

OPTIMIZING DISPERSAL CORRIDORS FOR THE CAPE PROTEACEAE USING NETWORK FLOW

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Abstract. We introduce a new way of measuring and optimizing connectivity in conservation landscapes through time, accounting for both the biological needs of multiple species and the social and financial constraint of minimizing land area requiring additional protection. Our method is based on the concept of network flow; we demonstrate its use by optimizing protected areas in the Western Cape of South Africa to facilitate autogenic species shifts in geographic range under climate change for a family of endemic plants, the Cape Proteaceae. In 2005, P. Williams and colleagues introduced a novel framework for this protected area design task. To ensure population viability, they assumed each species should have a range size of at least 100 km² of predicted suitable conditions contained in protected areas at all times between 2000 and 2050. The goal was to design multiple dispersal corridors for each species, connecting suitable conditions between time periods, subject to each species' limited dispersal ability, and minimizing the total area requiring additional protection. We show that both minimum range size and limited dispersal abilities can be naturally modeled using the concept of network flow. This allows us to apply well-established tools from operations research and computer science for solving network flow problems. Using the same data and this novel modeling approach, we reduce the area requiring additional protection by a third compared to previous methods, from 4593 km² to 3062 km², while still achieving the same conservation planning goals. We prove that this is the best solution mathematically possible: the given planning goals cannot be achieved with a smaller area, given our modeling assumptions and data. Our method allows for flexibility and refinement of the underlying climate-change, species-habitat-suitability, and dispersal models. In particular, we propose an alternate formalization of a minimum range size moving through time and use network flow to achieve the revised goals, again with the smallest possible newly protected area (2850 km²). We show how to relate total dispersal distance to probability of successful dispersal, and compute a trade-off curve between this quantity and the total amount of extra land that must be protected.

Key words: climate change; connectivity; corridor; dispersal; minimum range size; network flow; Proteaceae; reserve design; Western Cape, South Africa.

INTRODUCTION

Habitat connectivity is a basic concept in protected area design and more generally in landscape ecology (Margules and Pressey 2000, Turner et al. 2001). Ensuring habitat connectivity is an important element of conserving biodiversity, especially since global climate change will tend to cause many species to disperse along climate gradients (Noss 2001, Honnay et al. 2002). Climate change can contribute to habitat fragmentation (Bawa and Dayanandan 1998), increasing the need for explicit modeling of species dispersal and the spatial arrangement of habitat (Vos et al. 2002, Del Barrio et al. 2006). Here we show that an optimization paradigm called network flow (Ahuja et al. 1993) provides a

powerful new approach for measuring connectivity and for multispecies optimization of protected areas and corridors. Our approach takes into account species' varying dispersal abilities and the spatial and temporal distribution of suitable habitat, while making efficient use of conservation funds by minimizing the total area requiring new protection.

Our application of network flow falls within the general framework of systematic conservation planning (Margules and Pressey 2000). Our work mainly applies to the selection of additional conservation areas to meet the previously identified conservation goals (Stage 4 of Margules and Pressey 2000). It also applies to the review of existing conservation areas (Stage 3), as we use network flow to determine species' effective range size over time within areas with existing protection. More generally, we use network flow to evaluate the cost and impact of a specific set of conservation goals. Our

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findings can therefore inform the prioritization of conservation goals.

Network flow is a novel approach for measuring connectivity in a landscape, i.e., the degree to which components of the landscape such as habitat patches or protected areas are linked. A variety of other methods have been used to measure connectivity, and we outline them here in order to contrast them with network flow. The simplest notion of connectivity forms the basis of the patches-in-matrix model of landscape ecology (Turner et al. 2001): for a given species, two sites are considered connected, and therefore part of the same patch, if there is a path between them that uses only suitable habitat. Some species and ecological processes are better modeled by considering non-contiguous patches to be “functionally connected” if they are separated by a small gap that the species is likely to be able to cross (With 2002). The geographic distance of such a gap can vary depending on the quality of intervening areas between patches (the matrix) which may be more or less inhospitable for the given species. The effective distance between patches (also referred to as “least-cost path” or “cost-distance”) can be calculated using weighted shortest-path computations (Graham 2001, Ray 2005). Similarly, patch isolation measures the patch’s distance from other patches, and effective isolation uses potentially varying resistance in the matrix to weight paths between patches (Ricketts 2001). These models all involve questions of the form “Are two components of the landscape linked?” or “What is the effective distance between components?”, and the answers depend only on the shortest (possibly weighted) path between the components.

The network flow approach differs in that it addresses the question: “What is the capacity of the connection between two components?” It therefore considers the combined contribution of multiple paths between the components, and it is applicable when studying ecological processes involving quantification of flows of individuals or genes across the landscape (McRae 2006). Distance measures alone cannot effectively model such flows. For example, two elongated patches of suitable habitat a given distance apart in a landscape will likely have more interchange of organisms if they are arranged side by side rather than end to end, even though they have the same least-cost path distance in both cases. Therefore, there has been recent encouragement for the development of methods for modeling flows of organisms and genes directly (Forman 2002, Vos et al. 2002).

There are some existing methods for modeling the capacity of connections between components of the landscape. The conductance (or equivalently, the resistance) of electrical networks has been used to model gene flow and genetic differentiation among populations in heterogeneous landscapes (McRae 2006). Simulation models of dispersal use random walks on unweighted graphs (corresponding to binary habitat suitability) or

weighted graphs (for continuous habitat suitability), measuring, for example, the time to disperse to a distant part of the modeled landscape (Malanson 2003). This measure (mean dispersal time) is closely related to electrical conductance (Doyle and Snell 1984, Tetali 1991). Landscape connectivity, defined as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993) focuses on deriving a single measure of the capacity of all connections in the landscape. It has been measured in simulation models by randomly moving individuals and counting successful immigrants into habitat patches, i.e., dispersal success; and measuring the expected time to move between habitat patches, i.e., search time (Tischendorf and Fahrig 2000). These methods all model random movement of organisms or genes. In contrast, flow-based models measure how large or efficient a flow is possible, without assuming a particular model of organism movement.

We apply network flow to the task of designing protected areas for the Cape Proteaceae. The Proteaceae are the most charismatic plants of the South African Cape Floristic Region, a narrow mountainous coastal belt with an extremely high degree of richness, endemism, and diversity. For many species of Cape Proteaceae, the greatest threat to persistence is the low probability of dispersing from currently occupied areas to distant areas of predicted future suitable conditions, since many of the species are known not to disperse and establish easily over long distances (Midgley et al. 2002). We focus on autogenic shifts in species ranges because the ability to actively assist species migration is limited by lack of understanding and the complexity of the broader ecological system (Malcolm and Pitelka 2000). Williams et al. (2005) formalized and gave a heuristic solution for the task of designing protected areas to facilitate species shifts in geographic range in response to climate change. Here we use network flow to construct a set of protected areas achieving exactly the same conservation goals as Williams et al. (2005), while requiring only two-thirds as much additional protected area. Moreover, we prove that ours is the best solution mathematically possible, given this model and data. Network flow thus yields a much better assessment of the cost of planning for climate change. We also describe a number of ways that network flow supports generalizations of this design problem.

