Review

Temporal biodiversity change in transformed landscapes: a southern African perspective

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Landscape transformation by humans is virtually ubiquitous, with several suggestions being made that the world’s biomes should now be classified according to the extent and nature of this transformation. Even those areas that are thought to have a relatively limited human footprint have experienced substantial biodiversity change. This is true of both marine and terrestrial systems of southern Africa, a region of high biodiversity and including several large conservation areas. Global change drivers have had substantial effects across many levels of the biological hierarchy as is demonstrated in this review, which focuses on terrestrial systems. Interactions among drivers, such as between climate change and invasion, and between changing fire regimes and invasion, are complicating attribution of change effects and management thereof. Likewise CO₂ fertilization is having a much larger impact on terrestrial systems than perhaps commonly acknowledged. Temporal changes in biodiversity, and the seeming failure of institutional attempts to address them, underline a growing polarization of world views, which is hampering efforts to address urgent conservation needs.

Keywords: landscape change; biological invasions; conservation; fire; shrub encroachment; CO₂ enrichment

1. INTRODUCTION

Transformation of the structure and functioning of landscapes and ecosystems by humans is extensive. In terrestrial systems, the scale thereof has led to calls for the replacement of the more usually recognized biomes with a set of anthropogenic biomes, which cover more than 75 per cent of ice-free land and include 90 per cent of its net primary productivity (NPP; Ellis & Ramankutty 2008). Although some areas may yet be considered untransformed or wild (Sanderson et al. 2002), human activities have influenced these too. The impacts of anthropogenic climate change are almost ubiquitous (Parmesan 2006; Le Roux & McGeoch 2008; Lantz et al. 2009), or are forecast soon to become so (Deutsch et al. 2008), and very few regions globally are free of non-indigenous species, many of which have transformed the structure and functioning of the systems they have invaded (Mooney & Hobbs 2000; Blackburn et al. 2004; Frenot et al. 2005).

The biodiversity consequences of human impacts have recently been summarized in several large studies and reviews (e.g. Millennium Ecosystem Assessment (MEA) 2005; Parmesan 2006; Butchart et al. 2010). Notable among their many common messages is the absence of information for numerous areas and the influence that this might have on policy, which, irrespective of whether or not it is agreed by international convention, can only be given effect to by national legislation and rigorous implementation thereof. This information deficit is non-random, and related either directly or indirectly to the development status of the area or country concerned (e.g. McGeoch et al. 2010). At times it may also not be recognized explicitly. For example, in Root et al.’s (2003) review of climate change impacts, of the 143 examples used, less than 15 are from the Southern Hemisphere. While the extent of information is increasing rapidly for some areas (e.g. Hughes 2003; Mac Nally et al. 2009a,b), its absence in many others is concerning for several reasons, of which two are most notable.

First, nationally relevant demonstrations of impacts and their socio-economic consequences are often required to galvanize meaningful national responses (Braschler et al. 2010). Although at first this might appear to be partly a consequence of differences in scientific literacy among officials from various states, the position of small-island states relative to others in the climate change mitigation debate suggests otherwise. Moreover, without locally appropriate information, adaptation and mitigation practices are unlikely to succeed (Collier et al. 2008). While this might seem self-evident, it is typically not translated into science budgets in areas that are facing some of the most significant change, and often at rates faster

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than the global average. From a continental perspective, Africa is a notable example, having among the fastest rates of climate change, tropical forest removal and human population growth, and the lowest science budget votes on average (Collier et al. 2008; Pellikka et al. 2009).

