
Planning for Climate Change: Identifying Minimum-Dispersal Corridors for the Cape Proteaceae

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Abstract: *Climate change poses a challenge to the conventional approach to biodiversity conservation, which relies on fixed protected areas, because the changing climate is expected to shift the distribution of suitable areas for many species. Some species will persist only if they can colonize new areas, although in some cases their dispersal abilities may be very limited. To address this problem we devised a quantitative method for identifying multiple corridors of connectivity through shifting habitat suitabilities that seeks to minimize dispersal demands first and then the area of land required. We applied the method to Proteaceae mapped on a 1-minute grid for the western part of the Cape Floristic Region of South Africa, to supplement the existing protected areas, using Worldmap software. Our goal was to represent each species in at least 35 grid cells (approximately 100 km²) at all times between 2000 and 2050 despite climate change. Although it was possible to achieve the goal at reasonable cost, caution will be needed in applying our method to reserves or other conservation investments until there is further information to support or refine the climate-change models and the species' habitat-suitability and dispersal models.*

Key Words: area-selection algorithms, bioclimatic modeling, biodiversity conservation, connectivity, habitat suitability, species persistence

Planificación para el Cambio Climático: Identificación de Corredores de Dispersión Mínima para las Proteaceae del Cabo

Resumen: *El cambio climático representa un reto para la estrategia tradicional de la conservación de la biodiversidad que se basa en áreas protegidas fijas, porque se espera que el cambio climático cambie la distribución de áreas adecuadas para muchas especies. Algunas especies solo persistirán si pueden colonizar nuevas áreas, aunque sus aptitudes dispersoras pueden ser muy limitadas en algunos casos. Para abordar este problema ideamos un método cuantitativo para identificar múltiples corredores de conectividad en hábitats con diferentes aptitudes que primero busca minimizar las demandas de dispersión y el área requerida después.*

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Utilizamos software Worlmap para aplicar el método a Proteaceae en un mapa con cuadrícula de un minuto de la parte occidental de la región Florística del cabo en Sudáfrica, un área que suplementa a las áreas protegidas existentes. Nuestra meta era representar cada especie presente en al menos 35 celdas (aproximadamente 100 km²) entre 2000 y 2050 a pesar del cambio climático. Aunque era posible alcanzar la meta con un costo razonable, se requiere precaución al aplicar nuestro método en reservas u otras inversiones de conservación hasta que haya más información para sustentar o refinar los modelos de cambio climático y los modelos de aptitud del hábitat y de dispersión de especies.

Palabras Clave: algoritmos para la selección de áreas, aptitud del hábitat, conectividad, conservación de la biodiversidad, modelado bioclimático, persistencia de especies

Introduction

Anthropogenic climate change poses a challenge to the conventional approach to biodiversity conservation, which relies on fixed protected areas. With climate change, species' geographic distributions are expected to change. Some species may become locally extinct in existing protected areas so that conservation resources may (in effect) be squandered where they are no longer needed. Furthermore, conservation of some vulnerable species may require new areas that are currently both climatically unsuitable and unprotected (e.g., Peters 1991; Cowling et al. 1999; Rutherford et al. 1999a; Araújo et al. 2005). The dynamic nature of species' geographic ranges as they respond to climate change has been effectively ignored by previous conservation-planning approaches but needs to be accounted for in holistic conservation planning.

Climate change affects two key aspects of population processes. First, changing climate will change the distribution of habitat suitable for establishment, growth, and reproduction, so that an area protected as suitable for a species now may become unsuitable in the future (Peters & Darling 1985; Prentice 1986; Huntley et al. 1995; Sykes et al. 1996). Second, if with changing climate different suitable areas are needed for a species at different times, then the species would need to be able to disperse reliably to new suitable areas (Pitelka 1997). Consequently, how readily species disperse to new suitable areas could have a major effect on how well they persist as climate changes (Peters 1991; Pitelka 1997; Huntley 1998; Higgins & Richardson 1999). If species were able to disperse easily over any distance, then persistence despite changing patterns of suitability would require only additional areas to cover future suitability, without regard to distance. Current area-selection methods for identifying conservation priorities could already accommodate this situation by including the present and future suitable ranges for a species as two separate ranges to be represented. Unfortunately, because many species are poor dispersers and are unlikely to colonize distant areas, this approach is insufficient to ensure persistence, and new methods are needed.

We asked, how should we identify important areas for conserving biodiversity in the face of climate change, particularly when dealing with poorly dispersing species? We approach this from the convention of quantitative area selection, building on the general conservation-planning framework of Cowling and Pressey (2003). This type of framework can be extended for use with distribution data modeled to allow for climate change (Hannah et al. 2002). We started from the premise that for some species the greatest risk to persistence will be the low probability of dispersing between distant suitable areas. Consequently, the principle behind our method is to minimize the distances species are required to disperse. Fortunately, some species are expected to retain suitable areas within some of their present range, so these species could continue to be represented within the same areas (Hannah & Salm 2003; Midgley et al. 2003). As a starting point, we assumed that these species will be safer if they are conserved in these places. But for other species, survival will depend on dispersal to newly suitable areas because of loss of all formerly suitable areas. For these obligate disperser species, a rigorous design is needed to achieve multiple, appropriately managed corridors or stepping stones of connectivity that allow tracking of changes in suitable areas as climatic conditions change (Cowling et al. 1999; Midgley et al. 2003).

