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Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region

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Abstract

We assess the potential impact of climate change on plant diversity in the Cape Floristic Region (CFR) and its interaction with land transformation that has already occurred in the region. Predictions were made both at the scale of the Fynbos Biome (the dominant vegetation assemblage in the CFR) and for selected Proteaceae species. Bioclimatic modelling identified parts of the biome at particular risk from climate change. Species-level modelling (Generalised Additive Modelling) was done for 28 Proteaceae species selected from areas at high risk of biome loss, revealing individualistic range changes in a pattern broadly consistent with biome modelling results. Most species experienced potential range contractions (17 of 28), of which five showed range elimination. Several species (11 of 28) showed potential range expansions. For species showing range contractions, current land transformation had less impact on future potential ranges than did climate change, because many species ranges shifted to higher altitudes where land transformation is currently less prevalent. Fewer than half of the high-risk species showed overlap between current and future potential range, showing that propagule transport, establishment of species in novel ranges and conservation of landscape linkages will be critical for maintenance of biodiversity. Methods described here provide useful forecasts of potential climate change impacts that could guide conservation responses, but results need cautious interpretation in the light of the many assumptions underlying the techniques used.

Keywords: Bioclimatic modelling; Climatic niche; Corridor; Geographic range shift; Mediterranean-type ecosystem; Winter rainfall

1. Introduction

Recently documented biotic responses to possible human-induced climate change (Hughes, 2000; Peterson et al., 2002) raise a crucial question for conservationists: Are projected climate changes likely to be a threat to the conservation of biodiversity? Conservation efforts have generally assumed that climate is a constant feature of the environment, and that species distributions are effectively constant in space and time (Cowling, 1999). Both the former and latter assumptions are unjustifiable, as it is now well understood that the earth's climate has changed significantly and rapidly on time scales of decades to millennia (Broecker, 1999; Zachos et al., 2001); that species have shifted their ranges as climate has changed (Hewitt, 2000; Huntley and Birks, 1983; Parmesan, 1996; Parmesan et al., 1999); and that these range shifts are often individualistic responses to climate change (Graham and Grimm, 1990; Warren et al., 2001) as opposed to wholesale migrations of ecosystems or biomes. Several authors have begun to explore how conservation plans can begin to assess this threat and incorporate these insights into strategies that will be robust to climate change (e.g. Halpin, 1997; Hannah et al., 2002), and some planning to accommodate climate change impacts has been developed for the CFR (Cowling and Pressey, 2001; Cowling et al., 2003; Rouget et al., 2003) and for the winter rainfall

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Succulent Karoo Biome of South Africa (Cowling et al., 1999a). Nonetheless, explicit adaptations to conservation planning in the face of climate change are in their infancy.

The CFR boasts an exceptionally rich flora with high levels of endemism (Cowling et al., 1989), that may result, in part, from a unique climate and climate history (Cowling et al., 1998; Midgley et al., 2001). The mediterranean-type climate of the CFR may now be changing, characterised by increasing temperatures and reduced rainfall, especially in winter months (Tyson et al., 2002; Wand et al., personal communication). Conservation planning for the region has just begun to account for these significant changes and the impact they may have in concert with other threats (Cowling and Pressey, 2001; Cowling et al., 2003; Rouget et al., 2003).

If species range shifts are the likely dominant species response to future climate change, then spatially explicit planning will be fundamental to estimating the rate and direction of species movements required to ensure retention of sufficient range for their persistence. Modelling can help inform efforts to place land under effective conservation management, either in formally protected areas or in unprotected areas suitable as habitat. These tools must be relevant at regional and even sub-regional scales—the scales at which most practical conservation decisions, such as land acquisitions, are made.

In this paper, we develop a biome- and a species-based approach to assessing the regional impacts of climate change on the future distribution of a major floristic group (Proteaceae). We address a number of questions:

1. What biome-level patterns may be expected under future climate change, and what are the comparative potential range shifts in representatives of a dominant taxon, the Proteaceae, in areas of potential biome contraction?
2. How much has land transformation constrained the potential migration of species in response to climate change?
3. What proportion of species are under severe threat of extinction under the projected climate change scenarios?
4. What are the implications of these patterns for conservation planning?