Second, as Gore (1992, p. 37) succinctly recognized: ‘...even though we already know more than enough, we must also investigate any significant uncertainty’. Such uncertainty is commonplace. For example, the role of changing climates, relative to human development and changes in disease control interventions, in altering the nature and the extent of vector-borne disease prevalence is widely debated (Rogers & Randolph 2000; Patz et al. 2002; Lafferty 2009; Pascual & Bouma 2009), with the basis in data being very narrow in some instances (see Zhou et al. 2004; Hay et al. 2005; Paaijmans et al. 2009; Pascual et al. 2009). Similarly, although the fundamentals of biochemistry and ecology remain spatially unchanged, how these translate upwards into larger scale patterns of biodiversity variation and likely responses to change is spatially highly variable, often on very large, and sometimes unrecognized scales. Two examples serve to illustrate this point. First, the upper thermal tolerance limits to performance of ectotherms show narrow variation across the planet, especially by comparison with lower limits (Addo-Bediako et al. 2000; Gaston et al. 2009). In addition, environmental maximum temperatures are close to the limits of performance in tropical and sub-tropical ectotherms (Deutsch et al. 2008). Even small temperature increases are likely to cause extinction in these areas (Huey et al. 2009), especially because environmental maxima are spatially invariant across the tropics (Gaston & Chown 1999). Thus, migration is less suitable a response than it might be in temperate areas. Second, across a range of levels in the biological hierarchy, patterns in and processes underlying variation differ fundamentally among the hemispheres. North–south differences in responses to low temperature in insects, thermal tolerance in algae, life history and range size patterns of birds, and spatial variation in biodiversity and its underlying causes have all been documented (Chown et al. 2004; Orme et al. 2006; Fernández et al. 2009). Such variation has important and often unappreciated implications for forecasting and investigating environmental change-related impacts, though at times this might not be recognized (Simmons et al. 2004).

Bearing the importance of spatially explicit information on temporal changes in biodiversity in mind, this review therefore highlights several such changes that are largely the consequence of human activities in the terrestrial systems of southern Africa. The aim is not to be comprehensive, but rather to highlight significant examples of change associated with each of the broadly recognized global environmental change drivers—habitat alteration, exploitation, climate change, biological invasions and pollution (Millennium Ecosystem Assessment 2005). In some cases, information from this region has been instrumental in understanding the form of and mechanisms underlying temporal turnover in biodiversity associated with a particular driver (notably the dynamics and impacts of biological invasions—Richardson et al. 2000; Richardson & van Wilgen 2004; Wilson et al. 2009a). In others, the impacts of these drivers and their interactions with each other, and the influence thereon of conservation management responses remain less well appreciated.

2. HABITAT ALTERATION

Although western and central Botswana and the coastal regions of Namibia have been identified as among the last of the wild areas of the planet (Sanderson et al. 2002), much of the rest of southern Africa has been subject to extensive transformation, mostly through conversion to croplands and rangelands, as well as to urban areas (Fairbanks et al. 2000; Ellis & Ramankutty 2008). Habitat conversion for agriculture (including forestry) and urban settlement have had the largest impacts on the landscape and on biodiversity (Scholtz & Chown 1993; Biggs & Scholes 2002; Latimer et al. 2004; Biggs et al. 2008), and are predicted to continue to have substantial impacts into the future. Under the most extreme scenario of land-use change, by 2100 the condition of biodiversity (or its intactness) will have declined from about 90 per cent (in the 1990s) compared with untransformed areas, to 60 per cent, with the most profound changes occurring among amphibians and plants (Biggs et al. 2008). Poorly studied and poorly developed but biodiverse areas, such as Angola, are likely to show most change.

Temporal changes in biodiversity as a consequence of landscape transformation have typically been demonstrated by using space for time substitutions, with comparisons made among relatively untransformed protected areas (though see below) and matched transformed areas, with a few studies encompassing larger extents. These studies generally show substantial differences in richness, abundance and/or diversity among the protected/relatively untransformed areas and adjacent transformed landscapes (Samways & Moore 1991; van der Merwe et al. 1996; Gebeeyehu & Samways 2002; Meik et al. 2002; Fabricius et al. 2003; Davis et al. 2004; Witt & Samways 2004; O’Connor 2005; Botes et al. 2006; Blaum et al. 2007a,b, 2009; Krook et al. 2007; Sirami et al. 2009; Wallgren et al. 2009). However, the effects are rarely linear, and often depend on the trophic group and/or habitat preference of the taxon concerned (Krook et al. 2007; Greve et al. submitted), interactions among different biodiversity components (see Keesing 1998; Yarnell et al. 2007; Samways & Grant 2008; Hagenah et al. 2009), or the kinds of human interventions or impacts involved across the areas studied (Fabricius et al. 2003; O’Connor 2005; Botes et al. 2006, figure 1). Nonetheless, substantial changes to biodiversity have taken place in transformed areas by comparison with adjacent untransformed landscapes. At large spatial extents (and a quarter degree grid cell resolution), the efficacy of protected areas is reflected in a richness decline of ca 37 and 21 bird species in high and low NPP areas, respectively, in cells without any conservation
by comparison with those completely conserved (Evans et al. 2006a). The latter also often retain large-bodied species, now absent from the former (Greve et al. 2008). These studies demonstrate the value of protected areas in conserving diversity in the region (for general review of protected area efficacy see Gaston et al. 2008). Moreover, such space for time-substitution approaches often serve as the only means for doing so.

