# The View from the Cape: Extinction Risk, Protected Areas, and Climate Change

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*In the past decade, a growing number of studies have modeled the effects of climate change on large numbers of species across diverse focal regions. Many common points emerge from these studies, but it can be difficult to understand the consequences for conservation when data for large numbers of species are summarized. Here we use an in-depth example, the multispecies modeling effort that has been conducted for the proteas of the Cape Floristic Region of South Africa, to illustrate lessons learned in this and other multispecies modeling efforts. Modeling shows that a substantial number of species may lose all suitable range and many may lose all representation in protected areas as a result of climate change, while a much larger number may experience major loss in the amount of their range that is protected. The spatial distribution of protected areas, particularly between lowlands and uplands, is an important determinant of the likely conservation consequences of climate change.*

*Keywords: climate change, biodiversity, extinction risk, protected areas, modeling*

**C**limate change is likely to alter the species composition of protected areas, with important implications for conservation. For the last two decades it has been recognized that species might move into, or out of, parks and reserves as climate changes (Peters and Darling 1985). More recently, shifting range boundaries as a result of contemporary climate change have been observed for multiple species, underscoring the potential for climate change effects on species composition at fixed geographical points such as protected areas (Parmesan and Yohe 2003, Root et al. 2003).

Yet assessing the net effect of these movements has remained elusive—partly because observations of current range shifts are spotty, and partly because modeling of future range shifts for multiple species is data intensive and requires climate-change projections at a scale much finer than that offered by most global climate models. However, a variety of models of species responses to climate change are now available (figure 1, box 1), and multispecies modeling efforts are becoming more common (Bakkenes et al. 2002, Erasmus et al. 2002, Midgley et al. 2002, Peterson et al. 2002), including first attempts to assess the effects on species representation in protected areas (Araujo et al. 2004). These bioclimatic modeling studies have been important in highlighting the extinction risk associated with climate change (Thomas et al. 2004).
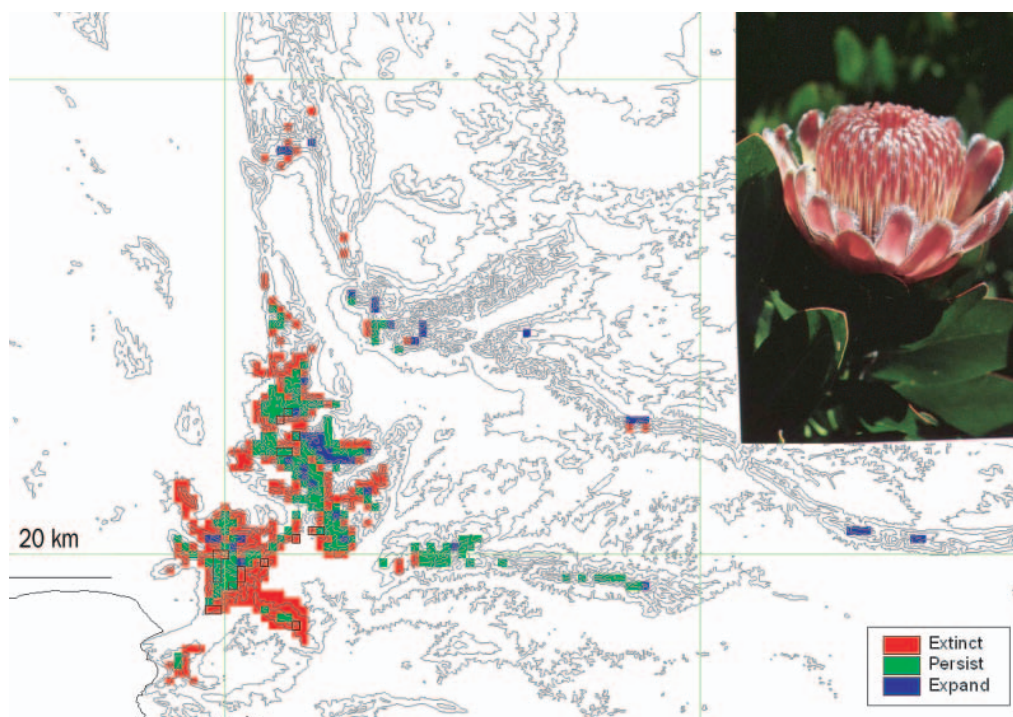
Each species responds to climate differently, so summary reports of multispecies modeling may be too brief to capture the full richness of either the methods or the results (Peter-

son et al. 2002). When multiple regions are combined (e.g., to estimate extinction risk; Thomas et al. 2004) or multiple species interactions are considered (e.g., to assess the effectiveness of protected areas; Araujo et al. 2004), it may be difficult for those not familiar with the regions or species to discern the underlying patterns of causation. One solution to this problem is to examine one region in depth and use it to illustrate general patterns that have been borne out in other regions.

Here we use a pioneering multispecies modeling effort that has been conducted for plants in the Cape Floristic Region of South Africa (figure 2) to illustrate how local biology, climate, and patterns of change combine to affect extinction risk and protected-area effectiveness. The Cape is a unique microcosm for such analysis, since it is both a biodiversity hotspot and one of the world's six plant kingdoms (Simmons and Cowling 1996). The multispecies modeling effort for the Cape provides an excellent example of the

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*Figure 1. Example of a bioclimatic model for* Protea lacticolor, *a species endemic to the Cape Floristic Region (shown in photograph inset). Present range retained in a 2050 climate change scenario is indicated in green. Present range lost in the 2050 scenario is in red, while new range projected to become suitable in 2050 is indicated in blue. Note range loss in the lowlands, range retention in the uplands, and limited opening of new range at higher elevations. Photograph: Colin Paterson-Jones.*

potential effects of climate change on efforts to conserve species in protected areas, answering questions such as whether climate change will increase or decrease the number of species in protected areas, how these changes will unfold over time, and what species and areas will be most affected. In this article, we review the results of this modeling effort, with emphasis on similarities with and differences from findings from other regions, and on implications for protected areas and their ability to constrain species extinctions as climate changes.

