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1. Introduction

Southern Africa has an exceptionally rich endemic flora and fauna. Besides its intrinsic value, biodiversity is also important for sustaining human livelihoods and for a number of formal and informal economic sectors.

The impetus for this project came out of work done in the late 1990s under the umbrella of South African country studies on vulnerability to climate change (Rutherford 1999). One of the "sectors" identified in those studies as being particularly at risk in South Africa was biodiversity. The likelihood of this threat is confirmed by Thomas et al. (2004), who predict that globally 15–37% of species in their sample (that covers 20% of the Earth's surface) may become extinct by 2050 due to anthropogenically caused global climate change. Models built on a completely different set of assumptions (Sala et al., in press) come to very similar conclusions. This predicted impact on biodiversity could have profound

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impacts on southern Africa, where biodiversity is of high importance to economic development and local livelihoods.

Southern Africa, and, in particular, South Africa has an exceptionally rich biological diversity (biodiversity). Seven broad terrestrial ecological zones (biomes) occur in the region: the savanna, grassland, nama karoo, succulent karoo, forest, desert, and fynbos biomes (Rutherford and Wesfall, 1986). An eighth biome, the thicket biome, is also recognized by some authorities (Low and Rebelo, 1996). Two of the biomes, the fynbos biome and succulent karoo biome have particularly high levels of biodiversity of vascular plants and exceptionally high levels of endemism. Within southern Africa, eight centers of plant endemism are recognized, with two of these, the Cape and succulent karoo, being effectively synonymous with fynbos and succulent karoo biomes (Cowling and Hilton-Taylor 1994; Cowling and Hilton-Taylor 1997).

The biomes of southern Africa are characterized by unique climatic parameters, although edaphic factors are also important in defining the habitats of individual species (Rutherford and Westfall, 1986). Global climatic change is therefore likely to impact on the future distribution patterns of the biomes. Early assessments of the possible impacts of climate change on biodiversity using simple biome-level climatic envelope approaches confirmed that severe impacts are likely to occur (Scholes, 1990; Rutherford et al., 1999). In general terms, it was found that existing biomes were shifted eastward and compacted into the eastern half of the country. Through using this approach, it was found that, on the basis of the predicted climatic futures of HadCM2 (including and excluding sulphates) and CSM scenarios, by 2050, 38–55% of the current area of South Africa would have a climatic

envelope that did not match any current biome. Hannah et al. (2002) suggest that future climate conditions are likely to produce species assemblages with no counterpart in present communities. Wide-scale species loss is also likely (e.g., Thomas, 2004).

Rutherford et al. (1999) predict the following biome-level changes. Of particular concern is the succulent karoo biome, which loses almost its entire current distribution, and is replaced by an area in which hotter and dryer conditions prevail. In addition, the main area of future distribution is disjunct from its current distributions and is separated by a range of mountains. Savanna, grasslands, and nama karoo are all reduced in total extent, with both the savanna and nama karoo invading into some of the previous grassland areas. The fynbos is the only biome to show limited changes in total extent, but there is evidence that many individual species may be impacted. The forest biome is very small and dispersed; the most likely impacts are to its distribution in the northeastern part of the country. Very little desert is found in South Africa. However, desertification is expected to increase with climate change, and this may increase the extent of the current desert biodiversity.

The Assessments and Impacts and Adaptations to Climate Change (AIACC)-funded project chose three of these biomes as pilot sites to develop a set of tools for better understanding the likely impacts on biodiversity. This was, in part, because of ongoing work in these biomes by team members, which means that data were readily available, but also for the following reasons:

The fynbos was chosen because of its biodiversity importance and because there is a large amount of fine-scale spatial data on the distribution of the current biodiversity.
Although the spatial extent of fynbos is not expected to be reduced as much as in

other biomes, there is a lot of concern as to how individual species will respond. As such, it was the perfect biome for testing of detailed individual species responses to climate change.

- The succulent karoo was chosen because of its unique biodiversity and because previous modelling has suggested that it is the biome that may experience some of the most severe impacts from climate change.
- The savanna was chosen because of its importance from a livelihood perspective and because it is such a widespread biome in Africa. A unique aspect of the savannas is the codominance of tree and grass life forms, and this provided a perfect situation in which to study systems-level responses of functional groups of plants to climate change.