We explored the conservation problem of climate-forced dispersal by considering the needs of the Proteaceae in the western part of the Cape Floristic Region of South Africa (their principal global hotspot). Proteaceae species are particularly well suited to our study. First, because they are highly valued for trade and tourism (Rebello 2001), plans are required to ensure their persistence (e.g., Rebello & Siegfried 1990). Second, many of the species are associated with the Fynbos Biome, which is expected to undergo a pronounced change in distribution with climate change (Midgley et al. 2003). Third, many of the species are known not to disperse and establish easily over long distances (Midgley et al. 2002). Fourth, their current distributions are well recorded (Rebello 2001). This application is used purely as an example to illustrate the method. Consequently, the results should not be interpreted as an attempt

to propose a new protected-area network for the study area.

Methods

Data Sources

We considered the western part of the Cape Floristic Region extending to 20°48' E and to 31°53' S, where it encompasses Fynbos communities. This is the part of the Cape Floristic Region that is most vulnerable to anthropogenic climate change (Midgley et al. 2002). We used a grid of 1 × 1 minute cells (average 1.85 × 1.55 km along their sides, area approximately 2.87 km²) because cells this size are small enough to be useful for practical planning and yet sufficiently large to be appropriate for modeling climate (Pearson & Dawson 2003).

Habitat transformation and changing land use compound the effects of climate change (e.g., Peters & Darling 1985; Peters 1991; Travis 2003). Based on information from the Council for Scientific and Industrial Research (CSIR 1999), we estimated that transformation of habitat to an unsuitable state has exceeded 66% of the area of each cell for 6036 of the one-minute grid cells. The distribution data for the Proteaceae were set to zero for these cells. In contrast, we estimated that there was adequate existing protection for 1525 of the grid cells in statutory protected areas (Rouget et al. 2003a).

Species' distribution data were taken from the Protea Atlas Project (PAP) database, which contains field-determined species presence and absence at more than 60,000 georeferenced sites. This is an unusually thorough sampling of localities, totaling more than 250,000 species records for 340 taxa (<http://protea.worldonline.co.za/default.htm>). Climate data were interpolated for

the 1-minute grid (Schulze 1997). Future projections were based on Schulze and Perks (1999), according to the 2050 projections for the region from the general circulation model HadCM2 (http://www.cru.uea.ac.uk/link/experiments/1b_experi_contents.html) with IS92a emissions assumptions for CO₂ equivalent greenhouse-gas concentrations and excluding sulfate-cooling feedback. Soil categorization relating to fertility (high, medium, and low), pH (acid, neutral, and basic), and texture (sand and clay) was derived for the 1-minute grid by interpolation of regional geology maps (R. Cowling and A. Rebelo, personal communication). Information on nomenclature and on species' dispersal modes was taken from Rebelo (2001).

Bioclimatic and Dispersal Time-Slice Modeling

Expected distributions were modeled separately for individual species of Proteaceae on the 1-minute grid (Table 1) by considering both the changing environmental suitability for each species (depending primarily on climate: Midgley et al. 2003) and its particular dispersal constraints (depending primarily on the dispersal agent). We made time-slice distribution models for each species for 2000, 2010, 2020, 2030, 2040, and 2050. Distributions for 2000 were modeled because the original sampling did not include all grid cells. Dispersal distances were assumed to be a maximum of one cell per time slice for ant- and rodent-dispersed species (which may be an overestimate), and a maximum of three cells per time slice for wind-dispersed species (corresponding to at least 4 km in 10 years or 400 m in 1 year, which may be considered long-distance dispersal: Cain et al. 2000). According to these models, 282 of the 316 Proteaceae species modeled would be expected to persist from 2000 to 2050 within the region, occupying 17,677 cells with a total

Table 1. Method to model expected distribution of Proteaceae species with climate change and dispersal constraints for time slices in 2000, 2010, 2020, 2030, 2040, 2050.

Step	Rule
1	Collate grid-cell data for environmental variables for now (2000) and for a future time (2050) with a standard climate change scenario.
2	Interpolate linearly for each environmental data for intervening decade time slice (2010 2020 2030 2040).
3	Develop general additive models (GAMs) for each species (e.g., Midgely et al. 2003; Thuiller et al. 2004a) and apply receiver operating characteristic (ROC) thresholds (Swets 1988) to define potential climatic range limits for each time slice.
4	Consider year 2000 range and buffer according to dispersal mode (add 1 grid cell around range periphery if ant or rodent dispersed or 3 grid cells if wind dispersed).
5	Consider year 2010 potential climatic range, see where this overlaps with the buffered 2000 range, and use this overlap for the expected 2010 range.
6	Repeat steps 4-5 by taking the 2020 potential climatic range and see where this overlaps with the buffered expected 2010 range and use this overlap for the expected 2020 range.
7	Repeat steps 4-5 by taking the 2030 potential climatic range, see where this overlaps with the buffered expected 2020 range, and use this overlap for the expected 2030 range.
8	Repeat steps 4-5 by taking the 2040 potential climatic range, see where this overlaps with the buffered expected 2030 range, and use this overlap for the expected 2040 range.
9	Repeat steps 4-5, considering the 2050 potential climatic range, see where this overlaps with the buffered expected 2040 range, and use this overlap for the expected 2050 range.

of 1,304,019 occurrences (ignoring habitat transformation).

Planning Framework and Goals

We identified important areas for conservation by using the planning framework described by Cowling and Pressey (2003, their Table 1). Our method relates most directly to their stage 7: the selection of additional conservation areas to extend the existing protection (a gap analysis, Scott et al. 1993).

