Potential vulnerability of Namaqualand plant diversity to anthropogenic climate change

G.F. Midgley[a,*], W. Thuiller[a,b]

[a]*Global Change research Group, Kirstenbosch Research Center, South African National Biodiversity Institute, P/Bag X7 Claremont 7735, Cape Town, South Africa*
[b]*Laboratoire d'Ecologie Alpine, UMR-CNRS 5553, Université Joseph Fourier, BP 53, 38041 Grenoble Cedex 9, France*

Abstract

We provide a position paper, using a brief literature review and some new modelling results for a subset of succulent plant species, which explores why Namaqualand plant diversity might be particularly vulnerable to anthropogenic climate change despite presumed species resilience under arid conditions, and therefore a globally important test-bed for adaptive conservation strategies. The Pleistocene climate-related evolutionary history of this region in particular may predispose Namaqualand (and Succulent Karoo) plant endemics to projected climate change impacts. Key Succulent Karoo plant lineages originated during cool Pleistocene times, and projected air temperatures under anthropogenic climate change are likely to exceed these significantly. Projected rainfall patterns are less certain, and projections of the future prevalence of coastal fog are lacking, but if either of these water inputs is reduced in concert with rising temperatures, this seems certain to threaten the persistence of, at least, narrow-endemic plant species. Simple modelling approaches show strong reduction in spatial extent of bioclimates typical of Namaqualand within the next five decades and that both generalist species with large geographic ranges, and narrow-range endemics may be susceptible to climate change induced loss of potential range. Persistence of endemics in micro-habitats that are buffered from extreme climate conditions cannot be discounted, though no attempts have been made to address this shortcoming of broader scale bioclimatic modelling. The few experimental data available on elevated temperature and drought tolerance suggest susceptibility of leaf succulent species, but high drought tolerance of non-succulent shrubs. Both species-level

*Corresponding author. Tel.: 27 21 7998707; fax: 27 21 7976903.
E-mail address: midgley@sanbi.org (G.F. Midgley).

monitoring and further experimental work is essential to test and refine projections of climate change impacts on species persistence, and the implications for conservation.

1. Introduction

Climate change represents a serious challenge to conservation, especially in species-rich regions of the world (Hannah et al., 2002). Biodiversity hotspots are acknowledged to face significant human threats, such as habitat fragmentation, land transformation, and many other significant human stresses at local and regional scales (Balmford, 1996). However, a changing climate will overlay and interact with all of these in ways that are difficult to predict, given uncertainties of the potential trajectory of climate change at the regional level, and a lack of scientific understanding of the potential biological responses (Lovejoy and Hannah, 2004).

The Succulent Karoo Biome, including the Namaqualand region, is now globally recognized as an example of a biodiversity hotspot under apparent imminent threat from climate change (Gitay et al., 2002). This region boasts an exceptionally rich flora (Milton et al., 1997), and is the world's only recognized desert biodiversity hotspot (Myers et al., 2000). Significant and diverse human threats to biodiversity exist and are not likely to reduce in intensity (Driver et al., 2003), while climate change will occur as a progressively intensifying stress, represented by increasing air temperature and potential changes in rainfall amounts and increasing rainfall variability (Houghton et al., 2001). Rising temperatures and rainfall changes will act independently to alter ambient drought and thermal stresses on living organisms, but also in combination to alter the timing and extent of soil water availability.

Planning to avoid or minimise human-induced threats to biodiversity in this region needs to take account of the potential trajectory of climate change, the uncertainties associated with this, and the impacts on the bioclimatic characteristics of this region and the resulting effects on its biota, as determined by their resilience under changing conditions. Climate change scenarios for the region remain uncertain, especially with regard to rainfall projections. The Namaqualand flora, comprising many hundreds of species, is also poorly understood in ecophysiological terms, which greatly limits a mechanistic understanding of potential impacts. In addition to improved ecophysiological knowledge, a far better understanding is needed of the population level responses of endemic species to climate variability and spatial micro-habitat structure, in order to assess population resilience and potential persistence under a changing climate regime (Thuiller et al., 2006).

