

Review

Temporal biodiversity change in transformed landscapes: a southern African perspective

Steven L. Chown*

*Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University,
Private Bag X1, Matieland 7602, South Africa*

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

*slchown@sun.ac.za

One contribution of 16 to a Discussion Meeting Issue 'Biological diversity in a changing world'.

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; Gebeyehu & 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

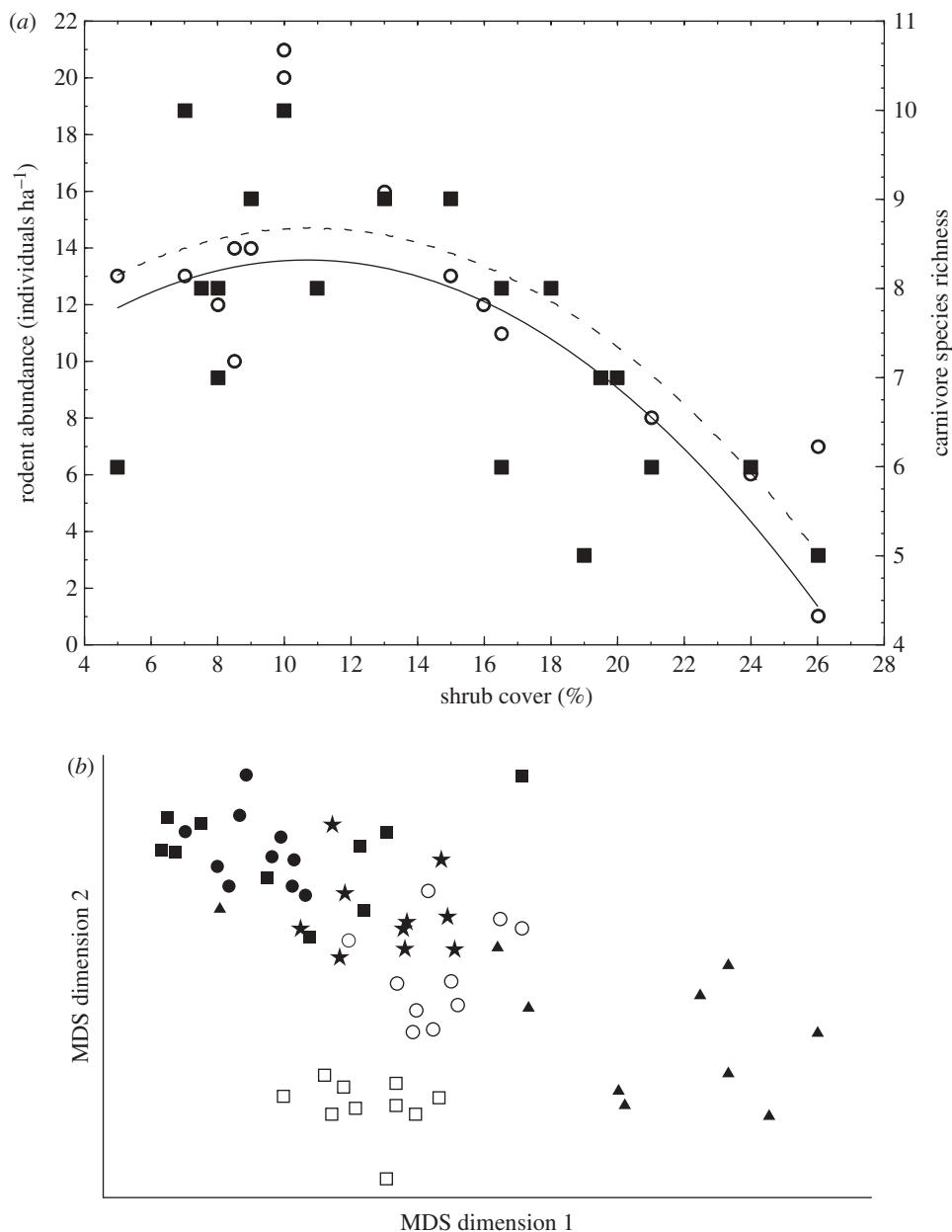


Figure 1. (a) Shrub encroachment effects on the abundance of rodents (open circles, dashed line) and species richness of small carnivores (filled squares, solid line) in the Kalahari Desert. Redrawn from data provided in Blaum *et al.* (2007a,b). (b) Non-metric multi-dimensional ordination of dung beetle 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).

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

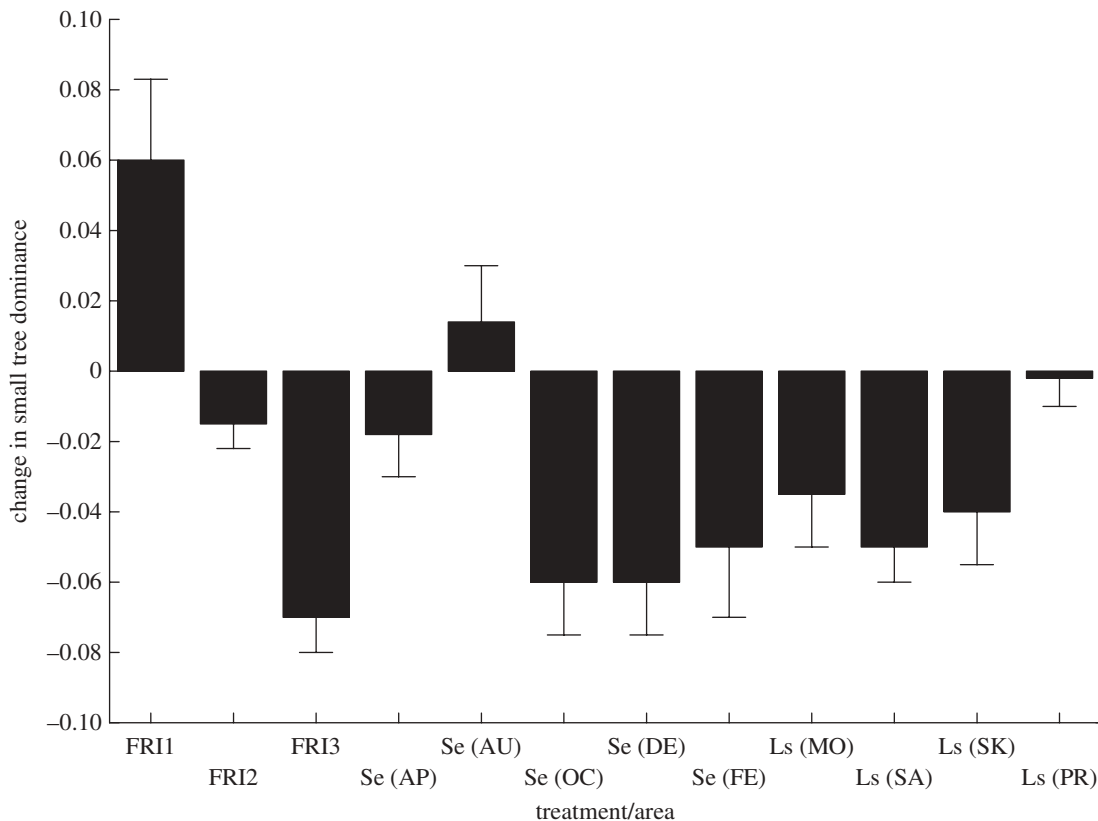


Figure 2. The effects of fire return interval (FRI; in years), season (Se; months of the year indicated by letters) and landscape productivity (Ls; from lowest to highest rainfall: MO, Mopani; SA, Satara; SK, Skukuza; PR, Pretoriuskop) on changes in the dominance of small trees following experimental burning regimes over a 40 year period in the Kruger National Park savanna. Redrawn from Higgins *et al.* (2007).

