

# Potential responses of terrestrial biodiversity in Southern Africa to anthropogenic climate change

Guy F. Midgley · Wilfried Thuiller

Accepted: 12 November 2010  
© Springer-Verlag 2010

**Abstract** Key studies supported by species-level data collection have provided early indications of the potential implications of unmitigated change for the ecosystems and biodiversity of southern Africa. These suggest a significant threat to biodiversity, both from changing bioclimatic suitability and changing atmospheric CO<sub>2</sub> level that seems to affect the competitive balance between woody and herbaceous plants in the dominant savanna biome of this region. Modeling efforts suggest significant implications of unmitigated climate change for this region, but assumptions underpinning methods such as bioclimatic modeling must be recognized, some of which might lead to over estimates of the rate and extent of the potential impacts. General trends and level of coincidence between various types of studies do support a high degree of concern for a substantial portion of southern African biodiversity under unmitigated climate-change scenarios. The most significant changes in ecosystem structure (both increases and decreases in woody plant cover), and associated faunal diversity changes, are projected in the dominant savanna vegetation type in this region, while the most significant biodiversity loss is projected for the winter rainfall region. Follow-up work to detect early signs of climate change identify regions of high- and low-potential impacts, and

experimental work to test some important hypotheses relating to the future evolution of climate-change impacts across the region are very few and urgently required.

**Keywords** Bioclimatic modeling · Conservation · Extinction risk · Fynbos · Savanna · Succulent karoo

## Introduction

Southern Africa is home to an appreciable portion of global biodiversity (Cowling et al. 1996; Myers et al. 2000), and many of its ecosystems retain relatively intact species assemblages across all trophic levels (Scholes and Biggs 2005). The region possesses an established network of protected areas that contribute both to conservation targets and to nature-based tourism (Brooks et al. 2001; Rodrigues et al. 2004). However, rising pressures on biodiversity are resulting from local and regional development pathways and direct extractive resource use (Scholes and Biggs 2004). It is now increasingly appreciated that anthropogenic climate changes are likely to progressively cause impacts on Africa and its biodiversity and that these will generally be negative from both ecological and economic perspectives (IPCC 2007a).

Southern Africa's natural biomes (Rutherford 1999) are overwhelmingly dominated by C<sub>4</sub> grasslands with varying cover of woody elements (Bond et al. 2005), either shrubs (in the case of the Nama-Karoo Biome) or trees, which include evergreen or drought-deciduous fine-leaved and broad-leaved forms, in Savanna and Forest Biomes. The natural geographic distribution of these biomes and local-to-regional dominance of dominant plant growth forms is determined largely by interactions between climate and disturbance regime. Below ~10°S latitude, maximum

---

G. F. Midgley (✉)  
Climate Change and BioAdaptation Division,  
South African National Biodiversity Institute,  
Claremont 7735, P/Bag X7, Cape Town, South Africa  
e-mail: Midgley@sanbi.org.za

W. Thuiller  
Laboratoire d'Ecologie Alpine, UMR-CNRS 5553,  
Université Joseph Fourier, Grenoble, France

woody plant cover, for example, is strongly rainfall controlled below  $\sim 500$  mm mean annual rainfall (MAR), somewhat affected by disturbance regime within MAR limits of  $650 \pm 134$  mm MAR and strongly disturbance determined above  $\sim 800$  mm (MAR) (Fig. 1, from Sankaran et al. 2005). Projecting climate change impacts in this region therefore requires an understanding of climate-disturbance interactions and their implications for assemblages of species (such as mammal browsers or grazers) that may be dependent on both climate and vegetation structure (habitat).

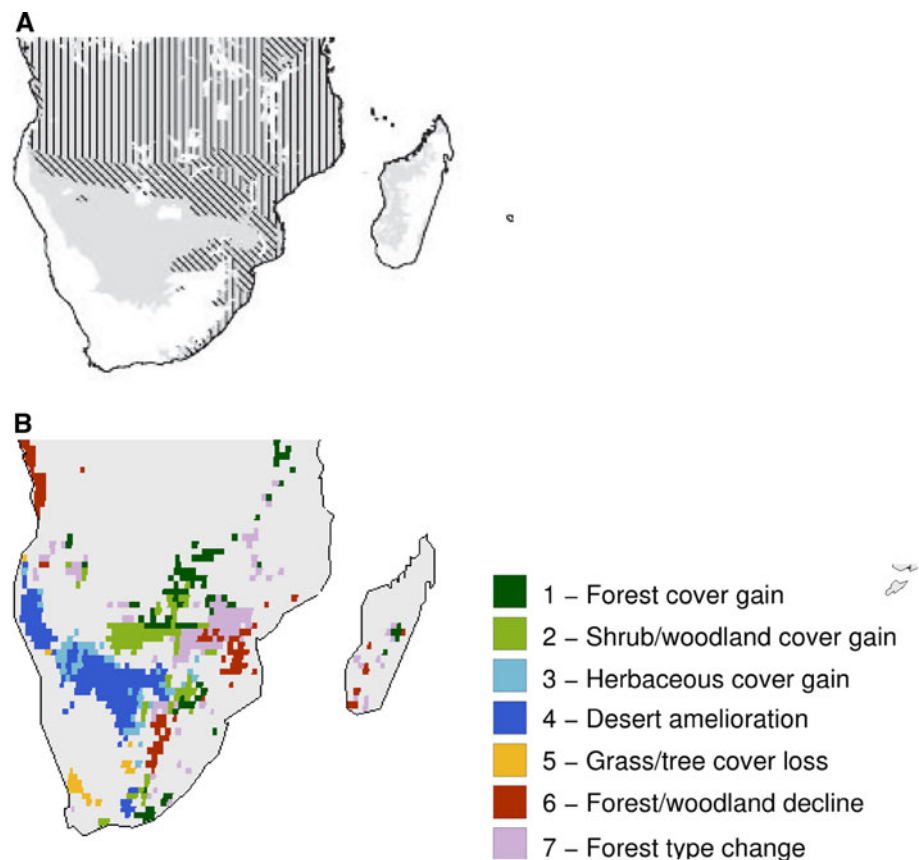
Global change pressures (land use, atmospheric composition  $\text{CO}_2$ , nitrogen deposition, climate, and biotic exchange) were summarized by Sala et al. (2000) and have been generally confirmed for Africa (Scholes and Biggs 2004; Hassan et al. 2005). Among leading pressures identified internationally, recent analyzes for southern Africa confirm an increasing prevalence of invasive species, primarily plants (Richardson et al. 2000), which poses challenges to conservation efforts in certain regions. By contrast, the pervasive stress of nitrogen pollution common in the northern Hemisphere (Sala et al. 2000) is not a significant current threat in the region. Climate change is increasingly viewed as a significant threat to African biodiversity (e.g., Meadows 2006), particularly to

