

Viewpoints

Human impacts in African savannas are mediated by plant functional traits

Summary

Tropical savannas have a ground cover dominated by C_4 grasses, with fire and herbivory constraining woody cover below a rainfall-based potential. The savanna biome covers 50% of the African continent, encompassing diverse ecosystems that include densely wooded Miombo woodlands and Serengeti grasslands with scattered trees. African savannas provide water, grazing and browsing, food and fuel for tens of millions of people, and have a unique biodiversity that supports wildlife tourism. However, human impacts are causing widespread and accelerating degradation of savannas. The primary threats are land cover-change and transformation, landscape fragmentation that disrupts herbivore communities and fire regimes, climate change and rising atmospheric CO_2 . The interactions among these threats are poorly understood, with unknown consequences for ecosystem health and human livelihoods. We argue that the unique combinations of plant functional traits characterizing the major floristic assemblages of African savannas make them differentially susceptible and resilient to anthropogenic drivers of ecosystem change. Research must address how this functional diversity among African savannas differentially influences their vulnerability to global change and elucidate the mechanisms responsible. This knowledge will permit appropriate management strategies to be developed to maintain ecosystem integrity, biodiversity and livelihoods.

African savannas face multiple anthropogenic threats

Savannas cover more than 50% of the African continent, encompassing diverse ecosystems with a wide range of woody cover, from densely wooded Miombo woodlands to Serengeti grasslands with scattered trees. Co-dominance of trees and grasses is common to these ecosystems, with the ground layer dominated by shade-intolerant C_4 grasses. This layer persists because woody plant recruitment is limited below its rainfall-based potential by disturbance, including recurrent grass fires and browsing (Sankaran *et al.*, 2005; Bond, 2008). Grasses also compete with tree seedlings for water, nutrients and light (February *et al.*, 2013; Vadigi &

Ward, 2013). The distinct physiology and ecology of C_4 grasses (Bond, 2008; Christin & Osborne, 2014) is therefore a defining characteristic of African savanna ecosystems and has driven the selection of woody plant traits since C_4 grasses increased in abundance during the late Miocene (Hoffmann *et al.*, 2003; Ratnam *et al.*, 2011).

The savanna biome is home to diverse endemic floras and faunas, including charismatic megafauna, which are central to wildlife tourism and hunting, contributing hundreds of millions of dollars to African economies (World Tourism Organization, 2015). Beyond this, people across the continent depend on a multitude of savanna ecosystem goods and services, including the provision of water and food, medicines, grazing for livestock, timber and grass for construction, fuelwood and charcoal, with a total annual value exceeding \$9 billion (e.g. Ryan *et al.*, 2016). However, as humans increasingly dominate the Earth system during the Anthropocene (Malhi, 2017), four anthropogenic drivers are causing rapid vegetation change across African savannas, threatening biodiversity and ecosystem services. These are: (1) land-cover change and transformation, (2) human-induced changes to fire, browsing and grazing regimes, (3) climate change and (4) rising atmospheric CO_2 (Fig. 1).

Land-cover change and transformation (Fig. 1a) accelerated during the 20th century (Riggio *et al.*, 2013). These are likely to continue to meet the food and energy requirements of a projected doubling-to-tripling of population by 2050 across most of the African savanna region (United Nations, 2017). The World Bank has proposed that the rapid economic development needed to support growing African populations and alleviate poverty could be catalysed by the large-scale expansion of commercial agriculture into savannas (World Bank, 2009). Important concerns have been raised about the suitability of available land for broad-scale commercial agriculture, but if this plan goes ahead the resulting destruction of savanna habitats would cause massive losses of biodiversity and carbon across the region (Searchinger *et al.*, 2015; Estes *et al.*, 2016). Simultaneously, increasing urbanization across southern and West Africa is raising local and regional demands for agriculture, fuelwood and charcoal, increasing pressures for land clearance and degradation (Wessels *et al.*, 2013; Kalema *et al.*, 2014). Indeed, recent land clearance rates across savanna regions in Tanzania and Zimbabwe have been at least as high as those of tropical forests in Nigeria and the Democratic Republic of Congo (FAO, 2015), an issue that receives virtually no political attention, even though wetter savannas contain similar levels of biodiversity to forests (Murphy *et al.*, 2016).

