Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot

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ABSTRACT

Aim To compare theoretical approaches towards estimating risks of plant species loss to anthropogenic climate change impacts in a biodiversity hotspot, and to develop a practical method to detect signs of climate change impacts on natural populations.

Location The Fynbos biome of South Africa, within the Cape Floristic Kingdom.

Methods Bioclimatic modelling was used to identify environmental limits for vegetation at both biome and species scale. For the biome as a whole, and for 330 species of the endemic family Proteaceae, tolerance limits were determined for five temperature and water availability-related parameters assumed critical for plant survival. Climate scenarios for 2050 generated by the general circulation models HadCM2 and CSM were interpolated for the region. Geographic Information Systems-based methods were used to map current and future modelled ranges of the biome and 330 selected species. In the biome-based approach, predictions of biome areal loss were overlayed with species richness data for the family Proteaceae to estimate extinction risk. In the species-based approach, predictions of range dislocation (no overlap between current range and future projected range) were used as an indicator of extinction risk. A method of identifying local populations imminently threatened by climate change-induced mortality is also described.

Results A loss of Fynbos biome area of between 51% and 65% is projected by 2050 (depending on the climate scenario used), and roughly 10% of the endemic Proteaceae have ranges restricted to the area lost. Species range projections suggest that a third could suffer complete range dislocation by 2050, and only 5% could retain more than two thirds of their range. Projected changes to individual species ranges could be sufficient to detect climate change impacts within ten years.

Main conclusions The biome-level approach appears to underestimate the risk of species diversity loss from climate change impacts in the Fynbos Biome because many narrow range endemics suffer range dislocation throughout the biome, and not only in areas identified as biome contractions. We suggest that targeted vulnerable species could be monitored both for early warning signs of climate change and as empirical tests of predictions.

Key words bioclimatic model, climate change, extinction risk, Fynbos, global change, HadCM2, Proteaceae, range displacement, South Africa.

INTRODUCTION

The early signs of human-induced climate change seem to be upon us (Hughes, 2000). Responses of biota include changes in physiology, productivity and growth (Cannel, 1998), and changes in species distribution and abundance due to migration and range shifts (Parmesan, 1996; Parmesan *et al.*, 1999). Within the field of conservation biology as a whole, and protected area management in particular, it is becoming increasingly urgent to develop predictions of how this significant change in the earth's environment will affect the abundance and distribution of species. These predictions need to be temporally and spatially explicit, to allow managers and designers of protected areas to plan for maximizing migration potential for the greatest number of species possible. Opportunistic selection of reserves is inefficient (Pressey *et al.*, 1993), and may be fatal for biodiversity conservation goals in the face of climate change. Spatially and temporally explicit predictions based on credible modelling can also guide the establishment of monitoring programmes to serve as early warning signs of the trajectory of climate change. Furthermore, explicit predictions will allow 'safe' limits of climate change to be defined (Schneider, 2001), and

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should soon become a component in guiding policy on carbon emissions.

Biodiversity is spatially highly variable (Myers *et al.*, 2000) and comprehensive spatial data are lacking for many species-rich areas of the world, so it is necessary to develop assessment techniques that can be applied in low-data situations. Bioclimatic modelling of biomes can serve as a first-cut estimate of risk of biodiversity loss even where species distribution data are poor. However, this approach involves many assumptions (Rutherford *et al.*, 1996), and it is not known whether this pragmatic approach over- or underestimates climate change risk to biodiversity, a situation that undermines its credibility and limits its application (Hannah *et al.*, 2002). It is desirable to apply both the broad biome modelling approach, and a more detailed species-level approach in the same region to assess this shortcoming.

The Cape Floristic Kingdom hotspot is particularly rich in plant species, has well-defined vegetation biomes (Rutherford & Westfall, 1994) and several excellent databases of plant species distributions (e.g. Rebelo, 1995). This provides the opportunity for a comparison of the biome and species-based methods for estimating risks of climate change for plant diversity. In this paper we describe results using both methods, and assess briefly their relative strengths and shortcomings. Finally, we describe a method to predict at a very fine (population) scale the effects of climate change, which may allow early detection of the rate and direction of climate change. This latter step is important in adding weight to climate change policy decisions, and in confirming the need for conservation bodies to take action.

