Protected area needs in a changing climate

Lee Hannah[1*], Guy Midgley[2], Sandy Andelman[3], Miguel Araújo[4], Greg Hughes[2], Enrique Martinez-Meyer[5], Richard Pearson[6], and Paul Williams[7]

Range shifts due to climate change may cause species to move out of protected areas. Climate change could therefore result in species range dynamics that reduce the relevance of current fixed protected areas in future conservation strategies. Here, we apply species distribution modeling and conservation planning tools in three regions (Mexico, the Cape Floristic Region of South Africa, and Western Europe) to examine the need for additional protected areas in light of anticipated species range shifts caused by climate change. We set species representation targets and assessed the area required to meet those targets in the present and in the future, under a moderate climate change scenario. Our findings indicate that protected areas can be an important conservation strategy in such a scenario, and that early action may be both more effective and less costly than inaction or delayed action. According to our projections, costs may vary among regions and none of the three areas studied will fully meet all conservation targets, even under a moderate climate change scenario. This suggests that limiting climate change is an essential complement to adding protected areas for conservation of biodiversity.

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Global climate is now rapidly changing, with consequent geographic rearrangement of species and recent climate-related extinctions (Root *et al.* 2003; Pounds *et al.* 2006). Yet protected areas (including national parks, nature reserves, and multiple-use conservation areas) are still the mainstay of modern conservation efforts (Rodrigues *et al.* 2004). Protected areas are geographically fixed and increasingly isolated by habitat destruction, and are therefore poorly suited to accommodating species range shifts due to climate change (Peters and Myers 1991). Here, we ask the question: are protected areas a relevant conservation response in an era of rapid climate change?

Evaluating the effectiveness of protected areas is a problem in conservation planning that is made more complicated by climate change. A major goal of systematic conservation planning is to ensure that all species are represented within the protected areas of a given geographic region (Margules and Pressey 2000). Completing an existing protected area system in a given region so that it represents all known species generally proceeds by assessing the species already protected and then systematically adding complementary areas until all species are represented. Multiple representations of populations or species occurrences are usually necessary to ensure the conservation of each species, so for large numbers of species the process can be quite complex. For this reason, computer-automated selection routines, known as "reserve selection algorithms", have been developed (Pressey and Cowling 2001).

The problem is more complex when species' ranges become dynamic as the result of climate change. One approach is to couple species distribution models and reserve selection algorithms (Araújo *et al.* 2004; Williams *et al.* 2005). Species distribution models use statistical or heuristic packages that simulate the present range of a species, based on relationships between known points of species' occurrence and climate at the time those points were recorded. A simulated present range is required because no species' distribution is perfectly known, while a simulation of future range is needed to account for the range shift likely to accompany changing climatic conditions.

When such modeled ranges are available for large numbers of species (ideally hundreds or thousands), a reserve selection algorithm can be used to design a protected-areas system that represents all species, both in the present and in the future. This is most easily done by starting with existing protected areas and adding additional areas to complete species representation.

One possible goal for such a process in a changing climate is maintenance of current species representation. However, some species' ranges cover large portions of current protected areas, while others are represented in only small areas, or not at all. This is because current protected areas have not been designed for efficient (or even complete) representation of species. As climate changes, it is not necessary or desirable to maintain large areas for over-represented species, nor is it logical to accept zero or very low representation for other species. A first step, therefore, is to add new areas to the existing protected areas system until practical representation targets are achieved. This provides a uniform baseline against which to judge our ability to maintain species representation.

Species representation targets are the most relevant mea-

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[1]*Conservation International, Washington, DC 20036 *(l.hannah@conservation.org); [2]Kirstenbosch Research Center, South Africa National Biodiversity Institute, Cape Town, South Africa; [3]National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, CA 93101; [4]Department of Biodiversity and Evolutionary Biology, National Museum of Natural Sciences, CSIC, Madrid 29006, Spain; [5]National Autonomous University of Mexico, Mexico City, Mexico; [6]American Museum of Natural History, New York, NY 10024*

Figure 1. *Protea species (mainly genus* Leucadendron*) on Jonaskop, within the Cape Floristic Province (Villiersdorp, South Africa). The several dead individuals may have experienced drought stress. Similar dieback has been observed in other parts of the fynbos biome in a wide variety of species at different sites.*

sure for investigating whether protected areas are an effective conservation response to climate change. If all species can maintain a desired target level of representation as climate changes, protected areas remain highly effective (Hannah *et al.* 2005). This would be the case, for example, in a situation where all current protected areas capture climate-driven shifts in species' ranges. Protected areas also remain effective if adding new protected areas can maintain species representation. However, if existing protected areas and potential additions to the system fail to maintain species representation, the role of protected areas is clearly limited.

