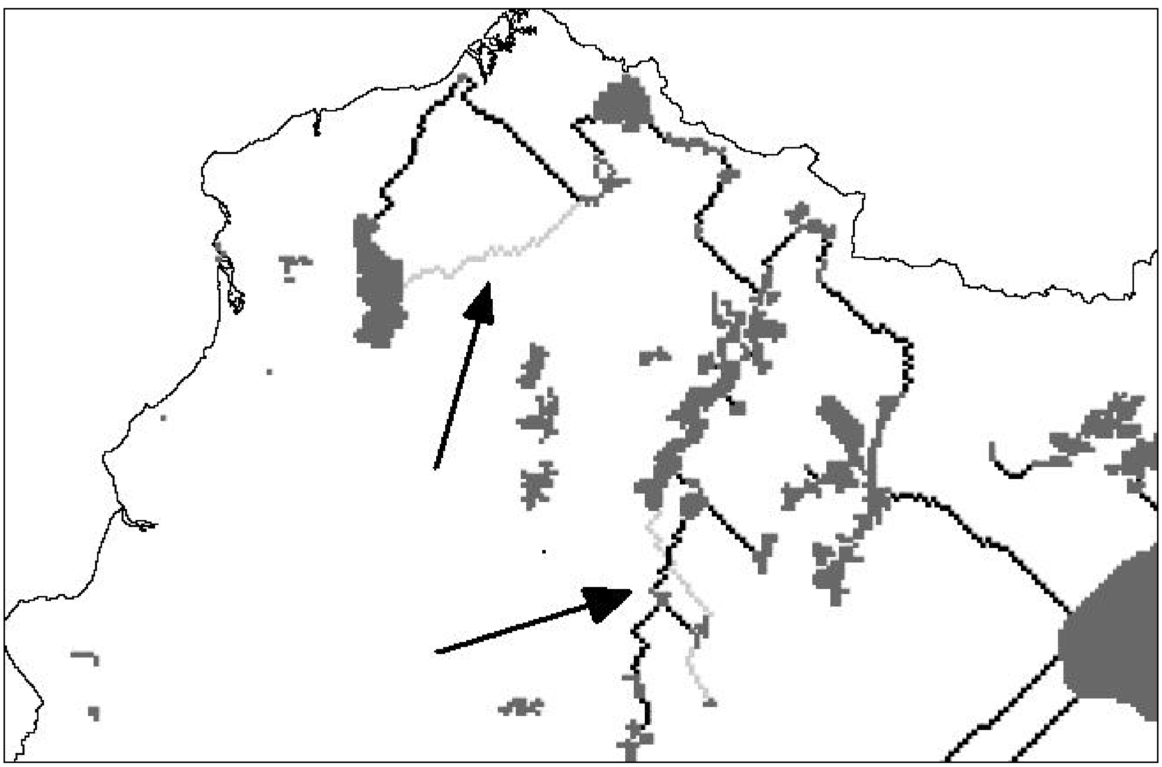


Figure 9. **Detail of 2 MSTs of the coarse-grained landscape quality model**.

Dark gray areas are conservation areas. The black lines are some of the edges of 1 MST of the largest component of the landscape quality graph. The light gray lines are some of the edges of a different MST. The arrows show areas where the edges of the 2 MSTs are discernibly different. In all other areas, the edges of the light gray MST overlap the edges of the black MST.



Fiigure 10. **The existing conservation areas of Ecuador**.

The black line around the perimeter of the shape represents the political boundaries of continental Ecuador. The areas in white inside the perimeter are anthropogenically-transformed sites (unavailable for conservation planning). Dark gray areas are the existing reserves.