2. A Description of the Biomes Studied

2.1 Fynbos

Fynbos, literally meaning fine-leaved bush, is a local term for the heath-like vegetation found in the areas of South Africa that have a Mediterranean-type climate with winter rainfall (Cowling et al., 1997). Evergreen, fire-prone vegetation on a low-nutrient substrate is a key feature of the fynbos. Fynbos is largely confined to the southwestern tip of South Africa in a relatively small area of ~71,000 km² on a landscape composed mostly of the rugged and steep quartzitic Cape Folded Mountains. The uniqueness of the Cape Floristic Region, which is largely coincident with the fynbos, has resulted in it being considered as one the world's six floristic kingdoms, the only one located entirely in one country (Good, 1974). The biome has exceptionally high species richness, especially of vascular plants, with an estimated 7300 species, of which 80% are endemic (Cowling and Hilton-Taylor 1994, 1997). Altitude, rainfall, aspect, and soil play important factors in determining vegetation structure. In addition, stochastic factors, such as fire frequency and intensity play an important role in determining species composition (Cowling et al., 1997). The plant species of the fynbos have a diverse and interesting array of plant reproductive strategies. The autecology of the species is likely to play an important role in how species will be able to adapt to a changing climate. This will be explored later in the paper, with only an overview of key ecological aspects to be presented in this section. In the fynbos, there is a strong dependency on insects as pollinators, but there is also a dependency on ants as seed dispersers (myrmecochory) in some species. Most species can resprout following fire. Bond (1984) warns that many fynbos species that do no resprout after fire and that are limited by seeds for recruitment face a high risk of extinction if their pollinator of disperser mutualisms collapse.

The ericoids are numerically the most dominant taxa comprising some 40% of the fynbos species. The Proteaceae, although not having as large a number of taxa, contribute the bulk of the shrub biomass. The protioids are both an ecologically and economically important plant group and form the basis of an extensive cut flower industry. Few protioids resprout after fire, the majority being obligatory reseders. Of these reseders, most are serotinous,, in other words, they store seeds in their canopy and only release them after fires. In these species, seeds are adapted to long distance wind dispersal. Nonserotinous seeds are passively dispersed or have fatty elaisomes that attract ants as dispersal agents (Bond and Breytenbach, 1985).

2.2 Succulent karoo

The succulent karoo biome is an area of about 100,000 km² that stretches along the west coast of southern Namibia and South Africa and as a narrow band across the northern edge of the fynbos. It is found predominantly on coastal plains and intermountain valleys, mostly at an altitude of less than 1,000 m. The biome receives only 20–290 mm of annual rain, of which >40% falls in winter. It is the high summer aridity and soils that are finer grained and more nutrient rich that differentiates this area from the fynbos. The biome has more than 5,000 plant species, of which about 50% are endemic (Milton et al., 1997).

It is the high concentration of leaf-succulents of the two dominant families, Mesembryanthemaceae and Crassulaceae, that gives this vegetation its uniqueness. Most species are insect pollinated, with more than 300 pollinators that have been identified. Seed dispersal occurs mostly by wind or water. Long-lived perennial species tend to have different seeding strategies from short-lived annuals. In the annuals, there are a number of mechanisms to delay germination to periods of suitable rainfall, and different species respond to different timing of rain. Disturbance of the landscape also promotes the establishment of annuals. Long-lived species tend to have a very low annual recruitment rate, whereas annuals have a high proportion of seedlings reaching reproductive maturity (Milton, 1995; Rosch, 1977; van Rooyen et al., 1979). Fire is not a feature in the succulent karoo. Re-establishment of long-lived plants onto disturbed areas is very slow and may take up to 80 years (Beukes et al. 1994; Dean and Milton, 1995). The vegetation is susceptible to drought, which can kill off many of the perennials. Though annuals recover rapidly from drought, perennials recover very slowly (Milton 1995).

2.3 Savanna

The codominance of trees and grass is what distinguishes savanna from other biomes. Savannas cover 54% of the land area of southern Africa, and 60% of sub-Saharan Africa. Savannas are found in predominantly frost-free areas with a moist hot season. It is the severity of the cold season that creates a differentiation between savannas and grasslands. The amount of rainfall separates savanna from nama karroo, at the low extreme, and forest, at the high rainfall extreme (Scholes and Walker, 1993; Scholes, 1997). At a whole-biome scale, plant species richness of southern Africa savannas is high, at about 5,780 species in an area of about 600,000 km². This species richness is second only to the fynbos in southern Africa. Although plant diversity at the small plot scale ("alpha diversity") is high, the species turnover ("beta diversity") and landscape ("gamma") diversity are generally low (Scholes, 1997). In other words, adjacent patches tend to have very similar species in them. This is in sharp contrast to the fynbos, which has high beta and gamma diversity.

