nature climate change

INSIGHT | PERSPECTIVES
PUBLISHED ONLINE: 21 AUGUST 2015 | DOI: 10.1038/NCLIMATE2753

Future of African terrestrial biodiversity and ecosystems under anthropogenic climate change

Guy F. Midgley[1]* and William J. Bond[2,3]

Projections of ecosystem and biodiversity change for Africa under climate change diverge widely. More than other continents, Africa has disturbance-driven ecosystems that diversified under low Neogene CO_2 levels, in which flammable fire-dependent C_4 grasses suppress trees, and mega-herbivore action alters vegetation significantly. An important consequence is metastability of vegetation state, with rapid vegetation switches occurring, some driven by anthropogenic CO_2-stimulated release of trees from disturbance control. These have conflicting implications for biodiversity and carbon sequestration relevant for policymakers and land managers. Biodiversity and ecosystem change projections need to account for both disturbance control and direct climate control of vegetation structure and function.

African ecosystems and biodiversity are biologically and ecologically unique, attract substantial tourism revenue, and provide significant ecosystem services at local, regional and global levels. It is projected that anthropogenic climate change is likely to have adverse impacts on African ecosystems and their biodiversity[1], but projections of impacts based on a range of methodologies diverge widely. This is partly due to contrasting scenarios of future precipitation, but much more importantly due to critical differences between approaches to modelling biodiversity impacts and their assumptions. These differences relate to the extent to which different modelling approaches incorporate the effects of atmospheric CO_2 and disturbance (fire, mammal herbivory) on ecosystem structure and productivity[2,3], and relative strengths in accounting for temperature- versus water-related controls on biodiversity. Projections of large declines in biodiversity under combined scenarios of climate and socioeconomic development[4,5] may not take these uncertainties into account. The most recent report by the IPCC on African vegetation change[1] reflects this well in stating with high confidence that "substantial uncertainties are inherent in these projections [future changes in terrestrial ecosystems] because vegetation across much of the continent is not deterministically driven by climate alone".

These issues require urgent resolution, because there are significant and immediate implications for biodiversity risk assessments, and adaptation and mitigation responses relevant for policymakers and land managers. The evidence necessary to resolve these divergences is indicative but far from adequate, primarily because of a dire lack of empirical evidence and information on both climate and atmospheric CO_2 impacts on the structure and function of water-limited and disturbance-dependent ecosystems in tropical and subtropical climates[6,7].

More than any other continent, Africa's ecosystems are water limited[8] and disturbance driven (by wildfire and mega-herbivores)[9], with a high representation of C_4 grass-dominated ecosystems[10,11]. Palaeoecological changes in climate and atmospheric CO_2 since the Miocene have strongly shaped the vegetation, disturbance regimes and biodiversity of these ecosystems[12]. Because the continent straddles the tropics and subtropics in both hemispheres, an enormous area over which climatic conditions are conducive to vegetation flammability emerged during the late Miocene[13]. The palaeoecological factors that led to the dominance of C_4 grasslands under these conditions are complex and possibly regionally specific[14], but after the prevalence of C_4 grassland systems gradually increased under the low atmospheric CO_2 of the early to middle Neogene[15], the ecological ascendancy of flammable grassland systems was triggered by increasing climate seasonality[16], and possibly entrained by reinforcing feedback between regional climate, vegetation and fire[17]. Africa's land surface today accounts for more than half the annual burnt area of the world[18,19]. Until a few centuries ago, Africa was also home to a near-intact megafauna, now becoming increasingly restricted to protected areas.

The late Miocene spread of grasslands provided novel habitats that supported high densities of grazing mammals, especially in Africa[20]. This included the evolution of mega-herbivores with very substantial impacts on vegetation structure and function[9]. Changes in vegetation structure and disturbance regime in the late Neogene led to the spread of disturbance-dependent and disturbance-enhancing C_4-dominated grasslands and flammable shrublands, at the expense of closed forests, that today cover more than 70% of Africa's vegetated surface[18]. This is the largest global anomaly to the assumption that world vegetation patterns are primarily determined by climate[21].