Projections of climate change impacts and the development of conservation responses in this region are therefore limited by many knowledge and information gaps. Nonetheless, early work using a simple bioclimatic modelling approach, and driven by earlier generation climate models such as HadCM2 (Hadley Center, UK) suggested that the Succulent Karoo as a whole, and selected component species, were at substantial risk from bioclimatic shifts (warming and drying) by as early as 2050 (Rutherford et al., 2000). Indeed, the Succulent Karoo has been identified as the biome in southern Africa at greatest risk from climate change (Rutherford et al., 2000). It is therefore critical to begin to fill these knowledge gaps

and from this to make more informed estimates of the risk of biodiversity loss under future climate change scenarios.

It might be argued that the extreme climatic conditions of deserts implies a high degree of stress tolerance in their endemic species, but the aim of this position paper is to propose that many (but not all) elements of the Succulent Karoo flora typical of the Namaqualand region may be particularly susceptible to anthropogenic climate change. We elaborate through brief review and presentation of new results what can currently be inferred about the potential impacts of climate change on this region of the world, while identifying key knowledge gaps, and suggesting some research questions and approaches that might address these.

2. Paleoclimatic perspectives

We argue here that an understanding of the relationship between rates and spatial patterns of past climate change and the distribution of endemic and range restricted species is fundamental in assessing the vulnerability of Succulent Karoo plant diversity to future climate change. As has recently been shown, the current global distribution of species richness is well described by the relative amplitude of glacial-interglacial climate change (Jansson, 2003)—simply put, regions with high endemic species richness such as Namaqualand, especially of species with low dispersal ability and vagility, are likely not to have experienced substantial Pleistocene climate change. It is useful to explore how this insight applies to Namaqualand, and then to consider the extent to which anticipated future change may exceed conditions under which vegetation and biota have developed in evolutionary time.

It is not the purpose of this section to review the paleohistory of southern Africa, but rather to highlight what little we know of key events that have contributed to the unique biota of Namaqualand. The origin of arid conditions is surely one of these events, and there is some evidence to suggest a long history of aridity in this region, even dating to the Cretaceous (Goudie and Eckardt, 1999). Work more relevant to the evolution of the modern Namaqualand flora suggests that cooling and drying trends during the Pliocene were associated with the establishment of the cold Benguela current and its increasing impact along southern Africa's west coast (Tankard and Rogers, 1978), and this triggered dominant vegetation change from subtropical woodland to an increasingly grassy savanna and open woodland with greater representation of sclerophyll shrubs. This view has been elaborated and generally supported by the analysis of mammalian fossils and ratite eggshell remains (Segalen et al., 2004), showing two episodes of drying in this region during the Neogene, the first during the Middle Miocene when the Antarctic ice-cap came into being, and the second during the Lower Pliocene when aridity intensified with the growth of the Arctic Ice Cap and greater influence of the Benguela.

An often overlooked aspect of atmospheric change during the middle to late Tertiary is that of dropping atmospheric CO_2 levels. Low atmospheric CO_2 is known to reduce the water and nitrogen-use efficiency of plants (Drake et al., 1997), and would thus combine with more extreme local aridity in creating a synergistic set of stresses for vegetation. While aridity *per se* is thought to encourage species diversification (Richardson et al., 2001), low CO_2 levels would have amplified this stress (Bond and Midgley, 2000; Bond et al., 2003; Cowling, 1999) and constraints on stomatal and photosynthetic function would have intensified (Robinson, 1994a, b). Current understanding of the ecophysiology of karroid

Aizoaceae shows that these groups have flexible gas exchange patterns (Veste et al., 2001), allowing limited water loss under drought conditions (CAM photosynthesis, with night time stomatal opening), but under wet conditions, high carbon assimilation rates with day time stomatal opening (C_3 photosynthesis). CAM photosynthesis, like C4, uses PEP-carboxylase as a primary carboxylating enzyme (Keeley and Rundel, 2003), and it is under-appreciated that this will raise carbon fixation efficiency especially under low CO_2 levels.