A variety of investigations of the impacts of human interventions on biodiversity through time have also been conducted in the region. Many involve the documentation and identification of the causes of shrub (or, colloquially, bush) encroachment, and the importance of interactions between ungulate density (or grazing and browsing intensity), fire regimes and rainfall, all of which are considered major drivers of vegetation dynamics (and other aspects of biodiversity dynamics) in the savannas, grasslands and shrublands that dominate the region (O’Connor & Roux 1995; Jeltsch et al. 1997; Roques et al. 2001; Parr et al. 2004; Govender et al. 2006; Owen-Smith & Mills 2006; Higgins et al. 2007; Asner et al. 2009; Hagenah et al. 2009; Staver et al. 2009; Todd & Hoffmann 2009; see also the review by Bond 2008). These studies include some of the longest running tropical ecology experiments (van Wilgen et al. 2003; Bond 2008) and have provided considerable insight into the biodiversity influences of management regimes in conservation areas. At least in savanna areas, they have also shown

Figure 1. (a) Shrub encroachment effects on the abundance of rodents (open circles, dashed line) and species richness of small carnivores (filled squares, solid line) in the Kalahari Desert. Redrawn from data provided in Blaum et al. (2007a,b). (b) Non-metric multi-dimensional ordination of dung beetle diversity illustrating the difference between two undisturbed habitats (Sand Forest (USF 1998, 2000) and Mixed Woodland (MW 1998, 2000)), and Sand Forest disturbed by elephants (EDSF 2000) and by human utilization (HDSF 1998). Open squares, MW 1998; open circles, MW 2000; filled squares, USF 1998; filled circles, USF 2000; filled triangles, HDSF, 1998; stars, EDSF 2000. Redrawn from Botes et al. (2006).
how different the interactions between rainfall, vegetation structure, ungulates and their predators are in these southern African systems compared with their East African counterparts (Owen-Smith & Mills 2006, 2008; Hopcraft et al. 2010; Stock et al. 2010). Thus, Roques et al. (2001) documented substantial (up to 40% increase), but variable changes in shrub cover across several land-use types over a 50 year period in a Swaziland savanna system. Frequent fires appeared to preclude encroachment (see the fire trap mechanism discussed by Higgins et al. 2007), with an increase in grazing pressure leading to a reduction in fire frequency and shrub encroachment. In the Hluhlwe-iMfolozi savanna studied by Bond and co-workers (e.g. Archibald et al. 2005; Krook et al. 2007; Staver et al. 2009; Stock et al. 2010), browsing and fire limit tree density. By determining the spatial distribution of grazers, fire also alters the balance between short grazing lawns and bunch-grasses, favouring the latter and so probably leading to a change in other components of diversity in this dynamic system. In the Kruger National Park savanna, exclusion of herbivores leads to a short-term increase in herbaceous cover in nutrient-rich areas, and a long-term increase in woody vegetation, with downstream effects on other biodiversity components (Asner et al. 2009).

Frequent burning, often justified as a means to provide forage for grazers, may in fact limit the extent of the short-grass habitats preferred by these species (Archibald et al. 2005). Indeed, the impacts of fire regimes on biodiversity and productivity have long occupied land managers in southern Africa (e.g. reviews by van Wilgen 2009a, b). In the Kruger National Park, a series of experimental fire treatments was established in 1954 and has been maintained ever since (van Wilgen et al. 2003). Typically, fire causes a change in tree structural diversity, favouring dominance by small trees, while tree density is not responsive to fire. Changes in fire return interval (or frequency) and season of fire have significant effects on small tree dominance, whereas the former, and landscape type (varying from dry to wet), have an influence on total tree biomass (figure 2). By contrast, ant assemblage structure (richness, abundance and identity) is influenced only by whether a plot has burned or not, and not by the specifics of the burn treatment, although landscape productivity clearly also has effects on richness (Parr et al. 2004; Parr 2008). Management activities thus benefit from these experiments because they provide explicit information on the influence of timing, season and frequency of burns on diversity in landscapes of different productivity.