endemic species (Hannah et al. 2005; Malcolm et al. 2006).

Early signs of anthropogenic climate change are emerging in southern Africa, especially in temperature records (Pollack et al. 1998; Hulme et al. 2001; Schulze 2005), but unlike the northern Hemisphere, very little information exists on observed responses of organisms, species, and ecosystems to climate-change trends. Such detection may be difficult to achieve, as biologic activity in this region is controlled mainly by water availability (Hawkins et al. 2003; Nemani et al. 2003), not minimum temperature as is the case in Northern Hemisphere latitudes where copious evidence reveals these emerging responses to recent climate change (IPCC 2007a). Water availability is a far more stochastic driver of ecological response and less amenable to analyzes of long-term trends and therefore less accessible to biologic impacts and their attribution (e.g., Root et al. 2005).

Furthermore, fire regime is an important determinant of ecosystem structure and function in this region (Bond and Van Wilgen 1996; Bond et al. 2003b; Bond and Keeley 2005), introducing further stochasticity and tightly linked species population-level responses. The region is also characterized by climate variability on a range of temporal scales (Tyson and Preston-Whyte 2000), driven most

**Fig. 1 a** Geographic distributions of mean annual rainfall-controlled ('stable') and disturbance-controlled ('unstable') savannas in southern Africa. Vertical hatching = 'unstable' savannas ( $>784$  mm MAR); cross-hatching = transition between 'stable' and 'unstable' savannas (516–784 mm MAR); gray shading = 'stable' savannas ( $<516$  mm MAR) (from Sankaran et al. 2005). **b** Projected "appreciable changes" in terrestrial ecosystem vegetation structure by 2100 relative to 2000 as simulated by Dynamic Global Vegetation Model LPJ (Sitch et al. 2003) for the IPCC SRES A2 emission scenarios (HadCM3-projected climate) (Lucht et al. 2006; Schaphoff et al. 2006). "Appreciable changes" exceed a structural change over at least 20% of the area of a simulated grid cell (adapted from IPCC 2007a)



notably by ENSO forcing (Diaz et al. 2001; Glantz 2001). All of these characteristics are likely to obscure clear and unambiguous detection of systematic species responses to climate trends. Nonetheless, since the late 1970s, significant drying and warming trends have been noted in the southern African subregion (Hulme 1996; Hulme et al. 2001) and strong contemporaneous warming trends have been noted in south western and central regions of South Africa (Warburton et al. 2005).

Several recent analyses suggest that projected climatic and atmospheric change may induce significant spatial shifts in optimal bioclimatic conditions for southern African species (Rutherford et al. 2000; Erasmus et al. 2002; Thuiller et al. 2006a) and may alter controls on ecosystem structure and function (Bond and Midgley 2000; Hulme et al. 2001; Bond et al. 2003a; Woodward and Lomas 2004; Thuiller et al. 2006c). Recent work in this field has been underpinned by increasing availability of geospatial data and a growing understanding of the driving forces behind ecosystem function (Bond et al. 2003b; Woodward and Lomas 2004; Bond and Keeley 2005). However, significant uncertainties remain at many levels, including those relating to climate projections, and species, habitat, and ecosystem responses (Midgley and Thuiller 2005; Neilson et al. 2005). This paper briefly reviews recent projections of climate-change impacts on southern African ecosystems and biodiversity at three main organizational levels—biome and ecosystem level, individual species geographic range, and species physiologic response.

### Climate-change projections for southern Africa

Rainfall gradients across much of southern Africa are thought to be strongly influenced by sea surface temperature (SST) contrasts between the southern Atlantic and Indian Oceans and their interaction with the near-meridional position of the inter-tropical convergence zone (Stokes et al. 1997). While West African and Sahelian rainfall fluctuations may be of long duration, those in southern Africa vary on a relatively short-time scale of between 2 and 5 years, broadly congruent with fluctuations in ENSO (Tyson and Gatebe 2001) and SST variability (Nicholson 2001). Rainfall in the region has shown few systematic trends during the twentieth century as a whole (Tyson and Gatebe 2001), though the 1950s were generally wetter, and rainfall has decreased consistently every decade since (Nicholson 2001), with some evidence for an increase in extreme rainfall events (Mason 1996). Drought extremes in Africa during the latter twentieth century are not unprecedented in the past two centuries (Nicholson 2001). Analyses of temperature trends for South Africa clearly show regions of consistent and significant warming during

the last two decades of the twentieth century (Warburton et al. 2005).

A compilation of seven GCM rainfall projections for the twenty-first century suggests a general summer drying trend ( $\sim 10\text{--}30\%$  by 2080) in parts of southern Africa, and some rainfall increases in eastern tropical latitudes, under high fossil fuel emission scenarios, but there is a wide range of inter-model variability (Hulme et al. 2001).