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; see also 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 Hluhluwe 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)

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; Krook *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

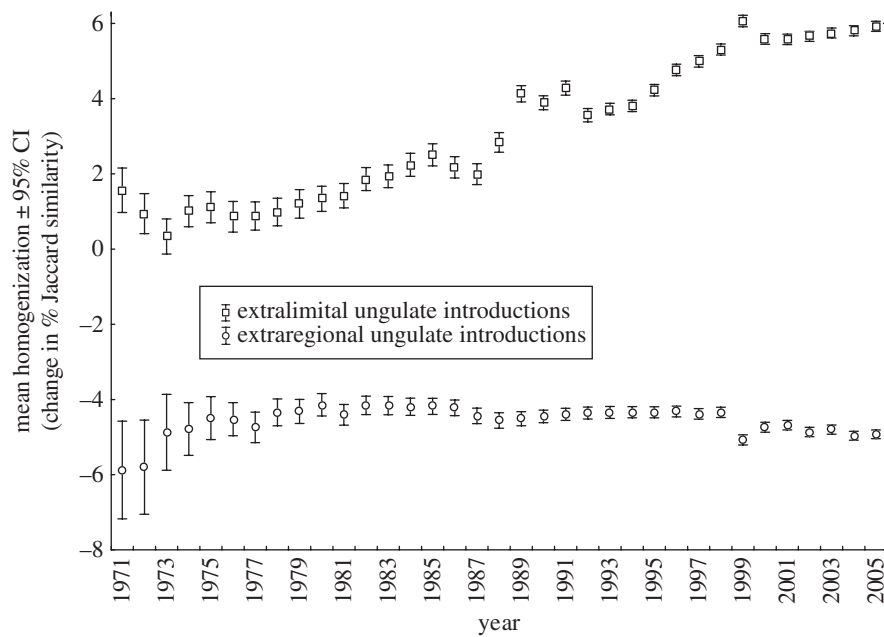


Figure 3. Temporal trends in homogenization of ungulate assemblages as a consequence of extralimital (i.e. movements within South Africa) and extraregional (importations of new species) introductions to South Africa at the quarter-degree grid cell level between 1971 and 2005. Redrawn from Spear & Chown (2008).

many forecast-based studies suggest that this is likely to be the case (Erasmus *et al.* 2002; Hannah *et al.* 2005; Thuiller *et al.* 2006*b,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.* 2009*a*). 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).

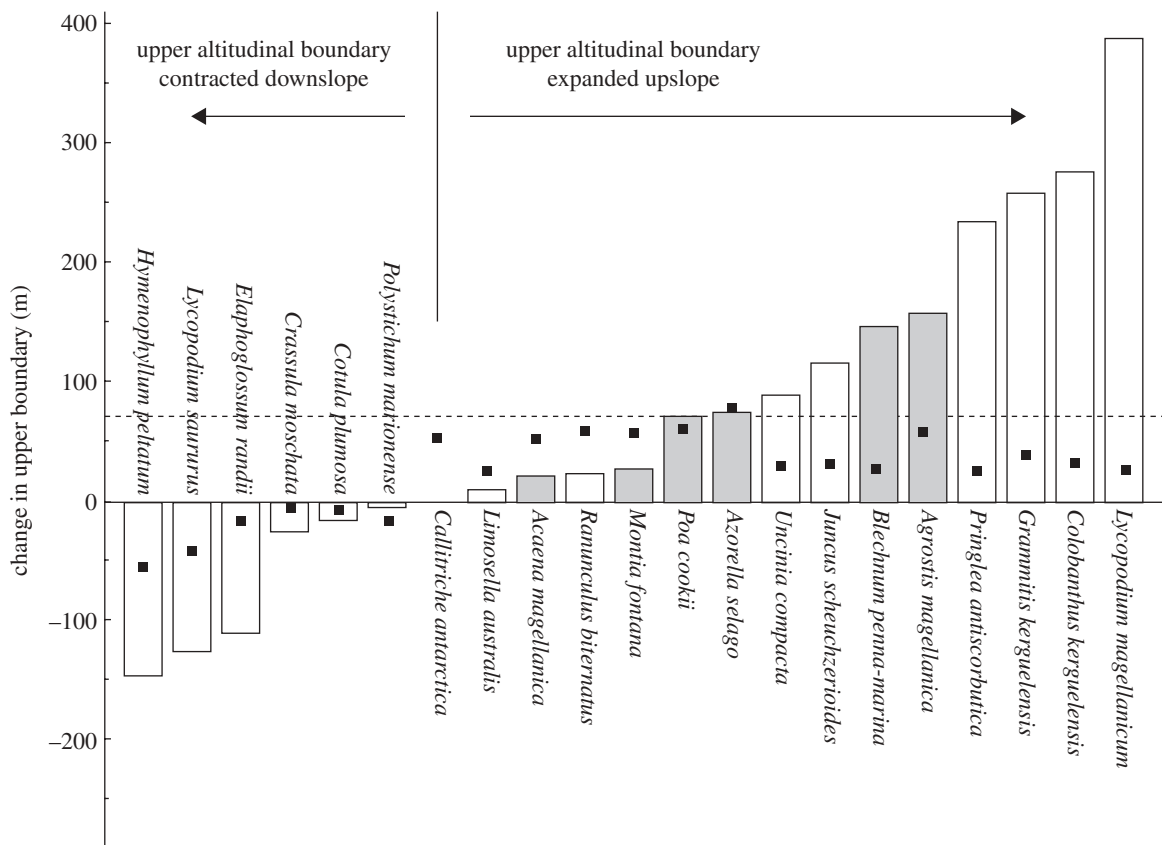


Figure 4. Changes in the upper altitudinal limit of the indigenous vascular flora of sub-Antarctic Marion Island between 1966 and 2006 indicated by the bars (filled bars indicate those species that dominate vascular plant biomass). The points indicate a simulated range boundary change of 10% of the altitudinal range in 1966, whereas the bars show the actual change. Redrawn from le Roux & McGeoch (2008).

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 extension 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 & Thiar 2007; Reinecke & Reinecke 2007; Chakona *et al.* 2009; de Villiers & Mkwelo 2009). In many cases, freshwater systems show exceptionally high levels of nutrient (especially P) loading

(de Villiers & Thiart 2007). 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.* 2005; Hendriks *et al.* 2010), and the impacts of changes in C:N ratios and stomatal conductance are being widely investigated (Coviella & Trumble 1999; Betts *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 perhaps 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 savanna (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.

Thanks to Maria Dornelas and Anne Magurran for the invitation to contribute to the Symposium '*Biological diversity in a changing world*' in celebration of the 350th anniversary of the Royal Society. Melodie McGeoch, Bernard Coetzee, two anonymous reviewers and the editors of this volume provided helpful comments on a previous version of the manuscript. Anel Garthwaite provided assistance with literature searches. This work was partly supported by the Working for Water programme and partly by Stellenbosch University's Overarching Strategic Plan.