METHODS

The overall purpose of our method is to select a set of areas to receive additional protection so that a collection of species can maintain viable populations, taking into account their dispersal limitations and changing habitat suitability under climate change. We use a quantitative model introduced by Williams et al. (2005) and applied to the Proteaceae of the Cape Floristic Region of South Africa, in which viability is ensured by protecting a minimum range size of 100 km² through time for each

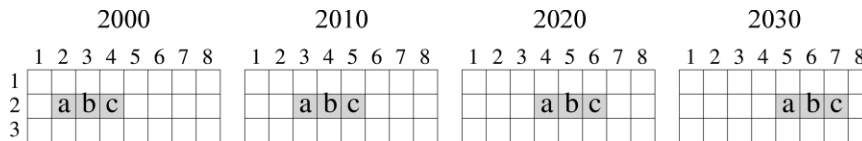


FIG. 1. Example chains and alternative definitions of nonoverlapping chains. A small area is divided into a 3×8 grid, shown for the years 2000 through 2030. Years 2040 and 2050 have been omitted for simplicity. Some of the cells, colored gray, have suitable conditions for a hypothetical species that can disperse at most one cell per decade. For the year 2000, only the three cells in row 2, columns 2 through 4 are suitable. Each decade, the suitable conditions are predicted to move a single cell to the right. There are three chains pictured, labeled a, b, and c, respectively: chain a uses cell (2,2) in year 2000, cell (2,3) in year 2010, cell (2,4) in year 2020, and cell (2,5) in year 2030. These three chains are nonoverlapping according to Definition 1 of nonoverlapping, which requires only that no two chains use the same cell in the same year. However, any two of the three chains overlap according to Definition 2 of nonoverlapping, which requires that no two chains ever use the same cell. For example, chains a and b overlap by Definition 2 since they both use cell (2,3): chain a uses it in year 2010, while chain b uses it in year 2000.

species, based on the area criterion of the World Conservation Union (IUCN); this translates to $35 \text{ 1}' \times 1'$ cells in the Western Cape.

Selecting protected areas to allow for dispersal

To model protection through time, Williams et al. (2005) introduced the concept of dispersal chains. For a given species, a dispersal chain is a sequence of six cells (possibly with repetitions), $c_{2000}, c_{2010}, \dots, c_{2050}$, such that each cell has predicted suitable conditions in the corresponding subscripted year (or is a presently occupied cell, for c_{2000}), and such that consecutive cells in the sequence are separated in the grid by no more than the distance that the species can disperse in a 10-year period. A dispersal chain therefore represents a feasible pathway for the species to disperse from cells where it is currently found to cells where it is predicted to have suitable conditions in 2050, using only suitable cells along the way. A set of chains represents a collection of independent pathways if the chains are “nonoverlapping” (Fig. 1). Combining the ideas of minimum range size and dispersal chains, Williams et al. (2005) model the task of designing dispersal corridors as follows:

- 1) Find dispersal chains for all species. For each species, the set of chains must:
 - a) be nonoverlapping;
 - b) use only untransformed cells with existing or proposed protection;
 - c) have at least 35 chains, if possible; if less than 35 nonoverlapping chains exist, then the set should have the maximum possible size.
- 2) Subject to these requirements, the number of cells with proposed protection should be as small as possible.

The nonoverlapping requirement is important, as it imposes the minimum area criterion. Without it, the set of chains for a species may occupy much less than 35 grid cells during some time period, compromising the species' viability (see *Discussion* for more analysis of this

requirement). However, there are at least two reasonable ways to define nonoverlapping chains:

- 1) No two chains use the same cell in the same year.
- 2) No two chains ever use the same cell, even in different years.

Under the first definition, two nonoverlapping chains may use the same cell, but only in different years. Fig. 1 shows an example that highlights the difference between these two definitions. The second (stricter) definition is the one used by Williams et al. (2005). We will focus primarily on the first definition, and then show how our methods extend to the second definition. The two definitions provide different levels of resilience against modeling errors. In the case of an incorrect prediction that a certain cell will be suitable at some particular future time slice, at most one chain will be affected (will not contribute to survival of the species) under both definitions. On the other hand, if a cell can be rendered permanently unsuitable despite being “protected,” then for the first definition, multiple chains may be affected, possibly leaving as many as five fewer pathways for the species to disperse to future suitable conditions (in the case where a different chain used that cell in each of the time slices $c_{2010}, c_{2020}, \dots, c_{2050}$).

Network flow concepts

We now introduce the basic concepts of network flow that we will need for designing dispersal corridors. Network flow is an optimization paradigm that is widely used in computer science and operations research (Ahuja et al. 1993). It has seen applications in such diverse areas as telecommunication networks, transportation networks such as roads and railways, warehousing and distribution, and production line and crew scheduling, though we believe it is new to ecology. These applications can all be seen as having an underlying graph (also called a network), and a commodity that flows over the graph (for example, telephone calls routed over a network of fiber-optic cables). Movements of species between habitat patches in a landscape or between protected areas can be seen in the same way, as flows in a graph that models the spatial and temporal

relationship between the patches or protected areas. Just as a telephone network should be designed to allow efficient routing of phone calls, networks of protected areas should be designed to facilitate flows of organisms. In this section, we give a brief introduction to two network flow problems that will be useful for optimizing dispersal corridors, namely “maximum flow” and “minimum-cost flow” (min-cost). For more details on these and other flow problems and their applications, see the comprehensive textbook by Ahuja et al. (1993). We will use only maximum flow to address the dispersal corridor design task introduced by Williams et al. (2005), and mention later how min-cost flow may be useful for variations on the model. We first define network flow in general terms for arbitrary graphs, then give an example where the graph represents a matrix of cells in a landscape. For the dispersal corridor application, we will use a more complex graph that represents a landscape changing over time.

Let G be a directed graph, consisting of nodes connected by directed arcs, and let each arc have a nonnegative value called its capacity (Fig. 2A). A flow from one or more nodes in the graph (sources) to one or more other nodes (sinks) is a function f that gives a nonnegative value $f(a)$ for each arc a , satisfying two constraints:

- 1) a capacity constraint, such that for each arc a , $f(a) \leq \text{capacity}(a)$;
- 2) flow conservation, such that at each node other than the sources and the sinks, the net flow is 0; i.e., the flow into the node equals the flow out of it.

For an analogy, arcs can be thought of as pipes, and the flow as the rate of water flowing through them. The nodes represent junctions where pipes meet, and the flow conservation constraint says that the amount of water flowing into any junction must equal the amount flowing out, unless the junction is a source (where water is being injected) or a sink (where water is escaping from the system). The capacity of an arc corresponds to the maximum flow rate allowed by that pipe. Directed arcs would correspond to pipes with unidirectional valves allowing flow only in the direction of the arc. Of course, ordinary water pipes allow flow in both directions, and we can model this by a pair of arcs between the same two nodes, pointing in opposite directions.