## The Cape as an example of multispecies modeling

The Cape studies are an example of bioclimatic (or "niche") modeling, which has been conducted for many species in several regions of the world (table 1). The Cape studies assess the impact of climate change on more than 300 species in the protea family (Proteaceae; Midgley et al. 2003). The proteas—many of which are internationally important in the floral trade because of their large, colorful flowers and their attractive fruits and foliage—are excellent subjects for modeling biotic responses to future climate shifts because they are well studied and have life histories that make them directly sensitive to climate change (Midgley et al. 2001). All successful bioclimatic modeling efforts depend on information on the current distribution of the species of interest. In the Cape, the Protea Atlas Project, an extensive cataloguing effort, provides

detailed information on current distribution of the proteas (Rebelo 2001). This information is used in bioclimatic models to establish how climate influences the current distribution of proteas and to model possible future changes (box 2).

The proteas studied are endemic to the Cape, another attribute important for multispecies modeling. Bioclimatic models perform reliably only when the climate and distribution information on which they depend is available for the entirety of a species' range, thus defining the complete "climate envelope" that the species currently finds suitable (Pearson and Dawson 2003). Using information from only a portion of a species' range may cause a bioclimatic model to ignore potentially broader tolerances represented by the species' range outside of the study area. For this reason, modeling should be restricted to species endemic to a study region, or should cover the full geographic range of the species in question.

The proteas are important conservation targets owing to their endemism and ecological significance. The family Proteaceae is one of the three floral elements that defines the fynbos, a vegetation type so diverse that it makes the region surrounding the Cape of Good Hope the world's smallest plant kingdom (Richardson et al. 2001). Proteas are the largest and showiest of the fynbos signature elements (Cowling 1992). The other defining fynbos elements are the ericas (Ericaceae), members of the heath family that have dwarf-shrub growth

## Box 1. Bioclimatic models: Climate change and species' range shifts.

Many assessments of the impact of climate change on biodiversity begin by creating bioclimatic models of a species' present and projected future range. Bioclimatic models establish a relationship between a species' current distribution and climate. That relationship may then be extrapolated to simulated future climates, giving an estimate of the species' possible future range. The simplest bioclimatic model creates a "climate envelope" for the species using the maximum and minimum values of various climate variables found within the species' range (Box 1981); a popular variation of this type of model is BIOCLIM. A variety of techniques may be used to establish a relationship between a species' distribution and environmental variables, including statistical approaches such as ordinary regression, generalized regression (e.g., generalized linear modeling, or GLM, and generalized additive modeling, or GAM), ordination (e.g., canonical correspondence analysis), and classification (e.g., classification and regression trees) as well as more complex techniques such as Bayesian frameworks, genetic algorithms, and artificial neural networks. For a detailed summary see Guisan and Zimmerman (2000).

Bioclimatic models have limitations, but are useful for assessing vulnerability and spatial dynamics. Limitations include the assumptions that species' ranges are in equilibrium with climate and that competition is a minor determinant of species' ranges relative to climate (Pearson and Dawson 2003). Both of these assumptions are debatable, vary from species to species, and are difficult to test. Another limitation stems from modeling range instead of populations. A species' range is comprised of a geographic extent (a polygon enclosing all occurrences, also known as extent of occurrence) and an area of occupancy—the habitats actually occupied within the geographic extent. Some bioclimatic models produce a probability surface of the species' likelihood of occurrence. This probability is often converted to a presence–absence surface by applying a cutoff value to yield a final product that is similar in appearance to a traditional range map (e.g., figure 1). At a coarse scale, the resultant map resembles the species' extent of occurrence, as does a range map in a typical field guide. However, at a fine scale, the resulting map approximates the area of occupancy for the species (the habitats within the extent of occurrence that the species actually occupies). The Cape modeling was conducted using data at a resolution of 1 minute (approximately 1.6 kilometers) by 1 minute, making it fine-scale relative to most bioclimatic modeling efforts but still coarse-scale relative to the area of occupancy of many plant species.

forms and small tubular or bell-shaped flowers, and the restios (Restionaceae), reed-like plants that resemble horsetails. The fynbos has arisen in the mediterranean climate and rugged, mountainous terrain of the Cape, and some evidence suggests that some groups have diversified and speciated widely in the geologically short period since the Miocene (Richardson et al. 2001). Most soils of the Cape are nutrient poor, forcing adaptation and specialization in the plants that occur there, and the vegetation that has developed is prone to fierce fires that recur at intervals of 10 to 30 years (Cowling 1992). Strong winds whip the Cape region, creating unique conditions for fire and plant dispersal, factors that are central to the diversity of the region (Simmons and Cowling 1996).

Species are the unit of study in the Cape protea modeling because abundant evidence from the past indicates that species respond individually to change in climate, rather than as coherent communities. No-analog communities—associations of prehistoric plants or animals that are unlike any that currently exist—are a common feature of the paleoecological record. Modeling of the Cape has been conducted at the community (biome) level, and this modeling shows a southward collapse of the fynbos biome that contains the proteas. But species-level modeling shows a variety of

species responses (range expansion and contraction) in areas where the biome is projected to contract, as well as in areas where the biome is projected to be retained (Midgley et al. 2002).

Warming trends have already been observed in the Cape region over the past 30 years by one of the authors (G. M.), working with Stephanie Wand. The Cape may therefore serve in many ways as a harbinger of climate change effects elsewhere. The fate of the protected areas of the Cape offers lessons that can inform conservation efforts throughout the world.