2. Methods

2.1. Study area and selected species

We modelled the Fynbos Biome (sensu Rutherford and Westfall, 1994) and selected endemic members of the family Proteaceae within the CFR. The Fynbos Biome is the dominant biome within the Cape Floristic Region. We focused attention on the western parts of the CFR, having established large potential impacts of climate change in this region (Midgley et al., 2003). The study area includes much of the western Cape (between 33–35° S and 18–22° E), a region that has a Mediterranean-type climate with more or less intense summer droughts and wet winters resulting from orographic rainfall and the passage of cyclonic cold fronts associated with westerly winds. Moisture derived from the Indian Ocean and the warm Agulhas Current can be transported onto the southerly coastal plains and southern mountains of the CFR at any time of the year, but this is of minor relevance in our area of interest. The soils of the CFR include mainly sandstone-derived, highly leached and dystrophic lithosols associated with the mountains, duplex soils (sand overlaying heavier subsoils) associated with the coastal platform, and relatively uncommon coastal calcareous soils, often associated with range-restricted plant endemics. The Fynbos Biome is a predominantly sclerophyll shrubland, characterised by the pre-eminence of hard-leaved shrubs (mainly of the species-rich family Proteaceae), narrow- and small-leaved subshrubs and leafless multi-stemmed grass-like growth forms (Taylor, 1978). On the whole, vegetation is fire-prone, with fire recurrence interval of between 4 and 40 years (commonly between 10 and 20 years).

We chose to analyse potential range shifts in Proteaceae species found mainly at low altitudes, with current distributions predominantly in areas of the Fynbos Biome predicted to contract significantly in our biome model.

2.2. Climate scenarios

Future climate scenarios were derived from $\sim 3 \times 3°$ coarse scale projections from the general circulation model HadCM2 for the southern African region interpolated finally to 1×1 minute scale (Schulze and Perks, 1999). The interpolation technique used established relationships between current climate and altitude, topography and continentality to derive finer scale data.

2.3. Vegetation shift modelling

Five climatically derived parameters considered critical to plant physiological function and survival were used to construct climate envelopes for the Fynbos Biome as a whole (e.g. Busby, 1991), and to build Generalised Additive Models (GAMs) of climate constraints for individual species (Yee and Mitchell, 1991). Parameters used were mean minimum temperature of the coldest month ($T_{\min}$), heat units [HU_{18}, annual sum of daily temperatures (°C) exceeding 18 °C], annual potential evaporation (PE), winter soil moisture days (SMD_{win}), and summer soil moisture days (SMD_{sum}—the latter parameters refer to the number of days for which soil moisture and air temperature were favourable for plant growth). These variables were among those derived for South Africa under present and projected 2050 climatic conditions by Schulze (1997) and Schulze and Perks (1999), and are consistent with variables chosen for similar studies in other regions (Bakkenes et al., 2002).

The minimum temperature of the coldest month is likely to discriminate between species based on their ability to assimilate soil water and nutrients, and continue cell division, differentiation and tissue growth at low temperatures (lower limit), and chilling requirement for processes such as bud break and seed germination (upper limit). Heat units discriminate between species based both on their requirement for a minimum temperature to complete growing cycles (lower limit), and ability to tolerate excess tissue temperature (upper limit). Potential evaporation discriminates through processes related to transpiration-driven water flow through the plant, and xylem vulnerability to cavitation and water transport efficiency. Soil moisture days in winter and summer discriminate through determining the intensity and duration of seasonal drought stress and growing opportunities, which are especially crucial for seedling recruitment and the survival of this sensitive plant life stage. However, it is important to note that there is little experimental work on local indigenous species to guide in the choice of any bioclimatically limiting variables, and these were chosen as a hypothetical minimum basic set for defining a bioclimatic envelope in South Africa's indigenous flora, in urgent need of testing.

A potential complication ignored by the techniques used here is that of changing atmospheric CO_2, which can improve the resource–use efficiencies of plants (Drake et al., 1997). However, what little work has been done on Fynbos species response to elevated CO_2 (Midgley et al., 1995, 1999) has revealed neutral effects of this atmospheric change on plant performance in the Proteaceae—furthermore, it can be expected that elevated CO_2 effects on plant growth will be muted in this nutrient-limited system (Stock and Midgley, 1995).

The spatial distribution of the Fynbos Biome as currently mapped was digitised from Rutherford and Westfall (1994), and modelled as described in Midgley

Table 1
Proteaceae species selected for this study, and their key physiognomic and habitat characteristics (after Rebelo, 2001)