The dispersal ability of species strongly affects these estimates (Pearson and Dawson 2003). A species maintains representation in a single protected area as long as any range shift due to climate change takes place within the boundary of that protected area (Peters and Myers 1991). If the range shift removes a species from within the boundary of a single protected area, it may still be protected if it is able to disperse to a second protected area. Dispersal ability, intervening land use, and distance to the second protected area will determine whether a species can "make the leap" (Midgley *et al.* 2002). Reasonable assumptions about species' dispersal ability and the suitability of habitat outside protected areas are therefore essential to estimating protected area efficacy as climate changes.

Over the past decade, many studies have modeled species range shifts caused by climate change (Peterson *et al.* 2001; Thomas *et al.* 2004; Thuiller *et al.* 2005) or applied reserve selection algorithms to assess the effectiveness of protected areas under the current climate regime (Pressey and Cowling 2001). However, few studies have combined these two techniques to address the continued effectiveness of protected areas as climate changes (but see Williams *et al.* [2005]). Now that researchers have modeled the response to changing climate of a large number of species in several regions, and existing protected areas and land use are known for these regions, the application of reserve selection algorithms to the problem is feasible.

We have used existing multi-species modeling efforts for three regions – tropical Mexico, the Cape Floristic Province of South Africa, and Western Europe – to assess protected area needs associated with climate change. Members of our group and co-workers have published a series of papers on multi-species distributional modeling and climate change in these three regions. Peterson *et al.* (2002) examined the range shifts of Mexican mammals, birds, and butterflies in response to climate change, using the genetic algorithm for rule set prediction (GARP), a species distribution model that uses multiple statistical and rule-based techniques for projecting range changes. Parra-Olea *et al.* (2005) performed similar analyses for herptiles in Mexico. Midgley (2002) and co-workers have used generalized additive modeling (GAM), a statistical modeling technique, to describe the effects of climate change on the endemic protea plant family of the Cape Floristic Province (Figure 1). Araújo *et al.* (2004) explored the effects of climate change on plants in Europe, also using GAM. These studies have indicated large range shifts upslope and poleward in many species, with most species moving independently of one another, just as predicted by theory and examination of paleoecological evidence. These studies have also borne out the theoretical prediction that climate change would drive species from reserves. Araújo *et al.* (2004) demonstrated that a reserve system in Europe optimized for current ranges might lose 6–11% of species under a changed climate, while Hannah *et al.* (2005) showed progressive loss of species representation from protected areas in the Cape region. We build on these previous modeling efforts by applying reserve selection algorithms to assess the implications for protected areas of climate change-driven species range shifts. Questions we answer include: can protected areas maintain species representation when ranges change? Would adding protected areas maintain representation of dynamic species, and, if so, how much more area will be required? The answers to these questions have important implications for conservation policy, our efforts to avoid species extinctions due to climate change, and the relevance of protected areas as a conservation tool in a changing climate.

Methods

We used data assembled for our previous studies on the effects of climate change in large numbers of species. The models of species distributions in these existing studies were adapted for the application of reserve selection algorithms. Simulated present and future ranges were available at high resolution for the Cape and Mexico (1.8 km^2 and 1 km^2, respectively) and at a much coarser resolution (50 km^2) for Europe. Focal taxa were plants in Europe and the Cape Floristic Region (protea family; Figure 1) and birds and mammals in Mexico. Table 1 lists the taxa and number of species modeled in each region. In total, species distribution models for 1695 species were used in the three regions combined.

Methods for modeling species distribution varied by region: the species distribution models were generated for the Cape and Europe using GAM and for Mexico using GARP. Although recent studies have demonstrated notable differences between predictions using alternative modeling methods (eg Thuiller 2004), the predictions we used provide both a projection of the environmental niche of a species and the best available estimate of the possible direction and magnitude of range shifts for the respective regions and species.