More recent projections summarized for the Intergovernmental Panel on Climate Change fourth assessment report (IPCC AR4) show a lack of agreement on the sign of rainfall change over much of southern Africa (IPCC 2007b). Downscaling using both statistical and dynamical methods reveals an emerging consensus for annual rainfall changes of 10% or less, slightly increased in MAR for some of the summer rainfall regions of southern Africa toward the end of this century, but decreased rainfall in the winter rainfall zone of the southern Cape, and western summer rainfall areas (Hewitson and Crane 2006; Engelbrecht et al. 2009). The few studies available under-sample the full range of IPCC AR4 scenarios. Overall water balance changes have been projected to reduce perennial drainage and river flow substantially in southern Africa by 2070–2099 (De Wit and Stankiewicz 2006). Mean annual temperature increases of up to almost  $5^{\circ}\text{C}$  have been projected for the interior of southern Africa by as soon as 2050 (Hulme et al. 2001), but IPCC AR4 suggest a range of between  $2.5$  and  $5.5^{\circ}\text{C}$  by the end of this century, with maximum warming centered on Botswana (IPCC 2007b).

### Biome and ecosystem level responses

Responses at biome and ecosystem scales have been addressed using two main approaches, the increasingly sophisticated DGVM (Dynamic Global Vegetation Model) ecosystem-level approach (e.g., Cramer et al. 2001; IPCC 2007a) and the correlative bioclimatic envelope approach (Box 1981). The bioclimatic approach is considered questionable at this level due to its many assumptions (e.g., unchanging species interactions, exclusive climate control of ecosystem distribution, equilibrium between ecosystem distribution and current climate), but nonetheless provides useful insights into initial risk assessment, hypothesis generation, and design of monitoring programs.

Bioclimatic approaches applied to biomes of South Africa were among the first local studies to raise concerns about the potential loss of bioclimatic niche space in that country (Rutherford et al. 2000). This approach revealed the potential loss of up to 65% of the area representing current optimal bioclimatic conditions for “sensitive” South African biomes, namely the Fynbos and Succulent Karoo (Rutherford et al. 2000). These studies assumed

earlier IS92a greenhouse gas scenarios and used older generation GCMs, such as HadCM2 (Perks et al. 2000). Follow-up studies using more recent climate simulations from HadCM3 based on IPCC TAR development scenarios and employing more sophisticated statistical methods, such as Generalized Additive Modeling (Guisan and Zimmermann 2000; Guisan and Thuiller 2005), have confirmed the essential conclusions of earlier biome-level work that endemic species rich biomes, such as the Succulent Karoo could show significant reduction in range of several tens of percent (Midgley and Thuiller 2007), though the spatial locations of persisting bioclimatic conditions may be somewhat revised. A study of the impacts of anticipated climate change on South African forest types suggests shifts in altitudinal and latitudinal range that will be constrained by current fragmentation of natural habitats (Eeley et al. 1999).

Hulme (1996) explored the impact of three climate scenarios for 2050 (core, dry, and wet) based on IPCC FAR methods (Carter et al. 1994), and employing the BIOME DGVM (from more recent climate future simulations, e.g., De Wit and Stankiewicz 2006, it seems that the “wet” scenario is least likely to develop, and results for this are therefore not considered here). This study found that the impacts of climate changes alone (excluding the effects of CO<sub>2</sub> fertilization and associated gains in vegetation water-use efficiency) caused an expansion of arid vegetation types (mainly thorn-scrub savanna) by up to 30%, at the expense of the Grassland type. However, with CO<sub>2</sub> fertilization effects included, mesic and tree-dominated Seasonal Forest vegetation more than doubled their extent at the expense of arid vegetation types.

A more recent study of Namibian ecosystems using the Sheffield DGVM and HadCM3 climate simulation under an SRES A2 scenario (Thuiller et al. 2006b) also found a strong sensitivity of vegetation structure and function to CO<sub>2</sub> enrichment, with NPP reductions due to climate change almost negated by CO<sub>2</sub> fertilization, and a strong increase in the success of C<sub>3</sub> forms at the expense of C<sub>4</sub> grasses. These findings are generally supported by DGVM simulations summarized in the IPCC AR4 (IPCC 2007a), which reveal that the most appreciable ecosystem structural change in southern Africa under an A2 scenario occurs in savannas and these range from both increases and decreases in woody plant cover (Fig. 1b).

The role of atmospheric CO<sub>2</sub> enrichment in grasslands and savannas could well be exacerbated by the mechanisms that maintain the current balance between grasses and trees. A key mechanism that prevents tree domination of savannas is mediated by grass fires that kill tree saplings, which are unable to gain sufficient carbon under low CO<sub>2</sub> conditions to recover from fire damage—but could well do so as CO<sub>2</sub> rises (Bond and Midgley 2000; Bond et al.

2003a). Despite this clear CO<sub>2</sub> sensitivity of southern African ecosystems, its regional and possibly global importance, and the uncertainties associated with it, no empirical field experiment exists in southern Africa to confirm or refute it. Greenhouse and early field-based studies have confirmed positive CO<sub>2</sub> impacts on grassland water-use efficiency (Wand et al. 2000, 2002; Motete et al. 2005; Stock et al. 2005), and a recent greenhouse study shows significant CO<sub>2</sub> dependence of the resprouting capacity of savanna trees (Kgope et al. 2010).

Patterns of increased woody plant cover have been recorded in South African savanna systems under diverse management regimes that now strongly implicate rising atmospheric CO<sub>2</sub> as a driver of this critical switch in ecosystem structure (Wigley et al. 2010). Studies on the impacts of such a thickening of woody cover show substantive impacts on animal diversity. Sirami et al. (2009) showed that savanna thickening is likely to lead to a loss in bird species richness at the landscape scale, and Muntiferi et al. (2006) showed that wild habitat for cheetah is significantly degraded by woody plant thickening.