Species	Adult height (m)	Habitat	Altitude range (m)
Diastella buekii (Gand.) Rourke	0.15	Moist sands	200–300
Diastella parilis Salisb. ex Knight	0.7	Sandstone foothills	250–500
Diastella proteoides (L.) Druce	0.5	Tertiary and recent sands	0–150
Leucadendron chamelaea (Lam.) I. Williams	2.3	Level sandstone sands	150–1000
Leucadendron cinereum (Sol. Ex Aiton) R.Br.	1	Level, sandy soil	15–100
Leucadendron corymbosum P.J. Bergius	2	Level, wet, clay subsoils	100–300
Leucadendron foedum I. Williams	2.5	Sandy soils	30–100
Leucadendron galpinii E. Phillips & Hutch	2–3	Sandy soils	0–200
Leucadendron lanigerum H. Buek ex Meisn. var. *lanigerum*	1.5	Level clays	180–200
Leucadendron levisanus (L.) P.J. Bergius	2	Damp, sandy soil	0–100
Leucadendron stellare (Sims) Sweet	2	Level, dry sands over clay	30–170
Leucadendron thymifolium (Salisb. ex Knight) I. Williams	2	Sands or gravels over clay	100
Leucospermum arenarium Rycroft	0.75	Deep, white, tertiary sands	120–170
Leucospermum hypophyllocarpodendron subsp. *canaliculatum* (H. Buek ex Meisn.) Rourke	0.2	Deep, white, recent sands	0–200
Leucospermum muirii E. Phillips	1.5	White tertiary sands	90–260
Leucospermum parile (Salisb. ex Knight) Sweet	1.5	Tertiary and recent sands	30–170
Leucospermum rodolentum (Salisb. ex Knight) Rourke	3	Tertiary and recent sand flats	0–300
Leucospermum tomentosum (Thunb.) R.Br.	0.4–1	Tertiary and recent sand flats near sea	0–80
Protea scolymocephala (L.) Reichard	0.5–1.5	Sandy flats and coastal lowlands	0–400
Serruria adscendens (Lam.) R.Br.	0.5–1	Sandstone soils	0–950
Serruria brownii Meisn.	0.3–0.5	Granite soils, shales and heavy sands	50–250
Serruria candicans R.Br.	0.4–0.8	Granite and sandy soils	60–160
Serruria cyanoides (L.) R.Br.	0.3–0.5	Sands	0–150
Serruria decipiens R.Br.	0.6–1	Sandstone and sandy soils	0–250
Serruria decumbens (Thunb.) R.Br.	0.1	Sandstone soils	150–310
Serruria fucifolia Salisb. ex Knight	0.8–1.5	Sandstone and sandy soils	150–920
Serruria linearis Salisb. ex Knight	0.4–0.8	Sands	120–190
Serruria trilopha Salisb. ex Knight	0.3–0.8	Sands	50–310

et al. (2003). Areas in which there were large differences between present and future modelled biome extent were deemed to be at high risk.

Based on biome-level projections of areas of high climate change impact, we selected for study a set of 28 Proteaceae species currently distributed in lowland regions (see Table 1). We used the Protea Atlas Database (Rebelo, 2001) which contains records of both species presence and absence at more than twenty thousand points within the CFR. These data allow the application of GAMs to derive bioclimatic relationships for the selected species (Hastie and Tibshirani, 1990). In addition to the climatic variables described earlier, we included in the species models three soils variables—fertility, sand and clay content, as defined and mapped by Schulze (1997). This is a minimum set of soil factors that is likely to influence plant performance through nutrient availability, and the impacts of soil texture on soil water availability.

The GAM approach maps out areas of differing probability of encountering the species modelled, ranging from 0 to 1. For the purposes of this paper, we chose probability levels of 0.5 and higher to define the bioclimatic and edaphic constraints for each species. This conservative cut-off reduces the risk of identifying areas as suitable for the species even if they are not—it therefore reduces the identification of false positives, or making errors of commission.

While GAMs do not have the same properties as models based on ordinary least squares regression, it is possible to derive a good indication of the performance of the model from a statistic which is analogous to R^2, but calculated as $1-$(residual deviance/null deviance), referred to here as “explained deviance”. If the model did not improve on a null (random) model for a given species, that species was assumed to have no current bioclimatic or edaphic limitation and its response to climate change not considered further (two species).

Generalised Additive Models for the selected species had adequate to good explanatory power (explained deviance ranged from 0.5 to 0.8, Table 2) for the 28 species modelled in detail. The relatively high coefficients obtained indicate that the species are likely to be climate-constrained, and that changes in the regional climate will have significant impacts on them. The 28 species selected were chosen by statistical screening of 33 candidate species. Two of the original 33 candidate species were excluded from the analysis due to poor statistical fit to null, and three were omitted from further analysis because the models could not identify any part of the study area in which they had a probability of occurrence greater than 0.5 in either the present or the future.

The impact of land transformation on future range was assessed by screening out areas currently mapped as transformed (CSIR, 1999), and assuming that these are unsuitable as habitat for the species.