The value of a flow is defined as the total net flow out of the source nodes, or equivalently, the total net flow into the sink nodes. For our example graph, Fig. 2B shows a flow of value 3 from node a (the source) to node e (the sink). The most basic network flow problem is the maximum flow problem, where we seek a flow of maximum value, among all flows from a given set of sources to a given set of sinks. It is easily verified that the flow shown in Fig. 2B is a maximum flow. Each arc may also have an associated cost, and the cost of a flow is then defined as the sum over all arcs of cost times flow. This leads to the minimum cost flow problem, where we seek a flow of minimum cost, among all flows of a

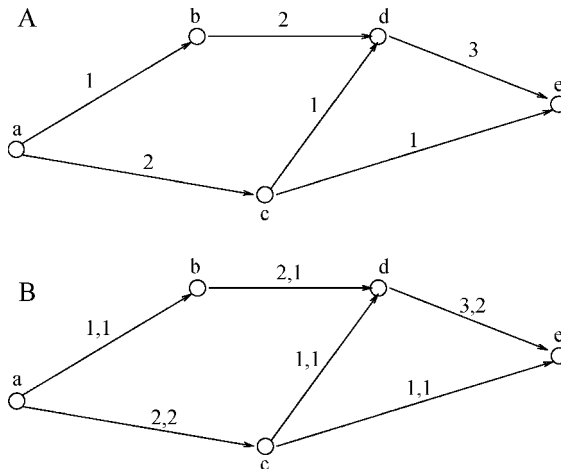


FIG. 2. (A) An example directed graph has five nodes (a, b, \dots, e) and six directed arcs. Each arc is labeled with a nonnegative “capacity.” In (B), the graph has been labeled to show an example “flow” from a single source node (a) to a single sink node (e). Each arc is labeled first with its capacity, then with the flow. The flow satisfies the following defining properties: it is nonnegative, obeys the capacity constraint on each arc, and satisfies flow conservation (flow in equals flow out) at each node that is not a source or sink. The flow has value 3, since that is the net flow out of the source (node a), or equivalently, the net flow into the sink (node e).

specified value between a given source and sink. For example, if the flow represents goods being trucked across a road network, arc costs may represent road lengths, so the cost of a flow is proportional to the amount of fuel required to transport the goods.

A fundamental property is that if all arc capacities are integers (and, in the case of min-cost flow, the specified flow value is also integral), there is always a maximum flow or min-cost flow that is integral, and that can therefore be decomposed into a set of paths from sources to sinks (Ahuja et al. 1993: Theorem 6.5). If the arc capacities are all equal to 1, such an integral flow can be decomposed into a set of arc-disjoint paths from sources to sinks; “arc-disjoint” means that no arc is in more than one path. Moreover, any set of arc-disjoint paths from sources to sinks constitutes a flow, so we have the following properties for any graph with unit capacities:

- 1) Finding the maximum flow is equivalent to finding the maximum number of arc-disjoint paths from sources to sinks.
- 2) Finding a minimum-cost flow of integer value F is equivalent to finding a set of F arc-disjoint paths from sources to sinks with minimum total cost.

In our example flow of Fig. 2B, the flow as pictured is integral. It can be decomposed into three paths from the source to the sink, namely the paths (a, b, d, e), (a, c, d, e), and (a, c, e). The paths are not arc-disjoint, because

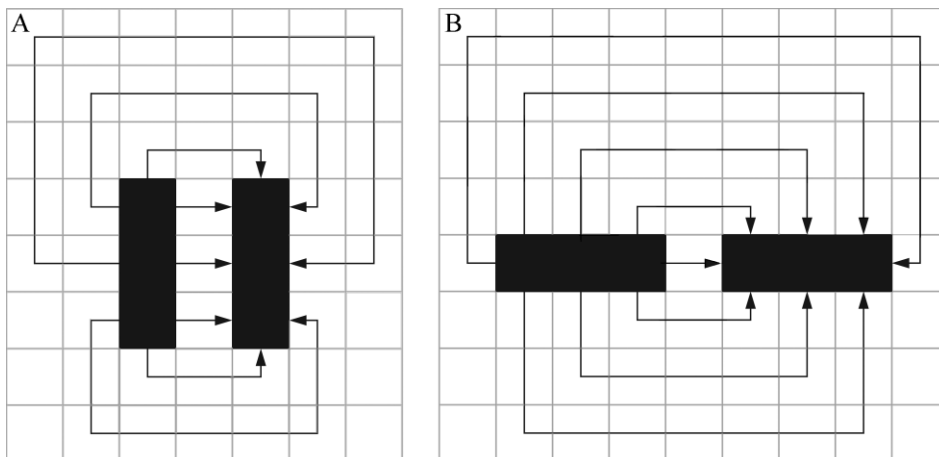


FIG. 3. Example of the use of network flow to measure connectivity between two patches in a matrix. An area is divided into a grid of cells (gridlines shown in gray). There are two 1×3 patches of suitable conditions for a hypothetical species (shown in black), arranged (A) side by side or (B) end to end. The cells are in a uniform matrix that has conditions that are unsuitable for the species, but that can be traversed. For each arrangement, the black arrows show a minimum-cost flow of value 8, for the graph defined as follows: there is a node for each cell, with unit-capacity arcs from each cell to each of its four neighboring cells. Cells in the left patch are sources, while cells in the right patch are sinks. If all arcs have unit cost, the flow in (A) has cost 52, while the flow in (B) has cost 68. Both flows are maximum flows, since there is a cut of value 8 (the boundary of either patch). A minimum-cost flow of value 3 has cost 6 for (A) vs. 10 for (B).

the first and second share the arc (d, e) and the second and third share the arc (a, c).

Another useful property of flows is the “max-flow min-cut theorem,” which says that the maximum flow from a set of source nodes to a set of sink nodes is equal to the minimum capacity among all cuts. A cut means a partition of the nodes into two subsets, one containing all of the sources and the other all of the sinks, and the capacity of a cut is the sum of the capacities of arcs crossing the cut from the source side to the sink side. In other words, the max-flow min-cut theorem says that finding the maximum flow value is the same as finding the bottleneck cut that most constrains flow from sources to sinks. This equivalence may find ecological applications, since the bottleneck that most constrains connectivity between areas of habitat for a species often warrants conservation attention; habitat corridors are examples of this.

Our second example uses min-cost flow to measure connectivity between two elongated habitat patches in a matrix (Fig. 3). The cost of a flow from one patch to the other is lower if the patches are arranged side by side (Fig. 3A) than if they are arranged end to end (Fig. 3B). Min-cost flow therefore allows us to model the availability and length (or more generally, some cost measure) of multiple paths between the patches, in contrast to least-cost path measures that depend only on a single path.