METHODS

A bioclimatic modelling approach (e.g. Busby, 1991) is employed within a geographic information system (GIS) framework (Rutherford *et al.*, 1996) to derive an apparent climate envelope for the Fynbos biome as it exists under current climate conditions (Fig. 1). In essence, bioclimatic modelling determines the environmental limits of an entity with a given spatial distribution by matching its known distribution to climatic surfaces.

The spatial distribution of the Fynbos biome was digitized from the map presented in Rutherford & Westfall (1994). A climatic database at a spatial resolution of 1×1 min (approximately 1.5×1.8 km at this latitude) provided temperature and water availability data for the entire area of interest (Schulze, 1997). These data were interpolated from 1946 weather stations with a 44-year continuous daily rainfall and temperature record, distributed countrywide (Schulze, 1997).

Five relatively independent climatically derived parameters considered critical to plant physiological function and survival are employed as environmental determinants. These are mean minimum temperature of the coldest month (T_{min}), heat units (annual sum of daily temperatures (°C) exceeding
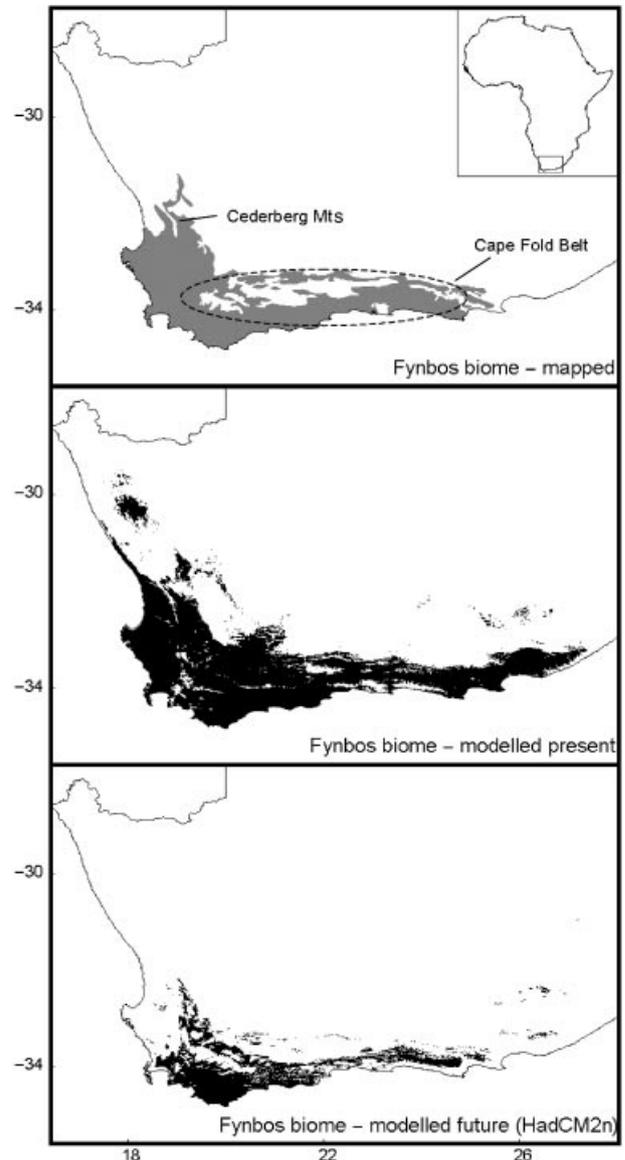
Fig. 1 Mapped Fynbos biome (*sensu* Rutherford & Westfall, 1994) and modelled Fynbos biome envelope, using limits of five parameters critical for plant growth and survival, at the present time and at ~2050 according to the climate scenario generated by HadCM2n. The approximate positions of the Cederberg mountain range and the mountains of the Cape Fold Belt are indicated.

18 °C [HU18]), annual potential evaporation (PE), winter soil moisture days (SMD_{win}) and summer soil moisture days (SMD_{sum}). Soil moisture days are calculated by a hydrological model (Schulze, 1997), and are defined as those days on which soil moisture is above a critical level for plant growth. All the above parameters are among those derived for South Africa by Schulze & Perks (1999).

While there is little experimental work to rely on locally, we consider these five environmental parameters as the minimum basic set for defining a bioclimatic envelope in South Africa's indigenous flora. T_{min} 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). PE 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 determine 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.