Anthropogenic activities also disrupt fire and mammalian herbivory regimes (Fig. 1b), two of the key spatial processes maintaining open savanna ecosystems (Fig. 2; Sankaran *et al.*, 2005). In particular, changes in land management, commercial agriculture and fragmentation by road networks alter the size,

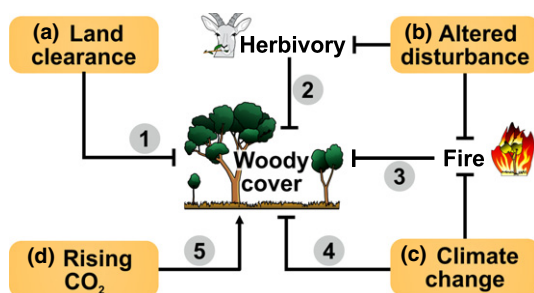


Fig. 1 Interacting effects of global change on savanna woody plant cover. Woody plant cover controls ecosystem services provided by savannas and is altered by four drivers of change: (a) land-use intensity, (b) human-induced changes to disturbance regimes, (c) climate change and (d) rising atmospheric CO_2 . Their effects are either exerted directly, or indirectly via herbivory and fire. The direction of these effects is indicated by pointed arrows (positive) and flat-ended arrows (negative). Land clearance limits herbivory and fire by fragmenting landscapes and reducing their connectivity, and therefore can potentially cause increased woody cover in uncleared areas. Drought can kill woody plants directly, but the effects of drought on fire depend on the underlying rainfall regime. Declining rainfall is associated with reduced burned area in the region of southern Africa where droughts are projected to become more intense during the coming century (Field *et al.*, 2012; Andela & van der Werf, 2014). This interaction could indirectly allow woody cover to increase. The numbered nodes indicate where biotic and abiotic interactions are controlled by a range of plant functional traits that differ among species and are discussed in the text.

season, frequency and intensity of fires, thereby altering natural fire regimes (Fig. 1b; Archibald *et al.*, 2013; Andela & van der Werf, 2014; Andela *et al.*, 2017). The effect is especially pronounced when economic development and increased population densities cause cropland expansion (Andela & van der Werf, 2014; Andela *et al.*, 2017). Indeed, much of the 25% decline in global fire can be attributed to increasing human influence in savannas (Andela *et al.*, 2017). People have similarly impacted herbivory regimes (Fig. 1b), with a continent-wide switch occurring across Africa from free-roaming native herbivores to largely sedentary grazing livestock. These changes in herbivory regimes are further exacerbated by the continent-wide poaching of iconic African megaherbivores, such as elephant and rhinoceros (Fig. 1b). The culling of wild mammals to prevent disease transfer to livestock has also drastically reduced population sizes (du Toit, 1995), while fences and roads hinder migration and restrict range sizes. Smaller and more fragmented populations, in turn, diminish the ecosystem-engineering effects of megaherbivores on vegetation openness and nutrient distribution (Asner *et al.*, 2016; Malhi *et al.*, 2016). Such engineering has likely influenced savanna structure and function since the Miocene (Charles-Dominique *et al.*, 2016).