It is the savannas that are home to most of Africa's large mammals, and this supports an important tourism industry. The savannas also support a large livestock ranching industry. As can be expected, herbivores are a key component of savanna dynamics. Historically, it was the savannas that supported most of the indigenous human populations of Africa, and the area is still of great importance in supporting subsistence economies through the supply of grazing, fuelwood, and other natural resources (Scholes, 1997).

A large proportion of savanna grasses have a C_4 photosynthetic pathway, whereas the trees (and other woody vegetation) all have a C_3 photosynthetic pathway. Seeds from savanna

grasses are largely animal or wind dispersed, whereas trees have ballistic dispersal, wind dispersal, and animal dispersal. The herbaceous layer is a mix of annual and perennial forbs and grass species, with annuals being more dominant in the arid areas. Trees can be exceptionally long lived (a few centuries in some species), and many species are able to resprout or coppice if damaged by animals or fire. Fire is a common occurrence, and its frequency and intensity are largely governed by rainfall and herbivory. A key feature of savanna dynamics is the codominance of grasses and trees. In this regard, fire and herbivory play an important role in determining the proportional representation between trees and grasses (Scholes, 1997)

3. Research Framework and Methodology

Three different approaches were developed to understand the vulnerability of biodiversity to climate change. Each approach was developed in one of the identified biomes. Detailed results from these studies are presented in separate publications. This report attempts to assimilate some of the general learning on the vulnerability of biodiversity from across the pilot studies. Because the objective of the pilots was to develop methodologies, there is not a consistent knowledge base between studies. In addition, a first attempt is made to link the vulnerability of biodiversity to climate change to the potential impacts that this will have on biodiversity-dependent human communities.

Before this study, attempts had been made to understand the impacts of climate change on the fynbos, using an approach that compared current climatic envelopes to the spatial location of future climatic envelopes (Midgley et al., 2002a, b). These approaches were

static in that they did not consider how species would respond to climate change but simply investigated whether they would have a suitable climatic envelope in the future. To overcome this shortcoming, the AIACC-funded project developed a "time-slice" modeling approach to investigate the migratory corridors needed for individual species to track climate change, and details of this approach are presented (G.F. Midgley et al., submitted manuscript "Migration rate limitations on climate change induced range shifts in Cape Proteaceae". G.F. Midgley personal communication. Williams et al., 2004). The Proteaceae were used to test this approach, as detailed distribution data already existed and because *Protea* are a charismatic and well-known species of economic importance. In addition, there is evidence that Proteas' distributions are closely correlated with the distributions of other fynbos species. Species' distribution data were taken from the *Protea* Atlas Project database, which contains field-determined species' presence and absence at more than 60,000 georeferenced sites. This is an unusually thorough sampling of localities totalling more than 250,000 species records for 340 taxa

(http://protea.worldonline.co.za/default.htm). Climate data were interpolated for the one-minute grid (Schulze, 1997). Future projections were based on Schulze and Perks (1999), according to the 2050 projections for the region from the general circulation model HadCM2 (http://cera-www.dkrz.de/IPCC_DDC/IS92a/Hadley-

Centre/Readme.hadcm2), using IS92a emissions assumptions for CO₂ equivalent greenhouse gas concentrations and excluding sulfate-cooling feedback. Soil categorization relating to fertility (high, medium, and low), pH (acid, neutral, and basic), and texture (sand and clay) were derived for the one-minute grid by interpolation of regional geology maps (R. Cowling and A. Rebelo, personal communication). Information on nomenclature and on species' dispersal modes was taken from Rebelo (2001).