There are a number of efficient algorithms to compute optimal solutions for the maximum flow and min-cost flow problems (Ahuja et al. 1993). Network flow type problems are also easily represented as linear programs,

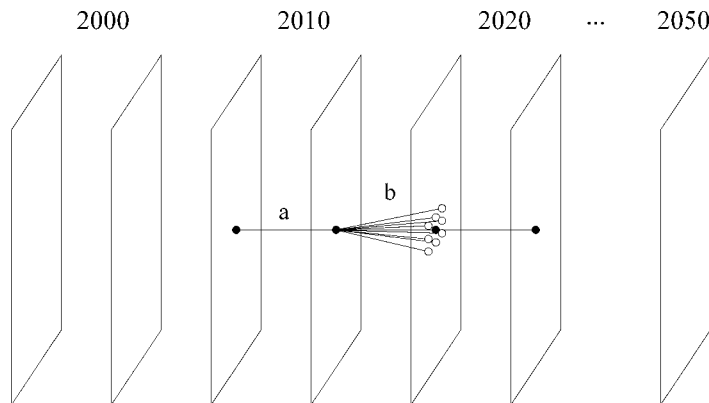
because flow conservation and capacity requirements are naturally represented as linear constraints. Some commercial linear program solvers can take advantage of the special structure of network flow constraints to quickly solve large flow problems.

Modeling dispersal chains as flow

Here we show how to represent nonoverlapping dispersal chains as flows in a directed graph that represents dispersal ability in the landscape. We focus on the first definition of nonoverlapping (see Appendix for modifications to represent the second definition). We assume that each species can disperse either one cell or three cells per time slice (as is the case with the Cape Proteaceae; see *Methods: The Cape Proteaceae*). There are therefore two versions of the graph, called G_1 and G_3 , corresponding to the maximum dispersal distance per time slice being either one cell (see Fig. 4) or three cells. The nodes of the graph consist of $2 \times \text{NYEARS}$ layers (where $\text{NYEARS} = 6$), numbered starting with layer 0; each layer l has one node $n_{l,c}$ for each grid cell c . The graph has the following collection of arcs, each with capacity 1:

- 1) In-year arcs. For each $y \in \{0 \dots \text{NYEARS} - 1\}$, and for each grid cell c , there is an arc from $n_{2y,c}$ to $n_{2y+1,c}$. The arc represents the ability of a species to establish and persist in the cell c during the y th time slice.
- 2) Between-year arcs. For each $y \in \{0 \dots \text{NYEARS} - 2\}$, and for each pair of cells c_1, c_2 that are within the maximum dispersal distance (one for G_1 and three for G_3), there is an arc from n_{2y+1,c_1} to n_{2y+2,c_2} . The arc represents the ability of a species to disperse from cell c_1 to the cell c_2 by the end of the y th time slice.

FIG. 4. The graph G_1 , representing dispersal and persistence possibilities for a species with maximum dispersal distance equal to 1. There are 12 layers, two for each of the years 2000, 2010, 2020, 2030, 2040, and 2050. Each layer has a node for each non-transformed cell. An example cell is shown as a black circle in some layers. White circles represent cells that are neighbors of the example cell. Representative examples of two types of arcs are shown. An in-year arc (labeled a) is present if the example cell is predicted to be suitable for the species in that year. Between-year arcs (labeled b) represent the ability of the species to disperse from the example cell to nearby cells. All arcs are left to right (arrowheads omitted for clarity) and have unit capacity.



The nodes in layers 0 and 1 represent the time slice 2000, layers 2 and 3 represent the time slice 2010, layers 4 and 5 represent the time slice 2020, and so on. A path through G_1 (or G_3) from the first layer to the last corresponds to a dispersal chain, constrained by a dispersal distance of 1 (or 3). For the graph G_1 , between-year arcs are analogous to the arcs in Fig. 3, the difference being that here the arcs all move forward in time (and that there are arcs to the four diagonal spatial neighbors in addition to the two horizontal and two vertical neighbors).

To model a particular species s , we choose G_1 or G_3 according to the maximum dispersal distance for s , and then delete nodes (and all adjacent arcs) corresponding to cells predicted to be unsuitable for s . In symbols, if a cell c is unsuitable for s in the i th time slice, we delete nodes $n_{2i,c}$ and $n_{2i+1,c}$ and all adjacent arcs. We call the resulting graph $G(s)$. To model a set P of protected areas, we delete from $G(s)$ all nodes corresponding to cells not in P . We call the resulting graph $G(s, P)$.

For any species s and set P of cells, let the maximum flow from the first layer to the last in $G(s, P)$ be denoted $\text{maxflow}(s, P)$. This is the maximum number of disjoint chains possible if exactly the cells in P are protected. Let P_0 be the set of already-protected cells, and let N be the set of all non-transformed cells. Define required flow(s) for a species s to be the smaller of 35 and $\text{maxflow}(s, N)$. We call a set P of cells feasible for a species s if P is a superset of P_0 and $\text{maxflow}(s, P) \geq \text{required flow}(s)$, or equivalently, if there exists a set of required flow(s) nonoverlapping dispersal-constrained chains within P . A set P of cells is feasible if it is feasible for all species. The task at hand is to find a feasible set whose size is as small as possible.

A similar graph was used by Williams et al. (2005), the essential difference being that we have doubled the number of nodes and added in-year arcs. The reason for doing this doubling is that network flow induces arc-disjoint paths. Arc-disjoint paths in the doubled graph correspond to node-disjoint paths (i.e., with no nodes being in two paths) in the graph of (Williams et al. 2005), i.e., nonoverlapping dispersal-constrained chains.

This method of mapping node-disjoint paths into arc-disjoint paths is called “node splitting” (Ahuja et al. 1993: Section 2.4). Finally, we note that there is no restriction on multiple species occupying a single cell, since the flow for a species is constrained only by suitable conditions for that species, and by the set of protected cells. The network flow for each species takes place in a different graph tailored for that species. The only element that ties these graphs together is that they use the same set of protected cells.

Optimizing flow via integer programming

We now show how to use the flow-based characterization of dispersal chains to formulate an integer program that minimizes the required protected area, while meeting the conservation goals. A linear program consists of a linear objective and a set of linear constraints, i.e., it takes the following form:

$$\begin{aligned} &\text{maximize } \mathbf{d} \cdot \mathbf{x} \\ &\text{subject to } \mathbf{Ax} \leq \mathbf{b} \end{aligned}$$

where \mathbf{b} and \mathbf{d} are fixed real-valued vectors, \mathbf{A} is a fixed real-valued matrix, and \mathbf{x} denotes the vector of variables. Here, \cdot denotes the vector dot product, and the inequality $\mathbf{Ax} \leq \mathbf{b}$ is meant to apply component-wise to the vectors \mathbf{Ax} and \mathbf{b} . An integer program takes the same form, with the added constraint that the variables in \mathbf{x} must have integer values, and a mixed integer program has some subset of the variables in \mathbf{x} constrained to be integral.