Table 2
Explained deviance for the Generalised Additive Models

Species	Explained deviance
Diastella buekii	0.77
Diastella parilis	0.74
Diastella proteoides	0.68
Leucadendron chamelaea	0.60
Leucadendron cinereum	0.65
Leucadendron corymbosum	0.62
Leucadendron foedum	0.57
Leucadendron galpinii	0.69
Leucadendron lanigerum var. *lanigerum*	0.58
Leucadendron levisanus	0.66
Leucadendron stellare	0.56
Leucadendron thymifolium	0.70
Leucospermum arenarium	0.71
Leucospermum hypophyllocarpodendron subsp. *canaliculatum*	0.65
Leucospermum muirii	0.70
Leucospermum parile	0.77
Leucospermum rodolentum	0.63
Leucospermum tomentosum	0.79
Protea scolymocephala	0.51
Serruria adscendens var. *decipiens*	0.54
Serruria brownii	0.58
Serruria candicans	0.72
Serruria cyanoides	0.58
Serruria decipiens	0.60
Serruria decumbens	0.68
Serruria fucifolia	0.68
Serruria linearis	0.68
Serruria trilopha	0.61

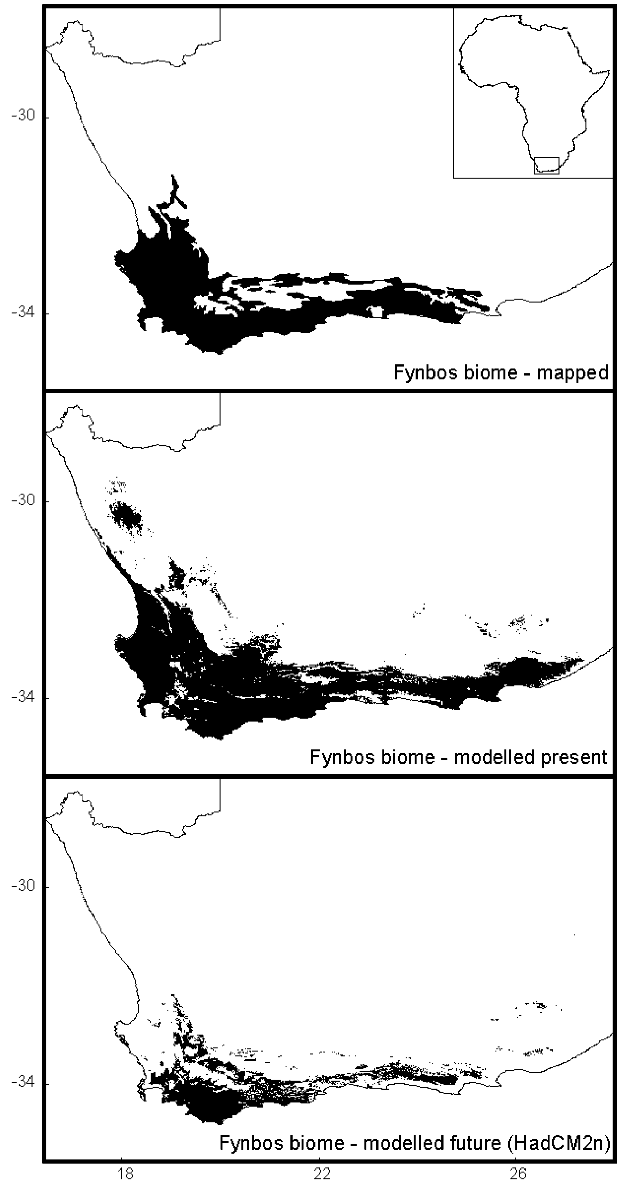
No attempt was made to refine species-specific models by variable selection, thus the models are termed “saturated” models. The GAM procedure used recorded presence/absence data from the Protea Atlas Database (Rebelo, 2001) for each of the species listed below as dependent variables, and physiologically significant substrate and bioclimatic variables (Schulze, 1997) as independent variables.

3. Results and discussion

3.1. Regional-level assessment

Biome-level modelling shows that the Fynbos Biome stands to lose significant areas near its northerly (equatorward) limits, especially in the coastal forelands and inland plains along the west coast (see Fig. 1) in response to projected climate change. The biome envelope suggests future contraction southwards onto the mountains of the Cape Fold Belt. Plains and slopes at lower altitudes along the west coast and northern borders of this mountain belt do not retain suitable bioclimates for vegetation of the Fynbos Biome. These areas are therefore of special conservation concern, as it is unlikely that their vegetation and habitats have experienced this extent and rapidity of warming and desiccation in the recent geological past.