REFERENCES

- Addo-Bediako, A., Chown, S. L. & Gaston, K. J. 2000 Thermal tolerance, climatic variability and latitude. *Proc. R. Soc. Lond. B* **267**, 739–745. (doi:10.1098/rspb.2000.1065)
- Altwegg, R. & Anderson, M. D. 2009 Rainfall in arid zones: possible effects of climate change on the population ecology of blue cranes. *Funct. Ecol.* **23**, 1014–1021. (doi:10.1111/j.1365-2435.2009.01563.x)
- Andrews, P. & O'Brien, E. M. 2000 Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *J. Zool.* **251**, 205–231. (doi:10.1111/j.1469-7998.2000.tb00605.x)
- Archer, S., Schimel, D. S. & Holland, E. A. 1995 Mechanisms of shrubland expansion: land use, climate or CO₂? *Clim. Change* **29**, 91–99. (doi:10.1007/BF01091640)
- Archibald, S., Bond, W. J., Stock, W. D. & Fairbanks, D. H. K. 2005 Shaping the landscape: fire–grazer interactions in an African savanna. *Ecol. Appl.* **15**, 96–109. (doi:10.1890/03-5210)
- Asner, G. P., Levick, S. R., Kennedy-Bowdoin, T., Knapp, D. E., Emerson, R., Jacobson, J., Colgan, M. S. & Martin, R. E. 2009 Large-scale impacts of herbivores on the structural diversity of African savannas. *Proc. Natl Acad. Sci. USA* **106**, 4947–4952. (doi:10.1073/pnas.0810637106)
- Beerling, D. J. & Osborne, C. P. 2006 The origin of the savanna biome. *Glob. Change Biol.* **12**, 2023–2031. (doi:10.1111/j.1365-2486.2006.01239.x)
- Betts, R. A. *et al.* 2007 Projected increase in continental runoff due to plant responses to increasing carbon dioxide. *Nature* **448**, 1037–1041. (doi:10.1038/nature06045)
- Biggs, R. & Scholes, R. J. 2002 Land-cover change in South Africa 1911–1993. *S. Afr. J. Sci.* **98**, 420–424.
- Biggs, R., Simons, H., Bakkenes, M., Scholes, R. J., Eickhout, B., van Vuuren, D. & Alkemade, R. 2008 Scenarios of biodiversity loss in southern Africa in the 21st century. *Glob. Environ. Change* **18**, 296–309. (doi:10.1016/j.gloenvcha.2008.02.001)
- Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L. & Gaston, K. J. 2004 Avian extinction and mammalian introductions on oceanic islands. *Science* **305**, 1955–1958. (doi:10.1126/science.1101617)
- Blaum, N., Rossmanith, E. & Jeltsch, F. 2007a Land use affects rodent communities in Kalahari savannah rangelands. *Afr. J. Ecol.* **45**, 189–195. (doi:10.1111/j.1365-2028.2006.00696.x)
- Blaum, N., Rossmanith, E., Popp, A. & Jeltsch, F. 2007b Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. *Acta Oecol.* **31**, 86–92. (doi:10.1016/j.actao.2006.10.004)
- Blaum, N., Seymour, C., Rossmanith, E., Schwager, M. & Jeltsch, F. 2009 Changes in arthropod diversity along a land use driven gradient of shrub cover in savanna rangelands: identification of suitable indicators. *Biodivers. Conserv.* **18**, 1187–1199. (doi:10.1007/s10531-008-9498-x)
- Bond, W. J. 2008 What limits trees in C-4 grasslands and savannas? *Annu. Rev. Ecol. Evol. Syst.* **39**, 641–659. (doi:10.1146/annurev.ecolsys.39.110707.173411)
- Bond, W. J. & Loffell, D. 2001 Introduction of giraffe changes acacia distribution in a South African savanna. *Afr. J. Ecol.* **39**, 286–294. (doi:10.1046/j.1365-2028.2001.00319.x)
- Bond, W. J. & Midgley, G. F. 2000 A proposed CO₂-controlled mechanism of woody plant invasion in grasslands and savannas. *Glob. Change Biol.* **6**, 865–869. (doi:10.1046/j.1365-2486.2000.00365.x)
- Bond, W. J., Midgley, G. F. & Woodward, F. I. 2003 The importance of low atmospheric CO₂ and fire in promoting the spread of grasslands and savannas. *Glob. Change Biol.* **9**, 973–982. (doi:10.1046/j.1365-2486.2003.00577.x)
- Botes, A., McGeoch, M. A. & van Rensburg, B. J. 2006 Elephant-and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputaland Centre of Endemism. *Biol. Conserv.* **130**, 573–583. (doi:10.1016/j.biocon.2006.01.020)
- Boutton, T. W., Archer, S. W. & Nordt, L. C. 1994 Climate, CO₂ and plant abundance. *Nature* **372**, 625–626. (doi:10.1038/372625a0)
- Bradley, B. A., Oppenheimer, M. & Wilcove, D. S. 2009 Climate change and plant invasions: restoration opportunities ahead? *Glob. Change Biol.* **15**, 1511–1521. (doi:10.1111/j.1365-2486.2008.01824.x)
- Braschler, B., Mahood, K., Karenyi, N., Gaston, K. J. & Chown, S. L. 2010 Realizing a synergy between research and education: how participation in ant monitoring helps raise biodiversity awareness in a resource-poor country. *J. Insect Conserv.* **14**, 19–30. (doi:10.1007/s10841-009-9221-6)
- Butchart, S. H. M. *et al.* 2010 Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168. (doi:10.1126/science.1187512)
- Carruthers, J. 2008 'Wilding the farm or farming the wild?' The evolution of scientific game ranching in South Africa from the 1960s to the present. *Trans. R. Soc. S. Afr.* **63**, 160–181.
- Castley, J. G., Boshoff, A. F. & Kerley, G. I. H. 2001 Compromising South Africa's natural biodiversity—inappropriate herbivore introductions. *S. Afr. J. Sci.* **97**, 344–348.
- Chakona, A., Phiri, C., Chinamaringa, T. & Muller, N. 2009 Changes in biota along a dry-land river in northwestern Zimbabwe: declines and improvements in river health related to land use. *Aquat. Ecol.* **43**, 1095–1106. (doi:10.1007/s10452-008-9222-7)
- Chown, S. L. & Froneman, P. W. (eds) 2008 *The Prince Edward islands. Land–Sea interactions in a changing ecosystem* Stellenbosch, South Africa: African Sun Media.
- Chown, S. L., Sinclair, B. J., Leinaas, H. P. & Gaston, K. J. 2004 Hemispheric asymmetries in biodiversity—a serious matter for ecology. *PLoS Biol.* **2**, 1701–1707. (doi:10.1371/journal.pbio.0020406)
- Chown, S. L., Spear, D., Lee, J. E. & Shaw, J. D. 2009 Animal introductions to southern systems: lessons for ecology and for policy. *Afr. Zool.* **44**, 248–262. (doi:10.3377/004.044.0213)
- Coetsee, B. W. T., Robertson, M. P., Erasmus, B. F. N., van Rensburg, B. J. & Thuiller, W. 2009 Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Glob. Ecol. Biogeogr.* **18**, 701–710. (doi:10.1111/j.1466-8238.2009.00485.x)
- Collier, P., Conway, G. & Venables, T. 2008 Climate change and Africa. *Oxford Rev. Econ. Policy* **24**, 337–353. (doi:10.1093/oxrep/grn019)
- Coviella, C. E. & Trumble, J. T. 1999 Effects of elevated atmospheric carbon dioxide on insect–plant interactions. *Conserv. Biol.* **13**, 700–712. (doi:10.1046/j.1523-1739.1999.98267.x)
- Cowling, R. M., Knight, A. T., Privett, S. D. & Sharma, G. 2010 Invest in opportunity, not inventory of hotspots. *Conserv. Biol.* **24**, 633–635. (doi:10.1111/j.1523-1739.2009.01342.x)
- Craig, M. H., Kleinschmidt, I., Nawn, J. B., Le Sueur, D. & Sharp, B. L. 2004 Exploring 30 years of malaria case data in KwaZulu-Natal, South Africa: Part I. The impact of climatic factors. *Trop. Med. Int.*