In the Karoo case study, a simpler approach was taken to consider the link between a single animal species and its habitat and food resources. Two species were used to test the methodology, the highly endangered riverine rabbit (*Bunolagus monticularis*) from the nama karoo and the padloper tortoise (Homopus singnatus) from the succulent karoo These studies are described in detail by G. O. Hughes et al. (submitted manuscript, "A fait accompli? Environmental change hastens the demise of the critically endangered riverine rabbit (*Bunolagus monticularis*)", 2006; G. O. Hughes, personal communication), G.O. Hughes, et al. (submitted manuscript, "Global change and an arid zone chelonian: The case of *Homopus signatus*: Environmental factors affecting modelled current and future distributions of *Homopus signatus* an arid zone chelonian endemic to South Africa" 2006 G.O. Hughes personal communication).

The savanna study took a different approach and investigates key functional properties (tree cover, fire frequency, grass and browse production, and carrying capacity for major guilds of herbivores and carnivores) rather than individual species interaction. This was done using a modeling approach (Scholes, personal communication) based on the Lotka-Volterra approach (Lotka, 1925; Volterra, 1926). The model, as developed in this study, attempts to predict the functional responses of grasses and trees to changes in temperature, rainfall, and CO₂ levels. This model does not look at individual species, but rather models the grass/tree ratio and the interplay of this with herbivory and fire.

4. Factors Impacting on the Vulnerability of Different Biomes and Species

The vulnerability of individual species depends on the interaction between the magnitude of the impact and the adaptive capacity of the species. Different global circulation models (GCMs) and emission scenarios result in a range of projections for future climate in southern Africa. Common to all is an increase in temperature, but the magnitude of this change varies from under 1°C to up to 3.5 °C for the year 2080 (Scholes and Biggs, 2004). (Note that the long-term equilibrium temperature change from the degree of radiant forcing that leads to these projections is about twice the amount recorded in 2080). In general terms, temperature change tends to be moderated by coastal influences; thus the change registered in the interior of the continent is higher than that at the coast.

There is less agreement between GCMs regarding the impacts of climate change on rainfall. Most models project reduced rainfall in the western half of southern Africa, though there may be increased rainfall in the eastern subcontinent (Scholes and Biggs, 2004). From the perspective of plants, the combination of an increase in temperature with reduced rainfall greatly decreases the available moisture for growth. In other words the ratio of rainfall to potential evaporation tends to decrease, resulting in more desert-like conditions. The increased CO_2 may, to some extent, mitigate the impacts of this increased aridity.

The fynbos as a biome appears less affected by climate change than many of the other southern African biomes (Rutherford et al., 1999). Does this mean that the richness of biodiversity is protected? A number of studies using the Proteaceae (a key and very diverse component of the fynbos) as an indicator group have investigated potential impacts on individual species. Midgley et al. (2002a), in a study of climate impacts on 28 *Protea* species, found that 17 will experience potential range contraction, whereas 5 species will

experience range elimination. Climate change was predicted to have greater impact than land transformation as the Proteas tended to move to areas of higher altitude in the mountains that are not likely to be impacted by land transformation. This study was repeated for 330 *Protea* species (Midgley et al., 2002b), with similar results. A loss of 51% to 65% of the area extent of the fynbos biome was predicted, depending on the climate scenario used. One-third of the *Protea* species were found to have complete range dislocation. In other words, there is no overlap between their future range and their current range. Only 5% would retain more than two-thirds of their current range. Ten percent of the species had no predicted range in the future scenario.

The predicted *Proteaceae* responses to climate change were further developed in this AIACC project by introducing a dynamic movement model, to see whether the Proteas could disperse from their current distribution to predicted 2050 habitats (Williams et al., 2004). The model assumed a shorter migration range for *Protea* species with ant-dispersed seeds than those where seeds are wind dispersed. A time-sliced approach was used to see whether suitable "stepping stones" habitats existed to allow the *Protea* to move from their current distribution to their future distribution. This study found that of the 282 species investigated, 262 maintained overlapping habitats and did not need to disperse (though their range may have reduced), 18 species were obligatory dispersers and could reach their new habitats, while two species could not disperse because of land transformation. Thirty-four species were removed from the analysis, as they had no future habitat and would therefore be predicted to go extinct unless ex situ conservation was initiated.

These detailed studies on the Protea are unique, and other genera of the fynbos have not been subjected to similar scrutiny. Although Proteas may serve as an example to represent general trends, they only account for a small proportion of the actual diversity, and the rest still needs more detailed analysis. Climatic envelope modeling, in general, and the dynamic movement models, in particular, have many assumptions and uncertainties, which are not taken into account in the current results.