Our goal was to conserve, where possible, a minimum range size for every species (a minimum-set problem). We used an illustrative range-size target of 100 km² for every species, based on the area criterion of the World Conservation Union (IUCN) for critically endangered species. This range-size criterion could be modified as better information on the sizes of viable ranges becomes available, such as on the relative needs of sprouting and nonsprouting species with climate change (cf. Pressey et al. 2003). For a 1-minute grid at the latitude of the Cape, 100 km² is approximately 35 grid cells. We did not constrain selection to choosing only contiguous blocks of grid cells because most Proteaceae do not require large blocks of contiguous habitat and because multiple scattered areas may promote persistence by spreading the risks of local extirpation among areas (Shafer 2001; Araújo et al. 2005). First we sought to facilitate dispersal ("dispersal chains") and then we tried to minimize costs or conflicts with other land-use interests ("area selection").

Dispersal Chains

Our primary criterion for choosing areas was to minimize the distances species would be forced to disperse to promote each species' probability of persistence. For some species, the minimum distance will be zero. We identified these "persistence areas" from a pattern of overlap of grid cells, where species are expected to continue to occur within the same cells in all six of our future time-slice models (without any implication for past or future persistence beyond the modeled time slices). Not all species can remain in persistence areas because habitat becomes unsuitable, so for the remaining (obligate disperser) species that will have to track the changing climate, we sought to give them the shortest possible dispersal distances. We identified these dispersal areas from a pattern of "chains of grid cells" across time-slice models, with the aim of providing connectivity, either as stepping stones or as more continuous corridors of suitable areas linked in space and time within the constraints of our dispersal models.

Accommodating both persistence areas and dispersal areas can be simplified within a single consistent method if we regard temporal overlap (persistence) cells as zero-length (dispersal) chains. If the goal had been simply to obtain a single representation of each species, then it would have been possible to reduce the size of the

computational problem. In this case, first we would identify persistence areas by looking for those cells in which all the time-slice models overlap. Second, we would deal with the remaining species separately, by seeking chains of cells that could form dispersal areas. However, our goal was to have multiple (35) representations for each species. For both this and the single-representation case above, we can simplify inclusion of both persistence areas and dispersal areas within a single consistent method by regarding temporal overlap (persistence) cells as zero-length (dispersal) chains. Some species can be represented with temporal overlap (persistence) cells alone, and some species can be represented with dispersal-constrained chains of cells alone. Other species, however, will require a combination of the two kinds of cells. Rather than tracking the number of overlap cells and the number of additional chains required for each species, it was simpler (although slower) to use the chains technique to find the shortest combination of overlap cells and chains for all species, treating overlap cells as zero-length chains of cells.

We identified dispersal chains of grid cells for a species by (1) finding suitable cells within successive time slices that lie within the maximum permitted dispersal step (of one or three grid cells, as appropriate) from previously suitable cells (Fig. 1) and (2) reiterating to find all such dispersal chains linking all time slices. In practice, the search for chains (Fig. 1) started from the 2050 time slice and worked backward to earlier time slices; it was more efficient because Proteaceae distributions were generally expected to become narrower over time. For a data set of this size, there were so many chains that it is impractical to store and select among them all on a personal computer. Therefore we stored a sample of up to 1000 of the shortest chains found for each species for the area-selection procedure. This sample size should be sufficiently large to increase efficiency by allowing the discovery of overlapping chains among the species during area selection. Less desirably, many of the chains for any one species overlapped in part, or even in total, because the dispersal jumps can occur between the same cells but between more than one pair of time slices. To ensure that we ended up with 35 independent chains for each species, we retained only completely nonoverlapping chains for the subsequent area-selection procedure. Which particular chains were selected first for the sample will affect which subsequent chains were found to be nonoverlapping. The effect of this was not addressed here.

Area Selection

Our secondary criterion for choosing areas was to minimize the total cost to society required to represent all the species (Faith & Walker 1996; Williams et al. 2003). Resources are limited, so minimizing the cost should reduce conflicts between conservation needs and society's other

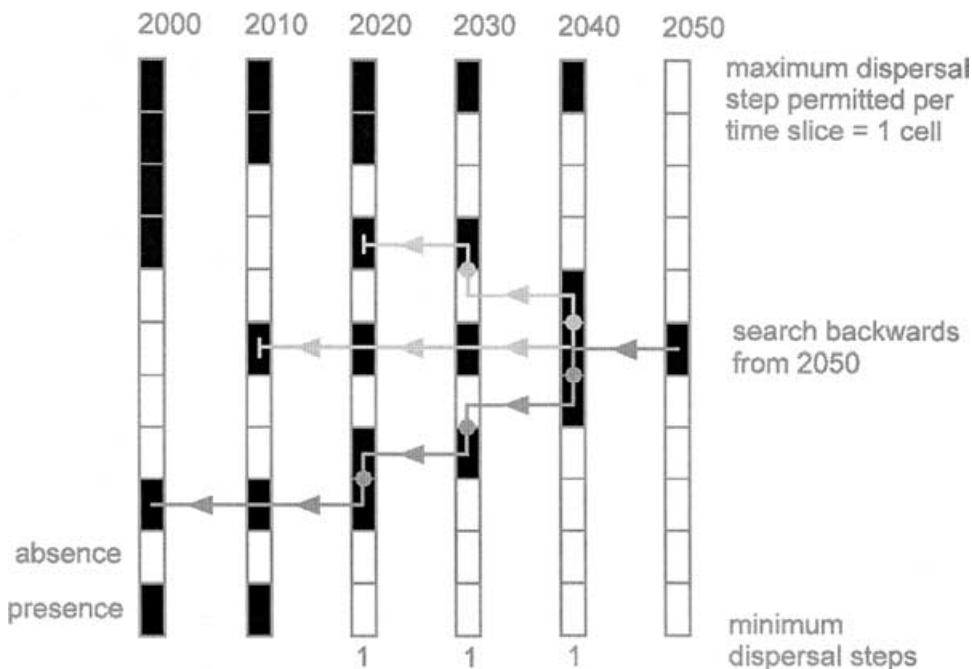


Figure 1. Procedure to identify dispersal-constrained chains of areas from modeled time-slice data on a grid for one obligate disperser species. Each vertical bar represents part of one dimension of a map grid. The series of bars represent the successive time slices. Black cells are modeled presences. The search for chains begins at 2050 because searching backward is more efficient when range sizes are decreasing over time. To proceed to the next time slice, there has to be a presence in the same grid cell or in a grid cell within one dispersal step (here the maximum dispersal step per time slice is one grid cell). Only examples of two incomplete chains and one complete chain are shown (other partly overlapping chains exist, but for clarity, are not shown).