- Health* **9**, 1247–1257. (doi:10.1111/j.1365-3156.2004.01340.x)
- Dabrowski, J. M., Peall, S. K. C., Van Niekerk, A., Reinecke, A. J., Day, J. A. & Schulz, R. 2002 Predicting runoff-induced pesticide input in agricultural sub-catchment surface waters: linking catchment variables and contamination. *Water Res.* **36**, 4975–4984. (doi:10.1016/S0043-1354(02)00234-8)
- Dallas, H. F., Janssens, M. P. & Day, J. A. 1999 An aquatic macroinvertebrate and chemical database for riverine ecosystems. *Water SA* **25**, 1–8.
- Davies, B. & Day, J. 1998 *Vanishing waters*. Cape Town, South Africa: University of Cape Town Press.
- Davis, A. L. V. 1996 Seasonal dung beetle activity and dung dispersal in selected South African habitats: implications for pasture improvement in Australia. *Agric. Ecosyst. Environ.* **58**, 157–169. (doi:10.1016/0167-8809(96)01030-4)
- Davis, A. L. V., Scholtz, C. H., Dooley, P. W., Bharm, N. & Kryger, U. 2004 Scarabaeine dung beetles as indicators of biodiversity, habitat transformation and pest control chemicals in agro-ecosystems. *S. Afr. J. Sci.* **100**, 415–424.
- de Villiers, S. 2007 The deteriorating nutrient status of the Berg River, South Africa. *Water SA* **33**, 659–664.
- de Villiers, S. & Mkwelo, S. T. 2009 Has monitoring failed the Olifants River, Mpumalanga? *Water SA* **35**, 671–676.
- de Villiers, S. & Thiar, C. 2007 The nutrient status of South African rivers: concentrations, trends and fluxes from the 1970s to 2005. *S. Afr. J. Sci.* **103**, 343–349.
- Dean, W. R. J. 1997 The distribution and biology of nomadic birds in the Karoo, South Africa. *J. Biogeogr.* **24**, 769–779. (doi:10.1046/j.1365-2699.1997.00163.x)
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C. & Martin, P. R. 2008 Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672. (doi:10.1073/pnas.0709472105)
- Ellis, E. C. & Ramankutty, N. 2008 Putting people in the map: anthropogenic biomes of the world. *Front. Ecol. Environ.* **6**, 439–447. (doi:10.1890/070062)
- Erasmus, B. F. N., van Jaarsveld, A. S., Chown, S. L., Kshatriya, M. & Wessels, K. J. 2002 Vulnerability of South African animal taxa to climate change. *Glob. Change Biol.* **8**, 679–693. (doi:10.1046/j.1365-2486.2002.00502.x)
- Evans, K. L., Rodrigues, A. S. L., Chown, S. L. & Gaston, K. J. 2006a Protected areas and regional avian species richness in South Africa. *Biol. Lett.* **2**, 184–188. (doi:10.1098/rsbl.2005.0435)
- Evans, K. L., van Rensburg, B. J., Gaston, K. J. & Chown, S. L. 2006b People, species richness and human population growth. *Glob. Ecol. Biogeogr.* **15**, 625–636. (doi:10.1111/j.1466-8238.2006.00253.x)
- Fabricius, C., Burger, M. & Hockey, P. A. R. 2003 Comparing biodiversity between protected areas and adjacent rangeland in xeric succulent thicket, South Africa: arthropods and reptiles. *J. Appl. Ecol.* **40**, 392–403. (doi:10.1046/j.1365-2664.2003.00793.x)
- Fairbanks, D. H. K., Thompson, M. K., Vink, D. E., Newby, T. S., van den Berg, H. M. & Everard, D. A. 2000 The South African land-cover characteristics database: a synopsis of the landscape. *S. Afr. J. Sci.* **96**, 69–82.
- Fernández, M., Astorga, A., Navarette, S. A., Valdovinos, C. & Marquet, P. A. 2009 Deconstructing latitudinal species richness patterns in the ocean: does larval development hold the clue? *Ecol. Lett.* **12**, 601–611. (doi:10.1111/j.1461-0248.2009.01315.x)
- Foden, W. *et al.* 2007 A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Divers. Distrib.* **13**, 645–653. (doi:10.1111/j.1472-4642.2007.00391.x)
- Forsyth, G. G. & van Wilgen, B. W. 2008 The recent fire history of the Table Mountain National Park and implications for fire management. *Koedoe* **50**, 3–9.
- Frenot, Y., Chown, S. L., Whinam, J., Selkirk, P. M., Convey, P., Skotnicki, M. & Bergstrom, D. M. 2005 Biological invasions in the Antarctic: extent, impacts and implications. *Biol. Rev.* **80**, 45–72. (doi:10.1017/S1464793104006542)
- Fusari, A. & Carpaneto, G. M. 2006 Subsistence hunting and conservation issues in the game reserve of Gile, Mozambique. *Biodivers. Conserv.* **15**, 2477–2495.
- Gaertner, M., Den Breeyen, A., Hui, C. & Richardson, D. M. 2009 Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Prog. Phys. Geogr.* **33**, 319–338. (doi:10.1177/0309133309341607)
- Gaston, K. J. & Chown, S. L. 1999 Why Rapoport's rule does not generalise. *Oikos* **84**, 309–312. (doi:10.2307/3546727)
- Gaston, K. J., Jackson, S. F., Cantu-Salazar, L. & Cruz-Piñón, G. 2008 The ecological performance of protected areas. *Annu. Rev. Ecol. Evol. Syst.* **39**, 93–113. (doi:10.1146/annurev.ecolsys.39.110707.173529)
- Gaston, K. J. *et al.* 2009 Macroecology: a conceptual re-unification. *Am. Nat.* **174**, 595–612. (doi:10.1086/605982)
- Gebeyehu, S. & Samways, M. J. 2002 Grasshopper assemblage response to a restored national park (Mountain Zebra National Park, South Africa). *Biodivers. Conserv.* **11**, 283–304.
- Geertsema, H. 2000 Range expansion, distribution records and abundance of some Western Cape insects. *S. Afr. J. Sci.* **96**, 396–398.
- Gilimee, J. H. 2000 Native insects expanding their ranges and becoming more abundant. *S. Afr. J. Sci.* **96**, 474.
- Gore, A. 1992 *Earth in the balance*. London, UK: Earthscan.
- Gore, A. 2007 *The assault on reason*. New York, NY: Penguin Press.
- Govender, N., Trollope, W. S. W. & van Wilgen, B. W. 2006 The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *J. Appl. Ecol.* **43**, 748–758. (doi:10.1111/j.1365-2664.2006.01184.x)
- Greve, M., Gaston, K. J., van Rensburg, B. J. & Chown, S. L. 2008 Environmental factors, regional body size distributions, and spatial variation in body size of local avian assemblages. *Glob. Ecol. Biogeogr.* **17**, 514–523. (doi:10.1111/j.1466-8238.2008.00388.x)
- Greve, M., Chown, S. L., van Rensburg, B. J., Dallimer, M. & Gaston, K. J. Submitted. The ecological performance of protected areas: a case study for South African birds.
- Hagenah, N., Prins, H. H. T. & Olf, H. 2009 Effects of large herbivores on murid rodents in a South African savanna. *J. Trop. Ecol.* **25**, 483–492. (doi:10.1017/S0266467409990046)
- Hamilton, C. 2010 *Requiem for a species. Why we resist the truth about climate change*. London, UK: Earthscan.
- Hannah, L., Midgley, G., Hughes, G. & Bomhard, B. 2005 The view from the Cape. Extinction risk, protected areas, and climate change. *BioScience* **55**, 231–242. (doi:10.1641/0006-3568(2005)055[0231:TVFTCE]2.0.CO;2)
- Harrington, R., Owen-Smith, N., Viljoen, P. C., Biggs, H. C., Mason, D. R. & Funston, P. 1999 Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biol. Conserv.* **90**, 69–78. (doi:10.1016/S0006-3207(98)00120-7)
- Hay, S. I., Shanks, G. D., Stern, D. I., Snow, R. W., Randolph, S. E. & Rogers, D. J. 2005 Climate