The impacts of anthropogenic climate change on African savannas (Fig. 1c) are more difficult to detect and attribute, and less well studied. Rising temperatures and changing distributions of rainfall have the potential to directly affect woody plant growth and mortality (Fig. 1c; Allen *et al.*, 2010), and to indirectly influence tree cover by disrupting fire regimes (Figs 1c, 2; Andela & van der Werf, 2014). The risk of heatwaves will increase across the continent in the coming decades (Battisti & Naylor, 2009). However, the amount and direction of precipitation change is likely to vary across sub-Saharan Africa (Engelbrecht & Engelbrecht,

2016), with climate models projecting increases in drought duration for southern Africa and more frequent extreme high rainfall events for Central and East Africa by the end of the century (Field *et al.*, 2012). The net effects of these climate changes on woody plant cover will depend on the resistance and resilience of plants to drought events and heat stress, and interactions with fire and herbivory regimes.

Finally, the fate of the African savanna biome may be bound intrinsically to rising atmospheric CO_2 (Fig. 1d) in ways that other biomes are not. This is because C_3 woody plants are potentially more responsive to the fertilization effect of rising atmospheric CO_2 than C_4 grasses. C_4 grassy vegetation first expanded globally in a low CO_2 atmosphere 5–10 Ma (Edwards *et al.*, 2010), an event linked to altered regional climates and fire regimes (Scheiter *et al.*, 2012), and the colonization of Africa by bovid mesoherbivores (Charles-Dominique *et al.*, 2016). During glacial times in the Pleistocene, low atmospheric CO_2 is thought to have further reduced the extent of closed tree cover (Harrison & Prentice, 2003), while woody vegetation expanded during higher CO_2 interglacials. Thus, as atmospheric CO_2 continues to rise during the Anthropocene, the demographic and competitive interactions between C_4 grasses and C_3 woody plants mediated by fire, herbivores and soil resources (Fig. 2) are predicted to shift increasingly in favour of the C_3 woody component. This process potentially leads to the encroachment of woody plants, and a transformation from open canopy savanna to closed canopy forest or shrubland (Bond & Midgley, 2000, 2012; Ward, 2010; Buitenwerf *et al.*, 2012; Higgins & Scheiter, 2012).

The diverse pressures of land clearance, alteration of fire and grazing regimes, climate change and increasing CO_2 likely interact to transform and degrade savannas at the continental scale in, as yet, unknown ways (Fig. 1). Regional differences in these interactions are suggested by recent examples from Africa, South America and Australia (Murphy *et al.*, 2015; Stevens *et al.*, 2016b). For example, African savannas may be more sensitive to fire than Australian systems (Murphy *et al.*, 2015), and the rates of change in Africa, but not Australia, are increasing over time (Stevens *et al.*, 2016b). However, Brazilian savannas, which have experienced the highest rates of land clearing and fire suppression (Durigan & Ratter, 2016), had the highest rates of woody encroachment in this analysis (Stevens *et al.*, 2016b), suggesting that fragmentation and fire suppression can have regional consequences. Hence, a key issue to reconcile is how regional changes in land clearance, fire, herbivory, climate and atmospheric CO_2 interact to influence the woody plant cover of savannas, mediated via tree growth and mortality (Fig. 1). The interactions between these factors are complex (Fig. 1), and we will only develop realistic scenarios of vegetation change and identify management options if we can disentangle the relative roles of each biotic and abiotic control, and their net effects. The observed rate of change and its potentially wide-reaching impacts set this apart as a research frontier requiring urgent action.

Here, we outline the major research challenges in understanding how vegetation changes across African savannas, showing how a mechanistic knowledge of savanna ecosystem ecology is needed to underpin realistic regional predictions of vegetation change and thus inform management strategies for mitigation and adaptation.