Climate change projections were from the Hadley Centre general circulation model (GCM; HadCM2 or HadCM3) and are for the 2050s (Johns *et al.* 2003). The projections are based on emissions scenarios that approximate business-as-usual (IS92a or A1FI) IPCC scenarios (IPCC 2001). For Mexico and the Cape, the GCM outputs were downscaled to the grain (resolution) of the species distribution modeling by standard splining methods, which take the difference between present and future GCM simulations and add it to current climate. This preserves the fine-scale structure of climate over the region (eg temperature variation with elevation) while introducing changes consistent with the GCM simulation of future conditions.

The effects of existing land use on habitat availability were included in Mexico and the Cape. In the Cape, land-use data were from the South Africa Landcover Database (CSIR 1999). In Mexico, a land-use map developed by Palacio *et al.* (2000) was employed. Changes in land use over time were not incorporated into this study, but have been addressed for the Cape and Europe by others (Rouget *et al.* 2003; Rounsevell *et al.* 2005). Habitat suitability of the various land-use classifications was assigned on a species-by-species basis. For example, urban areas were classified as unsuitable for all species studied, while farmland was classified as unsuitable for habitat specialists but suitable for species with more general habitat requirements.

Species' dispersal was simulated in the Cape and Mexico, but not for Europe, where the large study area, coarse scale, and large number of species involved made dispersal modeling impractical. A single, 50-year time-step with no dispersal was used for Europe. In the Cape and Mexico, dispersal was simulated in 10-year time-steps. Climatic variables were interpolated in 10-year increments and the species distribution models created for each decadal time-step. Each species was allowed to occupy suitable climate at each time-step within a dispersal radius defined by values from the literature or the authors' knowledge of the species and their dispersal capabilities. Proteas of the Cape were divided into three dispersal classes (insect, rodent, and wind), each with a characteristic dispersal distance allowed in each 10-year time-step, as described in Williams *et al.* (2005). In Mexico, mammals were assumed to occupy all contiguous climatically suitable habitat and birds all suitable habitat in each time-step.

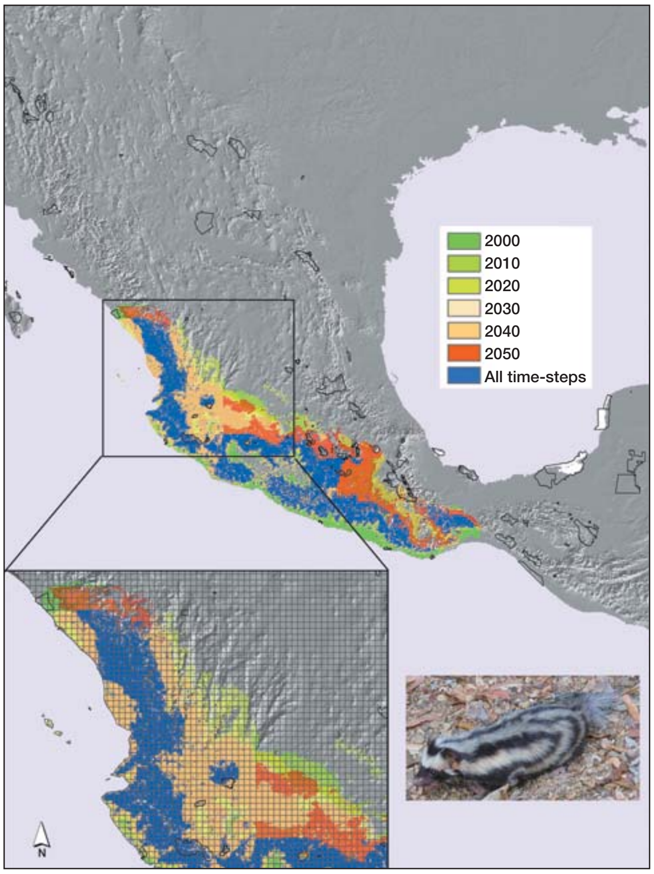

Figure 2. *Illustration of species distribution modeling for pygmy skunk (*Spilogale pygmus*; inset lower right), one of 179 species modeled for tropical Mexico. Colors show species distribution simulated for different time-steps. The gridded overlay shows the planning units (10 km x 10 km) used in reserve selection.*

The relevance of protected areas was assessed using reserve selection algorithms implemented within the Worldmap and SITES conservation planning software systems (Williams *et al.* 2000; Andelman and Willig 2002). Worldmap was employed for the Cape and Europe, while SITES was used for Mexico, because the study area was too large to be analyzed in Worldmap. Both Worldmap and SITES are grid-based systems, in which the size of the planning unit must be defined. Planning unit size was selected for each region based on the characteristics of the taxa being modeled. Planning units in the Cape were set equal to the modeling grid cells (1 minute, 1.8 km^2), since viable protea populations can be maintained in an area of this size. In Mexico, where birds and mammals are unlikely to maintain viable populations at the modeling scale of 1 km^2, a planning unit of 10 km x 10 km was used to approximate the minimum size of an effective vertebrate reserve (Figure 2). For Europe, the modeling scale of 50 km^2 was probably larger than needed for maintaining viable plant populations, so this scale was retained for planning units. A planning unit counted toward the representation target if it was selected to meet the target in any of the time-steps.