- variability and malaria epidemics in the highlands of East Africa. *Trends Parasitol.* **21**, 52–53. (doi:10.1016/j.pt.2004.11.007)
- Hayward, M. W. 2009 Bushmeat hunting in Dwesa and Cwebe Nature Reserves, Eastern Cape, South Africa. *S. Afr. J. Wildl. Res.* **39**, 70–84. (doi:10.3957/056.039.0108)
- Hendriks, I. E., Duarte, C. M. & Alvarez, M. 2010 Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. *Estuar. Coast. Shelf Sci.* **86**, 157–164. (doi:10.1016/j.ecss.2009.11.022)
- Higgins, S. I. *et al.* 2007 Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* **88**, 1119–1125. (doi:10.1890/06-1664)
- Hockey, P. A. R. & Midgley, G. F. 2009 Avian range changes and climate change: a cautionary tale from the Cape Peninsula. *Ostrich* **80**, 29–34.
- Hoffman, M. T., Carrick, P. J., Gillson, L. & West, A. G. 2009 Drought, climate change and vegetation response in the succulent karoo, South Africa. *S. Afr. J. Sci.* **105**, 54–60.
- Hopcraft, J. G. C., Olf, H. & Sinclair, A. R. E. 2010 Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends Ecol. Evol.* **25**, 119–128. (doi:10.1016/j.tree.2009.08.001)
- Huey, R. B., Deutsch, C. A., Tewksbury, J. J., Vitt, L. J., Hertz, P. E., Álvarez Pérez, H. J. & Garland, T. 2009 Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. B* **276**, 1939–1948. (doi:10.1098/rspb.2008.1957)
- Hughes, L. 2003 Climate change and Australia: trends, projections and impacts. *Austral Ecol.* **28**, 423–443. (doi:10.1046/j.1442-9993.2003.01300.x)
- Jeltsch, F., Milton, S. J., Dean, W. R. J. & van Rooyen, N. 1997 Analysing shrub encroachment in the southern Kalahari: a grid-based modelling approach. *J. Appl. Ecol.* **34**, 1497–1508.
- Keesing, F. 1998 Impacts of ungulates on the demography and diversity of small mammals in central Kenya. *Oecologia* **116**, 381–389. (doi:10.1007/s004420050601)
- Keith, D. A., Akçakaya, H. R., Thuiller, W., Midgley, G. F., Pearson, R. G., Phillips, S. J., Regan, H. M., Araújo, M. B. & Rebelo, T. G. 2008 Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biol. Lett.* **4**, 560–563. (doi:10.1098/rsbl.2008.0049)
- Kgope, B. S., Bond, W. J. & Midgley, G. F. 2010 Growth responses of African savanna trees implicate atmospheric [CO₂] as a driver of past current changes in savanna tree cover. *Austral Ecol.* **35**, 451–463. (doi:10.1111/j.1442-9993.2009.02046.x)
- Knoesen, D., Schulze, R., Pringle, C., Dickens, C. & Kunz, R. 2009 *Water for the future: impacts of climate change on water resources in the Orange-Senqu River basin. Report to NeWater, a project funded under the Sixth Research Framework of the European Union.* Pietermaritzburg, South Africa: Institute of Natural Resources.
- Krook, K., Bond, W. J. & Hockey, P. A. R. 2007 The effect of grassland shifts on the avifauna of a South African savanna. *Ostrich* **78**, 271–279. (doi:10.2989/OSTRICH.2007.78.2.24.104)
- Lafferty, K. D. 2009 The ecology of climate change and infectious diseases. *Ecology* **90**, 888–900. (doi:10.1890/08-0079.1)
- Lantz, T. C., Kokelj, S. V., Gergel, S. E. & Henry, G. H. R. 2009 Relative impacts of disturbance and temperature: persistent changes in microenvironment and vegetation in retrogressive thaw slumps. *Glob. Change Biol.* **15**, 1664–1675. (doi:10.1111/j.1365-2486.2009.01917.x)
- Latimer, A. M., Silander, J. A., Gelfand, A. E., Rebelo, A. G. & Richardson, D. M. 2004 Quantifying threats to biodiversity from invasive alien plants and other factors: a case study from the Cape Floristic Region. *S. Afr. J. Sci.* **100**, 81–86.
- le Roux, P. C. & McGeoch, M. A. 2008 Rapid range expansion and community reorganization in response to warming. *Glob. Change Biol.* **14**, 2950–2960. (doi:10.1111/j.1365-2486.2008.01687.x)
- Lee, J. E. & Chown, S. L. 2009 Breaching the dispersal barrier to invasion: quantification and management. *Ecol. Appl.* **19**, 1944–1957. (doi:10.1890/08-2157.1)
- Lindsey, P. A., Alexander, R., Frank, L. G., Mathieson, A. & Romañach, S. S. 2006 Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. *Anim. Conserv.* **9**, 283–291. (doi:10.1111/j.1469-1795.2006.00034.x)
- Lindsey, P. A., Roulet, P. A. & Romañach, S. S. 2007 Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biol. Conserv.* **134**, 455–469. (doi:10.1016/j.biocon.2006.09.005)
- Little, R. M., Crowe, T. M. & Villacastin-Herrero, C. A. 1996 Conservation implications of long-term population trends, environmental correlates and predictive models for Namaqua sandgrouse. *Pterocles namaqua*. *Biol. Conserv.* **75**, 93–101. (doi:10.1016/0006-3207(95)00031-3)
- Lloyd, P. 1999 Rainfall as a breeding stimulus and clutch size determinant in South African arid-zone birds. *Ibis* **141**, 637–643. (doi:10.1111/j.1474-919X.1999.tb07371.x)
- Lloyd, P. & Palmer, A. R. 1998 Abiotic factors as predictors of distribution of southern African bulbuls. *Auk* **115**, 404–411.
- Loveridge, A. J., Searle, A. W., Murindagomo, F. & Macdonald, D. W. 2007 The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biol. Conserv.* **134**, 548–558. (doi:10.1016/j.biocon.2006.09.010)
- Mac Nally, R., Bennett, A. F., Thomson, J. R., Radford, J. Q., Unmack, G., Horrocks, G. & Vesk, P. A. 2009a Collapse of an avifauna: climate changes appears to exacerbate habitat loss and degradation. *Divers. Distrib.* **15**, 720–730. (doi:10.1111/j.1472-4642.2009.00578.x)
- Mac Nally, R., Horrocks, G., Lada, H., Lake, P. S., Thomson, J. R. & Taylor, A. C. 2009b Distribution of anuran amphibians in massively altered landscapes in south-eastern Australia: effects of climate change in an aridifying region. *Glob. Ecol. Biogeogr.* **18**, 575–585. (doi:10.1111/j.1466-8238.2009.00469.x)
- MacDonald, I. A. W., Kruger, F. J. & Ferrar, A. A. 1986 *The ecology and management of biological invasions in southern Africa.* Cape Town, South Africa: Oxford University Press.
- MacKellar, N. C., Hewitson, B. C. & Tadross, M. A. 2007 Namaqualand's climate: recent historical changes and future scenarios. *J. Arid Environ.* **70**, 604–614. (doi:10.1016/j.jaridenv.2006.03.024)
- McGeoch, M. A., Butchart, S. H. M., Spear, D., Marais, E., Kleynhans, E. J., Symes, A., Chanson, J. & Hoffmann, M. 2010 Global indicators of biological invasion: species numbers, biodiversity impacts and policy responses. *Divers. Distrib.* **16**, 95–108. (doi:10.1111/j.1472-4642.2009.00633.x)
- McLoughlin, C. A. & Owen-Smith, N. 2003 Viability of a diminishing roan antelope population: predation is the threat. *Anim. Conserv.* **6**, 231–236. (doi:10.1017/S1367943003003287)
- Meik, J. M., Jeo, R. M., Mendelson, J. R. & Jenks, K. E. 2002 Effects of bush encroachment on an assemblage of