Disturbance-dependent African vegetation, including iconic savannas, has phylogenetic, functional and biodiversity characteristics that today are highly distinct from disturbance-sensitive biomes such as more ancient tropical forests[11,22]. Disturbance by fire and herbivores both limit tree cover[23] that to a first approximation differentiates plant forms that are tolerant of disturbance from those that are disturbance sensitive (although we acknowledge important differential aspects between these disturbance types that are less relevant for the purpose of this Perspective[9]). Importantly, these biomes are metastable, with interactions between disturbance, atmospheric CO_2 and climate drivers able to shift vegetation structure and composition rapidly[24], with strong feedbacks on patterns of animal and plant biodiversity[11,25,26]. The result is that over large areas of Africa, vegetation structure and ecosystem biodiversity is poorly predicted by climate alone, and thus cannot be described as climate controlled[27], but rather strongly determined by the disturbance regime[28], especially under CO_2 concentrations typical of pre-industrial times and lower[24,29] when carbon accumulation

[1]Global Change and Biodiversity Group, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa. [2]South African Environmental Observation Network, National Research Foundation, Private Bag X7, Claremont 7735, South Africa. [3]Department of Biological Sciences, University of Cape Town, Cape Town 7701, South Africa. *e-mail: gfmidgley@sun.ac.za

rate and carbon allocation differentials between C_4 grasses and C_3 woody plants were accentuated[30]. With CO_2 rising to levels[31] last seen several millions to tens of millions of years before the pivotal evolutionary events post-Miocene[32], it is difficult to see how the future of vegetation structure and biodiversity in Africa can be projected without incorporating an understanding of how disturbance regimes and climatic and atmospheric CO_2 controls will interact to determine biodiversity responses.

Unsurprisingly, there are divergent views on the future of African ecosystems and biodiversity, supported by a range of modelling and predictive approaches. Based on equilibrium assumptions of vegetation response to climate change, Africa shows among the lowest ecological sensitivity of any continent[33]. In contrast, when dynamic global vegetation model (DGVM) approaches[34] are applied, taking into account the role of disturbance by wildfire and growth responses to changing CO_2 levels, very significant shifts in major biomes are simulated, with expansion of woody elements and reductions in grass dominance in fire-prone savannas, woodlands and grasslands[35], and increases in grass dominance in fire-averse semi-arid shrublands[36]. DGVM simulations are based on a mechanistic representation of ecosystem function, and thus provide more defensible projections than correlative[37] analyses of biome determination[38,39] and species range shifts using climate drivers alone. The mechanistic DGVM projections suggest that active vegetation management[40], such as through the use of fire and mammal grazing and browsing, would be valuable elements of adaptation responses to protect both ecosystem services and biodiversity.

Long-duration observations of species range shifts in the Northern Hemisphere[41] support the general projections of species range response to climate change using niche-based modelling approaches[42], but these observations are limited mainly to regions where low temperatures limit biological activity[8]. Niche-based modelling techniques have also been applied in Africa, where water limitations to productivity are far more prevalent than low-temperature limitations[8]. These techniques project substantial biodiversity change through range reductions in indigenous and endemic species[3], and large spatial shifts in geographic ranges of plants[43] and animals[44] that indicate significant risk to biodiversity[6]. These studies support a paradigm of individualistic species response to climate change[45], and the consequent need for passive migration and corridor spatial planning approaches to climate change adaptation[46], which are more appropriate where climate control of species range limits is strong.

In this Perspective, we briefly summarize several recent advances in understanding of how disturbance regimes, rising atmospheric CO_2 and climate could interact to affect biodiversity and ecosystem structure and function in sub-Saharan Africa (SSA). We explore the implications for understanding and projecting African ecosystem and biodiversity trajectories in a rising CO_2 world, and briefly discuss the related implications for optimal mitigation and adaptation responses (passive versus active intervention) involving natural ecosystems, and for efforts to improve predictive knowledge in this area.