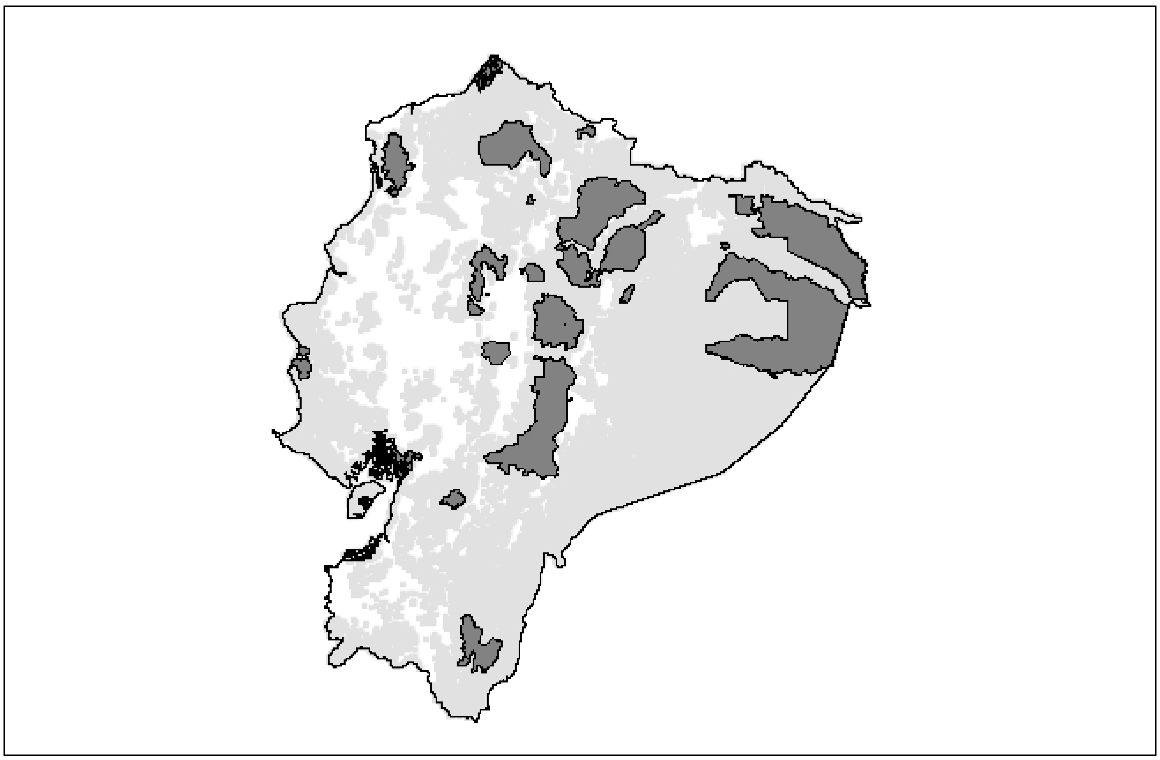


Figure 11. **Landscape quality graph of the Ecuador CAN** (**initialized with the existing conservation areas**).

Areas in dark gray represent conservation areas selected by ResNet when the place-prioritization algorithm was initialized with the existing conservation areas. Areas in black represent the edges of the landscape quality graph, that is, the shortest paths between conservation areas when the intermediate sites are scored using the landscape quality model described above. Some pairs of conservation areas are not connected by edges because they are separated by masked cells (shown here in white).