Thus, CAM and flexible C_3-CAM switching in the Aizoaceae would have conferred an advantage under the increasingly arid and low atmospheric CO_2 levels that developed since the late Tertiary. Furthermore, one particularly species-rich lineage of the Aizoaceae (Rushioideae) developed an apparent adaptive modification of xylem cell structure, termed wide-band tracheids, associated with an explosive rate of species diversification (Klak et al., 2004). This apparent key adaptation has also evolved in the Cactaceae in the New World (Landrum, 2002), and though its function is unknown, it is thought to confer superior survival of drought conditions, suggesting that the increasing aridity facilitated the diversification of these groups (Klak et al., 2004; Landrum, 2001). There is much experimental work to be done to explore the ecophysiological function of these key characteristics in relation to drought intensity and atmospheric CO_2 level, both of which are likely to increase in future.

Global climate oscillated between glacial and interglacial states through the Pleistocene, but especially during the last 750 000 years (EPICA, 2004) relatively short interglacials of about 10 000–20 000 years duration interrupted longer glacial conditions of roughly 100 000 years duration (see also Petit et al., 1999). Atmospheric CO_2 periodically attained levels low enough to be near the limit of effective C_3 photosynthesis (Robinson, 1994b) during peak glacial conditions. At a global scale, glacial climates have been interpreted as relatively dry, due partly to diminished water holding capacity of the atmosphere. However, because of its location in relation to westerly rain-bearing anti-cyclonic weather systems that provide winter rains, much of the west coast of southern Africa and its adjacent interior probably experienced an increase in rainfall (concentrated in winter months) out of phase with much of the rest of the world (Tankard and Rogers, 1978). This view is supported by recent analyses of sea-bed cores, showing activation of river systems during glacials, and wind blown dust accumulation during inter-glacial times, in a pattern of glacial wetting and inter-glacial drying repeated for all winter-rainfall regions of the southern Hemisphere (Stuut and Hebbeln, 2006).

Reconstructions have been carried out of how these climatic changes might have caused bioclimates currently suitable for the Succulent Karoo Biome to shift spatially (Midgley et al., 2001). These show a substantial northward migration of these bioclimates, even with conservative assumptions of regional cooling and northward shifts of rain-bearing frontal systems under cooler glacial conditions. However, even under peak glacial conditions of the Last Glacial Maximum, the Succulent Karoo Biome retained an appreciable core range within Namaqualand, namely in the "Knersvlakte", and further north in the arid mountains of the northern Cape (Richtersveld) (Midgley et al., 2005).

It is difficult to verify these vegetation shifts in the absence of paleobiological evidence available for sites in the Succulent Karoo Biome, and especially little is known about how the core of this region, and especially Namaqualand, may have responded to Pleistocene changes. Pollen evidence suggests some expansion of Fynbos elements during glacial conditions in the northern Cape (Shi et al., 1998), though not as far north as Namibia

(Scott et al., 2004), and evidence for Asteraceous shrubs ranging as far north as the Brandberg in Namibia (Scott et al., 2004).

In the relative absence of paleobotanical information it is interesting to ask how endemic karroid species in Namaqualand might have responded to these extended colder and wetter periods other than through migration. Preliminary results from a reciprocal transplant experiment that used altitude as a substitute for temperature regime (Agenbag et al., 2004), showed that two succulent species of the Succulent Karoo were able to survive, and indeed performed better at sites roughly 500–700 m higher than their current distributional limit—a drop in temperature of 3–4 °C, and representative of the difference between current and glacial temperature regimes. Thus it is possible that succulent species could have persisted and even thrived under cooler glacial conditions, and may not have been displaced even under peak glacial conditions in the core range of the Succulent Karoo. Far more experimental work could be done to test these ideas more rigorously.