Geography of sub-Saharan Africa

African ecosystems encompass mainly tropical and subtropical climates, but with significant areas of arid and hyper-arid climatic zones between 30° and 50° of the Equator, and some representation of temperate- and Mediterranean-type climates towards its poleward latitudes. The continent is therefore home to a great diversity of ecosystems, and to a significant proportion of the world's biological diversity that remains relatively intact[47]. With respect to vegetation biomes, the African land surface is covered by equatorial tropical forest ecosystems, tropical and subtropical woodlands and savannas, extensive tropical grasslands, arid shrublands and desert vegetation types, with small but biologically significant areas of Mediterranean-type ecosystems at its northern and southern fringes. There are also patches of temperate forest ecosystems in azonal sites scattered across the continent where altitude and latitude provide climatic conditions cool and wet enough to support them, or where topography affords protection from wildfire. Internal drainage of large rivers in the form of the Okavango Delta, for example, provides conditions suitable for unique azonal wetland ecosystems that contribute significantly to regional patterns of biodiversity[48]. Such azonal ecosystems are not considered further here due to their limited spatial extent, but advances are being made in assessing their vulnerability to climate change through the simulation of hydrological processes[49].

Biodiversity mapping has been advancing rapidly in Africa, with improving biogeographical understanding of the spatial distribution of plants[50], mammals[51], and herptile[52] and bird diversity[53]. This reveals that high biodiversity can be associated with regions where climate has been temporally more persistent and relatively less affected by Pleistocene climatic shifts[54]. High biodiversity has also been more recently established for systems exposed to long-established disturbance regimes[11,18]. Thus, both the relative stability of climate and disturbance regimes has been important in maintaining high biodiversity on the African continent.

Ecological understanding of African ecosystems has benefited from an increasingly sophisticated elaboration of biome and pyrome concepts[18,36], particularly in SSA, and now provides a strong basis for developing simulations of vegetation structure and function based on plant functional types[55]. Performance of these simulations can be assessed using remote sensing[56], which is a recent breakthrough for the study of interactive climate and disturbance control of African ecosystems[57].

Projections and observations

For the purposes of this Perspective, we consider three main clusters of biomes: tropical and subtropical disturbance-dependent (savanna and grassland) and disturbance-sensitive biomes (forest); arid and semi-arid water-limited shrubland and grassland ecosystems; temperate climate fire-dependent biomes (Mediterranean climate shrubland, high-altitude grasslands) and fire-sensitive biomes (temperate evergreen forest). The evidence base available, while far from complete, is sufficient to strongly suggest that climate, atmospheric CO_2 and disturbance changes are able to shift vegetation between states within and even between these clusters relatively rapidly.

Tropical and subtropical biomes. Tropical and subtropical SSA biomes comprise forest, savanna or grasslands, with grassland biomes occupying the broadest rainfall range from ±200 mm to ±3,000 mm mean annual precipitation (MAP)[11]. The distribution of the forest biome is well predicted by climatic variables, with a very high likelihood of occurrence of MAP above 2,000 mm (ref. 58). Savannas and grasslands are poorly predicted by climate, and exist in a metastable mix where MAP lies between 250 and 1,750 mm (refs 27,59,60). The weakness of climate alone as a predictor of biome dominance in this rainfall range has been coherently recognized and explored only in the past 15 years (refs 28,60,61). R. J. Whittaker recognized a climate zone where ecosystems were poorly predicted on a temperature–precipitation plane, while the full spatial extent of these metastable biomes was first mapped globally by Bond[9]. The recognition of the interactive role of fire and of atmospheric CO_2 (ref. 30) in determining the relative dominance of non-forested biomes was closely followed by simulations that showed that palaeoecological shifts in the extent of these biomes in response to glacial–interglacial climate change could only be fully explained if the limiting effect of low atmospheric CO_2 on tree growth was accounted for in DGVMs[62].