In each region, we first added protected areas until all species were represented at a uniform representation target for current climate. The representation target was 100 km^2 for plants and 100 km^2 or 10% of current range, whichever was larger, for other taxa (Rodrigues *et al.* 2004; Hannah *et al.* 2005). While it would be desirable to have individually derived representation targets for each species, based on their population dynamics and area needs, such individual treatment was not possible for the large number of species treated here.

Using these criteria, the current protected area system was "completed" for each region to achieve representation targets for all species under current climate. For future climate scenarios, we examined whether additional protected areas were required to maintain representation at target levels. This is the equivalent of investigating whether more protected areas will be needed due to the effects of climate change on species' ranges. If creation of new protected areas is not an effective management response to climate change, we would expect that adding additional area would not improve representation. Protected area was added until no further improvements in representation could be made under future climate projections, either because the species achieved its target, or because no further planning units existed that were climatically suitable for the species, either in the present or in the future. The species meeting the representation target were then counted.

Finally, we examined whether timing is important when incorporating climate change considerations into protected area planning. To do this, we included a variant in which consideration of climate change took place at the same time that representation was completed for the current system. In other words, the two-step process, in which representation for current ranges was improved and then representation to account for future ranges subsequently added, was replaced by a one-step process that simultaneously addressed representation for both present and future ranges. To do this, the reserve selection algorithm was provided with information on species' current and future ranges and asked to solve for both. The two-step process simulates current conservation efforts, which seek to improve representation of current ranges and leave accounting for climate change to be done later, while the one-step method simulates a more forward-looking conservation strategy, in which the impacts of climate change are anticipated and integrated into ongoing efforts to complete representation. We refer to the difference in area efficiency between the two-step and one-step process as "the cost of waiting".

Results

Protected area systems – completed to meet consistent targets for current ranges, and supplemented with additional protected areas to compensate for climate change – were able to represent most species' future ranges under the moderate climate change scenario used in this study. In the Cape, 246 of 316 species (78%) met the representation target for future range (see Table 1), in Mexico 160 out of 179 species (89%) retained full representation, and in Europe the corresponding figure was 1123 out of 1200 species (94%). Current protected area systems required a substantial area supplement to meet representation targets for both current and future ranges in all three regions. Some species failed to meet representation targets even for current ranges. The greatest shortfall was in the Cape, where 34 species (11%) did not meet the target for current ranges, while all species in Europe and all but one in Mexico met the target for current ranges. An additional group of species in each region failed to meet the representation target in the future scenario, even with the addition of new protected areas. In Europe and Mexico, all species that fell short of the target had at least some representation in the future scenario. In the Cape, 11% of species had no range in 2050, and the level of underrepresentation (number of species, area of shortfall per species) increased markedly in the future scenario (Figure 3).

The protected area required to achieve target levels of species representation was greater under future climate than under current climate in all three regions (Table 1, columns C and F). The climate change increment was always smaller than the area required for complete representation of current ranges (current protected area plus additional area required to meet baseline representation for current ranges) and smaller than the area required to complete baseline representation for current ranges in all but one case (Europe, using the two-step process). This is due to the ineffectiveness of current protected areas in meeting standardized representation targets, but also reflects the fact that moderate climate change can be accomodated with a relatively small increment of new protected areas (Table 1, columns C and F). The climate change increment was between < 1% and 34% of the area required for complete representation of current ranges (current protected area plus additional area required to meet baseline representation), depending on which approach (one-step or two-step) was used.

The one-step and two-step approaches to integrating consideration of climate change produced significantly different results. Table 1 summarizes the two-step approach in columns B-D and the one-step approach in columns E-F. The two-step approach simulates first completing representation to the target level using present ranges (column B), then compensating for the effects of climate change (column C). If we do not integrate climate change into our conservation strategies now, this is the likely sequence of events and the total area required will be the sum of the two steps, which is presented in column D.