needs. We used land area as a surrogate for cost because no more appropriate data were available. Cost-efficiency was achieved by selecting cells that are part of the most highly complementary sets of chains among species. The chains were sorted by length within the sample for each species so that the shorter chains could be chosen preferentially. The area-selection procedure consisted of three stages.

First, for the species that have a maximum of 35 or fewer chains, we selected all the unprotected cells within these chains. Selecting these goal-essential chains first is a modification of a procedure within popular heuristic algorithms that increases efficiency. For species that could not achieve 35 nonoverlapping dispersal-constrained chains, we could have included other cells from partly overlapping chains as conservation areas. We did not do this, but these cells could be added by backtracking to search again for partly overlapping chains.

Second, for species that did not reach the goal of 35 chains but could have, we identified all chains that were represented in part within the existing protected areas or within the goal-essential cells selected at the first stage. We then selected cells to complete these chains for up to 35 chains per species. Tests with the obligate disperser

species alone showed that including this stage increased area efficiency by 5-6%.

Third, for any remaining species that still did not reach the goal of 35 chains (i.e., those that could reach 35 chains but did not have chains partly represented within the existing protected areas), we used an iterative heuristic algorithm to select a set of complementary areas. We compared the efficiency of three of the most popular of these algorithms (Williams 1998): (1) greedy richness (Kirkpatrick 1983); (2) weighted rarity (Ackery & Vane-Wright 1984); and (3) progressive rarity (Margules et al. 1988). These algorithms have been modified for application to chains. At each step, all the algorithms select the highest scoring grid cell, but differ in the ways the cells are scored. Greedy richness counts simply the number of species that have not yet met their goals but which have a link from an unselected chain in that cell. Weighted rarity is similar, but weights each species by the inverse of the number of remaining chains for that species. Progressive rarity counts only the number of those species with the fewest (rarest) unselected chains. Once the highest-scoring cell was chosen, all the chains that fell within it were completed by selecting all of their additional constituent cells. Heuristic algorithms such as this do not guarantee truly optimal

Table 2. Dispersal-constrained chains of untransformed areas for the 18 obligate disperser species.*

Species	Maximum dispersal chain length (dispersal agent)	Minimum chain length	No. of dispersal-constrained (DC) chains	No. of nonoverlapping (NO) DC chains	No. of cells selected for this species	No. of NO-DC chains represented
<i>Diastella parilis</i>	5 (ant)	1	25	1	3	1
<i>Leucospermum heterophyllum</i>	5 (ant)	1	6,995	11	47	11
<i>Leucospermum parile</i>	5 (ant)	1	1,042	9	27	9
<i>Leucospermum praecox</i>	5 (ant)	1	46	1	1	1
<i>Paranomus abrotanifolius</i>	5 (ant)	3.8	4	1	0	1
<i>Paranomus centaureoides</i>	5 (ant)	1	227	2	2	2
<i>Paranomus longicaulis</i>	5 (ant)	1	3,548	8	17	8
<i>Serruria balanoccephala</i>	5 (ant)	1	14	1	0	1
<i>Serruria fucifolia</i>	5 (ant)	1	199,919	103	54	38
<i>Serruria linearis</i>	5 (ant)	1.4	206	1	0	1
<i>Sorocephalus scabridus</i>	5 (ant)	1	3,704	15	23	15
<i>Leucadendron modestum</i>	15 (wind)	1	677,645	33	13	33
<i>Leucadendron stelligerum</i>	15 (wind)	1	4,947	2	0	2
<i>Leucadendron thymifolium</i>	15 (wind)	7.1	3	1	3	1
<i>Leucadendron verticillatum</i>	15 (wind)	1.4	138	1	0	1
<i>Protea obtusifolia</i>	15 (wind)	1	1,718	3	0	3
<i>Protea pudens</i>	15 (wind)	2.0	2,291	2	1	2
<i>Protea susannae</i>	15 (wind)	1	843	3	0	3

*Chain lengths are measured in numbers of 1-minute grid cells. The maximum sample size of nonoverlapping dispersal-constrained chains is set to 1000 of the shortest chains.

results (e.g., Csuti et al. 1997; Rodrigues et al. 2000). Nevertheless, they can provide good, practical solutions to more complex problems of this kind, for which fully optimizing solutions are as yet not readily available (Moore et al. 2003). The chains-search and area-selection methods were written in C and implemented within the Worldmap software (see <http://www.nhm.ac.uk/science/projects/worldmap/index.html>).