The projected future temperature change represents a significant deviation from conditions in the CFR since the last glacial maximum (LGM), and probably since the inception of the Pleistocene. Modelled mean annual regional temperatures were on the order of 3.7 °C cooler during the LGM than today (Midgley and Roberts 2001; Midgley et al., 2001), and future projections suggest roughly 1.8 °C warmer mean annual regional temperatures, which is clearly a significant change within a very short time frame of 50 years. Future projected changes in precipitation regime are also without recent precedent.



Fynbos biome - mapped

Fynbos biome - modelled present

Fynbos biome - modelled future (HadCM2n)

Fig. 1. Current mapped Fynbos Biome (upper panel, after Rutherford and Westfall, 1994), and the modelled extent of the biome under current (middle panel) and future (~2050) climate conditions (lower panel), the latter based on climate change projections for the region generated by the GCM HadCM2.

Future predictions for the western Cape are for somewhat drier conditions, which will be exacerbated by higher air temperatures, together resulting in more intense plant water stress. This also is a change unprecedented in the past 20,000 years or more. In all likelihood, moisture availability during glacial conditions was significantly enhanced, due to more frequent and predictable arrival of frontal rainfall, which probably impinged on the west coast further north than is the case today, and resulted in more northerly distribution of currently mesic-associated groups such as the family Restionaceae (Shi et al., 1998), and proven greater prevalence of mesic forest elements north of the current northern limits of the CFR (Cowling et al., 1999b; Parkington et al., 2000). From the earlier, it is clear that the CFR faces significantly warmer and more arid conditions that may well be without precedent in the recent evolutionary history of many elements of the extant flora. As such, climate change could represent a significant threat to the persistence of these biota.

3.2. *Species-level assessment*

The 28 species modelled (Table 1) were selected from the area of projected biome loss, mainly low-altitude and coastal regions. They showed a diverse array of range change responses to the climate change scenario applied (see Table 3), and these provide some indication of risk due to climate change. Three major risks face species in a changing climate—range elimination, range reduction and range shift.

Range elimination: five of the 28 species (18%) are projected to have no suitable geographic range under the future scenario. These can be considered species most at risk of extinction under the given climate scenario, but cautious interpretation of this result is necessary. Modelled losses of range, even if they are derived from accurate knowledge of bioclimatic limits of species, may not represent immediate extinction. It is possible, for example, that established adults could persist in regions where climate has changed beyond their modelled limits because limits may be determined by the sensitivity of establishing seedlings. This effect would lead to a differential elimination of species dependent on seeds for post-fire regeneration (re-seeders), but allow plants which survive fire (resprouters) to persist. The resprouting habit is not evenly spread among the dominant genera in Fynbos (Le Maitre and Midgley, 1992)—this effect could therefore result in significant shifts in species composition and ecosystem function. The bioclimatic modelling approach fails to recognise this and other aspects of life history and population dynamics, which limits its ability to predict the detailed evolution of climate change effects in nature.

Range reductions: the projected climate change scenario reduces the modelled range sizes of 12 of the

28 species modelled (42% of the species, Table 3). Among these species the mean loss of range is 84% (median loss 90%), with the range of values falling between 27 and 99% of current range.

Although range losses predominate, a significant proportion (39%) of species show potential gains in range. This echoes the results of Warren et al. (2001) and Peterson et al. (2002) who have found that species display a range of responses to climate change, both positive and negative. Pimm (2001) has pointed out the difficulty this diversity of response poses for predictive modelling efforts.

Clearly, some species stand to gain from the climate change, but realisation of this theoretical new range depends on species dispersal capability, population size, fecundity and ability to penetrate new habitats. Experimentally derived information on seed dispersal distances, fecundity and establishment abilities are sorely lacking in indigenous Cape vegetation, and compromises the predictive power of this kind of modelling approach. Furthermore, the coarse soil fertility and texture classification we have used for this study may over-estimate the potential ability of species to occupy new ranges, and our range shift results could be seen as optimistic values.

Land transformation has a clear negative impact on potential range size (Table 3). Under current climate conditions, an average of 55% of potential range for the test species has been transformed, but perhaps surprisingly, this figure drops to only 27% under future climate conditions. This is the result of species ranges shifting to higher altitudes where land transformation is minimal (Fig. 2). These results do not account for future increases in land transformation, and are also subject to the modelling technique's assumptions discussed earlier.

Range shifts: twenty-three of the 28 species modelled showed range shifts (the remaining five species suffered range elimination). Thirteen of these 23 species had no geographic overlap between current and future projected ranges.