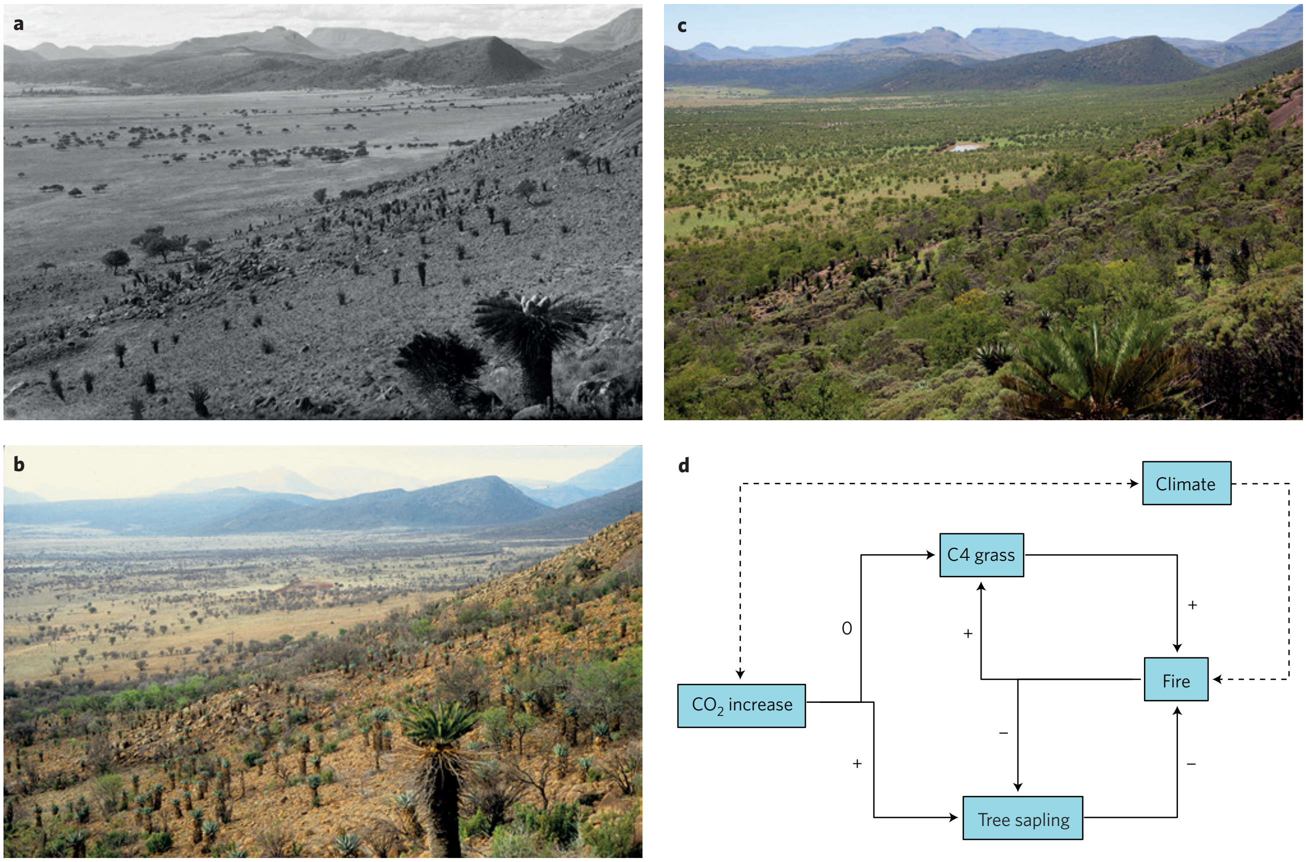

Figure 1 | Tree cover increase with CO_2 increase over the past century near Queenstown, Eastern Cape, South Africa. *Acacia karroo* is the most common tree species in this mesic savanna (~750 mm mean annual precipitation): **a**, 1925, 300–310 ppm CO_2; **b**, 1993, 360–370 ppm CO_2; **c**, 2011, 390–400 ppm CO_2. Tree cover increase has accelerated since the early 1990s. The 1925 photograph was taken by the late I. B. Pole-Evans (South African National Botanical Institute) and repeat photos courtesy of Timm Hoffman (1993) and James Puttick (2011) (Plant Conservation Unit, University of Cape Town), reproduced with permission from ref. 24, The Royal Society. **d**, Conceptual model of how rising CO_2 facilitates tree sapling recovery after fire but does not increase grass production (solid lines). Grass production increases fire frequency and intensity but sapling establishment can reduce these directly and via negative effects on grass production. The relationships between CO_2 and climate, and climate and fire regime (dashed lines) are not elaborated here, but could increase in importance with greater levels of anthropogenic warming, and are likely important in ecosystems where fire regime is responding directly to climatic signals.

Recent syntheses suggest further that the establishment of fire-dependent grasslands and savannas in Africa may have occurred through entrainment of strong vegetation and even regional climatic feedbacks[17,63]. This implies that landscapes within a large area of SSA can experience relatively rapid shifts in vegetation structure (and thus in biodiversity), driven by changes in fire regime, climate and atmospheric CO_2 concentration[12,24,27] (Fig. 1).

Numerous long-term field experiments in savannas that exclude fire have demonstrated relatively quick transitions from open grassland to closed woodland canopies in higher rainfall savannas[24,64]. These show very clearly that the typical grass-fuelled 'frequent, cool, small' wildfire types of the typically African pyrome[18] are critical in preventing trees from reaching escape height and becoming established[65]. Furthermore, the widely observed phenomenon of