Application of hydrologic modeling approaches suggests strong reductions in surface water flows across southern Africa (De Wit and Stankiewicz 2006), with likely significant negative impacts on endemic biodiversity that are as yet unquantified—especially for wetland environments such as the Okavango swamp system (Haman-dawana et al. 2008) whose feeder river could lose as much as 30% of its flow by 2050. Biophysical approaches applied to modeling dune field stability show a substantial risk of increasing dune mobility in the currently vegetated dunes of the Kalahari (Botswana and northern South Africa) by between 2050 and 2070 (Thomas and Leason 2005), with negative implications for subsistence livelihoods and biodiversity in this semi-arid region that hosts important protected areas.

Studies of interacting changes of vegetation cover on southern African climate are few—however, large-scale African tropical deforestation is simulated to alter rainfall patterns over much of the region due to climate teleconnections (Semazzi and Song 2001), with rainfall increases projected, with the exception of Mozambique where reductions are simulated.

### Species-level physiologic responses

Work on species-level responses to climate change factors is lacking in Africa, despite its high concentration of endemic species. What little has been done has focused on plant species and generally confirms findings from other continents. Dominant C<sub>4</sub> grassland species responses to elevated CO<sub>2</sub> show increased water-use efficiency (Wand



et al. 2000, 2002) that concur with widely reported responses (Midgley et al. 1999) and may scale up to impact on grassland water balance under field conditions (Stock et al. 2005). However,  $C_4$  species grown in elevated  $CO_2$  also show species-specific shifts in phenology (Motete et al. 2005) and increases in biomass (Wand et al. 2000) that concur with findings from short grass prairie in North America (Morgan et al. 2001).  $CO_2$  work on woody shrub species from nutrient-limited Mediterranean-type environments reveals muted growth responses (Midgley et al. 1999), while savanna tree saplings from resource-rich environments show significant growth and carbon status stimulation (Kgope et al. 2005, 2010). Succulent species that dominate the species-rich desert environments of the Succulent Karoo show a sensitivity to extended drought that contrasts with high drought tolerance of desert sclerophylls (Midgley and van der Heyden 1997), and succulents also appear susceptible to daytime warming-induced mortality (Musil et al. 2005).

### Geographic range and species population level responses

A growing body of work has attempted to project the potential response of wild species and biodiversity to anthropogenic climate change in southern Africa. This work has generally relied on the niche-based modeling approach (Guisan and Zimmermann 2000; Guisan and Thuiller 2005), which is supported by some excellent regional, national, and continental databases of species geographic distributions, climatic and human-use data sets. Apart from well-recognized limitations of this modeling approach (Guisan and Thuiller 2005), many such studies have attempted to account for uncertainties due to model variation and migration potential (Broennimann et al. 2006) and often make projections of impacts assuming both instantaneous (full) migration, and no migration (Bomhard et al. 2005).

Early work of Hulme (1996), as previously discussed, used IPCC First Assessment Report (AR4) methods (Carter et al. 1994) to develop climate scenarios and identified a prevalence of range size decreases over range increases by 2050 for 44 African ungulates, with negative effects concentrated in the high-altitude grasslands and interior savannas of South Africa. Projections for South African fauna based on HadCM2 climate scenarios for  $CO_2$  doubling showed a strong contraction of the ranges of animal species, including mammals, birds and reptiles, onto higher-altitude grasslands and toward more humid and cooler regions of South Africa (eastward shift) in response to regional warming (Erasmus et al. 2002), and the potential local extinction of many species in lower-lying regions.

More recent modeling of bird species ranges using HadCM3 scenarios has also revealed range contraction in endemic species of South Africa (Simmons et al. 2004), though this appears less significant for arid-system generalist species.

A comprehensive study of census records (1977–1996) for 11 ungulate species in South Africa's Kruger National Park showed severe population declines in seven species that could not be explained by ENSO forcing and its effects on annual rainfall (Ogutu and Owen-Smith 2003) but were correlated with an extreme reduction in dry season rainfall, interpreted as a possible fingerprint of regional climate change. This study noted that boundary fencing restricts potential range shifts by large mammals such as these in response to climatic variation and future climate change—and is a concern as model projections suggested local near-extirpation of three ungulate species under recurring dry summer conditions (Ogutu and Owen-Smith 2003).

In a study of 227 mammal species throughout the whole African continent, using HadCM3 climate scenarios, Thuiller et al. (2006a) found substantial shifts in geographic range, with a westward shift of species in the tropics and an eastward shift in the temperate zone, probably in response to aridification. A large fraction of species was also projected to become “critically endangered” or “extinct” by 2080, namely up to 40% with null migration, and up to 20% with full migration. These authors also noted that considerable change in species composition in response to climate change might occur across the region over this time frame. However, predictions of faunal responses to climate must be tempered by the finding that vegetation is, on its own, highly explanatory of animal species distributions (Andrews and O'Brien 2000); therefore, a better estimate of climate change effects will require the development of more inclusive explanatory models (climate, human-use impacts, and vegetation).

Studies on insect species are very few, but these may serve as sensitive indicators of climate change, as shown by Botes et al. (2006), who found that ant assemblage structure in the Cape Floristic Kingdom responded to site temperature characteristics which, together with area and vegetation variables, contributed significantly to species mix in major vegetation types and biomes on a bioclimatic gradient. Ant community change in response to climate change might also cause vegetation change, especially due to their importance in seed dispersal and regeneration of local plant species endemics.