- diurnal lizard species in central Namibia. *Biol. Conserv.* **106**, 29–36. (doi:10.1016/S0006-3207(01)00226-9)
- Millennium Ecosystem Assessment. 2005 *Ecosystems and human well-being: biodiversity synthesis*. Washington, DC: World Resources Institute.
- Miller, J. R. 2005 Biodiversity conservation and the extinction of experience. *Trends Ecol. Evol.* **20**, 430–434. (doi:10.1016/j.tree.2005.05.013)
- Mooney, H. A. & Hobbs, R. J. (eds) 2000 *Invasive species in a changing world*. Washington, DC: Island Press.
- Mucina, L. & Rutherford, M. C. (eds) 2006 *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19*. Pretoria, South Africa: South African National Biodiversity Institute.
- New, M. *et al.* 2006 Evidence of trends in daily climate extremes over southern and west Africa. *J. Geophys. Res.* **111**, D14102. (doi:10.1029/2005JD006289)
- O'Brien, E. M. 1993 Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *J. Biogeogr.* **20**, 181–198. (doi:10.2307/2845670)
- O'Connor, T. G. 2005 Influence of land use on plant community composition and diversity in Highland Sourveld grassland in the southern Drakensberg, South Africa. *J. Appl. Ecol.* **42**, 975–988. (doi:10.1111/j.1365-2664.2005.01065.x)
- O'Connor, T. G. & Roux, P. W. 1995 Vegetation changes (1949–1971) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. *J. Appl. Ecol.* **32**, 612–626.
- Ogutu, J. O. & Owen-Smith, N. 2003 ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecol. Lett.* **6**, 412–419. (doi:10.1046/j.1461-0248.2003.00447.x)
- Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E. & Fausch, K. D. 2004 Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* **19**, 18–24. (doi:10.1016/j.tree.2003.09.010)
- Orme, C. D. L. *et al.* 2006 Global patterns of geographic range size in birds. *PLoS Biol.* **4**, 1276–1283. (doi:10.1371/journal.pbio.0040208)
- Orr, J. C. *et al.* 2005 Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* **437**, 681–686. (doi:10.1038/nature04095)
- Owen-Smith, N. & Mills, M. G. L. 2006 Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecol. Monogr.* **76**, 73–92. (doi:10.1890/04-1101)
- Owen-Smith, N. & Mills, M. G. L. 2008 Predator–prey size relationships in an African large-mammal food web. *J. Anim. Ecol.* **77**, 173–183. (doi:10.1111/j.1365-2656.2007.01314.x)
- Paaijmans, K. P., Read, A. F. & Thomas, M. B. 2009 Understanding the link between malaria risk and climate. *Proc. Natl Acad. Sci. USA* **106**, 13 844–13 849. (doi:10.1073/pnas.0903423106)
- Parmesan, C. 2006 Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669. (doi:10.1146/annurev.ecolsys.37.091305.110100)
- Parr, C. L. 2008 Dominant ants can control assemblage species richness in a South African savanna. *J. Anim. Ecol.* **77**, 1191–1198. (doi:10.1111/j.1365-2656.2008.01450.x)
- Parr, C. L., Robertson, H. G., Biggs, H. C. & Chown, S. L. 2004 Response of African savanna ants to long-term fire regimes. *J. Appl. Ecol.* **41**, 630–642. (doi:10.1111/j.0021-8901.2004.00920.x)
- Pascual, M. & Bouma, M. J. 2009 Do rising temperatures matter? *Ecology* **90**, 906–912. (doi:10.1890/08-0730.1)
- Pascual, M., Dobson, A. P. & Bouma, M. J. 2009 Underestimating malaria risk under variable temperatures. *Proc. Natl Acad. Sci. USA* **106**, 13 645–13 646. (doi:10.1073/pnas.0906909106)
- Patz, J. A., Hulme, M., Rosenzweig, C., Mitchell, T. D., Goldberg, R. A., Githeko, A. K., Lele, S., McMichael, A. J. & Le Sueur, D. 2002 Climate change (communication arising): regional warming and malaria resurgence. *Nature* **420**, 627–628. (doi:10.1038/420627a)
- Pellikka, P. K. E., Lötjönen, M., Siljander, M. & Lens, L. 2009 Airborne remote sensing of spatiotemporal change (1955–2004) in indigenous and exotic forest cover in the Taita Hills, Kenya. *Int. J. Appl. Earth Obs. Geoinf.* **11**, 221–232. (doi:10.1016/j.jag.2009.02.002)
- Piao, S., Friedlingstein, P., Ciais, P., de Noblet-Ducoudré, N. L. D. & Zaehele, S. 2007 Changes in climate and land use have a larger direct impact than rising CO₂ on global river runoff trends. *Proc. Natl Acad. Sci. USA* **104**, 15 242–15 247. (doi:10.1073/pnas.0707213104)
- Radford, A. N. & Du Plessis, M. A. 2003 The importance of rainfall to a cavity-nesting species. *Ibis* **145**, 692–694. (doi:10.1046/j.1474-919X.2003.00198.x)
- Reilly, B. K., Sutherland, E. A. & Harley, V. 2003 The nature and extent of wildlife ranching in Gauteng province, South Africa. *S. Afr. J. Wildl. Res.* **33**, 141–144.
- Reinecke, S. A. & Reinecke, A. J. 2007 The impact of organophosphate pesticides in orchards on earthworms in the Western Cape, South Africa. *Ecotoxicol. Environ. Safety* **66**, 244–251. (doi:10.1016/j.ecoenv.2005.10.006)
- Richardson, D. M. & van Wilgen, B. W. 2004 Invasive alien plants in South Africa: how well do we understand the ecological impacts? *S. Afr. J. Sci.* **100**, 45–52.
- Richardson, D. M. *et al.* 2000 Invasive alien species and global change: a South African perspective. In *Invasive species in a changing world* (eds H. A. Mooney & R. J. Hobbs), pp. 303–349. Washington, DC: Island Press.
- Richardson, D. M., Rouget, M., Ralston, S. J., Cowling, R. M., van Rensburg, B. J. & Thuiller, W. 2005 Species richness of alien plants in South Africa: environmental correlates and the relationship with indigenous plant species richness. *Ecoscience* **12**, 391–402. (doi:10.2980/i1195-6860-12-3-391.1)
- Robinson, T. B., Govender, A., Griffiths, C. L. & Branch, G. M. 2007 Experimental harvesting of *Mytilus galloprovincialis*: can an alien mussel support a small-scale fishery? *Fisheries Res.* **88**, 33–41. (doi:10.1016/j.fishres.2007.07.005)
- Rogers, D. J. & Randolph, S. E. 2000 The global spread of malaria in a future, warmer world. *Science* **289**, 1763–1766. (doi:10.1126/science.289.5485.1763)
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. 2003 Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60. (doi:10.1038/nature01333)
- Roques, K. G., O'Connor, T. G. & Watkinson, A. R. 2001 Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *J. Appl. Ecol.* **38**, 268–280. (doi:10.1046/j.1365-2664.2001.00567.x)
- Rouget, M. & Richardson, D. M. 2003 Inferring process from pattern in plant invasions: a semi-mechanistic model incorporating propagule pressure and environmental factors. *Am. Nat.* **162**, 713–724. (doi:10.1086/379204)
- Rouget, M., Richardson, D. M., Nel, J. L., Le Maitre, D. C., Egoh, B. & Mgidi, T. 2004 Mapping the potential ranges of major plant invaders in South Africa, Lesotho and Swaziland using climatic suitability. *Divers.*