What is clear is that phylogenetic studies suggest that explosive species diversification occurred in the Succulent Karoo prior to and during Pleistocene times (Klak et al., 2004), indicating that cooler and potentially more moist conditions probably favoured the success of key lineages in this biome, or at least did not cause widespread extinctions. Phylogenetic studies that constrain the timing of diversification events are needed to provide further insights into the environmental drivers of species persistence and diversification, an approach that has been successfully pursued in the northern Hemisphere (e.g. Hewitt, 2000), resulting in substantial advances in understanding the origins of regional diversity.

From the above, it is clear that climate and atmospheric change may well have had a significant influence on speciation in the Succulent Karoo Biome from the late Tertiary. But in the absence of temporally constrained phylogenies it can be argued that events of either the late Tertiary or the Pleistocene were the dominant drivers of speciation of key lineages. The implications are critical for conservation biology under future anthropogenic climate change scenarios. The composition of the atmosphere is currently rapidly returning to early Tertiary-like conditions, with CO_2 levels expected to reach over 500 ppm at least, by the end of this century (Houghton et al., 2001). If Pleistocene glacial–interglacial conditions and oscillations generated diversification, it is likely that a return to pre-Miocene conditions will be far more significant for species extinctions than if diversification had originated during the Miocene itself.

3. Future climate scenarios and their potential impacts on plant diversity

The vegetation of the southern and western Cape has been well described and mapped at the landscape scale (e.g. Rutherford and Westfall, 1986), and several excellent databases of plant species distributions exist (Rutherford et al., 2003), allowing both biome and species-based methods for assessing impacts of climate change using bioclimatic modelling approaches (Guisan and Thuiller, 2005; Thuiller et al., 2005). The shortcomings of these methods are now well recognized (Pearson and Dawson, 2003). However, these serve as a useful first-cut assessment in the absence of alternative methods such as mechanistic modelling of plant functional types (PFT, e.g. Woodward and Kelly, 1997) using dynamic global vegetation models (DGVM, e.g. Prentice et al., 1992). This is especially true of the Succulent Karoo because succulent plant functional types have not yet been incorporated into mechanistic DGVM approaches. While it is commonly accepted that species of biomes and communities are not likely to respond in concert to anthropogenic climate

change (Woodward, 1992), studies in the adjacent Fynbos Biome have shown the utility of combining species- and biome-level assessments. These show that an assessment of the potential rate of change in biome-level bioclimatic conditions identifies vulnerable regions (Midgley et al., 2003), while species-based assessments provide more detailed vulnerability assessments (Midgley et al., 2002), and even allow the planning of adaptive strategies (Williams et al., 2005).

As mentioned above, early work on climate change impacts for the Succulent Karoo have been carried out (Rutherford et al., 2000) using climate scenarios from a previous generation of climate models, but not published in the peer-reviewed literature. We take the opportunity of this Special Issue to present some of these unpublished data using an older generation of climate scenarios, and in addition, to apply more modern techniques and an updated climate scenario. We therefore briefly describe here an updated modelling approach for the projected shifts in bioclimatic zones currently associated with the Succulent Karoo Biome, using niche-based methods implemented in the BIOMOD framework described in Thuiller (2003). Biome spatial distribution was digitised from Rutherford and Westfall (1986). A climatic database at a spatial resolution of 25×25 km provided climatically derived parameters employed as environmental determinants; annual and winter potential evapotranspiration, annual, winter and summer precipitation, annual and winter temperature (Schulze, 1997). Anthropogenic climate change was simulated by the general circulation model HadCM3 (Hulme et al., 1999), as driven by the IPCC A2 scenario for societal change (Nakicenovic and Swart, 2000), representing a socio-economically heterogenous world with unequal but generally slow economic growth, and continuous population and CO_2 emission growth. Projections were carried out for 2050 and 2080 time-frames.