The succulent karoo biome is expected to suffer the greatest impact from climate change, loosing almost all of its current range (Rutherford et al. 1999). The small area of future range is projected to be disjunct from the current range, separated by mountain escarpments (Rutherford et al., 1999). In the initial models of Rutherford et al., the small area of the biome in Namibia was excluded. It is possible that the parts of the projected future habitat might have similarities to this current area, which is already hotter and dryer. However, many of the species in Namibia are highly localized endemics that probably do not have the ability for long-distance migration. An observed decline in *Aloe dicotima*, one of the most "charismatic" and conspicuous species of the succulent karoo correlates with predictions from climate change modeling.

Results from the padloper study in the succulent karoo predict that the tortoise will likely adapt to the impacts of climate change. This is because the tortoise has a broad range of food sources, and most of these are from plants that grow over a widespread area. Impacts of climate on species with localized habitats were not investigated. By contrast, the riverine rabbit from the nama karoo is predicted to go extinct because its specialized habitat and

food requirements would not be met in the future climate (G. O. Hughes et al., submitted manuscript; G. O. Hughes, personal communication).

The core of the savanna case study was an investigation on the dynamics of trees and grass, given climate change. Trees and grasses have different responses to the changes in soil moisture and temperature, and CO_2 , which acts as a fertilizer and hence facilitates growth. The CO_2 effect is more pronounced in trees than in tropical grasses, but in both cases, CO_2 begins to saturate, in natural conditions, around 500 ppm (Scholes et al., 1999). Preliminary model runs for the northeastern lowveld savanna case study suggest that the decrease in soil moisture and the increase in temperature more than compensate for the small advantage that trees have as a result of elevated CO_2 levels. A slight increase in woodiness is, however, predicted as a consequence of climate change. The key control on future habitat structure is predicted to be the size of the elephant population and impacts of fires. On the basis of the model, it is predicted that the habitat suitability for browsers and grazers is likely to remain relatively constant in the 50-year timeframe, provided that fire and elephant management is appropriate. Overall, the carrying capacity for large herbivores is projected to decrease by about 10%.

5. General Factors That Are Likely to Contribute to Vulnerability of Ecosystems and Individual Species

5.1 Flatness of topography

Altitudinal gradients and aspect both lead to changes in climate. In hilly topography with steep environmental gradients, plants and animals will only have to move short distances to

find new habitats. This has been predicted by Cowling et al. (1999), and the models of Williams et al. (2004) confirm that many of the *Protea* species respond to climate change by moving up altitudinal environmental gradients. Although altitude provides an "escape" from the impacts of climate change, a potentially negative consequence is that species may be trapped on high-altitude "islands," which prevent them from dispersing to new areas.

By contrast, on a flat topography, such as is common in the succulent karoo, the horizontal rate of climatic envelope shift will be more rapid. This will make it extremely difficult for plants to disperse fast enough to track a changing climate. This may not be a problem for widespread species that are adapted to long-distance seed dispersal and rapid establishment, but it is likely to be devastating to species with localized distributions, short range seed dispersal, or slow rates of establishment (as is found in many of the long-lived perennial species).

5.2 Availability of refugia

Small climatically suitable refugia may well support remnant populations of a species in an otherwise changed climate. These refugia are generally linked to topography. A moist south slope of a mountain could be many degrees cooler and effectively much moister than a hot north slope. Similarly, a deep river gorge could provide moisture and temperature regulation, and protection from fire. Again, the fynbos biome is far more likely to have extensive refugia than the karoo biome. The savanna biome is also likely to have a number of refugia sites.

5.3 Edaphic barriers

Most plant species are adapted to specific soil conditions and are unlikely to be able to move over barriers of unsuitable soils. Similarly, the large mammals and birds of the savanna biome tend to be "fertile soil" specialists or "infertile soil" specialists. Factors such as texture, water holding capacity, nutrient status, and acidity are likely to be the most predictive in terms of soil suitability. Mountains are likely to form barriers, and this is especially true if the substrate on the mountains is very different from the surrounding plains, as is the case of the Cape Folded Mountains, which separate the existing succulent karoo from areas of future suitable habitat. *Colophospernum mopane*, a common species of the low-lying and hot savanna areas, is predicted on the basis of its climatic envelopes to expand extensively with global warming (Rutherford et. al., 1999), but may will show little or no response, as the species appears to be limited to the heavy soils of river valleys (Scholes, 1997).