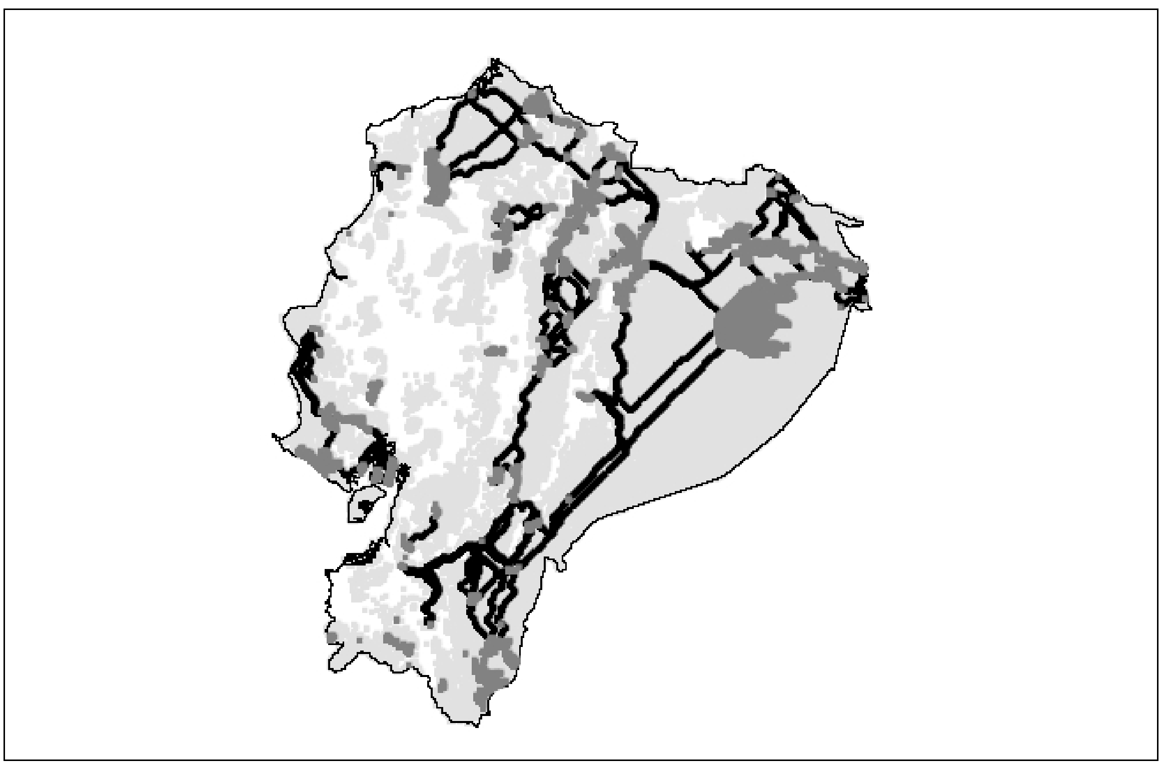


Figure 12. **Ecuador CAN initialized with the edges of the landscape quality graph**.

Areas in gray are cells in the edges of the landscape quality graph and cells in the conservation areas selected in a previous run of ResNet (see Figure 11). Areas in black are cells selected by ResNet initialized with the edges of the landscape quality graph. This method of selecting cells results in large clumps of cells clustered around the edges of the landscape quality graph.