Modelling results suggest significant reductions in surface area suitable for persistence of the Succulent Karoo Biome (Fig. 1), with a loss of ~40% of its current bioclimatically suitable range by 2050, increasing to ~65% loss by 2080. By 2050, the Succulent Karoo Biome is projected to be substantially reduced in extent on its eastern border along a south-north gradient. By 2080, the reduction in optimal bioclimatic habitat is projected to
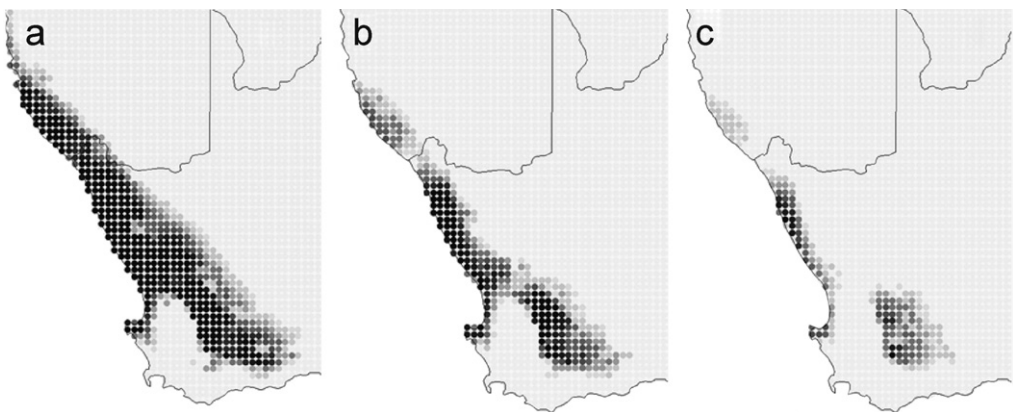

Fig. 1. Modelled habitat suitability for the Succulent Karoo Biome in southern Africa under current conditions (a), under future conditions by 2050 (b), and under future conditions by 2080 (c), according to the general circulation model HadCM3, using the BIOMOD approach of Thuiller (2004). Darker shading indicates high probability of occurrence.

be far more severe, with widespread reduction of bioclimatic suitability in many parts of the Succulent Karoo, and in particular in the central, Namaqualand region, of this biome. Under this scenario, models therefore project a division of the optimal Succulent Karoo bioclimatic distribution into two distinct ranges (excluding some marginally suitable habitat in southern Namibia), one situated in the Tanqua Karoo and eastward between the Cape Fold Mountains of the Cape Floristic Region, and another comprising a strip along the Atlantic coast. These projections are therefore less pessimistic than those originally suggested by Rutherford et al. (2000) which suggested a roughly 90% loss of bioclimatically suitable range by 2030 and up to 100% loss of suitable range by 2050 under older generation HadCM2 projections, but used less defensible modelling methods.

To model potential range shifts of individual endemic species we used a Generalised Additive Modelling (GAM) approach (Guisan et al., 2002; Guisan and Thuiller 2005). Anthropogenic climate change projections were mapped at $1' \times 1'$ grid scale (Perks et al., 2000), according to the general circulation model HadCM2, which projects temperature increases of between 1.3 and 2.5 °C for the southern Cape, and potential reductions of up to 25% in winter rainfall by 2050 (Hulme et al., 2001; Perks et al., 2000). Species distribution data were obtained from the Acocks Database (Rutherford et al., 2003) from which we selected 20 endemic leaf succulent species (Mesembryanthemaceae) with sufficient numbers of presence records to allow the development of models. We included soil fertility and soil texture (sand, silt, clay fraction) data sets (Schulze, 1997) as independent factors to account for species soil preferences. The predictive accuracy of each model for current range simulation was assessed using the area under the curve (AUC) of a received operating characteristic (ROC) plot of sensitivity against (1-specificity) (Table 1, Swets, 1988). Sensitivity is defined as the proportion of true positives correctly predicted, whereas specificity is the proportion of true negatives correctly predicted. A guide to the accuracy of the model is: 0.90–1.00 = excellent; 0.80–0.90 = good; 0.70–0.80 = fair; 0.60–0.70 = poor; 0.50–0.60 = fail (Swets, 1988). We transformed the probability of occurrence derived from the GAM to presence/absence using a probability threshold maximising the percentage of presence and absence correctly predicted (Pearce and Ferrier, 2000).