A final example of the analysis of long-term data on the impacts of habitat transformation illustrates how, within protected areas, management interventions can have substantial, though entirely unintended consequences for species of conservation significance. Between 1986 and 1995, the abundance of Roan antelope and Sable antelope declined precipitously (450 to 45 animals, and 2000 to ca 500 animals, respectively).

Figure 2. The effects of fire return interval (FRI; in years), season (Se; months of the year indicated by letters) and landscape productivity (Ls; from lowest to highest rainfall: MO, Mopani; SA, Satara; SK, Skukuza; PR, Pretoriuskop) on changes in the dominance of small trees following experimental burning regimes over a 40 year period in the Kruger National Park savanna. Redrawn from Higgins et al. (2007).
in the Kruger National Park. The decline was thought to be a consequence predominantly of substantial drought in the Park (Ogutu & Owen-Smith 2003) and this is an important contributing factor. However, further analyses (Harrington et al. 1999; McLoughlin & Owen-Smith 2003; Owen-Smith & Mills 2006) revealed that the provision of water points by managers in the drier, medium–tall grass areas of the park preferred by these species had led to an influx of water-dependent Burchell’s Zebra and Blue Wildebeest. The influx in turn precipitated an increase in Lion density, the major predator of large-bodied ungulates in the park (Owen-Smith & Mills 2008). Increasing predation was therefore a key factor, in combination with drought, leading to the decline in Roan and probably also Sable abundance. On this basis, Harrington et al. (1999) called for a review of the policy of augmenting water supplies for wildlife, and in the Kruger National Park substantial changes to the policy have been effected.

3. EXPLOITATION
Terrestrial impacts of exploitation, combined with land-use change, on vertebrates in the region are perhaps best reflected by the substantial differences in the numbers of ungulates seen in the landscapes of the region today by comparison with the 1800s. Arguably one of the clearest documentations of the change comes from the work of C. J. Skead, who converted old accounts of game numbers in the Eastern Cape of South Africa to realistic estimates of abundance (Skead 2007). By comparison with the late eighteenth and nineteenth centuries, the number of large mammals is now much depleted.

Exploitation of vertebrates (and other components of biodiversity) for subsistence continues in many areas across southern Africa (Shackleton & Shackleton 2004; Fusari & Carpaneto 2006; Kroom et al. 2007; Hayward 2009), but the emphasis has also changed with the growth of ecotourism and commercial hunting in the region (Van der Waal & Dekker 2000; Reilly et al. 2003; Carruthers 2008). While both activities clearly have conservation benefits, and are often argued in favour of because of these benefits (for discussion see Castley et al. 2001; Van der Merwe & Saayman 2003; Lindsey et al. 2006, 2007), they may also have disadvantages. For example, in the case of Lion, a single hunt may fetch up to US$ 130 000 (Loveridge et al. 2007), and it has been argued, on the basis of analyses and data from East Africa, that as long as males older than 5–6 years old are hunted, population growth can be sustained (Whitman et al. 2004). By contrast, in the Hwange National Park in Zimbabwe, males mature later than in East Africa, and even so, more than 30 per cent of the marked males that were killed by hunters were younger than 4 years (Loveridge et al. 2007). The hunting typically also caused territorial turnover, with one home range successively filled four times during the course of the 6 year study. Infanticide associated with territorial turnover was observed, and hunters also shot female lions. Together with increasing hunting off-take, changes in cub sex ratio and other forms of mortality (inadvertent mortality in snares), these practices suggested that the population may well be vulnerable in the region, with all the associated consequences given the role of this large predator in southern African savanna systems (Owen-Smith & Mills 2006, 2008).