### Extinction risk and multispecies modeling

Extinction risk for the proteas of the Cape due to climate change alone has been estimated at 21% to 40%, using midrange scenarios of greenhouse gas emissions (Thomas et al. 2004). The species–area relationship calculations on which these estimates are based remain the subject of debate (box

*Table 1. Multispecies (n ≥ 50) bioclimatic modeling efforts.*

| Region | Taxa | Number of species | Reference |
|---|---|---|---|
| Europe | Plants | 192 | Bakkenes et al. 2002 |
| Europe | Plants | 1200 | Araujo et al. 2004 |
| Europe | Birds | 306 | Huntley et al. 2004 |
| Britain and Ireland | Plants | 54 | Berry et al. 2002 |
| South Africa | Vertebrates, insects | 50 | Erasmus et al. 2002 |
| South Africa | Plants (Proteaceae) | 330 | Midgley et al. 2003 |
| Mexico | Birds, butterflies | 1870 | Peterson et al. 2002 |
| Brazil | Trees | 163 | Ferreira de Siqueira et al. 2003 |
| Amazonia | Trees | 69 | Miles et al. 2004 |
| Australia | Vertebrates, insects | 65 | Williams et al. 2003 |
| Canada | Butterflies | 111 | Peterson et al. 2004 |
| United States | Trees | 80 | Iverson and Prasad 1998 |

*Figure 2. Satellite image of the Cape region. The outlined box indicates the approximate location of figure 1. Note extensive north–south and east–west trending mountains of the Cape fold belt. Source: Image courtesy of MODIS Rapid Response Project at NASA/GSFC.*

3; Harte et al. 2004, Thuiller et al. 2004). It has been suggested that extinction risk due to climate change might be better estimated by counting the number of species whose climatic niche falls below a critical minimum size (Buckley and Roughgarden 2004). In the real world, climate change will act in synergy with other pressures, and most important will be the interaction of habitat loss with climate change.
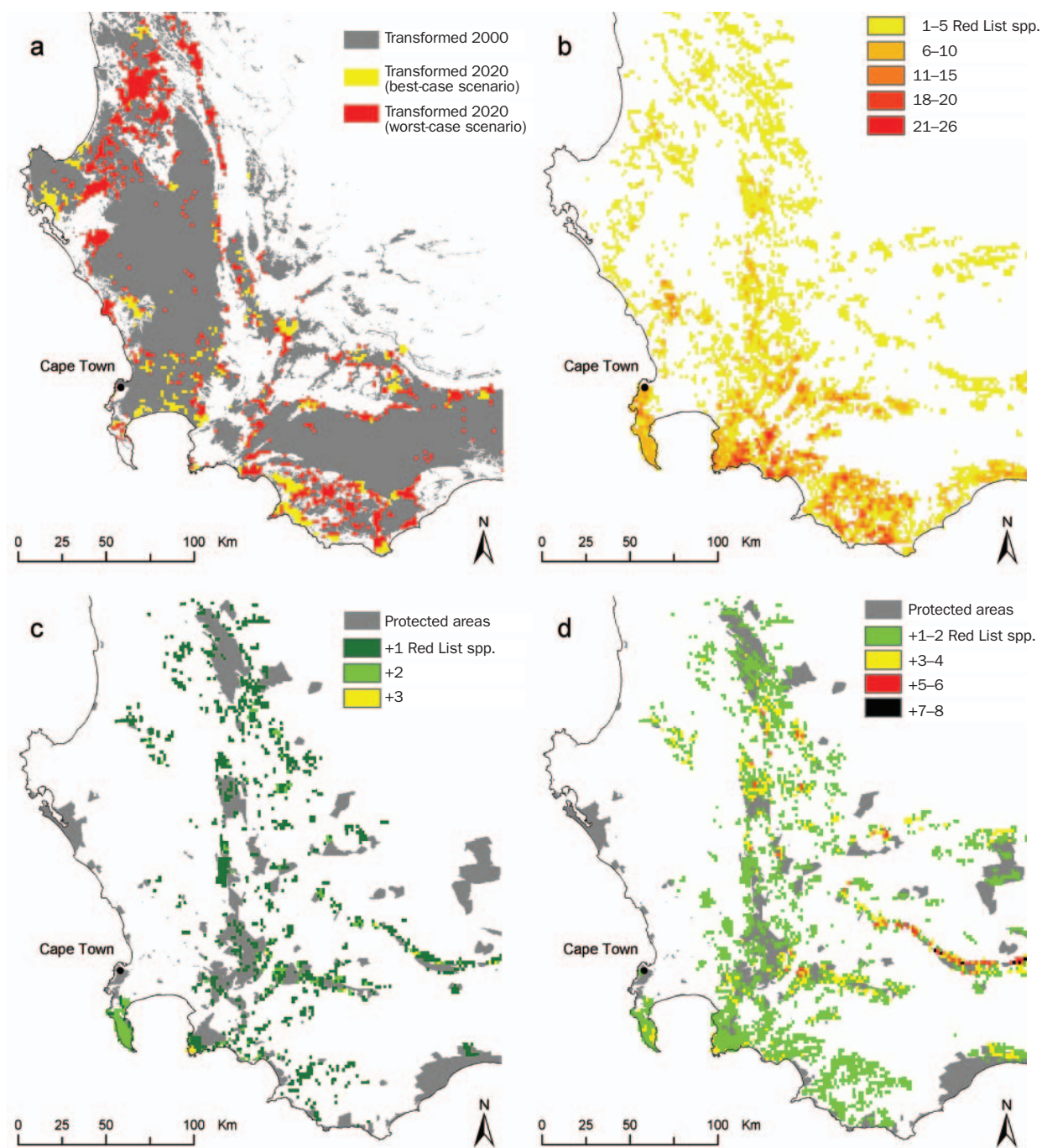
Extinction risk due to habitat loss is already high in the Cape, as evidenced by the number of threatened (Red List; IUCN 2001) protea species per unit area (figure 3b). At present, more than 30% of the region has already been heavily transformed by agriculture, urbanization, and dense stands of invasive alien plants, and much of the remainder has alien species present in low densities (figure 3a). Thirty percent of the remaining natural habitat is threatened by future extreme transformation (Rouget et al. 2003a). Some lowland habitats have lost more than 80% of their original extent already and have less than 5% of their remaining extent protected. Unsurprisingly, many proteas have disappeared from heavily transformed areas, and for many species, conservation areas harbor their last remaining populations. Overall, some 20% of the region is protected in some form of conservation area, but only half of this is in reserves with a high degree of protection (Rouget et al. 2003b).