Because of the limitations of minimum record numbers for acceptable species bioclimatic models, results for Succulent Karoo species are derived from endemics with generally large distributions, and do not represent the Namaqualand region alone. Thus, in relation to earlier species-level work reported for the Fynbos Biome, the mean range size of endemic Succulent Karoo species modelled is almost 30 times that of the endemic Proteaceae modelled in studies of the Fynbos Biome (Midgley et al., 2003). Three of the endemic Succulent Karoo species showed range increases, but no extinctions were predicted, and only two species were predicted to lose more than 80% of their range. The median range loss (8 of 20) is between 60% and 80% by 2050. Thus the larger range sizes of endemic Mesembryanthemaceae modelled appears to reduce the predicted range losses relative to Proteaceae (Midgley et al., 2003; Thomas et al., 2004), but suggest significant range size reductions nonetheless.

Illustrative spatial shifts for two species show one which experiences marginal range loss, and another which experiences significant range loss (Fig. 2). Southward migration and range fragmentation is evident in both species. Spatial shifts predicted for *Ruschia caroli* are likely representative of regional endemics with intermediate to large range sizes, with significant range contraction in the northern region of Namaqualand, and potential

Table 1

Current and future (∼2050 time frame) projected range sizes (in terms of $1' \times 1'$ grid squares) of 20 endemic karoo succulent species, relative change in range, and Area Under the Curve (AUC) statistic to judge model performance

Species name	Range size (number of $1' \times 1'$ grid squares)			AUC
	Current	Future	Change (%)	
Stoeberia frutescens	11647	105636	Gain	0.995
Apatesia sabulosa	115892	163000	Gain	0.830
Ruschia muricata	45134	58699	Gain	0.959
Ruschia robusta	51033	48097	5.8	0.967
Carpobrotus acinaciformis	5031	4358	13.4	0.979
Stoeberia utilis	20300	15859	21.9	0.987
Delosperma subincanum	60689	40623	33.1	0.906
Ruschia cymosa	37403	21699	42.0	0.962
Drosanthemum framesii	49843	26112	47.6	0.955
Prenia pallens	32767	14502	55.7	0.958
Ruschia multiflora	26190	9617	63.3	0.976
Psilocaulon junceum	59648	21730	63.6	0.931
Mesembryanthemum annuum	51452	17116	66.7	0.950
Ruschia caroli	14172	4435	68.7	0.981
Sceletium rigidum	50344	15080	70.0	0.896
Brownanthus ciliatus	53853	13595	74.8	0.937
Cleretum papulosum	29651	6512	78.0	0.963
Mesembryanthemum clandestinum	37978	7803	79.5	0.930
Antimima dasyphylla	20151	3959	80.35	0.966
Ruschia grisea	52090	5585	89.28	0.867

Range changes modelled for projected changes in climate according to the general circulation model HadCM2 simulating the A2 greenhouse gas emission scenario.

colonisation of novel range in the southern Cape. Results for *Ruschia robusta*, by contrast, indicate the higher resilience to climate change impacts conferred by a geographic range that spans both winter and summer rainfall regions, suggesting a far wider bioclimatic niche that facilitates the retention of a significant part of its range by 2050, and substantial potential for range expansion.

Migration of Succulent Karoo endemics therefore seems important for their persistence under climate change. The dispersal of Mesembryanthemaceae is thought to be highly limited because seeds are shed from persistent capsules during rainfall events, and are passively transported, and there appears to be a high degree of anti-telechory in desert species in general (van Rheede van Oudtshoorn and van Rooyen, 1999). However, it has been suggested that small seeds could be transported by wind to achieve significant long distance dispersal (Midgley et al., 2001)—a lack of understanding of dispersal and establishment potential in new habitats strongly constrains the estimation of extinction risk for endemic species in the Namaqualand region and the Succulent Karoo in general.