5.4 Land transformation and habitat fragmentation

The combined impacts of habitat loss through land transformation and climate change will make some species exceptionally vulnerable. The West Coast renosterveld of the fynbos has for instance already lost an estimated 97% of its habitat (Low and Rebelo, 1996). Many species struggle to migrate over transformed habitats, and just 100 m of cropland may be sufficient to prevent dispersal of some *Protea* species (Williams et al., 2004). Land transformation is typically most severe in areas suitable for crop production, and these are often the relatively flat areas (Haplin, 1997).

5.5 Plant life history characteristics

A large number of plant life history characteristics are likely to impact on species vulnerability to climate change. Some of these are discussed below.

5.5.1 Niche specialists versus generalists. Species with broad climate tolerances are less likely to be impacted than specialist species with narrow habitat niches. This is well illustrated by the Proteas, of which a number of species maintain habitats into the future, while for others, the habitat niche disappears (e.g., Williams et al., 2004, Midgley et al., 2002a, b). This is illustrated for animals by the case studies of the padloper tortoise and riverine rabbit (G. O. Hughes et al., submitted manuscript; personal communication).

5.5.2 Seed dispersal. For the obligatory dispersers, that is, those species that will have to move to find new habitats, seed dispersal is the key to movement. Wind, animal, bird, and water dispersal can lead to long-range dispersal of hundreds of meters or even kilometers. By contrast, many of the Proteas have ant-dispersed (myrmecohory) seed (Bond and Slingsbey, 1983), and this will greatly limit the distance that the species can move in any single generation. Many seeds have no long-distance dispersal mechanisms and tend to concentrate very close to the parent plant.

Animals and insects also differ in their movement, some birds and large mammals may travel hundred of kilometers, while others may be limited because of mobility or their reluctance to cross changed habitats. Samango monkeys, for example, though highly mobile, will not cross extensive open ground to move from one forest patch to another.

5.5.3 Species interactions: Competition and facilitation. Species will not move as total habitats (Hannah et al., 2000). Rather individual species in a habitat will move at different rates. When moving into a new area, a species is likely to experience new competition forces from those species already present. The impacts of this are exceptionally difficult to understand or model.

5.5.4 Dependency on pollinators and dispersers. Where species have a mutual dependency on a pollinator or seed disperser, then both organisms will have to adapt simultaneously to climate change for the long-term sustainability of each. Where there are generic pollinators such as the honey bee, the risk is far less. Obligatory pollinators and seed dispersers are common in the fynbos and succulent karoo, but relatively rare in the savanna (e.g., Milton et al., 1997; Cowling et al., 1997)

5.5.5 Species establishment. The establishment niche (Grubb, 1977) will be a key limiting process for many species. Once established, many species may well be able to cope with slightly modified climatic niches. This is well illustrated by the number of garden trees that once established growth way outside of their natural climatic niche. The time to seed set will also be important. If a plant takes many years to reach maturity and fruit, it may be more vulnerable to the impacts of climate change than an annual species.

5.5.6 Species longevity. It is probable that many species will be able to persist in a changed climate if they are already established. Some long-lived species may be able to persist for centuries, and if climate change mitigation is successful, may able to persist until

conditions are more optimal for regeneration. Short-lived species are likely to be more severely impacted and could go extinct within a few generations.

5.5.7 Seed ecology. Although poorly studied in South Africa, it is known that some species require a cool period to stimulate germination. Climatic warming could negatively affect such species ability to germinate. In the succulent karoo plant species seem to be dependent on seasonal rainfall for germination.

5.6 Impacts of alien invasive species

Alien invasive species are posing a strong threat to some biomes, most notably the fynbos. Any indigenous species attempting to establish in a new habitat may have to compete with alien vegetation that is simultaneously moving into the new niche. It has been suggested that invasive alien species may invade more rapidly under conditions of climatic change, as they are frequently opportunistic species adapted to a wide range of habitats (Macdonald, 1994)

5.7 Impacts of fire and herbivory

Both the fynbos and savanna are fire-dependent ecosystems (Cowling et al., 1997, Rutherford and Westfall 1986, Scholes 1997). Any change that changes fire frequency or intensity will change the dynamics of these systems. The succulent karoo is not adapted to fire, and fire limits the spread of succulent karoo species into habitats where fire occurs.