Results

Dispersal Chains

We found a total of 4.6×10^9 chains within the dispersal constraints for the 282 species among 11,649 untransformed grid cells with species presences. The search for these chains took 37.5 hours on a 2 GHz Intel Pentium 4 personal computer with a Windows 2000 operating system. The largest total number of chains for a single species (*Protea laurifolia*) was 4.8×10^8 . Large numbers of chains were found most often in extensive areas of overlap among expected distributions in the different time slices (e.g., for *P. laurifolia* there were 6471 cells in 2000 and 2285 cells in 2050, with an overlap of 2213 cells). For 262 of the species, there was sufficient overlap among all time slices for the shortest chains to be of zero length so that species could remain in at least one overlap cell without the need to disperse. There were just 18 obligate disperser species that would be able to persist in the region only if they could disperse along chains of cells in

every case (Table 2). Two other species (*P. odorata*, *Serruria scoparia*) could not be represented because habitat transformation removed all overlap cells and any possible chains within the dispersal constraints. Thirty-four species were not considered in our chains analysis because, according to the models, they were expected to lose all suitable cells within the mapped region in at least one of the time slices and therefore were expected to suffer extinction.

The sample of nonoverlapping dispersal-constrained chains from all species included 74,157 chains. For these obligate dispersers, forced to disperse for all 35 chains, it was possible to find very short chains within the dispersal constraints that minimized the dispersal challenge (Table 2). For Cape Proteaceae at the resolution of 1-minute grid cells, selected areas were thus mostly persistence areas or dispersal corridors, with little need for longer chains of dispersal stepping stones with intervening gaps. (We assumed gaps were up to two cells for the wind-dispersed species.)

The geographical distribution of dispersal chains in the sample can be shown (Fig. 2) with a color-overlay technique (adapted from Williams & Gaston 1998). Inevitably, there tended to be more chains where there were more species (red cells in Fig. 2, particularly in the mountains). Nonetheless, there were also regions with relatively many chains per species (green cells, e.g., inland from the Langeberg and around De Hoop) and regions with relatively few chains per species (blue cells, e.g., in the western coastal hills and coastal plain around Darling). Generally, the red, brown, and green cells show

areas that should be able to contribute more to dispersal and persistence among species, providing that the rest of each chain is preserved.

Area Selection

Starting with the 1631 one-minute grid cells with adequate existing protection, the area-selection procedures chose additional cells to complete the representation of every species at least 35 times where possible. Representation of every species was not always possible (Table 2, column 7) because (column 5) there were not 35 nonoverlapping dispersal-constrained chains for every species in untransformed areas. Area-selection procedures were much quicker to run (3 seconds) than the search for chains.

Most of the new cells (red in Fig. 3) were added at the first stage of selection because they were goal essential (931 new cells) for species that have very restricted ranges after habitat transformation and climate change. All nonoverlapping dispersal chains that were found were selected for these species (filled circles on the line $y = x$ in Fig. 4b). The largest block of goal-essential cells (red in Fig. 3) was in the hills east of Hermanus and extending eastward at higher elevations to the south of Napier. Many of the other goal-essential cells filled gaps between areas of existing protection in the mountains, for example, behind Simon's Town and in the Riviersonderend, Langeberg, Kouebokkeveld, Piketberg, and eastern Cedarberg mountains. In the second stage of selection, where part chains were completed (blue in Fig. 3), cells added were scattered around the edges of previously selected cells in the interior mountain ranges (372 new cells). These were concentrated particularly in the Piketberg and around the Cedarberg. Some species for which cells are selected at this stage ended up being represented by more than 35 chains (squares in Fig. 4b). This raises the possibility that more areas were selected than were strictly necessary to meet the goal (squares above the dotted goal line in Fig. 4b), which reduces efficiency in terms of the number of cells required. In principle, any areas not required to meet the goal might be removed at the end of the selection process, although we did not attempt this.

At the third stage (orange in Fig. 3), we used three alternative algorithms. The most efficient with these data was greedy richness (299 new cells, triangles in Fig. 4b), followed by progressive rarity (309 cells) and then weighted rarity (311 cells). Comparing the three area networks, 275 cells were shared by all three sets of choices, so the results were very similar. Fewer cells were selected at this than at earlier stages, in part because of the large number of cells (1631 cells, green in Fig. 3) with existing protection that already covered more than 35 chains for many of the more widespread species (open circles in Fig. 4b). Many of the new cells were in parts of the region distant from

cells selected previously, particularly in the hills inland from the Riviersonderend and Langeberg ranges.

Our procedure for representing 35 chains per species where possible was significantly more efficient than would be expected by chance. A simulation of picking at random 1602 cells to add to the 1631 cells with existing protection while avoiding transformed areas was repeated 1000 times. From this, we estimated the mean number of species expected to reach the goal of 35 chains (or if unachievable, the maximum number that they could achieve) by chance to be 172 species. The upper 1% tail of the distribution started at 177 species, much lower than the 280 species achieved with our procedure.

To examine the effect of overestimating the dispersal capabilities of the wind-dispersed species, which might be able to disperse by only one cell per time slice, we repeated the chains and selection methods for the same data (the modeling procedure in Table 1 was unmodified) but set the maximum dispersal step for all species to one cell. This reduced the total number of dispersal-constrained chains to 2×10^8 (a 95% reduction). A sample of 73,691 nonoverlapping chains was retained (a reduction of <1%). The total number of new grid cells selected (using greedy richness) fell from 1602 to 1523, a reduction of just 5%. But suppose, instead, we were dealing with more freely dispersing species. We repeated the chains and selection methods with the same data but with the maximum dispersal constraint set to three cells for all species. This increased the total number of dispersal-constrained chains to 9×10^9 (a 95% increase). A sample of 74,730 nonoverlapping chains was retained (an increase of <1%). The total number of new grid cells selected (using greedy richness) went up from 1602 to 1651, an increase of 3%. Therefore for these data the number of new cells required is relatively insensitive to changing the maximum dispersal distance within this range of changes.