A more efficient solution to the representation problem can be found by solving for current and present ranges simultaneously (Table 1, column E). This solution simulates incorporating climate change into conservation strategies immediately, and choosing new protected areas that satisfy representation targets for both current and

Table 1. Protected area requirements to meet defined species representation targets with and without climate change in the three study regions

	A	*B*	*C*	*D*	*E*	*F*	*G*
Region	Current protected area	Additional area required to meet baseline target (current ranges only)	Incremental area required to meet target with climate change, in addition to B (future ranges)	Total additional area required in two sequential steps (B + C)	Total additional area required in one step (current and future ranges simultaneously)	Incremental area required to meet target climate change, using one-step approach (E – B)	Cost of waiting (C – F)
Taxa	km^2	km^2	km^2	km^2	km^2	km^2	km^2
Number of species modeled		*Number of species meeting target at present*	*Number of species meeting target in 2050*	*Number of species meeting target in 2050*	*Number of species meeting target in 2050*		
Cape Floristic Region	4681	2330	1911	4241	3487	1157	754
Plants (Proteacea)		49% of A	41% of A 27% of A + B	91% of A 60% of A + B	75% of A 50% of A + B	25% of A 16% of A + B	39% of C 65% of F
316		*282*	*246*	*246*	*246*		
Tropical Mexico	104 000	44 000	12 800	56 800	44 500	500	12 800
Birds and mammals		42% of A	12% of A 9% of A + B	55% of A 38% of A + B	43% of A 30% of A + B	<1% of A <1% of A + B	96% of C 2460% of F
179		*178*	*160*	*160*	*160*		
Western Europe	20 850	3850	8450	12 300	7200	3350	5100
Plants (multiple families)		18% of A	41% of A 34% of A + B	59% of A 50% of A + B	35% of A 29% of A + B	16% of A 14% of A + B	60% of C 152% of F
1200		*1200*	*1123*	*1123*	*1123*		

Column A indicates the area currently protected. All subsequent area amounts must be added to these existing protected areas. Column B indicates the additional area required to meet the representation target for current species ranges. Column C indicates the area increment required to meet the target for future ranges in a second, subsequent step, once the target has been met for current ranges. Column D indicates the total additional area required to meet the target for current and future ranges in two steps, or the sum of the previous two columns (B+C). Column E is the area required to meet the target using the alternative approach of searching for solutions for present and future ranges in a single step. Column F is the incremental area needed to address climate change when existing representation and climate change are addressed in one step, or the difference between column E and column B. Column G is the area difference between meeting the target for present, then future ranges in two separate steps (D), versus meeting it for present and future ranges at once in a single step (E). This "cost of waiting" simulates the difference between completing representation for species present and future ranges now ("early action"), versus completing representation for species current ranges now, then waiting until sometime in the future to complete representation for future ranges ("waiting").

future ranges at once. This approach is more area-efficient in all three regions, resulting in smaller area requirements relative to the two-step approach (Table 1, compare columns E and D).

The incremental area required by climate change in the one-step solution was less than the increment required in the two-step approach in all three regions (Table 1, compare columns F and C), as would be expected in a more efficient solution. Note that the one-step increment must be approximated by taking the combined area required for present and future ranges in the one-step process and subtracting the area required for current ranges only from the two-step process (subtracting column B from column E in Table 1; the difference is given in column F).

The increased efficiency of the single-step solution suggests that there is a cost associated with waiting to address climate change. If this "cost of waiting" is large, then it may make sense to incorporate climate change into conservation strategies early, despite the uncertainty in current emissions, climate projections, and species distribution models. The cost of waiting is given in Table 1, column G, and ranges between 39% and 96% of the area increment required to address climate change in a two-step process and between 65% of, and 24 times more than, the amount of area required for climate change in the more efficient, one-step process. The cost of waiting was very large (greater than 100%) relative to the one-step solution in two of the three regions studied.