Early work on the iconic tree-succulent *Aloe dichotoma* supports this view, as populations of this species appear to be experiencing elevated rates of adult mortality, at least, in northern regions of its geographic range, while southerly populations are showing active recruitment suggestive of a southerly shift in optimum growing conditions for this species (Foden et al., in press), consistent with climate change trends and
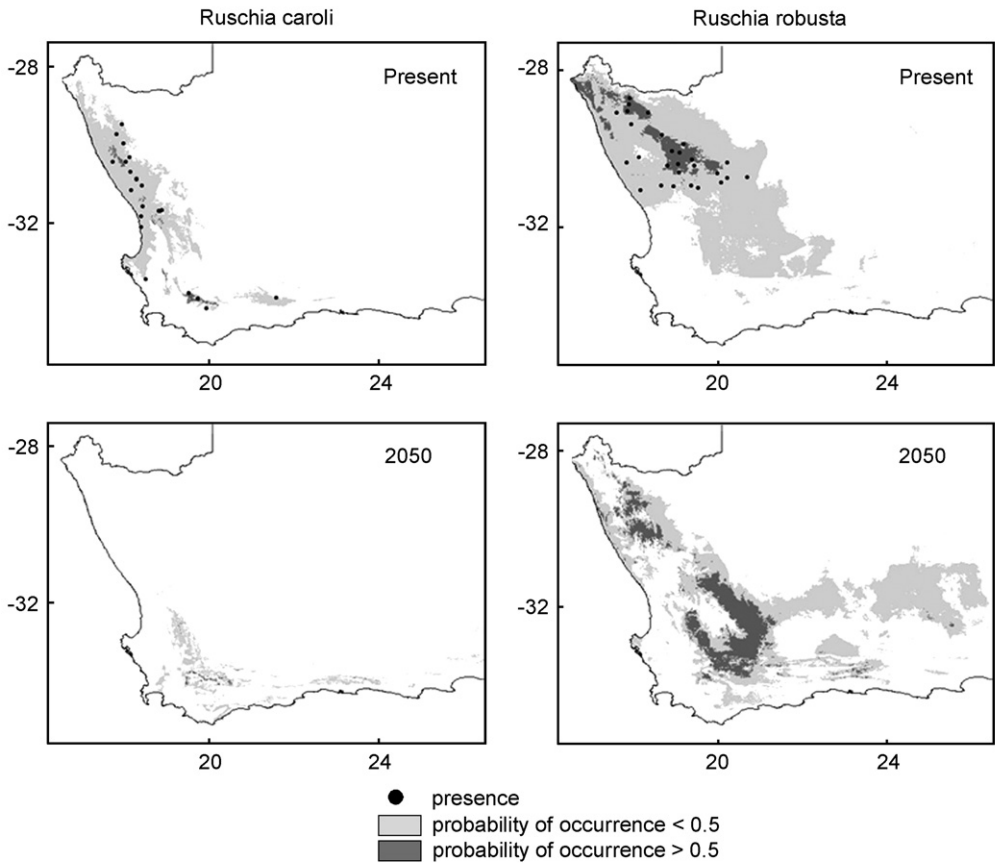
Fig. 2. Modelled habitat suitability for two endemic Succulent Karoo species under current conditions (present), and under future conditions (by 2050, according to HadCM2 projections). *Ruschia caroli* is a Succulent Karoo endemic, while *R. robusta* ranges across the 50% winter rainfall isohyet, into summer rainfall Nama-Karoo. The dots represent data for current positive (presence) distribution records. Shading indicates suitable bioclimatic habitat for the species, and darker blue shading indicates bioclimatically optimal habitat (probability of occurrence >0.9). Reproduced in grey scale with permission from Lovejoy and Hannah (2004).

projections. However, there is as yet little evidence of a southerly migration and range extension through the natural establishment of new populations, even though observations suggest that small populations rescued from sites zoned for development, and transplanted into regions far south of its current range are able to recruit without intervention (Ian Oliver *pers. obs.*).