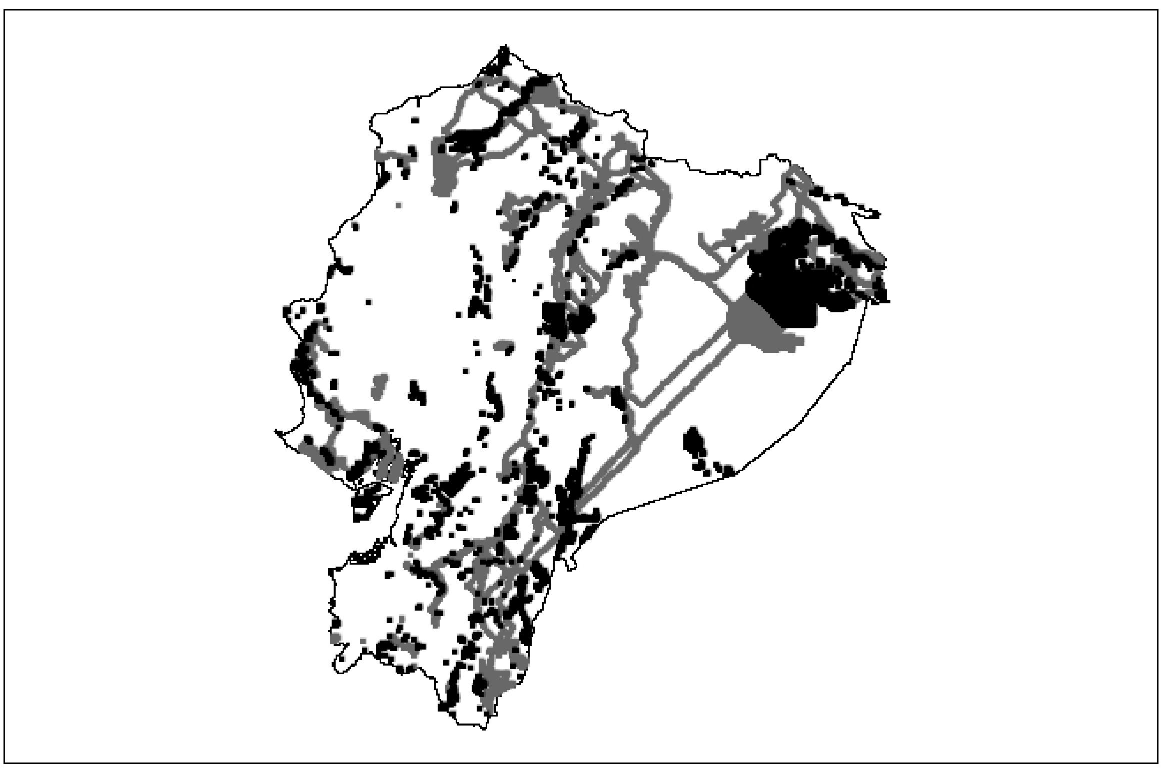


Figure 13. Landscape quality graph of the augmented CAN of the transvolcanic belt of central Mexico.

Areas in light gray are cells with primary or secondary vegetation (sites available for conservation planning). The existing national parks are shown in black. The dark gray areas are the conservation areas selected by the place-prioritization procedure and cells that can be used to link the conservation areas (the edges of the landscape quality graph).

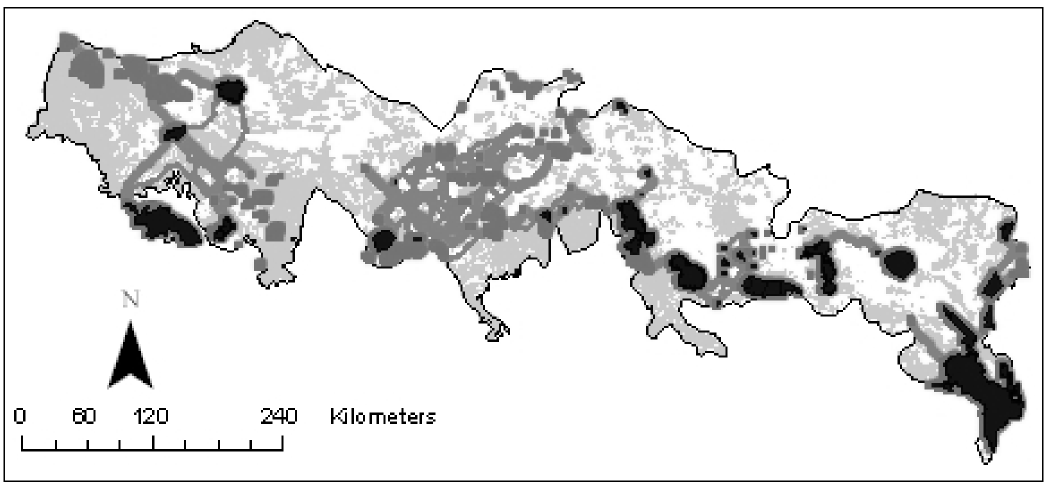


Figure 14. **MSTs of the landscape quality graph of the transvolcanic belt**: **solution frequency model**.

Sites available for conservation planning are shown in light gray. The dark gray areas are the CAN selected by ResNet and the set of cells that establish minimal connectivity between the units of the CAN when the weight of each edge of the landscape quality graph is the summed solution frequency of the cells in the edge. The arrow indicates an area where the edges included in the MST based on solution frequency differs from the MST based on physical distance.