Flow problems can be readily formulated as linear or integer programs, because the capacity and flow conservation constraints are all linear. We therefore formalize the corridor design task as a mixed integer program, with two types of variables:

- 1) Flow variables f_{sa} for each species s and each arc a of $G_1(s)$ or $G_3(s)$, depending on the maximum dispersal distance of s .
- 2) A preserve variable p_c for each non-transformed cell c indicating its protected status, with 0 representing unprotected, and 1 representing protected.

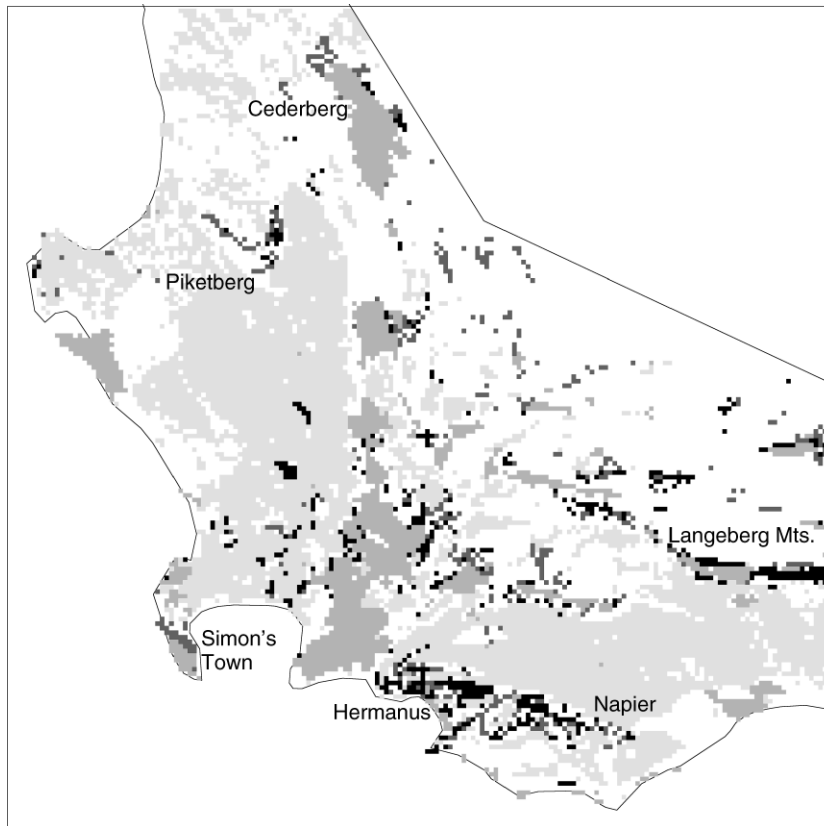


FIG. 5. Map of the western part of the Cape Floristic Region of South Africa showing areas chosen to allow dispersal of 282 species of Proteaceae along at least 35 paths, where possible, within areas of predicted suitable conditions under climate change. Key: pale gray, areas with 66% or more transformation of habitat; medium gray, existing protected areas; black, goal-essential cells (required by any feasible solution); dark gray, additional cells requiring protection, as determined by solving an integer program. There are 994 dark gray or black cells, and this is the minimum possible number for which the conservation goal is achievable.

The objective is to minimize the sum of the p_c variables, i.e., the total number of protected cells. The constraints are of four types:

- 1) Flow conservation. For each species s , these constraints ensure that the variables f_{sa} constitute a flow.
- 2) Required flow. These enforce the minimum area requirement. For each species s , the constraint is that the flow out of the source nodes (or equivalently, into the sink nodes) must be at least required flow(s).
- 3) Capacity. These ensure that the flows use only protected cells. For each in-year arc a corresponding to a cell c in time slice y , there is a constraint $f_{sa} \leq p_c$ for each species s for which cell c is suitable in year y . In other words, in the flow network for each species for which this arc exists, the capacity of the arc is set to p_c .
- 4) Existing protection. For all cells c that are already protected, $p_c = 1$. The preserve variables p_c must be explicitly constrained to be integers. Because of the integrality property of flows (mentioned earlier), having integer capacities p_c will automatically make the flow variables f_{sa} solve to integers.

The Cape Proteaceae

To demonstrate our approach, we apply it to the Proteaceae of the Cape Floristic Region of South Africa, using exactly the same data as Williams et al. (2005). The relevant data on these species consist of:

- 1) A grid of 32 400 $1' \times 1'$ cells covering the western part of the Cape Floristic region as far east as $20^{\circ}48' E$, as far north as $31^{\circ}53' S$, and all the way to the coast on the west and south (see Fig. 5).
- 2) The current (2000) distributions of 282 species of Proteaceae (presence or absence in each grid cell).
- 3) Predicted areas of suitable conditions for each species in years 2010, 2020, 2030, 2040, and 2050, derived from Schulze and Perks (1999), based on climate predictions from the general circulation model HadCM2 (Johns 1997). The climate predictions were fed into models of the species' bioclimatic requirements (trained on the current distributions) to predict areas of future suitable conditions. The bioclimatic models use the following variables, chosen for their direct physiological impact: mean minimum temperature of the coldest month, annual sum of daily

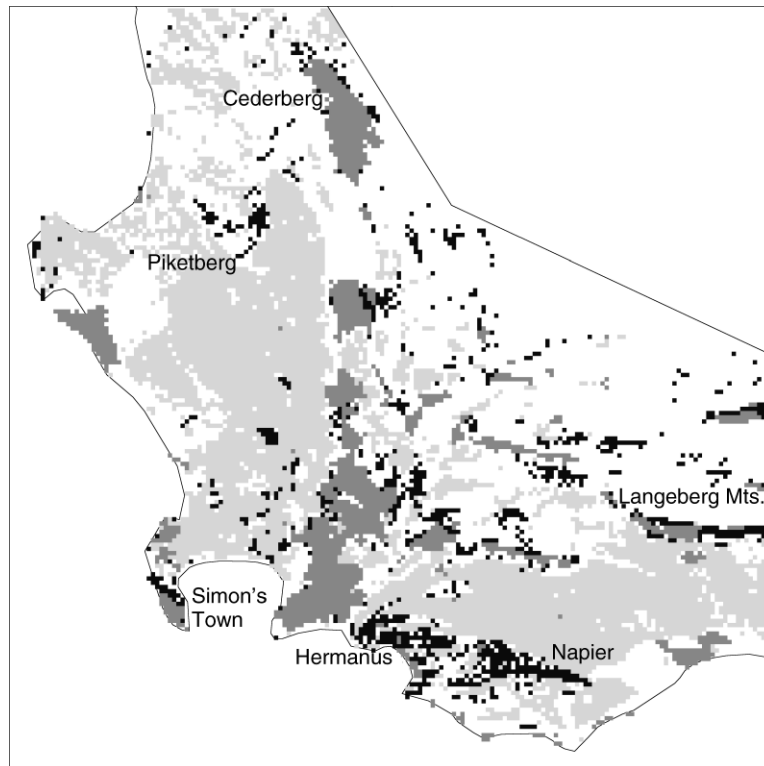


FIG. 6. Map of the western part of the Cape Floristic Region of South Africa showing areas chosen to allow dispersal of 282 species of Proteaceae along at least 35 paths obeying the Williams et al. (2005) definition of nonoverlapping, where possible, within areas of predicted suitable conditions under climate change. Key: pale gray: areas with 66% or more transformation of habitat; dark gray, existing protected areas; black, additional cells requiring protection, as determined by solving an integer program. There are 1068 black cells, and this is the minimum possible number for which the conservation goal is achievable. Goal-essential cells could be determined as in Fig. 5, if necessary, by solving additional integer programs.

temperatures exceeding 18°C, annual potential evaporation, and summer and winter soil moisture days (days where soil moisture is above a critical level for plant growth; Midgley et al. 2002).