Work on plant species ranges is currently further developed than that of animals and has been carried out for a much larger number of species. Much of this work (though not all) has focused on southern African biodiversity hotspots (*sensu* Myers et al. 2000) namely the Cape Floristic Region and the Succulent Karoo Biome. These

mainly winter rainfall regions represent a unique climate in the region and occupy only a small fraction of its land surface, yet may be important indicators of climate change due to incipient shifts in regional weather patterns such as the latitudinal position of rain-bearing westerly frontal systems.

Early work based on conservative climate scenarios of increased temperature but no change in precipitation, and using Bioclim-type modeling, provided first-cut indications of the potential climate change impacts on plant diversity within South Africa's protected area network (focusing on larger wildlife reserves) (Rutherford et al. 1999). Results indicated mixed impacts, with more than one-third of the species analyzed for one reserve indicated to become locally extinct with climate change, while another reserve in the same region had less than 1% local extinctions. This difference seemed to depend strongly on the different bioclimatic tolerances of species typical of each reserve. Potential species immigrations required to balance projected extinctions with climate change were surmised to exceed the migration potential of local species, and thus a net decrease in plant diversity was projected.

In the Cape Floristic Region iconic species groups, notably the *Proteaceae*, have been used to infer climate-change impacts on diversity (Midgley et al. 2003) and even to begin designing conservation responses (Hannah et al. 2005; Williams et al. 2005) and early-warning monitoring systems (Midgley et al. 2002). A comparison of biome- and species-level modeling approaches to estimate species extinction risk (using HadCM2 scenarios for CO<sub>2</sub> doubling) found that only 10% of endemic *Proteaceae* species had ranges restricted to the 51–65% of the biome lost under climate change, while range contractions and dislocations (no overlap between current and future modeled range) in up to one-third of species were spread throughout the biome (Midgley et al. 2002). Projected species range changes could also be sufficient to detect climate-change impacts within 10 years, allowing effective testing of model projections using targeted vulnerable species (Midgley et al. 2002).

In only one case has sufficient evidence been collected to suggest a species range shift response to recent climate change in southern Africa. The desert tree succulent *Aloe dichotoma* (quiver tree) shows unsustainable mortality in the warmer parts of its range in Namibia, but high rates of recruitment and population expansion in the cooler parts of its range in South Africa (Foden et al. 2007).

Impacts of climate change (HadCM2 scenarios for CO<sub>2</sub> doubling) and land transformation on species in regions of high risk of biome loss (Midgley et al. 2003) used 28 *Proteaceae* species to show that most species experienced potential range contractions (17 of 28), of which five showed range elimination, but several species (11 of 28) showed potential range expansions. For species whose

ranges contracted, current land transformation had less impact on future potential ranges than did climate change, because ranges tended to shift to higher altitudes with less land transformation pressure. Indeed, climate change has been shown to be potentially more important in increasing the risk status of endemic *Protea* species than projected land transformation over a short a time as two decades (Bomhard et al. 2005). These studies also reveal a substantial need for migration to allow the persistence of species, and efforts to address this need by designing effective links between protected areas using corridors have shown that this might be achievable (Williams et al. 2005), though highly dependent on climate scenario and thus currently risky for conservation implementation.

Modeling of 975 endemic plant species of a range of life forms over a far broader region of southern Africa, using HadCM3 scenarios (Broennimann et al. 2006), showed that the endemic flora of southern Africa on average could be reduced by about 40% in habitat-specific species richness even under the most optimistic SRES scenario (B1). Species and life form vulnerability to climate change could be partly explained by species' geographic distribution along climatic and biogeographic gradients, niche breadth, or proximity to physical barriers preventing migration and suggested promises for estimating species vulnerability.

A continent-wide study at rather coarse resolution using HadCM3 scenarios of potential geographic shifts of 5,197 African plant species (McClellan et al. 2005) shows substantial shifts for most species and widespread changes in species composition. Range size reductions or shifts were projected for 81–97% of the species modeled, with 25–42% projected to lose all suitable range by 2085. However, studies such as this, and others reviewed here, underscore the assumptions implicit in bioclimatic (niche-based) modeling that might lead to overestimates of the impacts of climate change on species persistence and community change. This shortcoming requires that ongoing monitoring programs are designed to test the evolution of the early impacts of climate change to allow confirmation of this threat and to improve the modeling approaches.

## Conclusions

Despite a fairly low overall investment in detecting and modeling projected climate change impacts across southern Africa, key studies supported by a long history of careful species-level data collection have provided early indications of the potential implications of unmitigated change for the ecosystems and biodiversity of the subcontinent. These first-cut assessments have been important, especially given the growing realization that significant concentrations of species are found in regions already threatened by human

development (biodiversity hotspots), and the direct dependence of many human livelihoods on diversity. These assessments, conducted at broad regional scales, suggest a significant threat to biodiversity across many taxonomic groupings both from changing bioclimatic suitability that to some extent control species geographic ranges and community composition, and changing atmospheric CO<sub>2</sub> level that might affect the competitive balance between woody and herbaceous elements of a region that is covered to a large extent by mixed tree-grass ecosystems. The most significant changes in ecosystem structure (both increases and decreases in woody plant cover), and associated faunal diversity changes, are projected in the dominant savanna vegetation type in this region, while the most significant biodiversity loss is projected for the winter rainfall region.

While modeling efforts have raised the alarm about the implications of unmitigated climate change for this region, assumptions underpinning methods such as bioclimatic modeling must be recognized, some of which might lead to over estimates of the rate and extent of the potential impacts. Nevertheless, the general trend and level of coincidence between various types of studies would support a high degree of concern for a substantial portion of southern African biodiversity under unmitigated climate-change scenarios. Follow-up work to detect early signs of climate change, identify regions of high- and low- potential impacts, and experimental work to test some important hypotheses relating to the future evolution of climate-change impacts across the region is very few and urgently required.