Conservation of the proteas will ultimately depend on protected areas to maintain critical minimum population sizes of species against the incursions of habitat loss and cli-mate change. Over the coming decades, human land transformation and fragmentation is likely to destroy most unprotected natural habitats (figure 3a), while climate change will accelerate, rendering many currently climatically suitable areas unsuitable for particular species even within protected areas (figure 3d). The net remaining populations will be primarily those that are protected from habitat loss in parks, reserves, and other conservation areas (conservancies on private lands are of growing importance in the Cape) and that can withstand the loss of climatically suitable space within those refuges. Adopting the premise that extinction risk will be determined for individual species by the intersection of protected areas and climatically suitable space, we use the results of the protea modeling to explore the complex conservation consequences of climate change and land-use change for the proteas and protected areas in the Cape.

## Protected areas and climate change

Bioclimatic models can be used to calculate the effect of climate change on species representation in protected areas. Current and future modeled ranges may be used to calculate the area of a species' range under protection at a given time, although it is important to keep in mind that a species' modeled potential range may not precisely match its actual range (Pearson and Dawson 2003). As the climate changes, the amount of range under protection will change, depending on the changes in the species' range relative to the geographic

*Figure 3. (a) Extent of habitat transformation in the southwestern Cape Floristic Region in 2000 and additional projected habitat transformation by 2020, assuming a low transformation rate (best-case scenario) and a high transformation rate (worst-case scenario) (Bomhard et al. 2005). (b) Number of species on the IUCN Red List (IUCN 2001) per 1-minute grid cell (2.9 km²) for 227 protea taxa endemic to the Cape Floristic Region. (c) Protected areas and increase in the number of Red List proteas per grid cell, based on a Red List assessment (IUCN 2001) that incorporates projected worst-case land-use change by 2020. (d) Protected areas and increase in the number of Red List proteas per grid cell, based on a 2020 Red List assessment that incorporates both land-use and climate change.*

location of protected areas. Projecting the change in climate carries considerable uncertainty. Future emissions of greenhouse gases into the atmosphere can only be estimated (through emissions scenarios; IPCC 1996, 2001), and the

resultant impacts on climate projected by general circulation models (GCMs) vary considerably (IPCC 2001). These uncertainties are critical to the global policy debate on constraining climate change, but multiple emissions scenarios and

## Box 2. The Cape protea models.

The models of protea range shifts conducted for the Cape are among the most detailed ever undertaken. Three key ingredients are required for such models: (1) species distribution data, (2) fine-scaled present and future climate data, and (3) data on other environmental variables (e.g., soil data) (Hannah et al. 2002b).

Species distribution data for the proteas came from the Protea Atlas Project (Rebelo 2001). The data from this project make it possible to model future range shifts of the proteas. The Protea Atlas Project provides records of species' presence and absence over large areas of the Cape. These records can be used to train a statistical model to predict the distribution of a species on the basis of key climate and soil variables. Once the variables most strongly influencing present distribution are determined, it is possible to assess how a species' range might shift under future climate change.

The South African national study on climate change provided fine-scale present and future climate data based on projections from a global climate model (general circulation model, or GCM) (Midgley et al. 2002). The future climate variables were derived from coarse-scale projections of the GCM known as HadCM2 (Hadley Centre coupled model version 2), which were converted to 1-minute resolution using a statistical downscaling technique (Midgley et al. 2002). Information on other environmental variables, such as soils, elevation, land-cover classes, and protected areas, from a GIS (geographic information system) database completed the information used in the Cape studies.

Several categories of bioclimatic models exist for projecting changes in a species' range as climate shifts (box 1). The Cape protea models were constructed using generalized additive modeling (GAM). GAM creates a statistical relationship between present range and present climate, then extrapolates future range on the basis of changes in climate variables projected by the GCM (figure 1). This process was followed for over 300 species of protea, producing a fine-scale, multispecies look at possible changes in biodiversity due to climate changes expected by 2050 (Midgley et al. 2002).

GCMs can greatly complicate general understanding of underlying patterns of climate-change impacts on species and protected areas. Here we treat species and protected areas first, using a single emissions scenario and the GCM from the Cape assessment (HadCM2, or Hadley Centre coupled model version 2) for simplicity, and then return to the issues of policy and uncertainty.

A species' range may shrink in response to climate change in an area where it is currently protected, but it may also expand in areas where it is not currently protected. Whether or not a species has the dispersal capacity to reach newly suitable range has a major impact on the size of future range, so we divided the proteas on the basis of primary dispersal

mechanism (wind, rodent, or ant dispersal) and estimated the likely maximum dispersal distance in 10-year time steps over 50 years. Most bioclimatic modeling studies use dual assumptions of "no dispersal" or "universal dispersal" (e.g., Peterson et al. 2002). Contiguous dispersal (dispersal into adjacent cells) is sometimes used (e.g., Peterson 2003), but it has limitations of its own, namely that it is arbitrarily linked to time step and spatial scale of modeling. The no-dispersal and maximum-dispersal assumptions used for the Cape protea modeling are a compromise that discounts the importance of unlikely long-distance dispersal events, the role of which remains controversial (Clark et al. 2003). The maximum-dispersal assumption is different from universal dispersal, in that it limts dispersal to range that is climatically suitable and within a maximum distance based on whether the species is dispersed by wind, ants, or rodents in each of five decadal time steps. The no-dispersal assumption is simply the overlap of the future range with the present range, which is critical for protected areas and conservation because it corresponds to the areas in which climate is projected to remain suitable for a species.