By complete contrast, the enthusiasm for increasing game diversity in particular areas is also having pronounced impacts in the region, largely by causing substantial changes in the ranges of many species. In the case of ungulates, range changes associated with the introduction of species to new areas, largely for ecotourism and hunting purposes, far outweigh any change that might be associated with changing climates in the region (Spear & Chown 2009a). Moreover, the movement of species to new areas is leading to homogenization of the fauna (Spear & Chown 2008). Between the early 1970s and the early 2000s, the ungulate fauna has increased its similarity among quarter-degree grid cells in South Africa by 6 per cent (figure 3). Homogenization has impacts distinct from those typically associated with invasions by single species (see Olden et al. 2004), but nonetheless also indicates the extent to which single species impacts might be concatenated. For example, Bond & Loffell (2001) showed that the introduction of Giraffe, a megaherbivore popular with tourists, to Ithala Game Reserve, an area where it was probably absent historically, is having substantial impacts on three Acacia tree species in the reserve, with one of the species showing complete mortality in those areas accessible to Giraffe. This outcome is in keeping with a global assessment of the consequences of ungulate introductions, where impacts on vegetation are often substantial (Spear & Chown 2009b).

4. CLIMATE CHANGE
Terrestrial systems across southern Africa show substantial spatial variation in average annual precipitation and its variability, as well as a quasi-periodic cycle of about 18 years (Tyson & Preston-Whyte 2000). Perhaps unsurprisingly, therefore, temporal variation in rainfall contributes significantly and often substantially to the population dynamics of a variety of southern African species (O’Connor & Roux 1995; Davis 1996; Little et al. 1996; Dean 1997; Lloyd 1999; Todd et al. 2002; Radford & DuPlessis 2003; Craig et al. 2004; Seely et al. 2005; Owen-Smith & Mills 2006; Thomson et al. 2006; Yarnell et al. 2007; Altwegg & Anderson 2009). Spatial differences in water availability are also significant contributors to correlative models of species distributions, species richness and patterns of vegetation structure, although spatial variation in temperature (typically minima, means and sometimes variability) and landscape heterogeneity are also important (O’Brien 1993; Lloyd & Palmer 1998; Andrews & O’Brien 2000; Erasmus et al. 2002; van Rensburg et al. 2002; Rouget et al. 2004; Richardson et al. 2005; Evans et al. 2006b; Mucina & Rutherford 2006; Thuiller et al. 2006a). Changes in these variables (as well as in composites such as evapotranspiration) therefore should have large influences on species distributions and on species richness in the region, and
many forecast-based studies suggest that this is likely to be the case (Erasmus et al. 2002; Hannah et al. 2005; Thuiller et al. 2006b,c; Coetzee et al. 2009, but see also Keith et al. 2008). However, predictions for and realized changes in temperature have been more straightforward to make and document, respectively (e.g. New et al. 2006; Knoesen et al. 2009), than those for rainfall (MacKellar et al. 2007; Knoesen et al. 2009). Thus, what the actual outcome of change will be in many areas is not simple to forecast (e.g. Hoffmann et al. 2009). Sound documentation of temporal changes in terrestrial diversity associated with climate change would therefore appear to be a pressing concern, and extensive records thereof in the literature might, in consequence, be expected.

Curiously, information on changes in some component of life history or distribution that is attributable to climate change is uncommon for the region. Perhaps, the most widely known example is the change in demography of the tree aloe, Aloe dichotoma, across its distributional range in western South Africa and in Namibia, which appears to be in keeping with expectations from forecast models for the region (Foden et al. 2007). A comprehensive dataset on changes in altitudinal range over a 40 year period also exists for indigenous vascular plants of the sub-Antarctic Marion Island (which geopolitically forms part of South Africa—see Chown & Froneman 2008). Over the period, an increase in upper elevational limit of 3.4 m yr$^{-1}$ on average has occurred, with one species showing a 388 m increase (Le Roux & McGeoch 2008; figure 4). Among terrestrial vertebrates, the only range extension currently ascribed to climate change is for the Common Swift (Hockey & Midgley 2009).