Two major drawbacks of the 'static' bioclimatic approach, apart from its inability to account for limitations of fecundity and dispersal, are that it ignores the limitation of species distribution by soil specificity and preference, and does not take account of the impact of rising atmospheric CO_2 on plant performance. All but the latter are likely to worsen the projected impacts of climate change on species distributions as predicted here, while the impacts of elevated CO_2 are likely to be neutral to modestly positive (Midgley *et al.*, 1995, 1999). In the case of species, climate envelopes are defined simply by the upper and lower limits of each of the five parameters, which is an approximation of the species' realized niche space or bioclimatic envelope (Cao, 1995; Rutherford *et al.*, 1995, 1996). In the case of the biome, limits were two standard deviations away from the mean value of each parameter where this value did not exceed the absolute upper or lower limit.

Predictions of future climate change were based on climate scenarios generated by the widely used general circulation models CSM and HadCM2, downscaled and interpolated for South Africa (Hewitson, 1999; Schulze & Perks, 1999). The HadCM2 model produced two scenarios by using different predictions of warming amelioration by sulphate emissions — HadCM2s (with sulphate amelioration) and HadCM2n (without sulphate amelioration). All models generated predictions of temperature and precipitation change for southern Africa for the mid-21st century (~2050), assuming an atmospheric CO_2 concentration of 550 p.p.m. Expected rates of change are not given by Schulze & Perks (1999) but, in general, more or less linear rates of temperature change are assumed for the next 50 years (Hulme, 1996). This assumption allows results for intermediate climate conditions to be interpolated between the endpoints (present and 2050). This interpolation was needed to predict which populations of the test species *Leucospermum tomentosum* (Proteaceae) would be subject to climate change-induced extinction within the next

decade. This species was selected as it is currently found within a region predicted to be lost to the Fynbos biome, and it suffers range dislocation under the HadCM2n climate scenario.

Species level data were supplied by the Protea Atlas Database (Rebelo, 1995). This database consists of georeferenced species presence and population size data for more than 210 000 sample records at more than 40 000 sample plots in the southern and western Cape of South Africa. For the purposes of this study, only species presence data were needed to construct the bioclimatic envelopes.

Results here are all expressed at the $1' \times 1'$ scale (a pixel resolution of ~300 ha), which is the minimum defined by the climatic data. This resolution allows individual species populations to be assessed for climate change risk and will facilitate field monitoring programmes to test predictions, but this application of the results is limited by the uncertainties inherent in both GCMs and spatial interpolation of the original baseline climate data.

RESULTS AND DISCUSSION

Application of the three climate models leads to similar predictions, namely that the Fynbos bioclimatic envelope contracts significantly by ~2050, resulting in a loss of biome area of 65% (HadCM2n), 51% (HadCM2s) and 58% (CSM). In order to simplify further analysis, we develop predictions only for HadCM2n (Fig. 1). As the most extreme prediction, this scenario should provide the most sensitive test of discrepancies between the two approaches used here to estimate risk of biodiversity loss.

Biome loss occurs over all altitudinal ranges, and is only less than 50% in a single altitudinal band, 1800–2100 m (Fig. 2a). Significant biome loss is noted at northern biome limits, with less than 10% retention of biome area north of 33°S (Fig. 2b). The high rate of biome loss in this topographically diverse region (mainly the northern coastal plain and the Cederberg Mountains) probably obscures the expected altitudinal dependence of biome loss. The strong latitudinal dependence of biome areal loss is in striking agreement with published studies of latitudinal range migrations in mobile organisms (Parmesan, 1996; Parmesan *et al.*, 1999; Hughes, 2000), and has important implications for reserve placement priorities, corridor establishment and genetic conservation and anticipatory rescue efforts. This result also suggests that monitoring for early warning signs of climate change should be focused on these northern limits.