The Cape protea models suggest that, if the current protected-area network does not change before 2050, the number of species represented in the protected areas of the region in the future depends strongly on dispersal assumption (table 2). In the Cape, the number of protea species in protected areas declines by 15% assuming no dispersal, and by 8% assuming maximum dispersal. In the only comparable study of large numbers of species, Araujo and colleagues (2004) found that 6% to 10% of European plant species would be lost from reserves as a result of climate changes projected for 2050 (the lower estimate associated with a universal-dispersal scenario).

These findings are significant for two reasons. First, the number of protected species declines in the Cape even under the maximum-dispersal scenario. Climate change will certainly rearrange species relative to protected areas, but it is not a foregone conclusion that this rearrangement will decrease the number of protected species. Some species will have future potential range within protected areas in which they do not currently occur. Others may exchange protected area in one part of their present range for protected area in a different reserve in their potential future range. In theory, the net effect of these changes could be neutral, or could even result in expanding representation of species in protected areas. Whether the potential future range could ever be occupied when species have to cross future heavily transformed and fragmented landscapes would then be debatable. But the Cape results show that even before species get to the challenge of crossing hostile intervening landscapes, the number of species in protected areas is reduced by climate change. The results of Araujo and colleagues (2004) for Europe support this interpretation.

The decline in the number of protected species is due to an overall strong decline in species range size with climate change. Part of this decline results from the dispersal constraint

**Table 2. Numbers of endemic protea species represented in protected areas of the Cape Floristic Region in 2000 and 2050 (projected).**

| Year (threshold) | Number of species (percent decline since 2000) | |
| --- | --- | --- |
| | No-dispersal assumption | Maximum-dispersal assumption |
| 2000 (presence only) | 327 (0) | – |
| 2050 (presence only) | 277 (15.3) | 301 (8.0) |
| 2050 (100-km$^2$ minimum threshold) | 202 (38.2) | 243 (25.7) |

*Note:* The number of species whose modeled ranges intersect protected areas in at least one grid cell (presence only) or at a minimum threshold of area (100 km$^2$) are given relative to two dispersal assumptions about species' ability to occupy newly climatically suitable areas.

placed on potential future range, but the pattern of overall decline exists even when this constraint is removed (Midgley et al. 2003). This effect has been demonstrated in multiple regions of the world, and the Cape is a good illustration of this pattern (Thomas et al. 2004). Similar findings have been reported for other regions and species of South Africa (Erasmus et al. 2002); Queensland, Australia (Williams et al. 2003); and Brazil (Ferreira de Siqueira and Peterson 2003). A major reason for this decline is that in warming climates, species move upslope into smaller and smaller areas as mountain peaks taper at higher elevations. The present global climate is at a warm interglacial level, one of the warmest in the past 2 million years, and future warming will push species further upslope as climate becomes the warmest in 40 million years or more (Overpeck et al. 2003). This effect may be particularly strong in the Cape, since there is no poleward continental landmass in which latitudinal range adjustments might take place.

The decline in number of protected species masks an even deeper erosion of protected-area effectiveness. Among those species that *are* represented in protected areas, the increased vulnerability to extinction due to reduced range size that accompanies climate change may be examined by looking at the area of species' ranges protected at present and in the future (table 3). Mean protected range of protea species declines by 36% to 60% under the future climate scenario. Declines in median protected range are markedly larger (39% to 72%), particularly under the no-dispersal scenario. The differences between median and mean values in the present indicate that protection is currently skewed toward species with small ranges. This bias in the distribution of protected range becomes even more pronounced in the future. In the 2050 scenario, many species have smaller protected ranges than at present, while a few have much greater ranges protected. This is another important lesson from the Cape studies: most species are projected to become rarer, while a few will prosper and become more widespread. This phenomenon has been noted in several other multispecies modeling efforts, including regions as diverse as Mexico (Peterson et al. 2002) and Britain and Ireland (Berry et al. 2002). The loss of species represented in protected areas by 2050 is modest, but is underlain by a deeper erosion of protected range that will turn into an explosion of unprotected species as climate change continues beyond 2050.

Loss of protected range may be compared with overall loss of species' ranges, to see whether protected areas are faring better or worse than the overall landscape. In comparison with overall range losses, the protected-range losses are less (36% to 72% compared with 57% to 86%) for the proteas. This is the result of the predominance of mountainous protected areas. Species are moving upslope with warming, and most protected areas are in the mountains. Therefore, the upslope portion of a species' range loses less area to climate change and is more protected, resulting in less loss in the protected parts of the range. This lesson from the Cape is not universally applicable but is universally relevant: regions that have predominantly lowland reserves will see disproportionately larger losses of protected range, while regions with abundant upland reserves, like the Cape, will see lesser losses of protected range.

## How much is enough?

Protected areas are a mainstay of conservation, and their utility relies on the assumption that extinction debt due either to habitat loss or to climate change can be forestalled within relatively small areas of the landscape if those areas are

**Table 3. Mean and median size of protected range of protea species modeled, with mean and median total modeled range size for comparison.**

| Year (threshold) | Range size (km$^2$) in protected areas (percent decline since 2000) | | Total range size (km$^2$) (percent decline since 2000) | |
| --- | --- | --- | --- | --- |
| | Mean | Median | Mean | Median |
| 2000 (present range) | 358 (0) | 206 (0) | 1948 (0) | 1454 (0) |
| 2050 (no dispersal; overlap of present and future range) | 144 (59.8) | 58 (71.8) | 495 (74.6) | 211 (85.5) |
| 2050 (maximum dispersal) | 228 (36.3) | 126 (38.8) | 845 (56.6) | 362 (75.1) |

## Box 3. Species–area relationships and climate change.

The species–area relationship (SAR) is an empirical relationship between the number of species and the land area of a continent or island. The larger the area, the more species, as one might expect; in many settings, this relationship is approximately linear when both scales (area and number of species) are log transformed. A variant of the SAR is the endemics–area relationship (EAR), which describes the relationship between land area and the number of species endemic to a region (Kinzig and Harte 2000). In both SAR and EAR, the slope of the log-transformed line, or z value, is the critical determinant of how species accumulate as area is added.

