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

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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 CO₂ 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

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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_4 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 $\sim 10^{\circ} S$ latitude, maximum



woody plant cover, for example, is strongly rainfall controlled below ~ 500 mm mean annual rainfall (MAR), somewhat affected by disturbance regime within MAR limits of 650 ± 134 mm MAR and strongly disturbance determined above ~ 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).

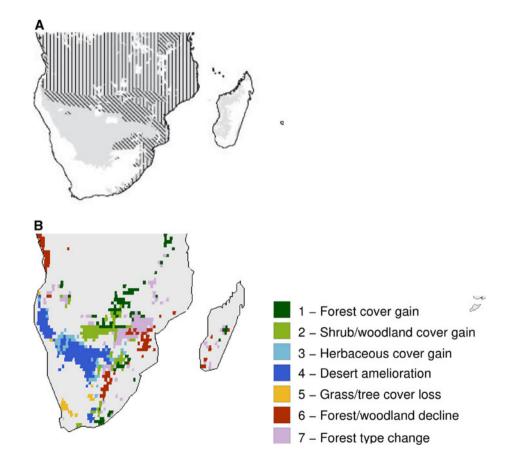
Global change pressures (land use, atmospheric composition CO₂, nitrogen deposition, climate, and biotic exchange) were summarized by Sala et al. (2000) and have been generally confirmed for Africa (Scholes and Biggs 2004; Hassan et al. 2005). Among leading pressures identified internationally, recent 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); crosshatching = 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 levelsbiome 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 nearmeridional 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 (~ 10 –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 undersample 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°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°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 CO₂ fertilization and associated gains in vegetation wateruse 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 CO₂ 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 CO₂ enrichment, with NPP reductions due to climate change almost negated by CO₂ fertilization, and a strong increase in the success of C₃ forms at the expense of C₄ 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 CO₂ 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 CO₂ conditions to recover from fire damage—but could well do so as CO₂ rises (Bond and Midgley 2000; Bond et al.

2003a). Despite this clear CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 Muntifering 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 (Hamandawana 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 C₄ grassland species responses to elevated CO₂ 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, C₄ species grown in elevated CO₂ 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). CO₂ 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 CO₂ doubling showed a strong contraction of the ranges of animal species, including mammals, birds and reptiles, onto higheraltitude 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 Had-CM3 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 climatechange 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 CO₂ 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 CO₂ 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 (McClean 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 (nichebased) 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 CO₂ 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.

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