The mean Proteaceae species richness at the quarter degree scale (QDS) shows a significant difference between areas retained within and areas lost to the Fynbos biome ($P < 0.001$, *t*-test). Areas retained have almost double the mean QDS richness value (39.3 ± 4.3 species, mean ± standard deviation) of those lost (21.7 ± 2.2 species) to the biome. This result seems to be a consequence of overall higher mean
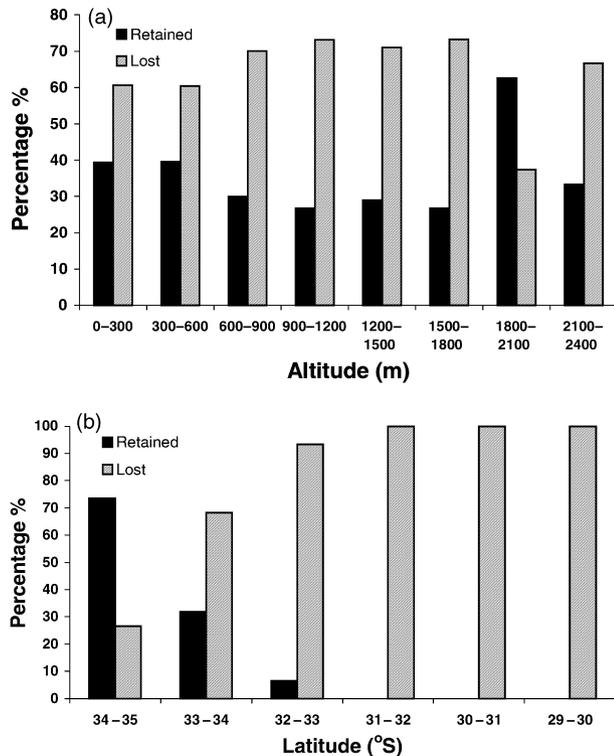
Fig. 2 Altitudinal (a) and latitudinal (b) distribution of proportions of the Fynbos biome either retained or lost after biome distributional shifts in response to climate change according to the HadCM2n scenario, by ~2050.

richness at more southerly latitudes, where biome retention is more prevalent. This result suggests (possibly optimistically, as we discuss below) that the impact of climate change may be reduced by the concentration of species in the southerly parts of the biome with high topographic diversity. The buffering potential of topographic diversity has long been noted as a key aspect of future reserve design efforts (Halpin, 1997), and has also been implicated in facilitating species persistence during glacial–interglacial climatic oscillations of the Pleistocene (Goldblatt, 1978; Midgley *et al.*, 2001).

A total of 29 species of the 330 endemic to the Fynbos biome have ranges completely within the area predicted to be lost from the Fynbos biome envelope. This approach therefore equates a ~50% loss of areal extent with a ~10% loss of individual species, a figure about half that (~20%) suggested for a temperate region from species:area relationships in the range of 1000–2000 km² (Rosenzweig, 1995). This result may be due to lower species richness in the area lost (lowland and generally more arid) than the area retained (cooler uplands, more topographically diverse).

What impacts are suggested by analysing climate change induced range shifts of all 330 endemic Proteaceae in the
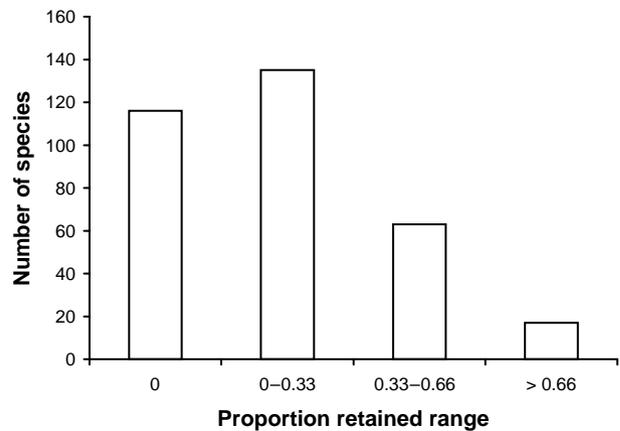
Fig. 3 Frequency histogram of the numbers of species suffering different levels of range displacement after distributional shifts in response to climate change according to the HadCM2n scenario, by ~2050.