- 4) A list of 1525 “already protected” cells (those with adequate existing statutory protection).
- 5) A list of 6036 “transformed” cells, for which more than two-thirds of the area in the cell has been transformed to an unsuitable state by human activity.
- 6) For each of the 282 species, a “dispersal distance” of one or three cells (for ant/rodent-dispersed or wind-dispersed species, respectively), representing the distance the species can reasonably be expected to disperse in a 10-year period. If the dispersal distance is one, the species can disperse from a given cell to any of the nine cells forming a square around the given cell; if the dispersal distance is three, the species can disperse from a given cell to any of the 25 neighboring cells arranged in a diamond around the given cell. (The nine and 25 numbers include the cell itself, modeling dispersal or survival within the cell.)

RESULTS

We solved the integer programs for the Cape Proteaceae to obtain solutions with the smallest possible number of protected cells, given the constraints (see Appendix for computational details). For the first definition of nonoverlapping, 994 cells are necessary and sufficient (Fig. 5), while for the second definition, 1068 cells are required (Fig. 6). The difference in the number of cells reflects the fact that the second definition gives resilience to more types of uncertainty in the input data, thus requiring more protected area for some species. For comparison, Williams et al. (2005) required additional protection for 1602 cells, which is 50% greater than our solution that meets the same conservation goals (using the second definition of nonoverlapping).

For 26 species, the required flow under the second definition of nonoverlapping is smaller than under the first definition, because fewer nonoverlapping chains are possible. For those species, therefore, a smaller minimum area is maintained over time in the solution to the integer program. The species with the largest difference is *Serruria bolusii* Phill. & Hutch. (Protea Atlas Code:

sebolu), which has at least 35 nonoverlapping paths by Definition 1, while only 25 nonoverlapping paths that satisfy Definition 2 are possible. The largest proportional decrease is for *Paranomus longicaulis* Salisb. ex Kn. (Protea Atlas Code: palong), which drops from 17 nonoverlapping paths to 8 nonoverlapping paths under Definition 2.

We note that the heuristic of Williams et al. (2005) does not find the true maximum possible number of chains for some species, including five of the 18 species (shown in their Table 2) that are obligate dispersers under the second definition of nonoverlapping. Our application of network flow does find the true maximum, thus allowing us to achieve stronger conservation goals for some of the species that are likely to be most vulnerable to climate change.

Despite being produced according to different requirements, the solutions of Figs. 5 and 6 are broadly similar: more than 80% of the newly protected cells in Fig. 5 are also protected in Fig. 6. The two solutions both contain cells clustered in a number of distinct areas, especially in the hills between Hermanus and Napier, the Piketberg, the peninsula east of Simon's Town, and the Langeberg Mountains. These areas were also highlighted by the solution of Williams et al. (2005). However, their solution also contains a large cluster in the Cedarberg, roughly doubling the existing amount of protected land, and in contrast, our solutions reveal that very little additional protection is required in the Cedarberg for the given conservation goals.

DISCUSSION

We have used network flow to exactly characterize the number of nonoverlapping dispersal constrained paths, which captures the notion of a species' range size during the time that its range is experiencing a geographic shift. Using network flow constraints in a mixed integer program, we found the optimum configuration of protected areas to support a minimum range size conservation goal simultaneously for 282 species of Cape Proteaceae, reducing by one-third the number of cells required to achieve the same conservation goal, compared to a previous study (Williams et al. 2005). The same method can be applied to any other group of species, as long as maps of predicted future suitable conditions can be generated for them. Similarly, the method can be used with updated future climate scenarios, as models of climate change evolve. Our results show that network flow can be a powerful tool for modeling and optimizing the capacity of connections between different components of a landscape, and we expect that it will find more applications in landscape ecology and reserve design.

Sources of uncertainty and potential errors

The optimization we have described depends on a number of levels of modeling, each of which comes with some potential sources of error. A major source of

uncertainty derives from the modeling of future climate conditions, especially since there is little agreement among climate models on likely future precipitation trends, and the distribution of Cape Proteaceae is strongly influenced by precipitation. A second major source of uncertainty is the projection of species distribution models onto future climate conditions. Models produced by different modeling methods may give very different future predictions (Pearson et al. 2006). Furthermore, we have assumed that the relationship between suitability for each species and climatic conditions is constant over time, and that generation times for the modeled species are similar to the 10-year duration of time slices. Continuous models were thresholded to give predictions of future suitable areas, so the predictions are sensitive to the choice of thresholding rule. The modeling of species' dispersal abilities and minimum area requirements and the treatment of habitat transformation are all quite simplistic, and open to future revision when more information is available (Williams et al. 2005). The similarity of our two solutions for different formalizations of the minimum-area requirement suggest that this detail of the approach is not a major source of uncertainty. However, given the significant uncertainties in climate and species models and their interaction, and other simplistic details of our modeling approach, the solutions that we have produced should be considered tentative, and subject to revision as the underlying models and data are improved. Nevertheless, our solutions identify areas that may be important for persistence of the Cape Proteaceae, given our current knowledge. By focusing on optimization, we have eliminated one source of uncertainty, the uncertainty due to the use of computational heuristics rather than exact optimization in the design of dispersal corridors. Indeed, we find that expanding the amount of protected area in the Cedarberg is not as important as was suggested by Williams et al. (2005), so more priority can be given to other areas.

Choice of optimization criterion

We note that it is possible to model more complicated dispersal mechanisms than we have considered here, for example allowing populations to branch and merge. However, to insure against stochastic events eliminating small populations or rendering small areas unsuitable, and to insure against uncertainty in the underlying data, it is important that a minimum number of separate populations be able to migrate along independent pathways that maintain suitable climatic conditions. Chains constitute the minimum requirement that ensures species viability through the existence of such independent pathways. By focusing on chains, we are primarily answering the question: "How much land must be protected to ensure viability during climate change?" However, given sufficient resources, we may desire protected area configurations that offer more than simple viability: we may prefer to maximize expected

population sizes, subject to the viability constraints we have modeled here. The latter optimization problem would probably require more explicit modeling of populations than the present study. We may also combine requirements on flows and chains with other optimization criteria, such as preferring contiguous protected areas.