- Distrib.* **10**, 475–484. (doi:10.1111/j.1366-9516.2004.00118.x)
- Roux, D. J. 2001 Strategies used to guide the design and implementation of a national river monitoring programme in South Africa. *Environ. Monitor. Assess.* **69**, 131–158. (doi:10.1023/A:1010793505708)
- Samways, M. J. & Grant, P. B. C. 2008 Elephant impact on dragonflies. *J. Insect Conserv.* **12**, 493–498. (doi:10.1007/s10841-007-9089-2)
- Samways, M. J. & Moore, S. D. 1991 Influence of exotic conifer patches on grasshopper (Orthoptera) assemblages in a grassland matrix at a recreational resort, Natal, South Africa. *Biol. Conserv.* **57**, 117–137. (doi:10.1016/0006-3207(91)90134-U)
- Samways, M. J. & Sharratt, N. J. 2010 Recovery of endemic dragonflies after removal of invasive alien trees. *Conserv. Biol.* **24**, 267–277. (doi:10.1111/j.1523-1739.2009.01427.x)
- Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. A., Wannebo, A. V. & Woolmer, G. 2002 The human footprint and the last of the wild. *BioScience* **52**, 891–904. (doi:10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2)
- Scholtz, C. H. & Chown, S. L. 1993 Insect conservation and extensive agriculture: the savanna of southern Africa. In *Perspectives on insect conservation* (eds K. J. Gaston, T. R. New & M. J. Samways), pp. 75–95. Andover, UK: Intercept.
- Seely, M., Henschel, J. R. & Hamilton III, W. J. 2005 Long-term data show behavioural fog collection adaptations determine Namib Desert beetle abundance. *S. Afr. J. Sci.* **101**, 570–572.
- Shackleton, C. & Shackleton, S. 2004 The importance of non-timber forest products in rural livelihood security and as safety nets: a review of evidence from South Africa. *S. Afr. J. Sci.* **100**, 658–664.
- Shelton, J. M., Day, J. A. & Griffiths, C. L. 2008 Influence of largemouth bass, *Micropterus salmoides*, on abundance and habitat selection of Cape galaxias, *Galaxias zebratus*, in a mountain stream in the Cape Floristic Region, South Africa. *Afr. J. Aquat. Sci.* **33**, 201–210. (doi:10.2989/AJAS.2008.33.3.2.614)
- Simmons, R. E., Barnard, P., Dean, W. R. J., Midgley, G. F., Thuiller, W. & Hughes, G. 2004 Climate change and birds: perspectives and prospects from southern Africa. *Ostrich* **75**, 295–308.
- Sirami, C., Seymour, C., Midgley, G. & Barnard, P. 2009 The impact of shrub encroachment on savanna bird diversity from local to regional scale. *Divers. Distrib.* **15**, 948–957. (doi:10.1111/j.1472-4642.2009.00612.x)
- Skead, C. J. 2007 *Historical incidence of the larger land mammals in the broader eastern cape* (eds A. F. Boshoff, G. I. H. Kerley & P. H. Lloyd), 2nd edn. Port Elizabeth, South Africa: Nelson Mandela Metropolitan University Bukani Print.
- Spear, D. & Chown, S. L. 2008 Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales. *J. Biogeogr.* **35**, 1962–1975. (doi:10.1111/j.1365-2699.2008.01926.x)
- Spear, D. & Chown, S. L. 2009a The extent and impacts of ungulate translocations: South Africa in a global context. *Biol. Conserv.* **142**, 353–363. (doi:10.1016/j.biocon.2008.10.031)
- Spear, D. & Chown, S. L. 2009b Non-indigenous ungulates as a threat to biodiversity. *J. Zool.* **279**, 1–17. (doi:10.1111/j.1469-7998.2009.00604.x)
- Staver, A. C., Bond, W. J., Stock, W. D., van Rensburg, S. J. & Waldram, M. S. 2009 Browsing and fire interact to suppress tree density in an African savanna. *Ecol. Appl.* **19**, 1909–1919. (doi:10.1890/08-1907.1)
- Stock, W. D., Bond, W. J. & van de Vijver, C. 2010 Herbivore and nutrient control of lawn and bunch grass distributions in a southern African savanna. *Plant Ecol.* **206**, 15–27. (doi:10.1007/s11258-009-9621-4)
- Swart, N. & Pool, E. 2007 Rapid detection of selected steroid hormones from sewage effluents using an ELISA in the Kuils River water catchment area, South Africa. *J. Immunoassay Immunochem.* **28**, 395–408. (doi:10.1080/15321810701603799)
- Thomson, M. C., Doblas-Reyes, F. J., Mason, S. J., Hagedorn, R., Connor, S. J., Phindela, T., Morse, A. P. & Palmer, T. N. 2006 Malaria early warnings based on seasonal climate forecasts from multi-model ensembles. *Nature* **439**, 576–579. (doi:10.1038/nature04503)
- Thuiller, W., Richardson, D. M., Pyšek, P., Midgley, G. F., Hughes, G. O. & Rouget, M. 2005 Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Glob. Change Biol.* **11**, 2234–2250. (doi:10.1111/j.1365-2486.2005.001018.x)
- Thuiller, W., Midgley, G. F., Rouget, M. & Cowling, R. M. 2006a Predicting patterns of plant species richness in megadiverse South Africa. *Ecography* **29**, 733–744. (doi:10.1111/j.0906-7590.2006.04674.x)
- Thuiller, W., Broennimann, O., Hughes, G. O., Alkemade, J. R. M., Midgley, G. F. & Corsi, F. 2006b Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Glob. Change Biol.* **12**, 424–440. (doi:10.1111/j.1365-2486.2006.01115.x)
- Thuiller, W., Midgley, G. F., Hughes, G. O., Bomhard, B., Drew, G., Rutherford, M. C. & Woodward, F. I. 2006c Endemic species and ecosystem sensitivity to climate change in Namibia. *Glob. Change Biol.* **12**, 759–776. (doi:10.1111/j.1365-2486.2006.01140.x)
- Todd, S. W. & Hoffman, M. T. 2009 A fence line in time demonstrates grazing-induced vegetation shifts and dynamics in the semiarid Succulent Karoo. *Ecol. Appl.* **19**, 1897–1908. (doi:10.1890/08-0602.1)
- Todd, M. C., Washington, R., Cheke, R. A. & Kniveton, R. 2002 Brown locust outbreaks and climate variability in southern Africa. *J. Appl. Ecol.* **39**, 31–42. (doi:10.1046/j.1365-2664.2002.00691.x)
- Tolley, K. A., Davies, S. J. & Chown, S. L. 2008 Deconstructing a controversial local range expansion: conservation biogeography of the Painted Reed Frog (*Hyperolius marmoratus*) in South Africa. *Divers. Distrib.* **14**, 400–411. (doi:10.1111/j.1472-4642.2007.00428.x)
- Tyson, P. D. & Preston-Whyte, R. A. 2000 *The weather and climate of Southern Africa*, 2nd edn. Cape Town, South Africa: Oxford University Press.
- Valkama, E., Koricheva, J. & Oksanen, E. 2007 Effects of elevated O₃, alone and in combination with elevated CO₂, on tree leaf chemistry and insect herbivore performance: a meta-analysis. *Glob. Change Biol.* **13**, 184–201. (doi:10.1111/j.1365-2486.2006.01284.x)
- Van der Merwe, P. & Saayman, M. 2003 Determining the economic value of game farm tourism. *Koedoe* **46**, 103–112.
- Van der Merwe, M., Dippenaar-Schoeman, A. S. & Scholtz, C. H. 1996 Diversity of ground-living spiders at Ngame State Forest, Kwazulu/Natal: a comparative survey in indigenous forest and pine plantations. *Afr. J. Ecol.* **34**, 342–350.
- Van der Waal, C. & Dekker, B. 2000 Game ranching in the Northern Province of South Africa. *S. Afr. J. Wildl. Res.* **30**, 151–156.
- van Kleunen, M. & Johnson, S. D. 2007 South African Iridaceae with rapid and profuse seedling emergence are more likely to become naturalized in other regions. *J. Ecol.* **95**, 674–681. (doi:10.1111/j.1365-2745.2007.01250.x)