Thomas and colleagues (2004) used SAR in a novel way to estimate extinction risk from climate change. These authors theorized that because species accumulate as one moves to larger and larger island or continental areas, the converse must also be true—species must be lost as their climatically suitable space becomes progressively smaller. A similar assumption had been used to estimate the number of extinctions that would eventually occur as the result of habitat loss (Brooks et al. 1999).

The SAR approach to estimating extinction risk from climate change has attracted criticism. Unlike other researchers who used SAR to estimate species losses due to habitat loss, Thomas and colleagues (2004) calculated range loss for each species individually, then used several alternative methods to estimate aggregated extinction risk. Some authors have argued that the aggregation methods used by Thomas and colleagues were not correct, while others have argued that combining individual range changes is not a valid use of SAR at all (Buckley and Roughgarden 2004). Thomas and colleagues addressed only endemic species, so that they could be sure their bioclimatic models were able to address all of a species' range, and it has been pointed out that EAR might have been more appropriate to apply than SAR in this case.

properly protected and managed. How much area is enough remains a largely unanswered question in conservation, however. Biologically meaningful targets at the regional and national levels have been elusive, while data deficiencies limit the ability to estimate the area needs of individual species (Soulé and Sanjayan 1998).

The extent of protection required matters greatly in terms of how many species are lost from protected areas as a result of climate change. In the Cape, if a single small area (under 3 square kilometers [$km^2$] at the resolution of this study) is sufficient for species persistence, then only 8% to 15% of proteas are projected to be lost from protected areas (depending on the dispersal assumption), whereas 26% to 38% of species are projected to be lost if species persistence requires a substantially greater area (table 2). Since most species require substantial area to maintain a viable population and resist chance extinctions, the higher estimates of the possible dam-

age to biodiversity conservation may be the more realistic. Significantly larger investments in protected areas and their management may be required to avoid extinctions due to climate change.

But how much *more* is enough? Arriving at an answer to this question for the future is difficult, because there is no agreed-upon standard for the present. Where population viability analyses have been conducted (e.g., for threatened species), a good approximation of the amount of habitat (range) required for a species' conservation may be available. For the vast majority of species, however, these data do not exist (Noss 1996). Simple presence is an inappropriate metric, as a single occurrence is unlikely to support a viable population for most species. A blanket percentage of range is unlikely to be appropriate, as different species have different range requirements. The current degree of protection (for species that are represented in the protected-area system) is one possible but largely arbitrary benchmark—most current protected-area networks have not been systematically designed, so some species are vastly overrepresented while others are vastly underrepresented.
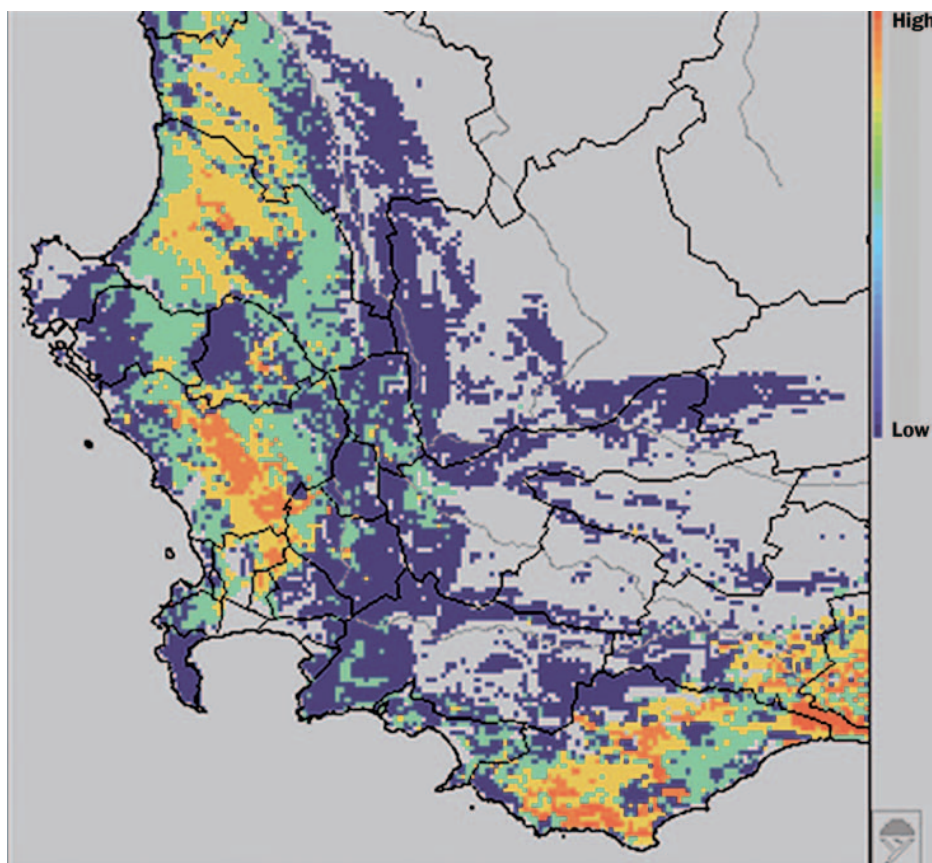
Protecting all the remaining range of species below a minimum rarity threshold has been suggested as a goal (Noss 1996). For assessing critically endangered species, the IUCN (the World Conservation Union) has set a threshold for rarity at 100 $km^2$ extent of occurrence (IUCN 2001). This 100-$km^2$ minimum threshold is used in table 2 to illustrate the difference between using a target threshold and using simple presence (at the scale of the study) as a criterion for protection. Until conservationists can answer the question "How much is enough?" in the present, it will be impossible to generate more precise estimates of protected-area requirements to compensate for climate change.