Fynbos biome? When range dislocation (i.e. no overlap between current range and future predicted potential range) of individual species is quantified at this scale, a more pessimistic estimate emerges. Under the HadCM2n scenario, fully one-third of all species are predicted to suffer range dislocation (Fig. 3). Is it reasonable to equate range dislocation with the possibility of extinction? We believe so, for a number of reasons. It is highly likely that the rate of climate change will exceed the potential of populations to track climate change by migrating. This is not only because of dispersal limitations, but more especially because regeneration opportunities are limited to periods immediately postfire. These opportunities are therefore limited by fire interval, which is in the order of 12–25 years in Fynbos, giving between two and five opportunities for range shifts over the timespan of the scenario in question. It is possible that higher ambient temperatures will accelerate the fire cycle, but it is uncertain how this effect will be modified by the impact of changing precipitation and rising atmospheric CO_2 on fuel accumulation in Fynbos (Stock & Midgley, 1995), as productivity is probably constrained by soil nutrient availability (Stock & Allsopp, 1992). Dispersal potential is limited also by: (i) patchy fires (Cowling, 1987), which form barriers of unburnt vegetation to retard the dispersal of wind-dispersed 'tumbleseeds' in the Proteaceae (Bond, 1988); (ii) the fact that significant numbers of Proteaceae (especially the genus *Leucospermum*) are ant-dispersed (e.g. Slingsby & Bond, 1985) and therefore have extremely limited potential dispersal rates; and (iii) strong soil type affinities in several species (Richards *et al.*, 1995).

Beyond those species that suffer complete range dislocation, a further 40% of Proteaceae may experience a loss of up to one-third of their range (Fig. 3), suggesting enormous threats to the genetic diversity of remaining populations.

Overall, if dispersal to novel sites is discounted, the range size of Proteaceae will suffer drastic losses, with only 5% of this group retaining more than two thirds of their current ranges.

This analysis suggests therefore that the biome approach underestimates significantly the threats of both species loss and within-species genetic diversity loss with climate change. Applying simple species:area relationships to coarse scale predictions of biome areal loss leads to an optimistic assessment of threats to biodiversity, mainly because species with limited ranges within biomes must also be expected to suffer range dislocations at a finer scale, even though their future potential range falls within the broader biome envelope.

Modelling of a sample species, *L. tomentosum*, typical of lowland Proteaceae, shows that it is possible to identify species populations that should suffer mortality due to the predicted changes in individual climate parameters (Fig. 4). If spatially specific predictions of mortality can be made and ascribed to a particular cause, field monitoring strategies and
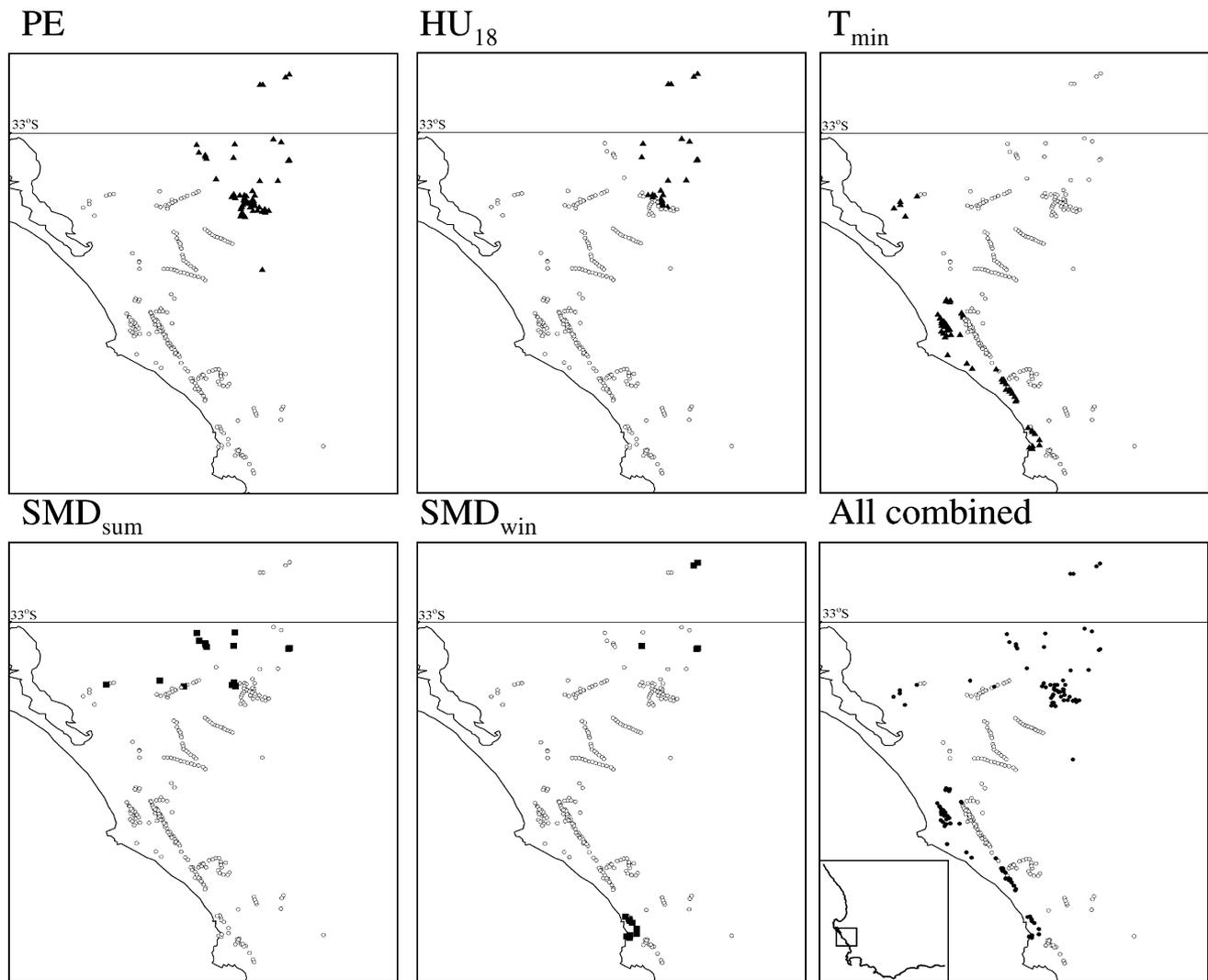
Fig. 4 Fine-scale modelling of all mapped populations of *Leucospermum tomentosum* (Proteaceae) identifying those predicted to fall either within (open circles), above (solid triangles) or below (solid squares) their modelled environmental limits after predicted climate change according to the HadCM2n scenario, by ~2010. Impacts of limiting factors have been disaggregated into five labelled panels: mean minimum temperature of the coldest month (T_{min}), heat units (annual sum of daily temperatures (°C) exceeding 18 °C [HU_{18}]), annual potential evaporation (PE), winter soil moisture days (SMD_{win}) and summer soil moisture days (SMD_{sum}). The combined effect of these limits on the mapped species distribution is represented in the panel labelled 'All combined'. The regional map inserted into this summary panel locates the area of the south-western Cape mapped in the panels.