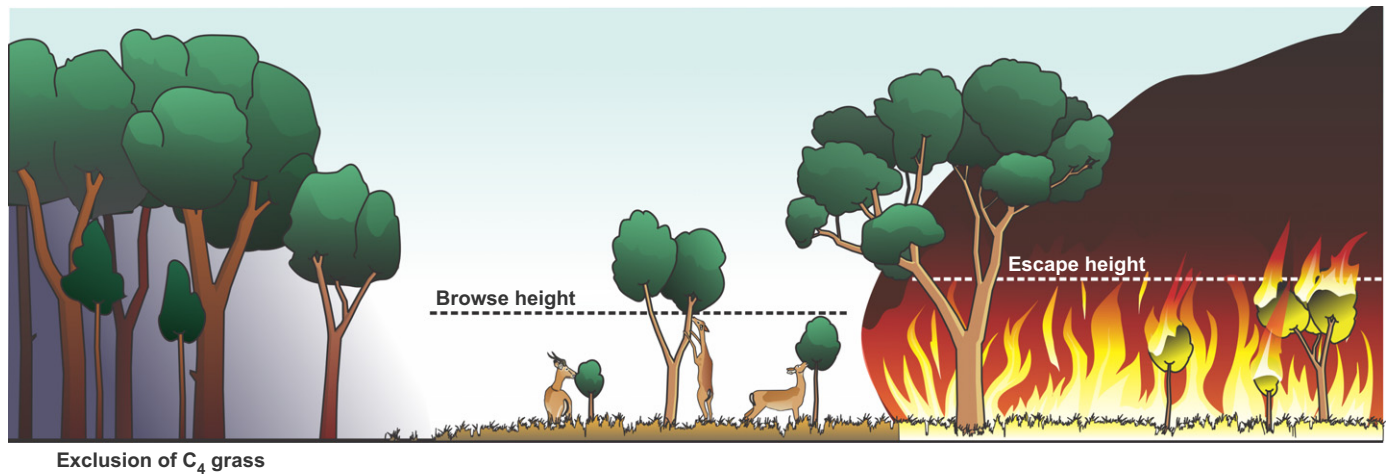


Fig. 2 Mechanisms of tree–grass coexistence in savannas. Fire and browsing cause demographic bottlenecks for tree recruitment into the grass layer, leading to the emergence of ‘escape heights’ in each case. When trees surpass these heights they are no longer suppressed by fire or browsing, and may reach mature sizes. Most C_4 grasses are excluded under closed tree canopies because they are intolerant of shading, a mechanism which suppresses fires. Each of these feedbacks is positive, leading to the emergence of tipping points beyond which the ecosystem transitions rapidly to an alternative stable state (Hoffmann *et al.*, 2012).

We begin by discussing how anthropogenic drivers cause the degradation of savanna ecosystems, and the crucial differences between degradation in savannas and forests.

The concept of degradation in savanna landscapes

Ecosystems become degraded when anthropogenic factors adversely affect ecosystem health, functions and services. This concept of degradation has achieved prominence in the context of tropical forests, whose high intrinsic value comes from their biodiversity and roles in the global carbon cycle (Lewis *et al.*, 2015). In these systems, hunting, fragmentation and disturbance cause species losses, and selective logging or land conversion for agriculture depletes carbon stocks, effects which clearly degrade the natural value of forests (Lewis *et al.*, 2015). However, uncritical application of the same degradation concept to savannas is problematic, because their biodiversity and ecosystem services depend on open-canopied grassy landscapes. In savannas, two opposing trends in woody plant cover may cause degradation (Veldman, 2016): the first is the total loss of ecosystems, driven by human land transformation (Fig. 1a), and the second is woody plant encroachment and afforestation of open savannas, caused by alterations to disturbance regimes (Fig. 1b), rising CO_2 (Fig. 1d) or tree planting (Veldman *et al.*, 2015a,b). Climate change may directly cause tree mortality or indirectly cause encroachment via its effects on fire regimes or the community composition of the grassy ground layer (Fig. 1c).