A focus on climate change impacts at population demographic level is virtually absent in southern Africa. There is very little evidence available to assess whether the early phases of anthropogenic climate change are affecting the biota of wild species and conserved nature areas in various and significant ways. Nature conservation agencies seem relatively unprepared and lack a strategic management response to the possible consequences of climate change, though records from extensive monitoring efforts could yield important insights (and have in a few cases). It seems unlikely that natural adaptation responses by biota beyond some level of geographic range shift in vagile organisms are likely, and thus conservation adaptive strategies require urgent attention, especially with regard to raising the level of protection for threatened species outside of official conserved areas, in order to minimize ancillary stresses on populations beleaguered by climate change.

## References

- Andrews P, O'Brien EM (2000) Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *J Zool* 251:205–231
- Bomhard B, Richardson DM, Donaldson JS, Hughes GO, Midgley GF, Raimondo DC, Rebelo AG, Rouget M, Thuiller W (2005) Potential impacts of future land use and climate change on the red list status of the Proteaceae in the Cape Floristic region, South Africa. *Glob Chang Biol* 11(9):1452–1468. doi:10.1111/j.1365-2486.2005.00997.x
- Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol Evol* 20(7):387–394
- Bond WJ, Midgley GF (2000) A proposed CO<sub>2</sub>-controlled mechanism of woody plant invasion in grasslands and savannas. *Glob Chang Biol* 6(8):865–869
- Bond WJ, Van Wilgen BW (1996) Fire and plants, vol 14. Chapman and Hall, London
- Bond WJ, Midgley GF, Woodward FI (2003a) The importance of low atmospheric CO<sub>2</sub> and fire in promoting the spread of grasslands and savannas. *Glob Chang Biol* 9(7):973–982
- Bond WJ, Midgley GF, Woodward FI (2003b) What controls South African vegetation—climate or fire? *S Afr J Bot* 69(1):79–91
- Bond WJ, Woodward FI, Midgley GF (2005) The global distribution of ecosystems in a world without fire. *New Phytol* 165(2): 525–537
- Botes A, McGeoch MA, Robertson HG, Niekerk A, Davids HP, Chown SL (2006) Ants, altitude and change in the northern Cape Floristic region. *J Biogeogr* 33(1):71–90
- Box EO (1981) Predicting physiognomic vegetation types with climate variables. *Plant Ecology* 45(2):127–139
- Broennimann O, Thuiller W, Hughes G, Midgley GF, Alkemade JMR, Guisan A (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Glob Chang Biol* 12(6):1079–1093. doi:10.1111/j.1365-2486.2005.01157.x
- Brooks T, Balmford A, Burgess N, Fjelda J, Hansen LA, Moore JL, Rahbek C, Williams PH (2001) Toward a blueprint for conservation in Africa. *Bioscience* 51:613–624
- Carter TR, Parry ML, Harasawa H, Nishioka S (1994) IPCC technical guidelines for assessing impacts of climate change. Intergovernmental Panel on Climate Change, WMO and UNEP, Geneva
- Cowling RM, Rundel PW, Lamont BB, Arroyo MK, Arianoutsou M (1996) Plant diversity in Mediterranean-climate regions. *Trends Ecol Evol* 11(9):362–366
- Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend AD, Kucharik C, Lomas MR, Ramankutty N, Sitch S, Smith B, White A, Young-Molling C (2001) Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Glob Chang Biol* 7(4):357–373
- De Wit M, Stankiewicz J (2006) Changes in surface water supply across Africa with predicted climate change. *Science* 311(5769): 1917–1921
- Diaz HF, Hoerling MP, Eischeid JK (2001) ENSO variability, teleconnections and climate change. *Int J Climatol* 21(15): 1845–1862
- Eeley HAC, Lawes MJ, Piper SE (1999) The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. *J Biogeogr* 26(3):595–617
- Engelbrecht FA, McGregor JL, Engelbrecht CJ (2009) Dynamics of the conformal-cubic atmospheric model climate-change signal over southern Africa. *Int J Climatol* 29:1013–1033
- Erasmus BFN, Van Jaarsveld AS, Chown SL, Kshatriya M, Wessels KJ (2002) Vulnerability of South African animal taxa to climate change. *Glob Chang Biol* 8(7):679–693
- Foden W, Midgley GF, Hughes G, Bond WJ, Thuiller W, Hoffman MT, Kaleme P, Underhill LG, Rebelo A, Hannah L (2007) A changing climate is eroding the geographical range of the Namib