bush encroachment[65] has been ascribed to overgrazing and removal of grass, which reduces fire frequency and intensity and allows woody plants to establish[66]. When this phenomenon is analysed more closely, woody plant increases are quantifiable over a wide range of land-management regimes[67]. This implies that there has been a recent release of trees from control by grass fires regardless of land management or fire regime, which must be linked to a change in a powerful driver operating at a large spatial scale, such as CO_2 increase[68].

The isolated effects of rising atmospheric CO_2 on growth and resilience to fire have only been quantified for a limited number of African savanna tree species, and under controlled experimental conditions. These show very significant effects on belowground carbon storage in roots, and aboveground resprouting rate[69]. If CO_2 fertilization effects such as these are incorporated into DGVMs, fundamental and widespread changes to vegetation structure and function are simulated across SSA[35]. These include not only large projected increases in dominance by woody plants with subsequent reductions in fire frequency in fire-dependent savannas and even some grasslands[35,70], but also increases in grass production and potential increases in fire in currently water-limited arid and semi-arid shrublands[71].

While these studies support the notion that rising atmospheric CO_2 could trigger widespread switches in vegetation structure, from open grasslands and savannas to woodlands and forests, some significant gaps remain. Chief among these is the role of soil nutrient availability in limiting species ranges[72], and in supporting a sustained CO_2 fertilization response[73,74]. Plant nutrient status has commonly been found to become limiting in long-duration CO_2 fertilization experiments, though few of these experiments have been conducted under dry and hot tropical to subtropical conditions[7] where CO_2 fertilization leads to replacement of one plant functional type by another. Large areas of African savannas are known to be nutrient limited[75], and this feedback is not captured[73] in most of the DGVM approaches that project woody plant expansions.