Discussion

Our findings indicate that (1) protected areas are a useful conservation response to climate change, (2) creation of new protected areas can substantially improve the likelihood of species conservation as climate changes, and (3) the sequence of implementing protected area responses to climate change influences the cost of such additions. An early response would result in cost savings (measured here in area set aside for conservation) and presents an important opportunity to combine completion of species representation for

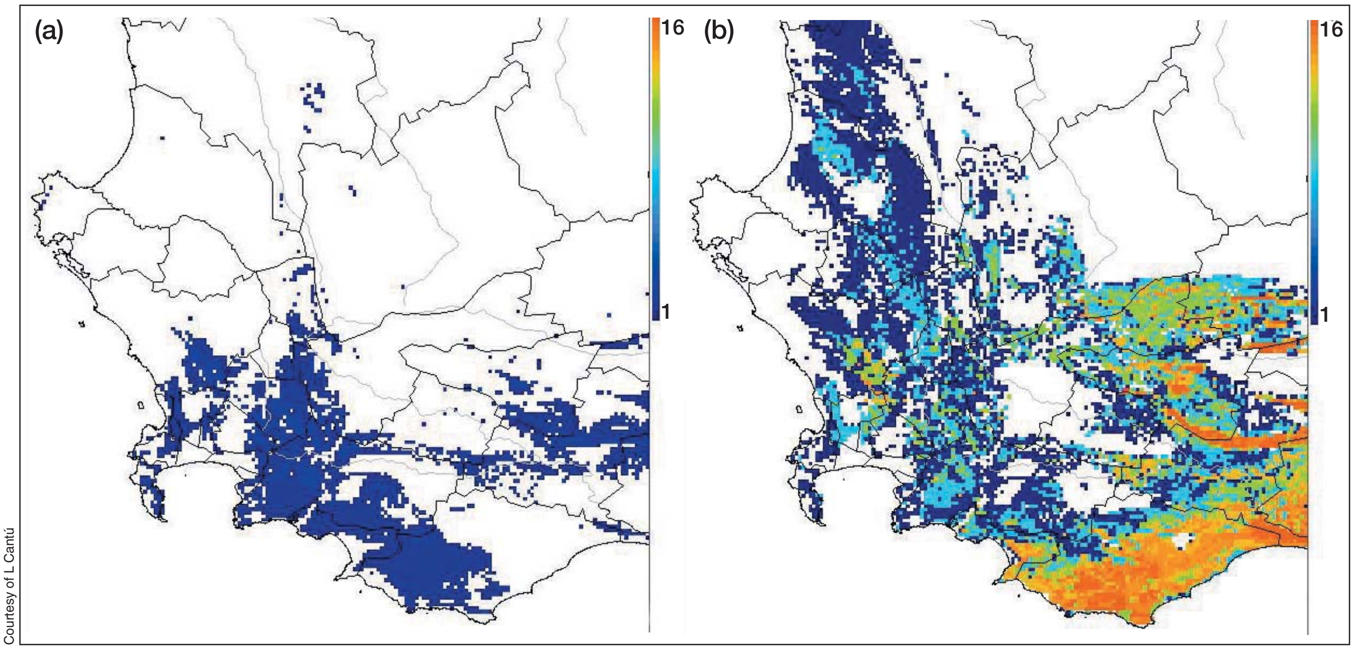

Figure 3. *Richness of underrepresented Cape protea species in an optimized protected areas system. (a) Richness of underrepresented species for a system of protected areas meeting a goal of 100 km^2 representation for the present modeled range of each species. (b) Richness of underrepresented species for a similar system meeting a goal of a 100 km^2 for the year 2050 modeled range of each species. Under-represented species are more geographically dispersed and concentrated in highlands in the future scenario, due to range limits contracting and moving upslope. The numbers in the color ramp legend (upper right of each panel) indicate the number of underrepresented species in each planning unit in the two time periods.*

current ranges with anticipation of climate change.

These results confirm the need for new protected areas in three highly varied regions and sets of taxa. Unless these regions are very unusual, investment in new protected areas to cope with climate change is likely to be required in most or all parts of the world. This represents a major new cost of conservation due to climate change. However, addressed proactively, it also offers opportunities to maximize other conservation benefits while extinctions due to climate change are reduced.

Most existing protected areas in these regions were created before the term biodiversity was coined, and certainly not under a system-wide mandate to represent and conserve biodiversity. As a result, species' representation in these systems is highly variable. There is a major need to upgrade protected areas to improve representation and a major opportunity to factor climate change into this process. As we show (Table 1, column G), it is more expensive to improve representation for current ranges and then wait to address climate change in a second, subsequent step. A more efficient course of action is to improve representation of current ranges and of (modeled) future ranges in a single step.