- Desert tree *Aloe* through population declines and dispersal lags. *Divers Distrib* 13(5):645–653. doi:10.1111/j.1472-4642.2007.00391.x
- Glantz MH (2001) *Currents of change: impacts of El Niño and La Niña on climate and society*, 2nd edn. Cambridge University Press, Cambridge
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8(9):993–1009
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Modell* 135(2–3):147–186
- Hamandawana H, Chanda R, Eckardt F (2008) Reappraisal of contemporary perspectives on climate change in southern Africa's Okavango delta sub-region. *J Arid Environ* 72(9):1709–1720. doi:10.1016/j.jaridenv.2008.03.007
- Hannah L, Midgley GF, Hughes G, Bomhard B (2005) The view from the Cape: extinction risk, protected areas and climate change. *Bioscience* 55:231–242
- Hassan R, Scholes R, Ash N (eds) (2005) *Ecosystems and human well-being—volume 1: current state & trends*, vol 1. Island Press, Washington, DC
- Hawkins BR, Field R, Cornell HV, Currie DJ, Guegan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117
- Hewitson BC, Crane RG (2006) Consensus between GCM climate change projections with empirical downscaling: precipitation downscaling over South Africa. *Int J Climatol* 26:1315–1337
- Hulme M (ed) (1996) *Climate change and Southern Africa*. CRU/WWF, Norwich, UK, 103 p
- Hulme M, Doherty R, Ngara T, New M, Lister D (2001) African climate change: 1900–2100. *Clim Res* 17(2):145–168
- IPCC, 2007a *Climate Change 2007: Impacts, Adaptation and Vulnerability*. Working Group II contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In: Parry M, Canziani O, Palutikof J, van der Linden P, Hanson C (eds) Cambridge University Press Cambridge, UK and New York, NY, USA
- IPCC, 2007b *Climate Change 2007: The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt K, Tignor MMB, Miller HL (eds) Cambridge University Press, Cambridge, UK and New York, NY, USA
- Kgope BS, Midgley GF, Bond WJ, Woodward FI (2005) Evidence for a CO<sub>2</sub> controlled mechanism to explain tree invasion of African savannas and adjacent grasslands. *S Afr J Bot* 71:267
- Kgope B, Bond WJ, Midgley GF (2010) Growth responses of African savanna trees implicate atmospheric [CO<sub>2</sub>] as a driver of past and current changes in savanna tree cover. *Austral Ecol* 35:451–463
- Lucht W, Schaphoff S, Erbrecth T, Heyder U, Cramer W (2006) Terrestrial vegetation redistribution and carbon balance under climate change. *Carbon Balance Manag* 1(6):1–7
- Malcolm JR, Liu C, Neilson RP, Hansen L, Hannah LEE (2006) Global warming and extinctions of endemic species from biodiversity hotspots. *Conserv Biol* 20(2):538–548
- Mason SJ (1996) Rainfall trends over the Lowveld of South Africa. *Climatic Change* 32:35–54
- McClellan CJ, Lovett JC, Küper W, Hannah L, Sommer JH, Barthlott W, Termansen M, Smith GF, Tokumine S, Taplin JRD (2005) African plant diversity and climate change. *Ann Mo Bot Gard* 92(2):139–152
- Meadows ME (2006) Global change and southern Africa. *Geogr Res* 44(2):135–145
- Midgley GF, Thuiller W (2005) Global environmental change and the uncertain fate of biodiversity. *New Phytol* 167(3):638–641
- Midgley GF, Thuiller W (2007) Could anthropogenic climate change threaten biodiversity in Namaqualand? *J Arid Environ* 70:615–628
- Midgley GF, van der Heyden F (1997) Growth form and function: perennial plants. In: Dean RJ, Milton SJ (eds) *The Karoo: ecological patterns and processes*. Cambridge University Press, Cambridge
- Midgley GF, Wand SJE, Pammenter N (1999) Nutrient and genotypic constraints on CO<sub>2</sub>-responsiveness: Photosynthetic regulation in congeners of a nutrient-poor environment. *J Exp Bot* 50:533–542
- Midgley GF, Hannah L, Millar D, Rutherford MC, Powrie LW (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Glob Ecol Biogeogr* 11(6):445–451
- Midgley GF, Hannah L, Millar D, Thuiller W, Booth A (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biol Conserv* 112(1–2):87–97. doi:10.1016/S0006-3207(02)00414-7
- Morgan JA, Lecain DR, Mosier AR, Milchunas DG (2001) Elevated CO<sub>2</sub> enhances water relations and productivity and affects gas exchange in C-3 and C-4 grasses of the Colorado shortgrass steppe. *Glob Chang Biol* 7(4):451–466
- Motete N, Midgley GF, Pammenter N (2005) Impact of elevated CO<sub>2</sub> on the phenology and canopy structure of a C<sub>4</sub> grassland microcosm. *S Afr J Bot* 70(5):797–803
- Muntifering JR, Dickman AJ, Perlow LM, Hruska T, Ryan PG, Marker LL, Jeo RM (2006) Managing the matrix for large carnivores: a novel approach and perspective from cheetah (*Acinonyx jubatus*) habitat suitability modelling. *Anim Conserv* 9:103–112
- Musil CF, Schmiedel U, Midgley GF (2005) Lethal effects of experimental warming approximating a future climate scenario on southern African quartz-field succulents: a pilot study. *New Phytol* 165(2):539–547
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403(6772):853–858
- Neilson RP, Pitelka LF, Solomon AM, Nathan R, Midgley GF, Fragoso JMV, Lischke H, Thompson K (2005) Forecasting regional to global plant migration in response to climate change. *Bioscience* 55(9):749–759
- Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Piper SC, Tucker CJ, Myeni RB, Running SW (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* 300(5625):1560–1563
- Nicholson S (2001) Climatic and environmental change in Africa during the last two centuries. *Clim Res* 17:123–144
- Ogutu JO, Owen-Smith N (2003) ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecol Lett* 6(5):412–419
- Perks LA, Schulze RE, Kiker GA, Horan MJC, Maharaj M (2000) Preparation of climate data and information for application in impact studies of climate change over southern Africa. In: Kiker G (ed) *Climate change impacts in Southern Africa*. Report to the National Climate Change Committee Department of Environmental Affairs and Tourism, Pretoria
- Pollack HN, Huang S, Shen P-Y (1998) Climate change record in subsurface temperatures: a global perspective. *Science* 282(5387):279–281
- Richardson DM, Bond WJ, Dean RJ, Higgins SI, Midgley GF, Milton SJ, Powrie LW, Rutherford MC, Samways MJ, Schulze RE (2000) Invasive alien species and global change: A South African perspective. In: Mooney HA, Hobbs R (eds) *Invasive species in a changing world*. Island Press, California, pp 303–350