protocols can be put in place to detect the early signs of climate change in plants. Such early signs of range displacement have been noted in animals (Parmesan, 1996; Pounds *et al.*, 1999; Warren *et al.*, 2001) but not yet in plants. Any monitoring programme should take careful note of particular stresses in particular regions — for example, mortality due to thermal and drought stress in the northern parts of this species' range are indicated by ~2010, while altered phenological patterns due to increasing minimum temperatures along the western seaboard seem more appropriate (Fig. 4). It would also be useful to establish detailed knowledge of the physiological and phenological behaviour of such a test species to hone sensitivity of detection methods. Xylem vulnerability to embolism, for example, would be a useful reference point for detecting evaporative and drought stress in the northern reaches of this species' range. Prediction followed by verification seems a powerful way to develop this important area of study.

CONCLUSIONS

Applying bioclimatic modelling techniques to predict the areal loss of the Fynbos biome under three future climate scenarios shows that the Fynbos bioclimatic envelope could contract significantly by ~2050, resulting in a loss of biome area of 65% (HadCM2n), 51% (HadCM2s), and 58% (CSM). The majority of this areal loss is predicted to occur in northerly (equatorward) latitudes, but is distributed more or less evenly with altitude. An analysis of potential plant species range dislocations biome-wide using the most extreme climate scenario yields even more disturbing results, suggesting the potential extinction of one third of the Fynbos-endemic Proteaceae, assuming that these species will not be able to disperse rapidly enough and establish in novel ranges. Only 5% of the Proteaceae species modelled are projected to retain more than two thirds of their current range. Coarse 'biome' level modelling may provide a quick and pragmatic route to assessing climate change impacts, especially where datasets are poor and no other option exists. However, when tested against a more detailed species-level approach in the Fynbos biome, the biome level approach significantly underestimated the potential loss of both species and within-species genetic diversity. Detailed species-level data are therefore essential for revising and fine-tuning biome-level predictions and designing effective response strategies. These could include methods to detect the early signs of climate change.

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