Extensive tracts of intact savanna across Africa are undergoing woody plant encroachment. Defined as an increase in woody biomass and cover, encroachment occurs via increases in the density and size of savanna trees, but also through the conversion of savanna into forest (Fig. 3a,b; Buitenwerf *et al.*, 2012; Mitchard & Flintrop, 2013; Stevens *et al.*, 2016a,b). Savanna tree cover does fluctuate naturally over decades, but numerous African savannas are now on a trajectory of increasing woody biomass, as noted by meta-analyses of long-term change (Stevens *et al.*, 2016b), analysis of photographic

records (Wigley *et al.*, 2010; Buitenwerf *et al.*, 2012; Ward *et al.*, 2014) and regional observations derived from remote sensing (Andela *et al.*, 2013; Mitchard & Flintrop, 2013; Stevens *et al.*, 2016a; Skowno *et al.*, 2017). Critically, observed rates of encroachment across Africa are accelerating (Stevens *et al.*, 2016b).

Encroachment causes degradation because it disrupts provisioning services and leads to biodiversity loss (Fig. 4; Parr *et al.*, 2014; Veldman, 2016). For example, an increase in tree cover within catchments depletes groundwater supplies upon which people depend (Bosch & Hewlett, 1982; Farley *et al.*, 2005), and limits the productivity of grasses grazed by livestock or game (Ryan *et al.*, 2016). Livestock has high social and cultural value in many African societies, and wild animals generate income via the tourism and hunting industries. For wild animals, encroachment is associated with significant faunal turnover (Sirami & Monadjem, 2012; Smit & Prins, 2015), and the potential loss of diversity is severe (Searchinger *et al.*, 2015), with adverse affects on tourism (Gray & Bond, 2013). While woody encroachment increases aboveground carbon storage, its impacts on soil carbon storage may be positive or negative (Jackson *et al.*, 2002; Li *et al.*, 2016), and net effects on the energy balance of the land surface are uncertain. Tropical deforestation increases albedo but reduces the latent heat flux, leading to a net warming and drying of regional climates (Hoffmann & Jackson, 2000; Lawrence & Vandecar, 2015), but whether woody plant encroachment has opposite effects remains unknown.

Degradation of savanna ecosystems therefore arises from somewhat different processes, and is marked by different indicators to those used for forests (Fig. 4; Veldman *et al.*, 2015a,b; Veldman, 2016). In the case of woody encroachment, savanna landscape management for ecosystem services must involve strategies for slowing tree recruitment and reducing woody plant cover, the opposite of strategies usually deployed for forested landscapes. The recognition of these points is important, because international and national forest and landscape restoration programmes are currently aiming to sequester carbon in woody biomass across 100×10^6 ha of Africa, while promoting sustainable development (Bonn