- Rodrigues ASL, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Cowling RM, Fishpool LDC, da Fonseca GAB, Gaston KJ, Hoffmann M, Long JS, Marquet PA, Pilgrim JD, Pressey RL, Schipper J, Sechrest W, Stuart SN, Underhill LG, Waller RW, Watts MEJ, Yan X (2004) Effectiveness of the global protected area network in representing species diversity. *Nature* 428:640–643
- Root TL, MacMynowski DP, Mastrandrea MD, Schneider SH (2005) Human-modified temperatures induce species changes: joint attribution. *Proc Natl Acad Sci USA* 102(21):7465–7469
- Rutherford MC (1999) Categorization of biomes. In: Cowling RM, Richardson DM, Pierce SM (eds) *Vegetation of Southern Africa*. Cambridge University Press, Cambridge
- Rutherford MC, Powrie LW, Schulze RE (1999) Climate change in conservation areas of South Africa and its potential impact on floristic composition: a first assessment. *Divers Distrib* 5:253–262
- Rutherford MC, Midgley GF, Bond WJ, Powrie LW, Roberts R, Allsopp J (eds) (2000) *Plant biodiversity: vulnerability and adaptation assessment. Climate change impacts in Southern Africa*. Report to the National Climate Change Committee. Department of Environmental Affairs and Tourism, Pretoria
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* 287(5459):1770–1774
- Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SILRX, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Frost PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J, Zambatis N (2005) Determinants of woody cover in African savannas. *Nature* 438(7069):846–849
- Schaphoff S, Lucht W, Gerten D, Sitch S, Cramer W, Prentice IC (2006) Terrestrial biosphere carbon storage under alternative climate projections. *Climatic Change* 74(1–3):97–122
- Scholes RJ, Biggs R (eds) (2004) *Ecosystem services in southern Africa: a regional assessment*. Council for Scientific and Industrial Research, Pretoria
- Scholes RJ, Biggs R (2005) A biodiversity intactness index. *Nature* 434(7029):45–49
- Schulze RE (ed) (2005) *Climate change and water resources in Southern Africa: studies on scenarios, impacts, vulnerabilities and adaptation*. Water Research Commission report 1430/1/05. Water Research Commission, Pretoria, Republic of South Africa
- Semazzi FH, Song Y (2001) A GCM study of climate change induced by deforestation in Africa. *Clim Res* 17(2):169–182
- Simmons RE, Barnard P, Dean WRJ, Midgley GF, Thuiller W, Hughes G (2004) Climate change and birds: perspectives and prospects from southern Africa. *Ostrich* 75(4):295–308
- Sirami C, Seymour C, Midgley GF, Barnard PB (2009) The impact of shrub encroachment on savanna bird diversity from local to regional scale. *Divers Distrib* 15:948–957
- Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W, Sykes MT, Thonicke K, Venevsky S (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Glob Chang Biol* 9(2):161–185
- Stock WD, Ludwig F, Morrow C, Midgley GF, Wand SJE, Allsopp N, Bell TL (2005) Long-term effects of elevated atmospheric CO<sub>2</sub> on species composition and productivity of a southern African C<sub>4</sub> dominated grassland in the vicinity of a CO<sub>2</sub> exhalation. *Plant Ecol* 178(2):211–224
- Stokes S, Thomas DSG, Washington R (1997) Multiple episodes of aridity in southern Africa since the last interglacial period. *Nature* 388:154–158
- Thomas DSG, Leason HC (2005) Dunefield activity response to climate variability in the southwest Kalahari. *Geomorphology* 64(1–2):117–132
- Thuiller W, Broennimann O, Hughes G, Alkemade JRM, Midgley GF, Corsi F (2006a) Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Glob Chang Biol* 12(3):424–440. doi:10.1111/j.1365-2486.2006.01115.x
- Thuiller W, Midgley GF, Hughes GO, Bomhard B, Drew G, Rutherford MC, Woodward FI (2006b) Endemic species and ecosystem sensitivity to climate change in Namibia. *Glob Chang Biol* 12(5):759–776. doi:10.1111/j.1365-2486.2006.01140.x
- Thuiller W, Midgley GF, Rouget M, Cowling RM (2006c) Predicting patterns of plant species richness in megadiverse South Africa. *Ecography* 29(5):733–744
- Tyson PD, Gatebe CK (2001) The atmosphere, aerosols, trace gases and biogeochemical change in southern Africa: a regional integration. *S Afr J Sci* 97:106–118
- Tyson PD, Preston-Whyte RA (2000) *The weather and climate of South Africa*. Oxford University Press, Oxford
- Wand SJE, Midgley GF, Stock WD (2000) Growth responses to elevated CO<sub>2</sub> in NADP-ME, NAD-ME and PCK C<sub>4</sub> grasses and a C<sub>3</sub> grass from Africa. *Aust J Plant Physiol* 28:13–25
- Wand SJE, Midgley GF, Stock WD (2002) Response to elevated CO<sub>2</sub> from a natural spring in C<sub>4</sub>-dominated grassland depends on seasonal phenology. *Afr J Range Forage Sci* 19:81–91
- Warburton M, Schulze RE, Maharaj M (2005) Is South Africa's temperature changing? An analysis of trends from daily records, 1950–2000. *Climate Change and Water Resources in Southern Africa: Studies on Scenarios, Impacts, Vulnerabilities and Adaptation*. Water Research Commission, Pretoria, RSA. <http://www.wrc.org.za/downloads/report%20lists/integrated%20resources.htm>
- Wigley BJ, Bond WJ, Hoffman MT (2010) Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Glob Chang Biol* 16:964–976
- Williams P, Hannah L, Andelman S, Midgley GF, Araujo M, Hughes G, Manne L, Martinez-Meyer E, Pearson R (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conserv Biol* 19(4):1063–1074
- Woodward FI, Lomas MR (2004) Simulating vegetation processes along the Kalahari transect. *Glob Chang Biol* 10(3):383–392