Table 3
Current modelled and future projected range sizes (total number of minute×minute squares with modeled probability of occurrence >0.5) with and without taking into account the impact of land transformation

Species	Modelled range size			
	Current		2050	
	Without transformation	With transformation	Without transformation	With transformation
Diastella buekii	12	4	3	3
Diastella parilis	15	9	0	0
Diastella proteoides	63	26	*114*	*53*
Leucadendron chamelaea	45	16	1	1
Leucadendron cinereum	154	55	*1317*	*538*
Leucadendron corymbosum	66	35	5	3
Leucadendron foedum	1	1	*83*	*73*
Leucadendron galpinii	218	112	1	1
Leucadendron lanigerum var. *lanigerum*	352	71	43	24
Leucadendron levisanus	17	3	*308*	*219*
Leucadendron stellare	103	11	*366*	*147*
Leucadendron thymifolium	15	0	*257*	*206*
Leucospermum arenarium	27	10	5	0
Leucospermum hypophyllocarpodendron subsp. *canaliculatum*	263	114	30	19
Leucospermum muirii	45	26	0	0
Leucospermum parile	81	39	1	1
Leucospermum rodolentum	1276	707	3	3
Leucospermum tomentosum	513	319	372	216
Protea scolymocephala	2	0	*35*	*24*
Serruria adscendens var. *decipiens*	9	8	*165*	*131*
Serruria brownii	1	0	0	0
Serruria candicans	22	22	9	9
Serruria cyanoides	0	0	2	2
Serruria decipiens	149	78	0	0
Serruria decumbens	0	0	*18*	*17*
Serruria fucifolia	744	377	21	19
Serruria linearis	28	15	0	0
Serruria trilopha	0	0	*108*	*102*

Italicised values for 2050 highlight range size gains.

The vector of potential species range shifts (derived by connecting centroids of the current and future species ranges) suggest a general south-eastward displacement in response to projected climate change, although some species show large eastward shifts (Fig. 3). The vector distances linking current and future population centroids range from 8 to 483 km (Table 4). These distances reflect the distance the main body of a population must traverse to be maintained.

A significant proportion of Fynbos species possess directed dispersal syndromes with short potential distances, such as myrmecochory (Le Maitre and Midgley, 1992). Many of the high-risk lowland species modelled here are ant-dispersed, and cannot be expected to maintain the pace of dispersal indicated by these centroid distances in a timeframe of decades. Interestingly, habitat loss due to existing land transformation does not significantly alter either the distance or direction of range displacement (Fig. 3, Table 4).

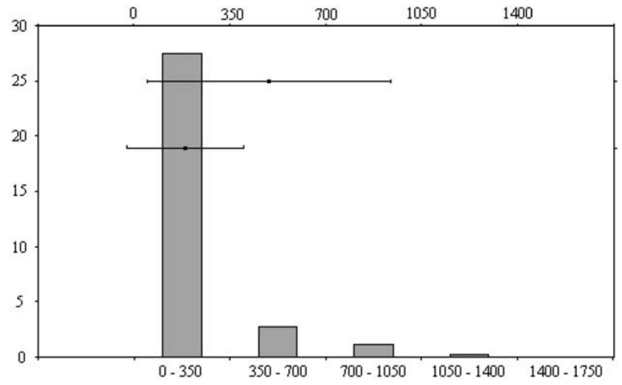


Fig. 2. The current altitudinal distribution of transformed land in the study region (Columns, lower *X*-axis), and the present and future (~2050) altitudinal distribution of the 28 species modelled in this study (Filled circles and error bars, Upper *X*-axis).

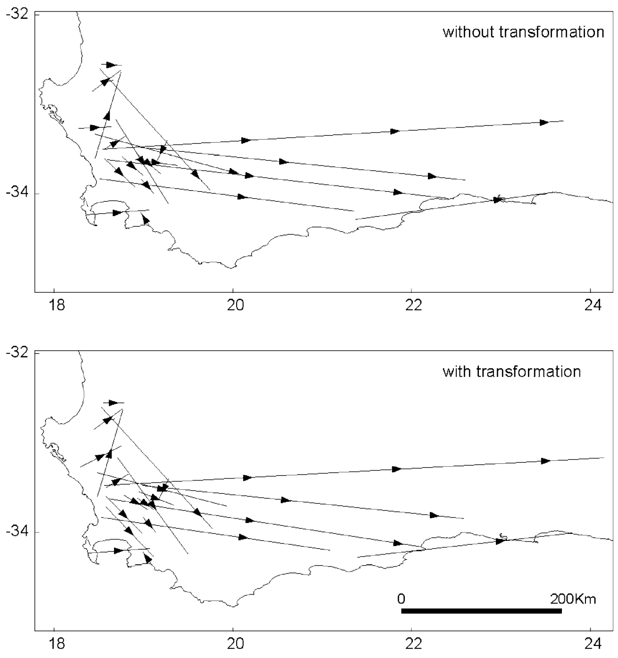


Fig. 3. Modelled range shifts in response to climate change, required for species to retain their optimum bioclimatic range. Arrows join the geographic centroids of the current and future (~2050) ranges of modelled species, without (upper panel) and with (lower panel) the effects of land transformation.