Common Swift is one of 18 species that have extended their range to the Cape Peninsula over the past 60 years, but it is the only one for which a combination of increasing afforestation, availability of water (through dams and other irrigation schemes) and urbanization cannot explain the range shift (Hockey & Midgley 2009). Indeed, these authors caution that range shifts in the region should be examined carefully for the extent to which human development factors may be the underlying cause of range shifts, before attributing these to climate change, so echoing similar concerns relating to climate-related changes in vector-borne diseases on the continent (Craig et al. 2004; Lafferty 2009). Claims have also been made for climate change-related range shifts in various invertebrate species (Giliomee 2000), but at least some of these have been the subject of contention (Geertsema 2000).

5. INVASIONS

Biological invasion by vascular plants is arguably one of the most comprehensively investigated global change drivers for the region, largely because of extensive work undertaken in South Africa. Indeed, the country has a long history of research in the area, which has contributed substantially to the development of the field of invasion biology (MacDonald et al. 1986; Richardson et al. 2000; Rouget & Richardson 2003; van Kleunen et al. 2008; Wilson et al. 2009a). Investigations either using space for time substitutions, or involving time series have shown not only how non-indigenous species have moved from being alien to invasive, but have also documented a wide range of impacts on biodiversity at a range of levels (Richardson & van Wilgen 2004; Gaertner et al. 2009). The focus has not only been on changes to biodiversity as a consequence of species entering the country, but also on traits, vectors and pathways that enable species from South Africa to alter biodiversity in other regions (Thuiller et al. 2005; van Kleunen & Johnson 2007; Lee & Chown 2009).
Although biological invasions by animals have perhaps been less extensively investigated (though e.g. Robinson et al. 2007; Shelton et al. 2008), temporal changes at a number of spatial scales have been explored. Range expansion of the Painted Reed Frog into the Western Cape has also been well documented, and the underlying causes of the expansion shown to be less than straightforward (Tolley et al. 2008). Thus, populations of this species in the far Western Cape are clearly a mixture of three genotypes from areas across the country, and a consequence of human introduction. By contrast, in the eastern part of the Western Cape, it appears that newly documented localities for the species are probably a consequence of range extension from the most westerly part of the range, possibly owing to a shift in rainfall patterns and to the construction of small dams on farmlands. Thus, the range expansion includes aspects of direct human movement of the species, indirect facilitation and climate change. Such complex dynamics are forecast to be an increasing feature of future biological invasions across the globe (Walther et al. 2009).

Similarly complex interactions among human activities and invasion seem to be favouring the ongoing transformation of the fynbos biome (a globally significant biodiversity hotspot) by alien pine species, which are also grown commercially as plantation species in the region and elsewhere in the country. Because pines are serotinous, fires stimulate seed release and soil-stored seeds are stimulated to germinate by fire. An increase in fire frequencies in the region (Forsyth & van Wilgen 2008) and an absence of seed-feeding biological control agents (because of industry concerns) suggest that substantial additional transformation of this area by pines, which form dense stands even in the absence of other human disturbance, can be expected (van Wilgen 2009b). If fynbos is to be conserved, in keeping with various conservation strategies for the country, the costs of unplanned fires in the region could amount to an additional US$ 13 million annually (i.e. above the current substantial investment made by local conservation organizations and the national Working for Water programme; van Wilgen 2009b).

6. POLLUTION
The effects of heavy metal and pesticide pollution and nutrient loading have been the subject of a variety of studies in the region, most notably using longitudinal investigations of freshwater systems or comparable kinds of space for time substitutions, although monitoring of abiotic variables stretches back to the early twentieth century (Davies & Day 1998; Dallas et al. 1999; Dabrowski et al. 2002; de Villiers 2007; de Villiers & Thiart 2007; Reinecke & Reinecke 2007; Chakona et al. 2009; de Villiers & Mkwele 2009). In many cases, freshwater systems show exceptionally high levels of nutrient (especially P) loading.
A substantial programme of monitoring of river health in the country has been undertaken at least since the 1990s, including assessments both of abiotic variables and of changes in biota typically using a family-level, invertebrate-based scoring system (the South African scoring system or SASS, Davies & Day 1998; Dallas et al. 1999; Roux 2001). Similar studies have now commenced on other pollutants such as endocrine-disrupting compounds, though these are more recent, with much less temporal extent (e.g. Swart & Pool 2007). In terrestrial systems, the likely significance of nutrient loading, and other forms of pollution from aerial sources, has frequently been noted, but the number of studies of effects on diversity is low (van Tienhoven & Scholes 2004; Wilson et al. 2009b).