### Which species and when?

In the Cape models, lowland species and species with small ranges lose protection first. This pattern follows the trend for small-range and lowland species to lose the most range, regardless of whether the range is in protected areas or outside. The present range sizes of species that are lost from the protected areas are much smaller than those of the species that are retained. Protea species projected to lose all protected range have a mean range size of 2290 $km^2$, compared with the mean range size of 5590 $km^2$ for all species. This is consistent with the theory suggesting that species with smaller ranges will have a smaller envelope of environmental variables within that range, and hence greater sensitivity to climate change (Hughes 1996, Pimm 2001).

Lowland species are also disproportionately affected. Figure 4 shows the species richness of species that lose all protection. Lowland species dominate, while only a few montane species lose all protection; large parts of the Cape fold mountains are outlined in cool, low-richness blue. This follows the general pattern for proteas in the Cape, in which most lowland species rapidly lose range—possibly because the Cape's situation at the southern tip of the African continent makes
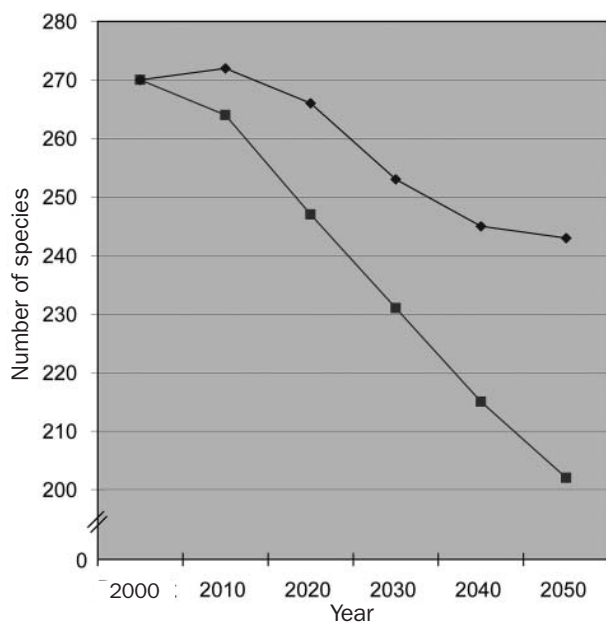
*Figure 4. Richness of species that lose all protected range in the southwestern Cape Floristic Region. Warmer colors indicate higher numbers of species. Worldmap software and map courtesy of Paul Williams.*

latitudinal adjustments poleward largely impossible. Other studies in regions where latitudinal adjustments are possible have noted losses in lowland species range ranging from moderate (Peterson et al. 2002) to pronounced.

This "lowland loss" effect is in apparent conflict with other estimates that most extinctions due to climate change will occur in mountains, as species moving upslope find less and less habitat, and eventually have nowhere to go. In fact, both perspectives may be correct. Required migration distances for range shifts due to climate change are shorter in uplands, where steep climatic gradients prevail, than in lowlands, which have a more uniform climate. Although lowland species therefore suffer a larger absolute range loss, they usually exhibit a lower extinction risk, because many of them tend to be widespread (Dynesius and Jansson 2000). Many upland species, in contrast, have relatively small range sizes, so that a major proportional range loss leaves them with little absolute range and a higher extinction risk. Effects in both lowlands and uplands will depend strongly on patterns of land use (Peterson 2003). Even widespread lowland species with good dispersal ability may face extinction if extensive transformed and fragmented landscapes (figure 3a) lie between their present and future ranges.

The timing of species loss under different dispersal assumptions in the Cape is illustrated in figure 5. No-dispersal protected range (future protected range that overlaps with current protected range) is lost first and continues to decline, while the loss of protected range under the maximum-dispersal assumption starts more slowly and levels off with time. This is because species' ranges move into the Cape fold mountains and then track the changing climate by moving to other parts of the mountain chain. Future new range opens up in montane reserves, causing the protected-range loss to decrease if species are assumed to be able to realize their maximum dispersal potential. Protected range under the no-dispersal assumption, on the other hand, exhibits continuous decline, as overlap between present and future range progressively erodes. Although the absolute level and rate of climate change are likely to be different from those shown in this graph because of uncertainties in climate models and emissions scenarios, this relative pattern is likely to be robust in the Cape under all model and scenario combinations, because of the extensive and well-protected mountains of the region. The distinctive L shape of the Cape mountains, extending both north–south and east–west (figure 2), provides expanding areas of refuge to the east as species ranges move south, which is unusual. In most montane settings, steady loss of

*Figure 5. Number of protea species protected through time according to a model of the Cape Floristic Region, showing number of species with 100 square kilometers (km²) of protected total range (diamonds) and with 100 km² of overlap between protected present and future range (i.e., no-dispersal assumption; squares).*

range over time (due to decreasing area at higher elevations) even with maximum dispersal, such as that observed by Williams and colleagues (2003) in upper montane species of Queensland, Australia, is probably the norm. In nonmontane regions, loss of range under all dispersal assumptions may be rapid, as discussed above.

These patterns of vulnerability and timing are consistent with upslope and poleward movements expected with warming. In the Cape, warming dominates the modeled biotic responses to future climate change, as it does in many other systems that have been modeled. In other regions, precipitation may be more important. For example, precipitation changes and interruption of moisture recycling have been implicated in the modeled retreat of Amazonian forests under future climate change (Betts et al. 1997, Miles et al. 2004).

### Can more protected areas compensate?
Species whose future range has no overlap with their present range may have trouble tracking climate change, even when their future range is projected to be substantial. Overlap between present and future range is therefore an important attribute to represent in protected areas. This overlap range is equivalent to the range under the no-dispersal assumption.

In the Cape, a few species that are projected to lose all protected overlap range by 2050 have untransformed but unprotected overlap range that could be protected to fill the gap. Of the 62 proteas that have no protected overlap range in 2050, 20 have overlap range outside of protected areas on

lands that could be considered as candidates for protection. In addition to the species that have no overlap range protected, a further 12 species have less than 1000 hectares (ha) of overlap range in protected areas, but substantial (more than 1000 ha) of overlap range outside of protected areas in untransformed areas suitable for conservation.