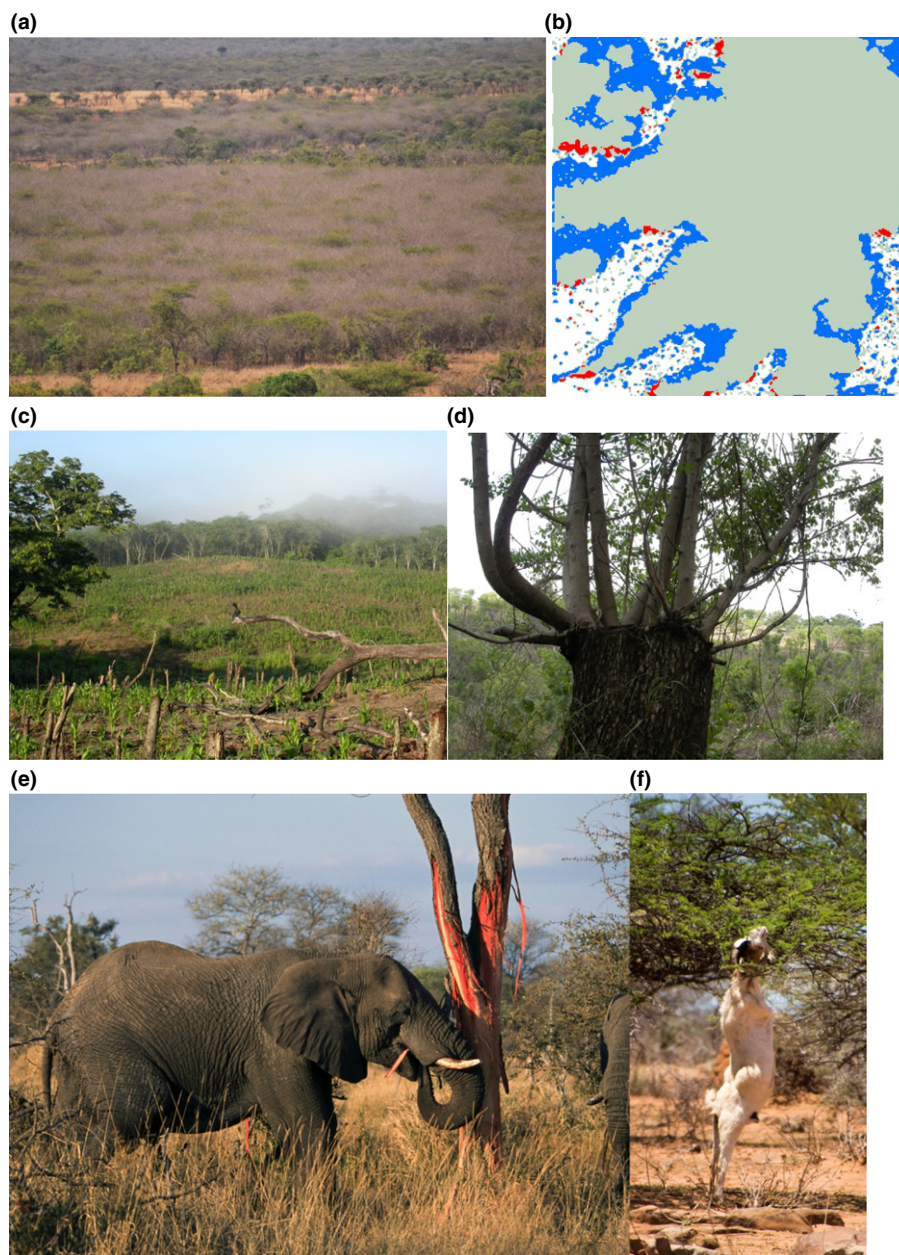


Fig. 3 Drivers of change in savannas. Woody plant encroachment threatens the ecosystem services provided by savannas across Africa; for example: (a) an encroached area in northern KwaZulu Natal, South Africa; (b) an analysis of aerial photographs at a savanna–forest ecotone in the north of Mbam Djerem National Park, Cameroon, showing encroachment over the last 50 yr in a 1 km square area: blue, tree gains; red, tree losses; white, no trees; grey, forest. However, agricultural clearance (c) is also a major threat to savanna woodlands, but the adaptation of tree species to disturbances from fires and herbivores can mean that woody plants recover rapidly (d). Populations of wild animals, such as elephants (e), and domestic livestock, such as goats (f), may both maintain open woody canopies. Photo credits: (a) Nicola Stevens; (b) Edward Mitchard; (c, d) Casey Ryan; (e) Godot13, CC BY-SA 3.0, (<https://commons.wikimedia.org/w/index.php?curid=24516228>); (f) Nicola Stevens.

Challenge, 2016; World Resources Institute, 2016). Arguments against the afforestation of savannas have been made elsewhere (e.g. Veldman *et al.*, 2015a,b; Bond, 2016a,b; DeWitt *et al.*, 2016; Veldman, 2016). However, to avoid this problem, it is vital that forest and landscape restoration programmes develop clear criteria for identifying degraded areas and developing appropriate restoration strategies (Veldman *et al.*, 2015a,b; Veldman, 2016). In the case of savannas degraded by woody plant encroachment, these appropriate strategies may controversially include tree removal.