Bi-criteria optimization

In this paper, we are primarily trying to minimize the number of additional grid cells requiring protection. That is, we seek a solution of minimum cost that satisfies the survival requirements, where each grid cell we use is assigned a cost of one. The model could also accommodate different costs for each grid cell, simply by changing the coefficient in the mixed integer program's objective function that corresponds to that cell. Here we also consider attaching costs to the arcs, in order to model how likely the species is to survive and disperse at each step in a dispersal chain. We set the cost of each between-year arc to be the Euclidean distance between the endpoints of the arc; in-year arcs had cost 0. This results in the cost of a chain being the sum of the Euclidean distances of its implied dispersal events.

Adding the flow cost to the objective function of our mixed integer program combines the financial cost of creating new protected areas with the biological cost of requiring the species to disperse further. On its face, it seems that adding these costs is comparing apples and oranges. This is a common difficulty in bi-criterion optimization problems. We want to maximize the chances of species survival, but protecting grid cells is difficult and has other costs that push us to minimize the number of grid cells we protect. We need to somehow balance these two criteria. One approach is to place a hard limit on one of the two costs while optimizing the other. Another approach is to multiply one of the costs by a scaling parameter and add it to the other. Both approaches allow us to vary the appropriate parameter over a range, in order to fill out a trade-off curve of total dispersal distance required (and implied reduction of survival probability) vs. grid cell protection cost; we chose to implement the former approach. We started with the number of protected cells at 994, the minimum for which the goal is achievable, and then increased it in steps of 10 from 1000 to 1340, the point at which adding more protected cells does not help to reduce the flow cost (Fig. 7). On the left of the plot we see that a 5% increase in the number of protected cells allows the flow cost to be reduced 20%. Conversely, the right end of the plot shows that many more cells must be protected if we want to keep the flow cost at or near its minimum possible value. A lower flow cost means that the species are not required to disperse as far, so their probability of successfully dispersing along the chains is increased. Therefore, we conclude that a small increase above the absolute minimum number of protected cells may be justified, in order to increase the probability of the

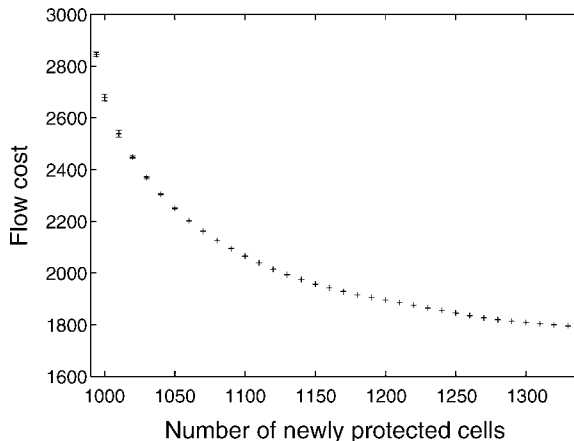


FIG. 7. Trade-off curve for the bi-criteria optimization of the number of protected cells and the flow cost. The flow cost is the sum of the Euclidean distances of the dispersal chains. The minimum possible number of protected cells is 994, while the minimum possible flow cost is 1794.37. The points on the graph show selected solutions trading off the two measures. At each point, the y-value gives the minimum possible flow cost for the given number of protected cells, if CPLEX solved the corresponding mixed integer program within a few days; otherwise the upper and lower bounds found for the minimum flow cost are shown with an error bar.

species' survival, but that maximizing survival probability (by minimizing flow cost) is not likely to be a cost-effective use of conservation funding.

Variable dispersal likelihood and habitat suitability

The network flow and integer programming approach offers some new possibilities for solving variations of the corridor design task. We have seen this already in the use of two notions of nonoverlapping; here we describe some variations that use min-cost flow instead of maximum flow. One possibility is to represent species ranges with continuous values rather than binary ones, denoting varying levels of suitability for the species. In addition, a given species may be more likely to disperse to nearby cells than to further away cells, or to cells in a certain direction, due to prevailing winds. A simple way of modeling varying dispersal likelihood is given by the bi-criteria optimization described above, where there is an implied cost for each dispersal event, proportional to the dispersal distance. We can represent varying probabilities of persistence and dispersal more explicitly and with more detail by varying arc costs. For example, we can make the cost of an in-year arc be the negative log probability that the species would persist in the corresponding cell for the corresponding 10-year period. Similarly, we can make the cost of a between-year arc be the negative log probability that the species would disperse between the corresponding two cells in a 10-year period. The cost of a source-sink path, being the sum of the costs of its arcs, is then equal to the negative log probability that the species manages to persist and then disperse as required at each step in the correspond-

ing dispersal chain, assuming each of these events is statistically independent. Finding a min-cost flow of a particular value v would then be equivalent to finding a set of v dispersal chains that maximizes the probability of successful dispersal along all the chains simultaneously. Cost here represents biological cost; economic costs (such as variations in land price) can also easily be modeled.

Alternatively, we may be able to estimate the size of the population that each cell can sustain in each time slice. If we set the capacity of in-year arcs to this estimate, then a flow can be interpreted as modeling the dispersal of a whole population. Such a flow may no longer be decomposable into nonoverlapping chains, and it might use a different number of cells in each layer. For example, it might use 35 highly suitable cells in one year, and 50 fairly suitable cells in the next.

Another possibility for adding realism to the model is to use what is known as generalized flow. In ordinary network flow, the flow entering an arc is the same as the flow leaving the arc. Generalized flow allows for there to be multiplicative gains or losses. (For a multiplicative loss, think of the arc as a leaky pipe.) This would be another potential way to model the probability of dispersal between two grid cells. Generalized flow has also been well-studied in the operations research and computer science communities, and there are efficient computational techniques known for dealing with it.

Varying conservation goals

If model outputs will be used to prioritize new areas for conservation, it may be useful to propose more contiguous or compact areas of new protection. This can be achieved by adding a boundary length modifier, which adds a penalty to the objective function for each pair of neighboring cells with different protection status (Possingham et al. 2000). The mixed integer program will then compute the optimum trade-off between boundary length and number of proposed sites. A larger penalty value will produce more contiguous designs.

Similarly, it may be useful to propose protection only for sites that are needed by multiple species. This can be achieved by making the required flow value for each species be a variable, rather than a constant, and adding a penalty to the objection function for flow values that are less than the conservation goal. The penalty can vary per species, depending on the maximum achievable number of chains, or other measures of the conservation importance of each species. This will allow the mixed integer program to find the optimal trade-off between the conservation goals and number (or economic cost) of proposed sites.