Discussion

We used atlas data of a kind (if not yet of a quality) that is commonly available to demonstrate one possible method for incorporating climate change considerations into conservation planning. Many researchers from different parts of the world have proposed that stepping stones or corridors be used to provide connectivity between protected areas, but rarely have the criteria behind the proposals been explicit or quantitative and none, as far as we are aware, have used a quantitative species-based approach to deal with climate change. However, caution will be needed before applying our method to conservation management. The method is necessarily sensitive to

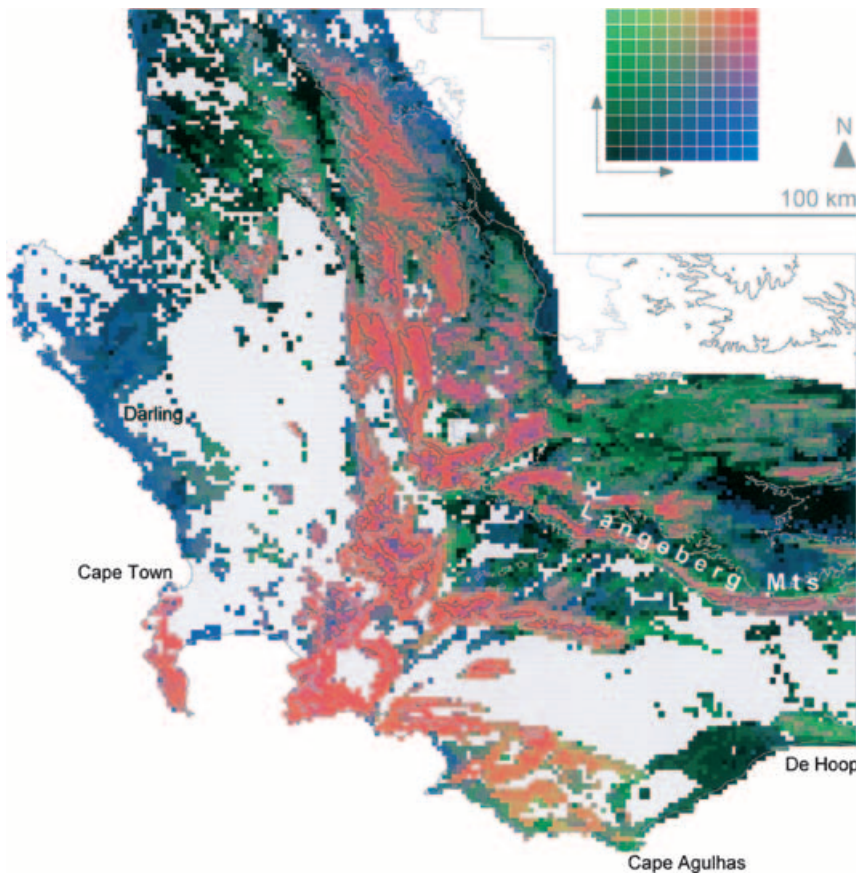


Figure 2. The western part of the Cape Floristic Region of South Africa showing the relationship between (x-axis of color scale) species richness in 2000 and (y-axis of color scale) the numbers of chains for 280 species of Proteaceae in untransformed cells on a 1-minute (2.8 km²) grid. Both axes are transformed to give uniform frequency distributions among classes along these axes. Chains are counted as the density of links from all time slices 2000-2050 in all nonoverlapping dispersal-constrained chains of cells. Color classes: red, relatively high counts of 2000 species richness and high numbers of chains; green, an excess of chains relative to 2000 richness; blue, an excess of 2000 richness relative to chains; black, low counts for both; light grey, cells with 66% or more transformation of habitat; medium grey, 600-m contour; and dark grey, 1000-m contour.