5.8 Impacts of misaligned conservation strategies

Strategic conservation planning typically attempts to ensure that all current habitat types are conserved in at least one location. Climatic change will result in new species assemblages and it is likely that the spatial location of at least some of the species will change. As a consequence, it is likely that in the future, the current conservation network may not adequately protect biodiversity. In addition, the alignment of current reserves, which may be well aligned to maintain static biodiversity, may be poorly aligned to facilitate the movement of biodiversity, or may not cover the biodiversity refugia of the future. It may be better to protect gradients and transitional areas rather than, or in addition to, core areas (Peters and Darling, 1985; Haplin, 1997; Hannah et al., 2002; Williams et al., 2004). Strategic expansion of the conservation network may be needed to ensure effective conservation in a changing environment. Enhancing conservation outside of the protected areas (what is sometimes referred to as managing the matrix), may be even more important. The only South African biome where this has been studied in any detail is the fynbos case study of this AIACC project (Williams et al., 2004). This study found that for effective conservation, a doubling of the current conservation network is needed. It also recommends the conservation of "persistence areas," those areas that remain suitable over time despite climate change.

On the basis of the literature, our case studies, and the rationale presented above, it is predicted that the species in the succulent karoo are likely to be more vulnerable to climate change than those of the savanna or fynbos. This is primarily because of the extent of impact that climate change is likely to have on this habitat, but this will be compounded by

factors, including the relatively flat topography, the influence of edaphic factors specialist pollinators, and the slow rate of re-establishment of long-lived perennial species.

Impacts on the fynbos will, to some extent, be mitigated by the mountainous terrain, but individual species studies indicate that some of species loss is still probable. The high level of transformation in the lowland fynbos habitats makes species in these habitats especially vulnerable.

By contrast, the savannas, as a system, are considered to be less vulnerable to climate change. We did not study individual species in this biome, but the analysis of functional groups suggests that most of the functional aspects are likely to be maintained. Direct impacts on individual species are less certain and currently unstudied, but our prediction, based on the factors likely to have an impact on biodiversity as presented above, suggest that the biodiversity of the savanna biome is less likely to be severely impacted than the fynbos and karoo because of the widespread and generalist nature of most savanna species.

6. Human Dependencies on Biodiversity From the Selected Biomes

Biodiversity has an intrinsic value, but it also has a direct and indirect human benefit value. It currently contributes to human livelihoods in the succulent karoo, fynbos, and savanna. It also contributes to human well-being of people who live outside these areas, but who, for instance, visit them as tourists, or use medicinal or horticultural products derived from them. The value of biodiversity to human well-being is poorly researched. An initial attempt is made here to predict likely impacts from climate-induced biodiversity change on

livelihoods based on use of biodiversity. This is done on a biome basis for our three case study biomes.

6.1 Succulent karoo

This near-desert area has low plant production potential and a very low human population density. It has historically been used prominently for livestock grazing, though even with borehole water it is still an inhospitable environment. Livestock stocking rates have decreased over the last two decades, and this is attributed to species changes in response to herbivory (Dean and McDoanald, 1994; Milton et al., 1997). It can be assumed that with increasing aridity, as predicted by most climate models, that this area will become less suited to livestock production. Changes in the global economics of livestock production are likely to exacerbate this impact.

Increasingly, the succulent karoo has been used by the tourism industry for ecotourism during its annual wild flower blooms. These blooms are all from annual species, mostly of the families Asteraceae, Liliaceae, and Mesembryanthemaceae. The extent of these blooms is related to seasonal rainfall. A decline in rainfall, or shift in seasonality of rainfall, may therefore have a direct impact on this industry.

6.2 Fynbos

The fynbos is an area of high human population, especially on the plains, although the mountains have relatively low population density. Transformation to agricultural and settlement has had strong impacts on biodiversity, but natural biodiversity per se is not the basis of the main economic activity in the biome. Individual species of the fynbos are extensively used for the cut flower and dry flower industry, for flavoring brandy (buchu)

and for herbal tea (rooibos tea). The vegetation is also used for fuelwood, although much of this is from alien invasive species. Changes in availability and location of the commercializable species will impact directly on these industries. In addition, the fynbos is a major tourist attraction, although how closely tourism can be linked to actual species biodiversity is unclear and is unlikely to be a linear relationship. Loss of biodiversity is unlikely to be measured in direct loss of tourism.