Finally, geographic range limitation through climate variables on widespread and locally dominant tree species cannot be ignored and replaced purely by an understanding of atmospheric CO_2 and fire constraints. While empirical information is generally lacking, recent studies[76–78] have started to uncover how climate and growing season length may limit geographic range in important tree species. In the case of *Colophospermum mopane* and *Acacia* species, these studies show[76,77] that the main explanatory variable underlying range limitation is growing season duration (although simple cold tolerance limits are also important). The mechanism by which growing season duration operates is through setting the time available for carbohydrate storage accumulation after seasonal aboveground growth ceases, and in turn is likely to be tightly linked to resprouting capacity and therefore to resilience to disturbance. It is also likely that rising atmospheric CO_2 would shorten the required growing season duration to achieve the same carbohydrate storage status.

Taken together, this set of studies suggests that climate change impacts on biodiversity in metastable savanna in Africa cannot be credibly considered without including responses of vegetation structure, and therefore habitat, to changing climate, disturbance and CO_2 concentration.

Temperate biomes. Temperate systems in SSA, similar to tropical and subtropical systems, often occupy landscapes as a metastable mix of fire-dependent and fire-averse structural types, often with distinct phylogenetic composition[79]. In this climatic range, the biomes that can be recognized are forest and thicket (fire averse), and grassland and shrubland (fire dependent). However, these structural types probably transform less rapidly between states than is the case for tropical systems discussed above[80], and soil nutrient and texture characteristics may also play more of a role in constraining structural state, disturbance regime and phytosociology[81].

Indications are that high endemic biodiversity in flammable shrublands accumulated rapidly post-Miocene with the establishment of a winter rainfall regime, and is also attributable to muted climate change during the Quaternary[82]. High-altitude temperate grassland diversity also originated post-Miocene. High biodiversity is maintained by recurrent fires in both the shrubland and grassland biomes, but forest patches exist where there is protection from fire or where MAP is high enough through the year to support evergreen forest and exclude fire[83]. Rainfall seasonality appears to play a key role in limiting the spread of C_4 grasslands to the southwestern region of South Africa, where the exceptionally rich Mediterranean shrubland biome is one of very few in Africa that remains almost free of C_4 grass. Palaeoevidence indicates that the shrubland biome is currently in refugium typical of interglacial conditions, and may have been more widely distributed under cooler and wetter glacial conditions[84].

Indications are that fire frequency and area burned are increasing in flammable shrublands[85], which become flammable once a threshold biomass is reached[80]. Increasing temperatures and drought could advance this threshold, as well as leading to larger fires due to greater realized fuel continuity[85]. Niche-based models indicate substantial risk of range losses by largely endemic species in Mediterranean-climate shrublands[86], but these do not take account of potential increases in fire frequency that would exacerbate climate-driven range losses in slower-maturing species that are killed by fire and regenerate from seed banks[87]. The position of Mediterranean-type ecosystems at the southern tip of Africa strongly limits potential for species migration with a warming and drying climate, exacerbating extinction risk.

Observations under field conditions indicate the decline of endemic gymnosperm tree populations due to increasing fire damage in Mediterranean shrublands[88]. Experimental evidence shows that the CO_2 fertilization effects on endemic plants may be constrained in these biomes due to nutrient limitations[89], suggesting that an increasing risk of fire will override the tendency for endemic woody plant expansion with higher CO_2. However, CO_2-accelerated growth and spread of woody invasive alien species that avoid nutrient limitation via nitrogen fixation cannot be excluded. Unfortunately, DGVM approaches are not well developed for these vegetation types due to inadequate treatment of the shrub functional type[90], and the incomplete incorporation of soil nutrient feedback control on production. Better-developed mechanistic modelling approaches would allow the implications of these trends on vegetation structure, function and biodiversity to be explored.

Taken together, such a range of threats suggests potential for significant biodiversity loss in the southern temperate zone, although persistence through previous episodes of rapid warming during glacials[91] implies that there is at least some potential for landscape-level resilience until warming exceeds palaeo-historical limits, which could occur this century.