Distances between the edge of current distributions and the nearest edge of a future potential range (separation distances) provide a better assessment of the risk of species extinction than do the centroid–centroid distances (range shifts). Separation distances are significantly less than 25 km in most cases and are normally only marginally increased if land transformation is taken into account (Table 4).

Ten species show overlap between their current and future potential ranges, and can be considered least at risk under this climate scenario. However, this number drops to eight when land transformation is considered (Table 4), showing that habitat destruction increases the risk from climate change by accentuating the need for dispersal in a subset of species.

It is noteworthy that even among the species whose ranges are projected to expand, the majority are obligate range-shifters (no overlap between present and future ranges). These species must migrate across considerable distances to avoid extinction, despite the fact that their ranges are projected to increase. This indicates that range expansion is not a reliable index of range overlap or species' vulnerability to climate change. Land transformation is certain to be critical in determining potential landscape linkages for those species without range overlap, but this aspect requires analysis beyond the scope of this paper.

Taken together, and taking cognisance of the assumptions underlying the modelling techniques used here, the majority of the species modelled seem to be at risk of range size reduction and even extinction under the given climate change scenario. Five species have zero future potential range, six lose more than 90% of their range, and a further four are required to migrate more than 10 km between their current and future ranges. These 15 of the 28 species modelled (53%) appear to be at highest risk of extinction under this climate change scenario.

3.3. Implications for conservation planning in the region

These first phase results indicate several important conclusions for the region and several for conservation planning in other areas. At the regional scale, it is clear that west coast lowlands of the Fynbos biome are most vulnerable to climate change impacts. This region is home to a considerable biodiversity (Cowling, 1992), but is relatively poorly conserved (Cowling et al., 1999c; Younge, 2000). Considerable species range shifts forecast

Table 4
Shortest distance (km) between the species' present distributional range and potential future range (nearest edge to edge), with and without taking into account the impact of land transformation (E indicates species has no future range, i.e. it goes extinct under the climate change scenario, and 0 km indicates overlap between current and potential future range)

Species	Centroid-centroid (km)		Closest edge-edge (km)	
	Without transformation	With transformation	Without transformation	With transformation
Diastella buekii	22	22	15	15
Diastella parilis	E	E	E	E
Diastella proteoides	49	59	0	5
Leucadendron chamelaea	28	28	8	8
Leucadendron cinereum	154	142	0	0
Leucadendron corymbosum	36	40	0	0
Leucadendron foedum	40	40	0	0
Leucadendron galpinii	206	224	7	7
Leucadendron lanigerum var. *lanigerum*	33	31	0	0
Leucadendron levisanus	267	239	0	3
Leucadendron stellare	119	141	8	17
Leucadendron thymifolium	357	328	11	38
Leucospermum arenarium	190	190	157	157
Leucospermum hypophyllocarpodendron subsp. *canaliculatum*	483	523	2	6
Leucospermum muirii	E	E	E	E
Leucospermum parile	29	29	22	22
Leucospermum rodolentum	10	10	5	5
Leucospermum tomentosum	35	50	0	0
Protea scolymocephala	111	111	21	21
Serruria adscendens var. *decipiens*	19	17	0	0
Serruria brownii	E	E	E	E
Serruria candicans	340	340	0	0
Serruria cyanoides	7	7	0	0
Serruria decipiens	E	E	E	E
Serruria decumbens	65	63	2	2
Serruria fucifolia	22	22	2	2
Serruria linearis	E	E	E	E
Serruria trilopha	101	80	5	22

in this area suggest that sympathetic management from landowners will be important for maintaining corridors for dispersal of these biota. Detailed modelling of montane species is necessary to confirm that their level of risk is lower than for the mainly lowland species modelled here.

Spatial overlap between current and future ranges is present in a substantial portion of species, even in this high-risk group. Ten species showed overlap between present and future ranges, and eight of these ten maintained overlap even when land transformation was considered. Protected area planning can be directed at these areas with relatively straightforward adaptations of existing systematic protected areas planning tools (reserve selection algorithms).

Two counter-intuitive results emerged. First, range expansion was present in some species with substantial populations in the area projected to experience biome loss. This supports the principle that species, rather than communities, are the unit of response to climate change. Paleoecological studies have shown community dissociation and species individualistic range shifts in periods of past climate change (Huntley and Birks, 1983). Other assessments of the biotic impact of future climate change have shown similar species individualistic patterns (Bakkenes, 2002; Peterson et al., 2002).