Although typically not thought of as a form of pollution, but more a contributor to climate change, alterations in CO₂ concentrations (or carbon loading of the atmosphere) may nonetheless be having a profound effect on southern terrestrial systems. While acidification in marine systems is a topic of substantial concern globally (Orr et al. 2009; Hendriks et al. 2010), and the impacts of changes in C:N ratios and stomatal conductance are being widely investigated (Coviella & Trumble 1999; Bett et al. 2007; Piao et al. 2007; Valkama et al. 2007), other potential impacts on terrestrial systems may be less well appreciated. For example, the contribution of increasing CO₂ concentrations to ongoing shrub encroachment has been the source of some controversy (Boutton et al. 1994; Archer et al. 1995). Experimental work from the sub-region has demonstrated that increasing CO₂ concentrations certainly promote woody plant growth (e.g. Kgope et al. 2010) and a carbon allocation, physiological mechanism generally bears out this expectation (Bond & Midgley 2000). Indeed, changing CO₂ concentrations (along with fire, precipitation changes and the evolution of grazers) probably had a major impact on the past (as far back as the Miocene) extent and spread of grasslands and savannas (Bond et al. 2003; Beerling & Osborne 2006; Kgope et al. 2010). To date, however, it has proven difficult to disentangle the impacts of land-use variation (i.e. extent of grazing and browsing), fire frequency, rainfall variation and CO₂ concentration on shrub encroachment. However, a study from the Hluhluwe Imfolozi area (see §2) across three very different land-use types, and using a time series covering the period 1937–2004, has shown that irrespective of land use, shrub/tree encroachment has taken place, and dramatically so (Wigley et al. 2010). Tree cover increased over the period from 14 to 58 per cent in the conservation area, 3 to 50 per cent on a commercial farm and 6 to 25 per cent in a communal grazing area. These areas all have very different grazing pressures and fire regimes, and have shown no systematic trend in rainfall variation. Likewise, although nitrogen deposition may be a driver of the change, the herbaceous component should have been more responsive, leaving the only explanation an increase in CO₂ concentration (Wigley et al. 2010). If, as seems likely, the increase in tree cover is a consequence of increasing CO₂ concentration, then similar changes can be expected across the subregion, perhaps over-riding human management interventions. The implications are profound not only for biogeochemistry (Kgope et al. 2010) and the shifting balance among indigenous species (see §2), but also because invasive alien woody species are a major agent for biodiversity change across the region (Richardson et al. 2000).

7. CONCLUSIONS
Temporal changes in biodiversity in southern African terrestrial systems, as a consequence of direct or indirect human activities, have been both extensive and profound. While the majority appear to be having negative consequences for diversity, this is not always the case. One demonstration thereof is the return of endangered species following clearing of riparian invasive trees (Samways & Sharratt 2010). Moreover, few investigations have been made of how changing climate may reduce the impacts of currently invasive species, or diseases, though obviously this has to be the case in some instances (Bradley et al. 2009; Lafferty 2009). Nonetheless, it is clear that, on balance, human activities are profoundly altering biodiversity in the region, often resulting in a substantial impoverishment thereof. That this should be the case for a region often valued for its biodiversity is perhaps not surprising given global trends (Millennium Ecosystem Assessment 2005), but it is alarming. It also raises the issue, again, of why institutional responses from the national (e.g. Chown et al. 2009) to the international level have typically been so slow and often so unsuccessful (Hamilton 2010). Perhaps increasing urbanization, a burgeoning human population and the associated extinction of experience are partly to blame (Miller 2005). However, wilful denial and increasing tendencies to polarize discussions in an attempt to promote particular worldviews may be another (Gore 2007). In this case, which seems likely to lead to relentless environmental change, it might seem prudent to devote as much of the available resources as possible to conservation action, rather than to further documentation of biodiversity and its change (see Cowling et al. 2010). However, given the success of reasoned argument in improving our livelihoods (Ziman 2007) and the occasional demonstration by our institutions that well-supported evidence can lead to swift changes in policy and its rigorous implementation (Gore 1992), a more balanced approach might be most successful at slowing the change.

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