It is also important to point out that many succulent endemics may persist in sub-habitats such as shaded crevices and south-facing slopes that are less susceptible to climate change impacts than suggested by the "mean" conditions at the $1' \times 1'$ scale. This dependence on micro-site conditions is especially problematic for coarse scale modelling (Pearson and Dawson, 2003) in species such as this that are often of small stature and associated with specific parts of the landscape. For this reason, it is important to test the

predictions of species persistence by employing field-based experiments to manipulate water and temperature conditions in situ to simulate those expected under various scenarios of climate change (e.g. Musil et al., 2004). Such experiments need to estimate both lethal levels of change for established individuals, in addition to impacts on acclimation, selection of tolerant individuals and demographic processes before unambiguous projections of extinction risk can be made.

At this time, preliminary experimental results for dwarf succulents suggests that they may currently grow close to their thermal tolerance limits (Musil et al., 2004), raising concerns about even relatively mild projections of future warming. In another manipulative study (Midgley and van der Heyden, 1999), the effects of rain exclusion on succulent and non-succulent growth forms were investigated and demonstrated greater susceptibility to drought induced mortality in succulents than in non-succulents.

It is also interesting to note that the Namaqualand annuals *Dimorphotheca pluvialis* and *Dimorphotheca sinuata* show some resilience of both growth and reproductive output under elevated UV-b levels, and little impact on these performance measures by elevated CO_2 levels (Wand et al., 1996), although there is some evidence to suggest a gradual accumulation of genetic damage under these conditions (Midgley et al., 1998; Musil, 1996; Musil et al., 1999). Therefore, although succulent species may be susceptible to climate change impacts, it is very likely that other plant growth forms will be more resilient, and may at least persist or even thrive under changing conditions.

4. Conservation responses

Up till now, regional climate predictions have been considered too uncertain to develop detailed conservation plans that allow resilience to climate change. Significant uncertainties associated with regional predictions of future climate trends unfortunately remain, and this constrains spatially explicit projections of the optimal geographic ranges of species (Thuiller, 2004) and the estimation of species and population vulnerability to a changing climate. Adaptive conservation strategies proposed up till now to facilitate resilience to climate change are therefore general—such as conserving topographic diversity within a protected areas network (Hannah et al., 2002), or conserving processes to ensure future evolutionary potential (Driver et al., 2003). Until a clearer indication is obtained of likely regional climate change and also the rate and extent of species responses, more precise and concrete plans to facilitate species persistence will remain elusive.

Nonetheless, at this stage monitoring and early warning systems could be designed to reduce several uncertainties, most importantly by selecting target species (e.g. Burke, 2004) in a wide range of sites that are most likely to show early responses. Species range and population-level monitoring should also be combined with modelling approaches to test the reliability of projections, and maximise the chance of improving their predictive power. If widespread species range shifts are the likely dominant species response to future climate change (e.g. Schroter et al., 2005), these skills will be critical in developing spatially explicit projections to estimate the rate and direction of species movements required to ensure retention of sufficient range, either in protected areas or in unprotected areas suitable for their persistence (Araújo et al., 2004; Rodrigues et al., 2004; Williams et al., 2005), and indeed the need for human intervention in maximising the chance that these range shifts can be realized.

All in all, conservationists cannot take the view that more detailed planning of conservation responses needs to wait for greater certainty in regional climate prediction, especially in the Namaqualand region—tools and contingencies can be developed now, and even tested (for e.g., species translocation studies, *ex situ* propagation, or even tests of seed longevity in storage) in anticipation of improved regional climate forecasts and projections of their impacts on species and ecosystems. Given that modelling approaches suggest that this region may be impacted relatively early by climate change, the Succulent Karoo in general and Namaqualand region in particular could serve as a globally important test case for developing and testing effective climate-integrated conservation strategies (sensu Hannah et al., 2002).

Acknowledgements

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