Functional traits mediate the differential responses of savanna species to global change

Woody plant cover in savannas is controlled by the interacting effects of land clearance, herbivory, fire, climate and atmospheric

CO₂ on plant growth and mortality (Fig. 1). These impacts are, in turn, mediated by the ecological adaptations of woody plants and grasses characterized by their functional traits (indicated by the numbered nodes in Fig. 1). Where these traits have been characterized, they contrast significantly among the Detarioideae, Combretaceae and Mimosoideae species that dominate different floristic regions of African savanna (Fig. 5; Table 1). Known trait differences among these dominant tree species include defences against herbivores and resistance to fires, nitrogen-fixing nodulation and mycorrhizal status, canopy architecture and clonal reproduction, and current knowledge of these is detailed in Table 1.

A specific example of these trait contrasts is the nature of tree mutualisms with microbes. High-rainfall savannas are associated with leached and infertile dystrophic soils particularly low in phosphorus (Högberg, 1986). As a consequence, most woody

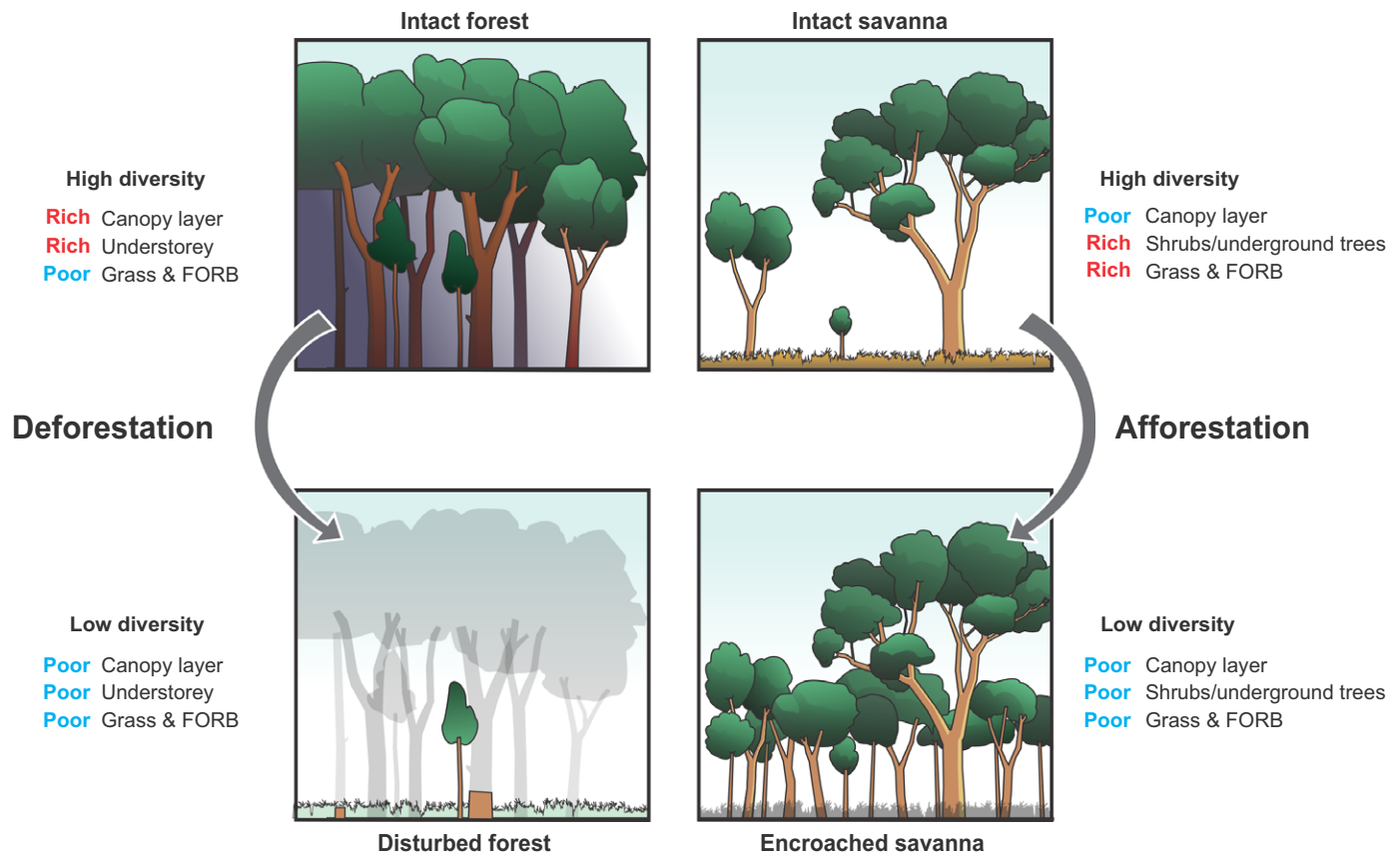


Fig. 4 Mechanisms of degradation in tropical forests and savannas. Degradation is associated with biodiversity losses in both tropical forests and savannas, but through different mechanisms in each case. In savannas, afforestation eliminates the species-rich ground cover of grasses, forbs, shrubs and underground trees. This schematic of the general principles involved was produced using the reviews of Bond & Parr (2010) and Veldman *et al.* (2015a,b), and references therein. See also Zaloumis & Bond (2011) and Abreu *et al.* (2017).

species across the Detarioideae savannas (Fig. 5) are nonnitrogen-fixing legumes that acquire nutrients via ectomycorrhizal (EM) symbioses (Högberg, 1986). For example, the Detarioideae-dominant genera *Brachystegia* and *Julbernardia* are EM (Högberg, 1986). Conversely, in the Combretaceae-dominated savannas (Fig. 5), the genera *Combretum* and *Terminalia* are arbuscular mycorrhizal (Högberg, 1986). The distinction is important for two reasons. First, elevated CO₂ tends to fertilize growth in EM species irrespective of soil fertility, whereas the CO₂-fertilization effect in arbuscular mycorrhizal species is lost when soils are infertile (Terrer *et al.*, 2016). Second, by affecting the nitrogen content of leaves and the availability of crude proteins for herbivores, these symbioses have the potential to alter the overall forage quality of the vegetation (Owen-Smith & Cooper, 1987), with potential cascading consequences to higher trophic levels (Fornara & du Toit, 2008).