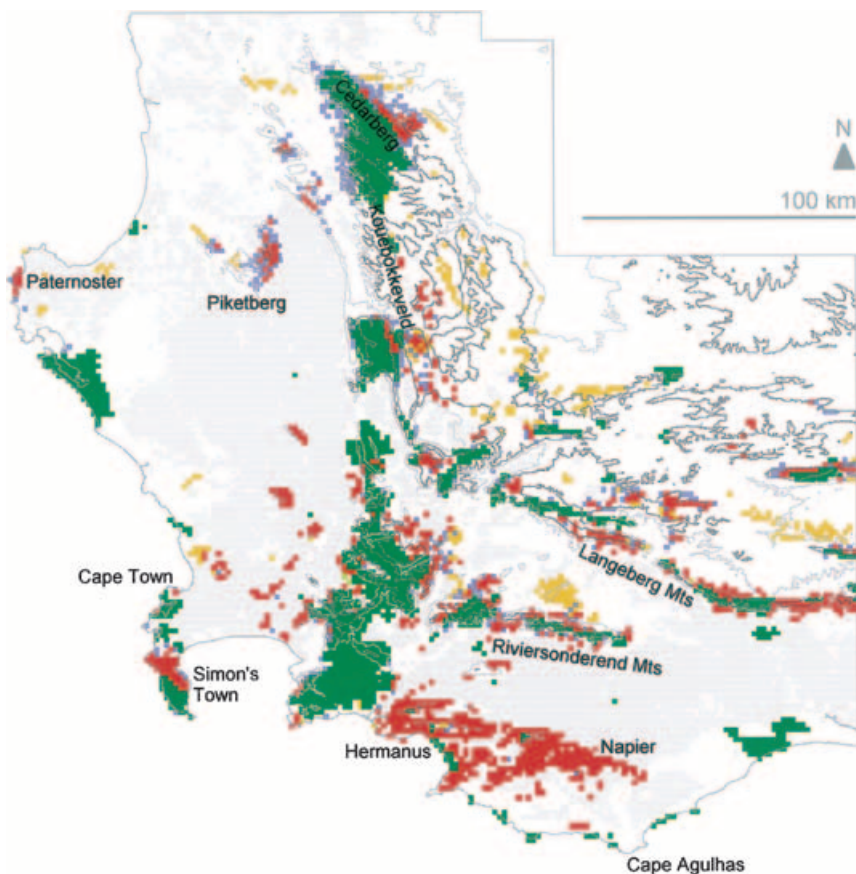


Figure 3. Map of the western part of the Cape Floristic Region of South Africa showing areas selected to continue to represent 280 species of Proteaceae in at least 35 untransformed 1-minute (2.8 km²) cells, where possible, through a scenario of climate change: light grey, cells with 66% or more transformation of habitat; green, cells with existing protection; red, cells chosen to represent goal-essential chains; blue, cells chosen to complete chains for species partly represented within existing protected cells and goal-essential cells; orange, cells chosen using an iterative complementarity algorithm based on greedy richness (600-m contour in medium grey, 1000-m contour in dark grey).

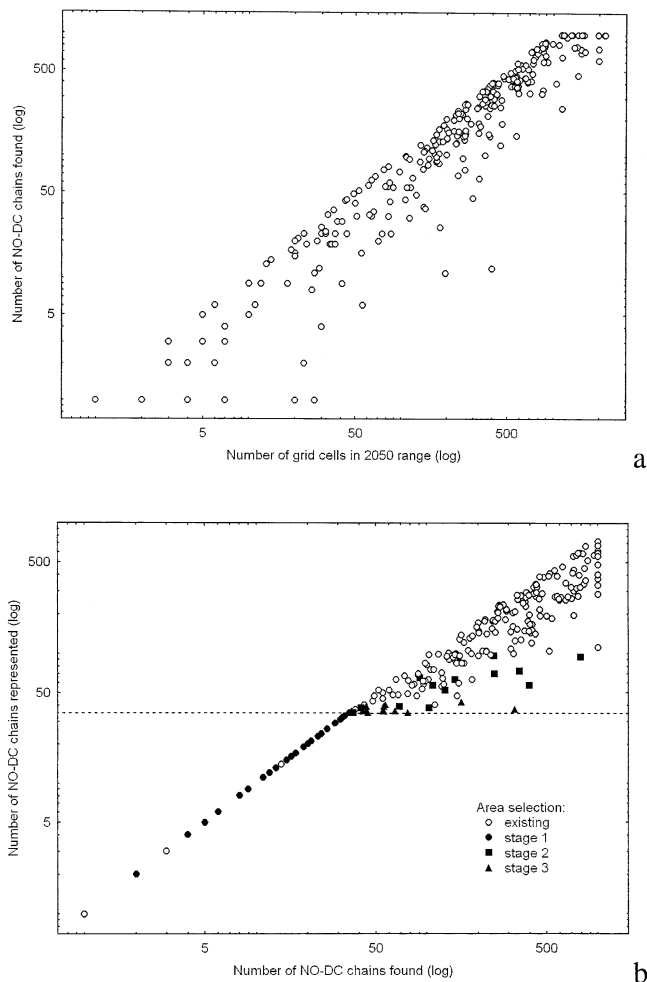


Figure 4. (a) Relationship between range size for 280 species of Proteaceae within the region in 2050 in number of one-minute (2.8 km^2) cells and the number of nonoverlapping dispersal-constrained (NO-DC) chains (limited to a sample of 1000) within the selected areas for a goal of at least 35 untransformed 1-minute (2.8 km^2) cells, where possible, through a scenario of climate change. (b) Relationship between the number of NO-DC chains (limited to a sample of 1000) and the number of NO-DC chains represented among the existing protected areas and the areas selected. Symbols show the stage of area selection at which representation of a species is completed (Fig. 3): open circles, species in cells with existing protection; filled circles, species in cells chosen to represent goal-essential chains; squares, species in cells chosen to complete chains partly represented within existing protected cells and goal-essential cells; triangles, species represented in cells chosen using an iterative complementarity algorithm based on greedy richness. Dotted line corresponds to the goal of at least 35 chains per species (species below the line have all of their representations selected).

the choice of climate-change model, to the assumptions about habitat suitability and species' dispersal, and to the scale of planning units or grid cells employed. Sensitivity to broad changes is expected, although robustness to small changes would be desirable in the face of uncertainty. Refinement of the models and of the assumptions is likely to be needed. However, with our approach these components are at least explicit and accountable.

Assumptions, Biases, and Sources of Error

Modeling of future bioclimatic suitability is expected to be the largest source of error because of the significant uncertainties in the climate models (and only one of several possible models was considered here) and because of uncertainties in identifying the factors that truly govern species' distributions, both now and in the future (Pearson & Dawson 2003; Vaughan & Ormerod 2003; Thuiller et al. 2004b). The suitability models we used assume further that relationships between species and climate and soils are unchanging over time, the rate of climate change is uniform through time, species' interactions do not affect distributions strongly, and generation times approximate the 10-year time-slice duration, which requires pollination, seed set, and an appropriate fire-disturbance frequency. As with most modeling, it was assumed that distributions reach equilibrium with expectations from the models, in this case within each of the 10-year time periods (in this region, fires do approximate a 10-year cycle, with dispersal following within 6 months). Area selection is known to be sensitive to the choice of suitability model (Loiselle et al. 2003), but as yet we have no data with which to explore the effects of inadequacies in the models for the Cape Proteaceae.