Second, climate change had a greater impact on projected ranges than did current land transformation. The direction of range shifts upslope and the pattern of reduced upland land transformation combine to reduce the effect of habitat loss in future ranges. These results show the importance of species-level modelling and indicate that climate change may be critical to the medium- and long-term success of conservation efforts in the region. As land transformation and climate change are both accelerating, the combined impact of future transformation and climate change may be much larger than indicated here. A conservation window exists, in which near-term actions are much more likely to be feasible and cost-effective.

3.4. Implications for conservation strategies

This study presents unique insight into the relation between modelled biome changes and possible underlying species range shifts. Comparison of biome modelling and species modelling has seldom been attempted. Most studies focus either on global biome modelling (e.g. Prentice et al., 1992; Cramer et al., 2001) or on regional species modelling (e.g. Peterson et al., 2002) and seldom, on biome and species modelling at the same location and scale.

In the CFR, species range shift modelling results support the broad conclusions of biome modelling, but with species-specific characteristics important for conservation. Most species lose range from the area of modelled biome loss. The median range loss within the area of biome loss is 97.8%. Nearly half of the species modelled lose all of their range within the area of biome loss. Yet a substantial number of species expand their ranges within the area of biome loss. Six of 28 species (21%) gain range within the area of projected biome loss. Three of these species more than double their range. An additional three species expand their ranges outside the area of projected biome loss. The proportion of range expanders and species with total loss of range was about the same even in those species that are endemic or near-endemic ($>90\%$ of range) to the area of biome loss. Of the 14 endemic and near-endemic species, 21% showed range expansion, while 29% lost all range.

Thus, the area of biome loss indicates an area of wholesale range loss and re-arrangement, but it does not indicate direct climate-driven extinctions for many species. The implication for conservation strategies is that areas of modelled biome loss are priorities for species-level modelling, landscape analysis, and attempts to refine both regional climate predictions and modelling techniques. These are *not* indicated as conservation write-offs, even ignoring the model assumptions discussed above. Even those species (5 of 28) modelled to have no future range at all may persist for sometime in unfavourable climatic conditions or in micro-refuges.

Finer-scale modelling can reveal possible micro-refuge locations. For other species, coordinated creation of new protected areas and landscape linkages across the region will be key to allowing potential future range to be occupied (Hannah et al., 2002). Conservation strategies must expand protected areas efforts and encompass larger landscape conservation efforts. A new, more complex conservation paradigm is required.

Such strategies have been termed Climate Change–Integrated Conservation Strategies (CCS) (Hannah et al., 2002). A CCS begins with climatic and range shift modelling, which in turn informs four later stages. The five elements of a CCS are:

1. Regional Modelling;
2. Protected Areas Revision;
3. Matrix Management (creation of landscape linkages);
4. Regional Coordination of Conservation; and
5. Global Transfer of Resources.

Biome modelling may be a useful first-cut assessment in the regional modelling portion of a CCS. However, the results of this study show that species-level modelling is essential for detailed conservation planning. Range elimination, range contraction and range shifts are all possible climate change outcomes which must be considered both independently and in concert.

Protected areas planning and management must be expanded based on modelling results. These efforts can begin by focusing on areas in which present and future ranges overlap. The CFR modelling shows that even in areas projected for major bioclimatic changes (biome collapse) some species may still show range overlap. A general strategy is to use site selection algorithms to plan protected areas and conservation management in those areas where present and future ranges are projected to overlap. These sites will be adequate to meet minimum range (or population) requirements for some species. For other species, a combination of present range and potential future range will be required to meet conservation targets.

For the remaining species whose ranges do not overlap (the majority in this study), management of the matrix of land uses between protected areas is essential for persistence. Species-level modelling is a major asset in this planning process. Information on the direction and magnitude of range shifts can be used to design landscape connectivity of habitats useful to each target species. This can ultimately lead to a matrix of land uses between protected areas that allows complex multiple range shifts to occur.

Regional coordination of protected areas planning and matrix management efforts will be necessary across political divisions and administrative jurisdictions for such landscape-based approaches to be effective. In the Cape, this coordination is within sub-divisions within a single country. In other regions, coordination across international boundaries will be equally important.

International transfer of resources is necessary to underwrite the modelling and research efforts, additional protected areas, landscape conservation management and conservation coordination required in Climate Change–Integrated Conservation Strategies. Cooperation among international and national conservation groups has initiated this support for the initial stages of modelling in the CFR. Major new funding mechanisms are called for to extend this support to other CCS elements in the Cape and to developing CCS in other regions of the world.

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