For species unrepresented in the current protected-area network, protecting their overlap range offers a double opportunity. The representation of their 2050 overlap range can be improved, and at the same time their present range can be represented in protected areas for the first time. In the case of the Cape proteas, however, this promise goes unfulfilled. All of the protea species unrepresented in the current protected areas of the Cape have very small present ranges. Like other small-range species, their ranges quickly disappear as the climate changes, and they are projected to have no range at all in 2050. Thus, portions of their present range may be captured in protected areas, but their future modeled ranges appear to present no opportunity for overlap conservation.

In sum, a significant but limited proportion of the proteas that have no overlap range in the current protected-area network might be saved through new protected areas. Other measures will be necessary to ensure the conservation of the remaining species. As climate change progresses, the number of species requiring extraordinary measures will increase.

### Conservation implications
In regions such as the Cape, not only the climate will change; human population and the resulting pressures on ecosystems will continue to evolve, often in ways unfavorable to biodiversity. The synergies between these multiple changes will ultimately have major implications for conservation. For example, agriculture in the Cape may move upslope to retreat from the warming and drying lowlands and to retain optimal environmental conditions for crops (e.g., optimal temperature for vineyards or cold duration for orchard fruits), in the process destroying natural habitats in areas that today are of little agricultural value. In addition, climate change and growth-stimulating effects of rising carbon dioxide ($CO_2$) may accelerate the spread of invasive alien plants, which already outcompete slow-growing and $CO_2$-nonresponsive indigenous fynbos plants in many areas of the Cape, with serious implications for water resources and fire regimes. Much of the protected range in the maximum-dispersal scenarios discussed above could never be occupied because of present incompatible land uses, and land use will continue to change, often in response to changing climate.

More than twice as many additional proteas may be threatened if land use and climate change are considered together, compared with estimates considering changes in land use alone. Presently, 126 of the proteas modeled are classified as threatened (critically endangered, endangered, or vulnerable) according to Red List criteria (IUCN 2001). If only future land-use change as predicted for 2020 is considered, 4 to 13 additional species would be classified as threatened, compared with an additional 30 to 37 species if land use and

climate change are considered together (no-dispersal assumption) (Bomhard et al. 2005). The spatial distribution of these species is remarkable (figure 3). Compared with a Red List assessment that does not look into the future, the number of Red List proteas could rise by up to three species per 1-minute grid cell because of future land use change alone (figure 3c). The number of Red List proteas could, however, rise by up to eight species per 1-minute grid cell, if climate-change effects as predicted for 2020 are added to the land-use change effects on species' ranges (figure 3d), with considerable changes occurring within and outside protected areas. The good news is that the predominance of mountainous protected areas seems already to provide critical refuge for some upland species affected by future climate change. However, for many lowland species, and for upland species outside current protected areas, there is no such good news.

Why does this matter? Conservation planning for additional reserve site selection, for example, is heavily based on available information on the distribution of threatened species and ecosystems. Knowledge of future changes in the distribution of threatened species can certainly help to identify those areas that hold the maximum potential for biodiversity conservation in the face of future threats. Furthermore, knowledge of where, when, and how future threats may affect species can help to identify the most appropriate conservation measures for each species. Species most affected by climate change are likely to require additional measures (e.g., facilitated range shifts) compared with those most affected by land-use change, which can be saved through protection of their remaining natural habitat. Improved conservation strategies can compensate for some of the future changes, but clearly even the most forward-looking of these strategies will break down in the face of unlimited change.

For species without overlap range, one possible conservation strategy is the creation of corridors that will allow species to track climate changes (Hannah et al. 2002a). Another is moderate to intensive management to maintain populations and facilitate range shifts through translocation. Either strategy will require major new resources. Corridors carry uncertainty, as it is unknown whether all species will be able to migrate fast enough to track climate change of the magnitude projected for the coming century. However, it is possible to identify "chains" or "tracks" of suitable habitat for species migration using bioclimatic models. Areas in which these tracks overlap for many species could be protected as corridors for multispecies migration (Williams et al. 2003). The alternative—intensive management—may be incompatible with the conservation of natural processes in many areas, but it could have a higher likelihood of successful conservation of species.

## Regional change and global policy

For biodiversity conservation, it is time to take these future changes into account when developing climate change–integrated conservation strategies ("adaptation" measures in IPCC parlance) (Hannah et al. 2002a, 2002b). In widely used conservation tools such as the IUCN Red Lists of threatened species, the consideration of future threats to biodiversity may not be adequate at present, given the challenge ahead.

Ultimately, improved conservation responses must be accompanied by global policies to halt climate change. The Kyoto Protocol is now in force, a tremendous step in collaboration and collective international action, but a small step in substantive reduction of greenhouse gas emissions. The challenge ahead is staggering—halting climate change, the critical goal for biodiversity, requires stabilizing atmospheric greenhouse gas concentrations. A stable level of greenhouse gases in the atmosphere implies zero net emissions, which would require the total transformation of the global energy supply system to renewable sources. Accomplishing this in the space of several decades without huge environmental costs is a gargantuan task (Lackner 2003). Biologists need to be informed and engaged in the global debate about climate change, or these changes may overwhelm hard-won and still incomplete gains in habitat protection. The ultimate solutions are not immediately apparent, but this is not a reason to avoid action, but rather an imperative to engage now and help formulate solutions that work for society *and* biodiversity. Biologists, particularly those in the United States, have a stake in advocating this course.

Climate change is a dangerous and uncertain game for biodiversity. We know that the present ranges and the present degree of protection of many species will rapidly erode as a result of climate change. The degree to which these losses can be compensated for by occupation of newly suitable range is highly uncertain. Some refinements to protected-area networks can clearly reduce the damage that might be expected by mid-century. Past that, uncertainty rises, but considerable negative consequences for biodiversity loom. The only sure way of improving the odds is to limit climate change itself—a huge task with huge benefits for biodiversity and, ultimately, for all of us.

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