Arid and semi-arid biomes. The deserts of SSA are among the most ancient on Earth, and have expanded and contracted multiple times since the establishment of arid conditions roughly 80 million years ago, with hyper-arid conditions prevalent since the early Miocene[92]. There is evidence for significant expansion of unstable dune systems in the Kalahari and Namib deserts through the driest periods of the late Pleistocene[93], when CO_2 concentrations were very low, and when climate drivers favoured enhanced aridity. Warm deserts tend to expand globally during glacial periods, despite cooler conditions, and this is generally ascribed to increasing dryness. However, the role of lower atmospheric CO_2 in contributing to this pattern has not yet been fully considered.

While SSA deserts retain some ancient floristic elements, such as *Welwitschia mirabilis*, that may date back to more than 100 million years ago (discussion in ref. 94), there is considerable evidence for recent diversification of desert groups, particularly in the Aizoaceae, which diversified as recently as the Pleistiocene[95]. Arid-adapted C_4 grasses have also diversified widely[96], and thus significant floristic biodiversity in SSA arid systems is associated with modern atmospheric CO_2 and climatic conditions. These systems have an ecological history of grazing with sporadically high herbivore densities[97] that has been replaced by consistent stocking rates that can transform vegetation composition[26].

The potential importance of aridlands for the global carbon cycle has recently been recognized after a major positive sink anomaly was detected in 2011 (ref. 98), over 50% of which has been attributed to semi-arid ecosystems particularly in the Southern Hemisphere[99]. Increased moisture availability due to La Niña conditions was the trigger for the enhanced 2011 land sink in semi-arid regions[100].

Recent projections for SSA arid systems based on DGVM modelling reveals a greening of the aridlands[6] with increasing vegetation cover, driven largely by increasing CO_2 levels. On the other hand, projections based on climate-only correlative approaches indicate increased potential for vegetation decline, and desert expansion through, for example, sand dune remobilization[101]. It is important to reconcile these contrasting views given that adverse effects may often be emphasized[1].

Net primary production in SSA deserts is strongly water constrained[8], and therefore can be altered by changes in factors affecting water-use efficiency[102]. Apart from the obvious rainfall change, these include the factors that determine evapotranspiration (temperature, humidity, wind speed) and rising CO_2. At the high levels of potential evapotranspiration in deserts, quite significant changes in potential evapotranspiration components are needed to have a biologically relevant effect. On the other hand, relatively small atmospheric CO_2 increases result in appreciable effects on gas exchange and leaf-level water-use efficiency. The particular role of atmospheric CO_2 has been highlighted by work that shows how large an area globally, and in Africa, has responded through an ~10% increased cover following ~15% CO_2 increases in just under three decades[103].

Desert net primary production and vegetation cover are therefore expected to respond strongly to shifts in rainfall patterns and rising atmospheric CO_2. DGVM projections suggest future strong enhancement of vegetation cover for African arid and semi-arid ecosystems[36,104,105], partly because of the strong effect of increasing atmospheric CO_2 via increasing plant water-use efficiency. Such effects are likely to counteract significantly the projected decreases in plant production[101] that are realized in climate-only projections.

Observations based on remote sensing show a tendency towards increased vegetation cover and productivity[8,99], and these are supported by *in situ* observations using matched photographs that reveal stable or increasing vegetation cover[106], particularly of the grass component[107]. Historically, grassland shifts have been responsive to climatic changes[108]. However, there is a question about the permanence of these increases in biomass, especially the grass component, because of the likely increase in fire frequency. Fire occurrence and intensity increased after exceptionally productive years where grassiness increased in semi-arid shrublands[109], with adverse impacts on shrub diversity and biomass due to local extinction and weak resprouting response resulting from low fire tolerance. Therefore, the increase in carbon sequestration driven by anomalously wet years and by CO_2 fertilization may provide short-term impacts on regional and even global carbon sink strength, but may not represent a permanent sink[99]. This uncertainty represents an important knowledge gap in a warming world.