Adding new area now to conserve both present and future ranges of species was less costly (in area) than using a two-step process, suggesting that early action to adapt conservation strategies to climate change may be more efficient than strategies that delay response. The reason for this increased efficiency is that it is more effective to deal with two variables simultaneously than it is to solve for them sequentially. In practice, reserve selection algorithms add area (planning units) in a step-wise manner. At each step, it is common for several planning units to have equivalent scores. The algorithms use simple tie-breakers to choose between these equivalently scoring units (eg random draw or planning unit closest to point-of-origin of the planning grid). When a second selection criterion such as climate change is available, these ties are broken in a more systematic manner. For example, if five planning units have equivalent scores for current range, but only one contains future range, the one containing the future range will be selected in the one-step process. In the first step of a two-step process, that planning unit has only a one-in-five chance of being selected, so it is highly likely that a second planning unit will need to be selected in the second step, effectively doubling the cost of selecting that unit. Multiplied over dozens of species, the lower cost of a single-step process results in significant area savings.

It may be possible to meet the target for climate change (ie future ranges) at little or no additional area cost if enough planning units exist with equivalent scores for the current ranges. This was the case for Mexico in this study, where almost no area increment was required for climate change in the one-step process. Not all areas will have clear "no-regrets" options, but where gains in efficiency are large and model uncertainties are modest, it will almost always be less costly (in area) to implement early conservation responses.

The amount of new protected area required in our projections varied widely, with regions where more species were modeled requiring more new area to compensate for climate change. Since species are expected to move individually in response to climate change, adding additional species is likely to increase area requirements. This effect may have been magnified in Europe by the coarse scale of the planning units. Species dispersal assumptions are also likely to influence estimated area requirements. In Mexico, where birds, butterflies, and mammals were all assumed to disperse more readily than the plants of the Cape or Europe, the estimates of new protected area requirements were lower. It is therefore likely that estimates of new area required to deal with climate change would decrease for Europe and increase for Mexico if modeling were repeated at a finer scale for Europe and with more included taxa (particularly plants) for Mexico. This would reduce some of the variation observed in our results. However, the climate, species, topography, and current protected areas of all regions are unique and there is strong reason to believe that regional variation is to be expected. It is exactly for this reason that modeling and protected area design for individual regions is so important.

Uncertainties arise in our emissions projections, climate change models, species distribution models, and other sources of information (IPCC 2001; Araújo and Rahbek 2006). Species distribution models depend on assumptions (eg species ranges being in equilibrium with climate) that may not always be valid. Additional research is warranted to explore these sources of uncertainty and their possible impacts on estimates of protected area needs. In addition, as noted above, the amount of new protected area required is likely to vary by region and by taxa, although it is notable that increasing the number of species included in such analyses can only increase the estimate of protected area needs. Our dispersal assumptions are also conservative, since future range that was greatly distant from species' current ranges was not considered. This approach discounts rare, long-distance dispersal mechanisms (Higgins and Richardson 1999; Pearson and Dawson 2003), consistent with recent paleoecological evidence suggesting that long-distance dispersal may not play a major role in facilitating rapid migrations (Pearson 2006). In light of these various uncertainties, we emphasize that quantitative refinement of our estimates is essential; nevertheless, we believe that our results are qualitatively robust.

While the new protected area required by climate change in our calculations is a fraction of current protected area, adding new protected area may be difficult in regions already beset by high and increasing levels of habitat destruction. At the same time, it is clear that fixed protected areas alone will not be sufficient to safeguard biodiversity from the impacts of climate change. Between 6% and 22% of species in our analysis failed to meet representation targets for future ranges. These losses would increase under more severe climate scenarios. Lost representation can be compensated by the creation of corridors or "stepping stones" that link species' current and future ranges. We have explored this option and found it to be relatively area-intensive (Williams *et al.* 2005). Unchecked climate change will thus force increasingly area-intensive and costly conservation measures, ultimately outstripping all possible responses as available land for new protected areas and pathways for connectivity are exhausted. Constraining climate change and adding protected areas to make conservation strategies robust to unavoidable change are therefore necessary complements to one another in efforts to avoid climate-related extinctions.

International policy may also need to balance equity issues that arise when some regions develop markedly higher costs and lower ability to compensate for climate change than others. For instance, in the Cape, extensive area additions were required and the number of species meeting representation targets (Figure 3) was low relative to the other two regions studied, indicating that this region may be particularly vulnerable to climate-driven biodiversity loss. This is an important point for policy makers seeking to define the level at which climate change should be constrained. Evidence from the Cape and other regions may provide early warning signs of "dangerous interference" under the United Nations Framework Convention on Climate Change (UNFCCC) criterion of allowing "ecosystems to adapt naturally" (O'Neill and Oppenheimer 2002).