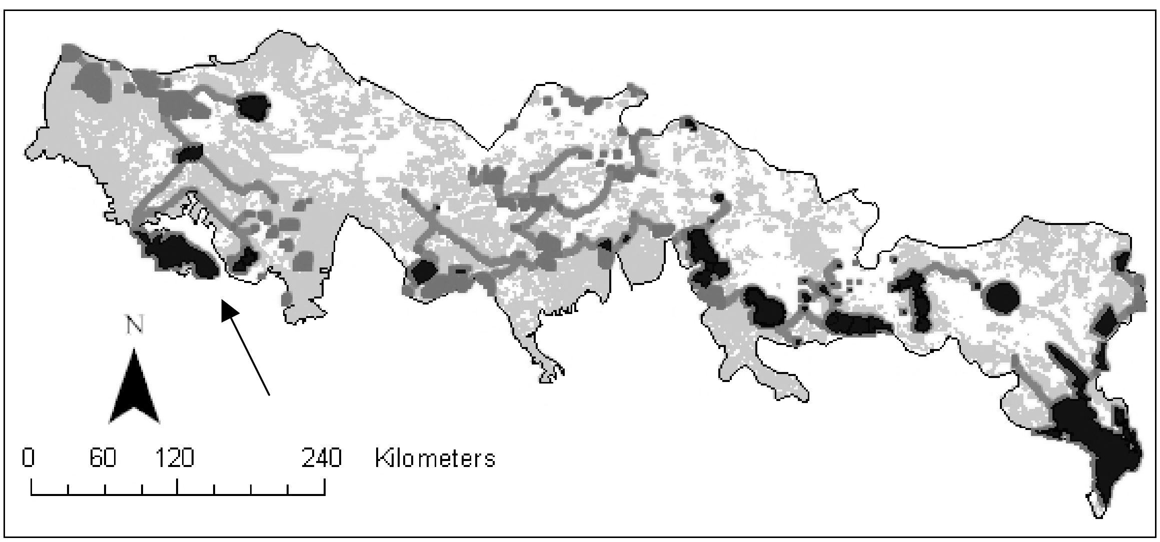
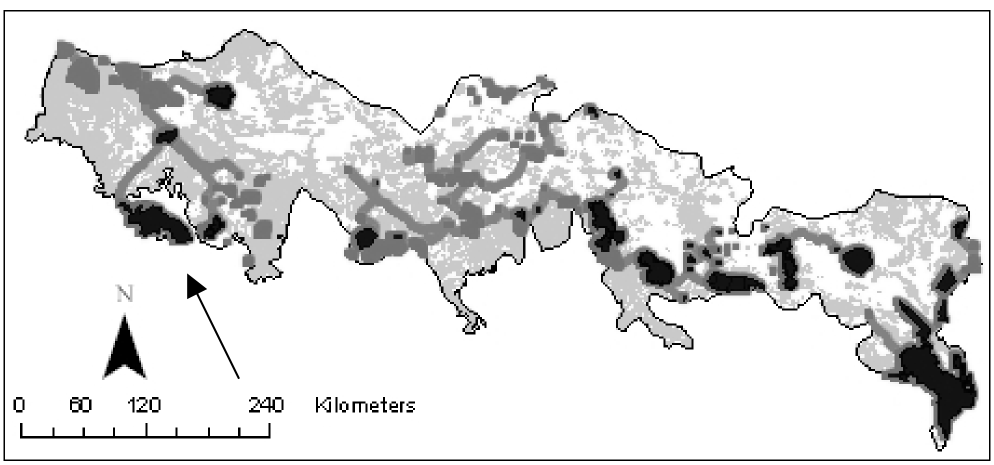


Figure 15. **MSTs of the landscape quality graph of the transvolcanic belt**: **physical distance model**.

Sites available for conservation planning are shown in light gray. The dark gray areas are the CAN selected by ResNet and the set of cells that establish minimal connectivity between the units of the CAN. The dark gray areas are the CAN selected by ResNet and the set of cells that establish minimal connectivity between the units of the CAN when the weight of each edge of the landscape quality graph equals the number of cells in the edge. The arrow indicates an area where the MST based on physical distance differs from the MST based on solution frequency.



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