Our knowledge of effective dispersal processes was very limited, particularly in regard to the importance of rare, long-distance events (Clark et al. 1998; Higgins & Richardson 1999; Cain et al. 2000; Clark et al. 2003). If alternative dispersal rules were preferred, these could be accommodated for future studies. We consider that dispersal and its effect on persistence should be more important to planners than the crude area-efficiency of species representation. But many new questions arise. How realistic is it to expect corridors of anything other than uninterrupted pristine habitat to function effectively for dispersal? How important is the nature of the matrix (Gustafson 1998; Lindenmayer & Franklin 2002)? We know from our own observations in the study area that many small relic patches of Proteaceae species remain on rocky outcrops and in stream ravines within otherwise intensively agricultural landscapes. Many Proteaceae species will not disperse across gaps of unsuitable habitat of even 100 m in these landscapes. Can dispersal areas ever be expected to work for these species? How important are sheltered microrefugia (which cannot be represented adequately

by broad-scale bioclimatic models) within some of these landscapes for persistence?

Our treatment of habitat transformation was also simplistic but again could easily be extended in the future when more information becomes available. First, we could include models of how transformation is expected to proceed (e.g., Rouget et al. 2003b), even if not all changes are predictable. Second, although we considered cells with < 34% of their area remaining untransformed to have no value, some species are known to persist in small fragments just a few meters across, or even in seed banks for at least three generations (A. Rebelo, personal communication). Such fragments may provide some persistence in the face of climate change. Because of their isolation, however, these fragments are unlikely to contribute to dispersal and migration, and are almost certainly subject to increased risk of extinction through stochastic events. As in most studies, our knowledge of threats, vulnerabilities, and viabilities remains poor.

Implications

The 1602 cells added by our gap analysis represented an increase of 98% on the cells with existing protection. This near doubling of the area for which conservation-friendly management is required might seem ambitious, but it was still much less than in some recent plans. For example, Cowling et al. (2003), dealing with many more species, considered extending conservation management to 52% of the broader Cape Floristic Region (and disproportionately more within our study area) as opposed to the 18% of the study area required here. Most of the areas we selected (Fig. 3) are considered irreplaceable by Cowling et al. (2003, their Fig. 3). We have selected some areas that may be overlooked, however, unless future climatic conditions and species' dispersal abilities are explicitly considered, for example, areas near Simon's Town and Paternoster, areas around the Cedarberg and east of the Kouebokkeveld, and areas north of the Rivieronderend and Langeberg mountains.

How does the distribution of persistence areas and of dispersal areas compare with the distributions of environmental features such as mountains? Cowling et al. (1999) suggest that areas with short and steep environmental gradients better accommodate poor dispersers. Such areas are likely to be in the mountains. Our newly selected grid cells were indeed significantly more likely to contain the higher median elevations associated with mountain ridges in this region (mean of 605 m median elevation within the selected set of 1,602 cells, compared with 571 m from the 95% [upper] tail from 1000 sets of 1,602 cells drawn at random from among the 10,259 cells that were candidates for area selection). In the medium term, an escape by species to new elevational ranges could be effective. Consequently, dispersal problems might be most severe for poor dispersers in regions of low relief (Ruther-

ford et al. 1999a, 1999b; Peterson 2003). In the long term, however, because there is often less land area available at higher elevations, shifts toward higher elevations may result in range contraction and increased risk of extinction. Ranges might ultimately become "trapped" on isolated mountain tops with nowhere to move within realistic dispersal distances.

Comparing Figs. 2 and 3, there appears to be a weak tendency for goal-essential cells (red in Fig. 3) to have been chosen from among cells rich in species and chains (red in Fig. 2), but furthermore these cells were chosen preferentially from the eastern highland regions (e.g., more in the Langeberg and less in the Kouebokkeveld mountains). This may reflect the general eastward shift of biomes expected with climate change in southern Africa (Midgley et al. 2003).

Proteaceae are just one among many groups of highly valued organisms that need to be accommodated within regional conservation plans and budgets. Surrogacy among taxonomic groups for complementary area networks based on current distributions has received some attention (e.g., Jaarsveld et al. 1998; Andelman & Fagan 2000; Williams et al. 2000; Manne & Williams 2003). Our question here, however, is different and novel: Would the areas identified as important for Proteaceae provide continuing protection with climate change for these other organisms? Proteaceae might be expected to mirror distribution patterns for most of the Fynbos species, which are mesic and schlerophyllous, but not for the more arid Fynbos, the Renosterveld, or for the Succulent Karoo (A. Rebelo, personal communication).

Conclusions

In the absence of other viability information, the conservation problem for some species can be reduced by identifying persistence areas that remain suitable for species over time, despite climate change. This is expected to be the most reliable approach, because dispersal is uncertain. Where dispersal is unavoidable, our results identify species requiring urgent action and species for which there is little hope. Dispersal might be facilitated by providing connectivity across the shortest corridors or chains of stepping stones over time. Our method could be integrated easily with a variety of implementation strategies, simply by incorporating the appropriate values for social cost or conflict within the area-selection procedure. Given the many uncertainties in the models and the relatively small number of Proteaceae species that have to disperse, however, it may be that the method is most useful for identifying species that are expected to face particular difficulties (e.g., the species in Table 2). Some of these species may require a different approach. For a few species, transplantation and intensive management ("gardening in the wild") may be a more reliable solution. We

see these as two complementary approaches that could support each other. Nonetheless, when faced with the problem of accommodating climate change in conservation plans for larger numbers of species that have to disperse, if adequate information is available, our method for identifying dispersal areas may still be more practical for most species.

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