Climate-only niche-based approaches generally project expansion and eastward migration of arid and semi-arid systems in SSA, with only the winter-rainfall desert region projected to see significant decreases in the spatial extent of its current bioclimatic niche[110]. Species models using the same approach also project these shifts, with the large endemic flora of the winter-rainfall desert region projected to suffer very significant biodiversity loss[111]. Observations of increased cover of C_4 grasses[107], greater productivity and novel fire regimes[109] towards the eastern margins of the semi-arid shrublands do not support these projections. On the other hand, there is some evidence from observations of the desert tree succulent *Aloe dichotoma* (Quiver tree) that rising temperatures may be driving population declines in the northern parts of its range, and population increases towards the south[112]. The flora of this winter-rainfall desert has a high representation of plants using CAM photosynthesis whose productivity may not be significantly influenced by atmospheric CO_2, and thus the climate-only projections may be more relevant in this region.

As is the case for the other biome clusters, there is limited empirical information available to provide robust tests of model projections. In addition, poor understanding of how shrubs function limits the applicability of DGVM approaches to results on C_4 grasses, and the absence of a CAM functional type limits their applicability to the rich succulent flora of this region.

Mitigation and adaptation

Almost 50% (2000–2005) of African greenhouse gas emissions were from land-use and land-cover change[113], and thus land-based mitigation projects are attractive for Africa in the context of United Nations Framework Convention on Climate Change mitigation instruments. Large tracts of land that are currently grassland and savannah have been identified for potential afforestation in SSA[114], but with little to no regard for ancillary adverse impacts on biodiversity and local ecosystem services, such as water delivery and grazing. This analysis suggests that projected shifts in vegetation structure and function significantly change prospects for mitigation potential (largely positively but with high uncertainty in semi-arid lands), and we note that bush-encroachment calculations feature as a major CO_2 removal term (sink) in the greenhouse gas inventory of at least one country in SSA (Namibia, Table 3.1 in ref. 115).

We project that large-scale afforestation via woody cover increase and biome switches driven by rising atmospheric CO_2 and climate change has the potential to transform and thus to reduce the biodiversity of some of the most species-rich and iconic African vegetation types, and their delivery of vital services, such as freshwater, over extremely large areas. Such an outcome directly undermines conservation adaptation efforts to maintain these. Maintaining ecosystems in an un-encroached state in the face of climate and atmospheric CO_2 change will involve active management through the use of fire and browsing, practices that have been in place for millennia[116], but are decreasing due to agricultural expansion[117], and risk becoming the victims of incomplete theory[118] about their role in maintaining iconic African ecosystems. Passive conservation efforts based only on projections of species range shifts and appropriate placing of protected areas are doomed to fail if not coupled with an active disturbance management approach, which itself may not be achieved through replacement of indigenous grazing and browsing systems by domestic stock alone.

Urgent choices relating to trade-offs between biodiversity, carbon sequestration and direct-use benefits from ecosystems now face African policymakers and stakeholders. These choices will be critical for maintaining unique African biodiversity, but the key empirical evidence needed to make well-informed decisions is incomplete. This could be addressed with well-replicated experimentation, synthesis of available information, and development of appropriate modelling tools that incorporate emerging concepts on the role of uniquely African disturbance regimes. Encouraging progress is being made on ecological–economic tools for assessment of optimal investments in wildfire management[119]. Species-based approaches would benefit by taking into account the fundamental role of habitat structure as determined by disturbance, climate and atmospheric CO_2 drivers, and mechanistic modelling of ecosystem structure and function would benefit from improved simulation of fire in the typically African pyrome[18], important plant functional types, such as shrubs, and browsing and grazing processes.

Received 14 March 2015; accepted 13 July 2015; published online 21 August 2015

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Acknowledgements

Funding via the South African National Research Foundation 'Global Change Grand Challenge: Solutions for Sustainability' Grant 92463 (G.F.M.) and the NRF/CSIR Applied Center for Climate and Earth System Studies (W.J.B.) made this work possible.

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Competing financial interests

The authors declare no competing financial interests.