6.3 Savanna biome

The savanna biome is used predominantly for livestock grazing or wildlife management, including nature-based tourism. There is a growing literature on the importance of the savannas for the provision of livelihood benefits to poor rural communities (e.g. Campbell, 1996; Shackleton et al., 2004). Within South Africa, most of the communally managed areas occur in the savannas, and these have extensive rural communities that derive a large proportion of their livelihoods from the natural biodiversity of the savanna. This trend is even more prevalent in other southern African countries where there is less of a cash economy and a poorer state social support network. By far, the most important resource from the savannas to these subsistence communities is fuel wood and grazing, although many other resources, including construction timber, edible plants, medicinal plants, and craft material are also collected. Although specific species may change, it is likely that the range of services derived from savannas will still be maintained (though possibly at a somewhat lower level), but because of climate, these areas may become less hospitable to crop production, and hence, reliance on natural products may increase.

The potential of the savannas to support a wildlife-based tourism industry is not envisaged to collapse as a consequence of climate change. The same is probably true of the livestock industry, although climate change may accelerate the current change that is being observed in areas where there is a switch from livestock to wildlife management. This switch is predicted as a result of greater resilience of wildlife in a hot environment and the possibility of increased problems from pathogens.

7.0 Conclusion

The vulnerability of individual species depends on the interaction between the magnitude of the impact and the adaptive capacity of the species. Two South African biomes, the fynbos and succulent karoo, are predicted to be the most vulnerable to projected climate changes in the 21st century, while the savanna is predicted to be more resilient. The plant species-rich succulent karoo is at risk, partly because of the magnitude and nature of the projected climate change (in the most extreme scenarios, the climate niche that it currently occupies is not represented in the future) but also because the relatively flat topography, which does not provide altitudinal or aspect-based refugia. This means that species need to disperse very rapidly to keep track with a changing environment. Their capacity to do so is constrained by their strong soil specificity, in this geologically complex location. The slow establishment rates of many long-lived species place them at greater risk than annual species with more rapid establishment and greater seed dispersal. Not only is there a large probability of extensive species loss, but in addition, the biomes ability to support livelihoods is expected to decline.

Within the fynbos, the extent of species loss may exceed that predicted from simply considering the loss of habitat, but it is predicted to be less severe than in the succulent karoo. The complex reproduction ecology of many of the species adds to the species vulnerability, and this is not taken into consideration in simple climatic envelope-based modeling predictions. Species loss is an important concern considering the international importance of this biome as an international biodiversity hotspot. The mountainous terrain of the biome will, to some extent, assist in the adaptation to climate change. Economic sectors depending on the biodiversity, such as the wild flower industry, may suffer severe impacts from climate change.

A key consideration in both fynbos and succulent karoo biomes is the close and obligatory association between species, for instance between plant species and their pollination and seed dispersal agents. The entire suite of organisms would have to move jointly in response to a changing environment for the long-term integrity and viability of the community and its constituents. The current knowledge base and models are not adequate for this analysis.

The savanna biome is predicted to have relatively limited functional or species change. Although the biome overall is species-rich, the mean range size of the organisms is large (i.e., the same species are found over extensive areas and across a wide climate niche). The diverse mammals and birds for which this biome is world renowned are relatively mobile and not highly dependent on particular plant species, but on broad functional categories of plants, which are projected to persist. There is some evidence that enhanced CO_2 may promote C3 trees over C4 grasses, but our models suggest that this effect may be overwhelmed by differences in the temperature and water response functions between trees

and grasses. In interaction with changing fire regimes and elephant densities, this could impact savanna structure, which would have consequences for savanna habitat structure and the proportions of various species in the community, though not necessarily their persistence The ability of the biodiversity of the savanna biome to support rural subsistence livelihoods or the wildlife and tourism industry is not expected to change very substantially, although climate change may accelerate the current shift from cattle to wildlife ranching.

From a human vulnerability perspective, it is the savannas that have the highest density of human settlement, and it is these areas where there is a high dependency on the use of the savanna resources, particularly for fuel, but also for numerous other livelihood-enhancing products. These areas are also exceptionally important for their support of nature-based tourism and wildlife-based production. By contrast, the fynbos and succulent karroo has a lower level of subsistence livelihood dependency, though a number of enterprises have developed around the commercial harvesting of particular plant species, such as *Proteaceae* for the flower market, and herbal teas and brandies.

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