Long-range dispersal events

The potential usefulness of the approach we describe relates to the ongoing debate about the migration capacity of species under climate change. For example, fossil pollen records have been interpreted as indicating

that tree populations migrated much faster during post-glacial warming in North America and Europe than our current knowledge of seed dispersal mechanisms would suggest (Davis 1981, Huntley and Birks 1983). Rare and poorly understood long-distance dispersal events could therefore be an important factor in the ability of these and other species' ranges to track suitable conditions during periods of rapid climate change (Clark 1998, Pearson and Dawson 2005), but such events are not included in the dispersal models considered in this paper. However, there is recent genetic evidence that tree migration rates at the end of the last glacial period were much slower than fossil pollen data suggests, reducing the need to posit rare long-distance dispersal events (McLachlan et al. 2005). Indeed, range expansion into areas predicted to become suitable may be slow, lagging trailing edge population extinction (Foden et al. 2007). It is clear that further research is warranted to understand the full range of dispersal mechanisms. This is especially true for any species expected to undergo pronounced range shifts, like many Proteaceae (Midgley et al. 2003). Meanwhile, conservation planning must be done with respect to our current understanding of species' dispersal abilities, and flexible planning methods must be developed to be able to incorporate and adapt to future insights into species' dispersal abilities. In general, we prefer to err on the side of caution, and use conservative estimates of species' dispersal abilities.

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LITERATURE CITED

- Ahuja, R. K., T. L. Magnanti, and J. B. Orlin. 1993. Network flows: theory, algorithms, and applications. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- Bawa, K. S., and S. Dayanandan. 1998. Global climate change and tropical forest genetic resources. *Climatic Change* 39(2-3):473-485.
- Clark, J. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152:204-224.
- Davis, M. 1981. Quaternary history and the stability of forest communities. Pages 132-153 *in* D. West, H. Shugart, and D. Botkin, editors. *Forest succession: concepts and application*. Springer-Verlag, New York, New York, USA.
- Del Barrio, G., P. A. Harrison, P. Berry, N. Butt, M. Sanjuan, R. Pearson, and T. Dawson. 2006. Integrating multiple modelling approaches to predict the potential impacts of climate change on species' distributions in contrasting regions: comparison and implications for policy. *Environmental Science and Policy* 9:129-147.
- Doyle, P., and J. Snell. 1984. Random walks and electric networks. Mathematical Association of America, Washington, D.C., USA.
- Foden, W., G. F. Midgley, G. Hughes, W. J. Bond, W. Thuiller, M. T. Hofman, P. Kaleme, L. G. Underhill, A. Rebelo, and L. Hannah. 2007. A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through

- population declines and dispersal lags. *Diversity and Distributions* 13(5):645–653.
- Forman, R. T. 2002. Foreword. Pages vii–x in K. J. Gutzwiller, editor. *Applying landscape ecology in biological conservation*. Springer-Verlag, New York, New York, USA.
- Graham, C. H. 2001. Factors influencing movement patterns of Keel-billed Toucans in a fragmented tropical landscape in Southern Mexico. *Conservation Biology* 15(6):1789–1798.
- Honnay, O., K. Verheyen, J. Butaye, H. Jacquemyn, B. Bossuyt, and M. Hermy. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters* 5(4):525–530.
- Huntley, B., and H. Birks. 1983. *An atlas of past and present pollen maps for Europe: 0–13,000 B.P.* Cambridge University Press, Cambridge, UK.
- Johns, T. C., R. E. Carnell, J. F. Crossley, J. M. Gregory, J. F. B. Mitchell, C. A. Senior, S. F. B. Tett, and R. A. Wood. 1997. The second Hadley Centre coupled ocean-atmosphere GCM: model description, spinup and validation. *Climate Dynamics* 13(2):103–134.
- Malanson, G. P. 2003. Dispersal across continuous and binary representations of landscapes. *Ecological Modelling* 169:17–24.
- Malcolm, J. R., and L. F. Pitelka. 2000. Ecosystems and global climate change: a review of potential impacts on U.S. terrestrial ecosystems and biodiversity. *Pew Center on Global Climate Change*, Arlington, Virginia, USA.
- Margules, C., and R. Pressey. 2000. Systematic conservation planning. *Nature* 405:243–253.
- McLachlan, J. S., J. S. Clark, and P. S. Manos. 2005. Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86:2088–2098.
- McRae, B. 2006. Isolation by resistance. *Evolution* 60:1551–1561.
- Midgley, G. F., L. Hannah, D. Millar, M. C. Rutherford, and L. W. Powrie. 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography* 11:445–451.
- Midgley, G. F., L. Hannah, D. Millar, W. Thuiller, and A. Booth. 2003. Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic region. *Biological Conservation* 112:87–97.
- Noss, R. F. 2001. Beyond Kyoto: forest management in a time of rapid climate change. *Conservation Biology* 15(3):578–590.
- Pearson, R. G., and T. P. Dawson. 2005. Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. *Biological Conservation* 123:389–4001.
- Pearson, R., W. Thuiller, M. Araújo, L. Brotons, E. Martinez-Meyer, C. McClean, L. Miles, P. Segurado, T. Dawson, and D. Lees. 2006. Model-based uncertainty in species' range prediction. *Journal of Biogeography* 33:1704–1711.
- Possingham, H., I. Ball, and S. Andelman. 2000. Mathematical methods for identifying representative reserve networks. Pages 291–305 in S. Ferson and M. Burgman, editors. *Quantitative methods for conservation biology*. Springer-Verlag, New York, New York, USA.
- Ray, N. 2005. Pathmatrix: a geographical information system tool to compute effective distances among samples. *Molecular Ecology Notes* 5:177–180.
- Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. *American Naturalist* 158:87–99.
- Schulze, R. E., and L. A. Perks. 1999. Assessment of the impact of climate. Final report to the South African Country Studies Climate Change Programme. School of Bioresources Engineering and Environmental Hydrology, University of Natal, Pietermaritzburg, South Africa.
- Taylor, P., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68:571–572.
- Tetali, P. 1991. Random walks and the effective resistance of networks. *Journal of Theoretical Probability* 4:101–109.
- Tischendorf, L., and L. Fahrig. 2000. How should we measure landscape connectivity? *Landscape Ecology* 15:633–641.
- Turner, M., R. Gardner, and R. O'Neill. 2001. *Landscape ecology in theory and practice*. Springer, New York, New York, USA.
- Vos, C. C., H. Baveco, and C. J. Grashof-Bokdam. 2002. Corridors and species dispersal. Pages 84–104 in K. J. Gutzwiller, editor. *Applying landscape ecology in biological conservation*. Springer-Verlag, New York, New York, USA.
- Williams, P., L. Hannah, S. Andelman, G. Midgley, M. Araújo, G. Hughes, L. Manne, E. Martinez-Meyer, and R. Pearson. 2005. Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology* 19(4):1063–1074.
- With, K. A. 2002. Using percolation theory to assess landscape connectivity and effects of habitat fragmentation. Pages 105–130 in K. J. Gutzwiller, editor. *Applying landscape ecology in biological conservation*. Springer-Verlag, New York, New York, USA.

APPENDIX

Modeling the second definition of nonoverlapping chains (*Ecological Archives* A018-043-A1).