- van Kleunen, M., Manning, J. C., Pasqualetto, V. & Johnson, S. D. 2008 Phylogenetically independent associations between autonomous self-fertilization and plant invasiveness. *Am. Nat.* **171**, 195–201. (doi:10.1086/525057)
- van Rensburg, B. J., Chown, S. L. & Gaston, K. J. 2002 Species richness, environmental correlates, and spatial scale: a test using South African birds. *Am. Nat.* **159**, 566–577. (doi:10.1086/339464)
- van Tienhoven, A. M. & Scholes, M. C. 2004 Air pollution impacts on vegetation in South Africa. In *Air pollution impacts on crops and forests. A global assessment* (eds F. Emberson, M. Ashmore & F. Murray), pp. 237–262. Air Pollution Reviews vol. 4. London, UK: Imperial College Press.
- van Wilgen, B. W. 2009a The evolution of fire and invasive alien plant management practices in fynbos. *S. Afr. J. Sci.* **105**, 335–342.
- van Wilgen, B. W. 2009b The evolution of fire management practices in savanna protected areas in South Africa. *S. Afr. J. Sci.* **105**, 343–349.
- van Wilgen, B. W., Trollope, W. S. W., Biggs, H. C., Potgieter, A. L. F. & Brockett, B. H. 2003 Fire as a driver of ecosystem variability. In *The Kruger experience. Ecology and management of savanna heterogeneity* (eds J. T. Du Toit, K. H. Rogers & H. C. Biggs), pp. 149–170. Washington, DC: Island Press.
- Wallgren, M., Skarpe, C., Bergström, R., Danell, K., Bergström, A., Jakobsson, T., Karlsson, K. & Strand, T. 2009 Influence of land use on the abundance of wildlife and livestock in the Kalahari, Botswana. *J. Arid Environ.* **73**, 314–321. (doi:10.1016/j.jaridenv.2008.09.019)
- Walther, G.-R. *et al.* 2009 Alien species in a warmer world: risks and opportunities. *Trends Ecol. Evol.* **24**, 686–693. (doi:10.1016/j.tree.2009.06.008)
- Whitman, K., Starfield, A. M., Quadling, H. S. & Packer, C. 2004 Sustainable trophy hunting of African lions. *Nature* **428**, 175–178. (doi:10.1038/nature02395)
- Wigley, B. J., Bond, W. J. & Hoffman, M. T. 2010 Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Glob. Change Biol.* **16**, 964–976. (doi:10.1111/j.1365-2486.2009.02030.x)
- Wilson, J. R. U., Dormontt, E. E., Prentis, P. J., Lowe, A. J. & Richardson, D. M. 2009a Something in the way you move: dispersal pathways affect invasion success. *Trends Ecol. Evol.* **24**, 136–144. (doi:10.1016/j.tree.2008.10.007)
- Wilson, D., Stock, W. D. & Hedderson, T. 2009b Historical nitrogen content of bryophyte tissue as an indicator of increased nitrogen deposition in the Cape Metropolitan Area, South Africa. *Environ. Pollut.* **157**, 938–945. (doi:10.1016/j.envpol.2008.10.021)
- Witt, A. B. R. & Samways, M. J. 2004 Influence of agricultural land transformation and pest management practices on the arthropod diversity of a biodiversity hotspot, the Cape Floristic Region, South Africa. *Afr. Entomol.* **12**, 89–95.
- Yarnell, R. W., Scott, D. M., Chimimba, C. T. & Metcalfe, D. J. 2007 Untangling the roles of fire, grazing and rainfall on small mammal communities in grassland ecosystems. *Oecologia* **154**, 387–402. (doi:10.1007/s00442-007-0841-9)
- Zhou, G., Minakawa, N., Githeko, A. K. & Yan, G. 2004 Association between climate variability and malaria epidemics in the East African highlands. *Proc. Natl Acad. Sci. USA* **101**, 2375–2380. (doi:10.1073/pnas.0308714100)
- Ziman, J. 2007 *Science in civil society*. Exeter, UK: Imprint-Academic.