Conserving biodiversity as climate changes is a two-pronged challenge, requiring both adaptation – improved conservation strategies – and mitigation – stabilization of greenhouse gases in the atmosphere (IPCC 2001; Hannah *et al.* 2002). The results presented here indicate that increases in protected areas will be necessary to compensate for altered species distributions caused by climate change. The amount of additional area required depends on the physical and biotic geography of individual regions and taxa, as well as the level of climate change experienced. Protected area additions will eventually be overwhelmed unless they are coupled with limitation of atmospheric greenhouse gases. By the 2050s, many species in some regions may be unable to meet even the modest representation target used in this study, indicating that greenhouse gas levels in the atmosphere of as little as double pre-industrial CO_2 might already exceed the capacity of improved conservation systems to maintain biodiversity.

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References

Andelman SJ and Willig MR. 2002. Alternative configurations of conservation reserves for Paraguayan bats: considerations of spatial scale. *Conserv Biol* **16**: 1352–63.

Araújo MB Cabeza M, Thuiller W, *et al.* 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Glob Change Biol* **10**: 1618–26.

Araújo MB, and Rahbek C. 2006. How does climate change affect biodiversity? *Science* **313**: 1396–97.

CSIR (The Council for Scientific and Industrial Research). 1999. South African national land cover database project – data users manual. Pretoria, South Africa: CSIR.

Hannah L, Midgley GF, Hughes G, and Bomhard B. 2005. The view from the Cape: exinction risk, protected areas and climate change. *BioScience* **55**: 231–42.

Higgins SI and Richardson DM. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. *Am Nat* **153**: 464–75.

IPCC (Intergovernmental Panel on Climate Change). 2001. Climate Change 2001: the scientific basis; contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Port Chester, NY: Cambridge University Press.

Margules CR and Pressey RL. 2000. Systematic conservation planning. *Nat London* **405**: 243–53.

Midgley GF, Hannah L, Millar D, *et al.* 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecol Biogeogr* **11**: 445–51.

Pearson RG. 2006. Climate change and the migration capacity of species. *Trends Ecol Evol* **21**: 111–13.

Pearson RG and Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecol Biogeogr* **12**: 361–71.

Peters RL and Myers JP. 1991. Preserving biodiversity in a changing climate. *Issues Sci Technol* **8**: 66–72.

Peterson AT, Ortega-Huerta MA, Bartley J, *et al.* 2002. Future projections for Mexican faunas under global climate change scenarios. *Nature* **416**: 626–29.

Peterson T, Sanchez-Cordero V, Soberon J, *et al.* 2001. Effects of global climate change on geographic distributions of Mexican Cracidae. *Ecol Model* **144**: 21–30.

Pounds JA, Bustamante MR, Coloma LA, *et al.* 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**: 161–67.

Pressey RL and Cowling RM. 2001. Reserve selection algorithms and the real world. *Conserv Biol* **15**: 275–77.

Rodrigues ASL, Andelman SJ, Bakarr MI, *et al.* 2004. Effectiveness of the global protected area network in representing species diversity. *Nature* **428**: 640–43.

Root T, Price JT, Hall KR, *et al.* 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57–60.

Rouget M, Richardson DM, Cowling RM, *et al.* 2003. Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biol Conserv* **112**: 63–85.

Rounsevell MDA, Ewert F, Reginster I, *et al.* 2005. Future scenarios of European agricultural land use. II: Projecting changes in cropland and grassland. *Agr Ecosyst Environ* **107**: 117–35.

Thomas CD, Cameron A, Green RE, *et al.* 2004. Extinction risk from climate change. *Nature* **427**: 145–48.

Thuiller W. 2004. Patterns and uncertainties of species' range shifts under climate change. *Glob Change Biol* **10**: 2020–27.

Thuiller W, Lavorel S, Araújo MB, *et al.* 2005. Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci USA* **102**: 8245–50.

Williams P, Hannah L, Andelman S, *et al.* 2005. Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conserv Biol* **19**: 1063–74.

Williams PH, Burgess N, and Rahbek C. 2000. Flagship species, ecological complementarity and conserving the diversity of mammals and birds in sub-Saharan Africa. *Anim Conserv* **3**: 249–60.