Examples like this indicate the importance of major trait divergences among the species dominating different floristic regions of African savannas, but the values for many of these traits remain unknown. Future research must systematically characterize the trait combinations of savanna tree and grass species, their roles in mediating plant responses to disturbance, climate and CO₂, and the diversity of these traits among species. The traits considered may need to extend beyond those commonly considered by ecological screening approaches (e.g. Cornelissen *et al.*, 2003).

Given current knowledge about the distributions of savanna floristic regions in relation to continental environmental gradients (Fig. 5), and the known contrasts in traits between their characteristic taxa (Table 1), it seems sensible to begin this work by systematically comparing the functional traits of savanna species between the floristic regions. However, functional diversity also exists within each savanna type, arising from coexistence mechanisms and species sorting along fine-scale landscape gradients. It will therefore be important to understand the relative significance of functional variation both between and within savanna communities.

In the following we provide a rationale for identifying the traits to include in this comparative work, using Fig. 1 as an organizing framework because the cover of woody plants determines savanna biodiversity and ecosystem services. We first review how functional traits mediate plant responses to felling/clearance, herbivory, fire, drought and rising CO₂, and then outline how these vary among savanna trees and grasses. We also explain how each biotic or abiotic driver varies in relation to the continental climatic gradient shown in Fig. 5.

Table 1 provides a detailed list of the functional traits and their ecological interactions. Improving the mechanistic understanding of these ecological interactions will enable better simulation of plant functional diversity within process-based ecosystem models

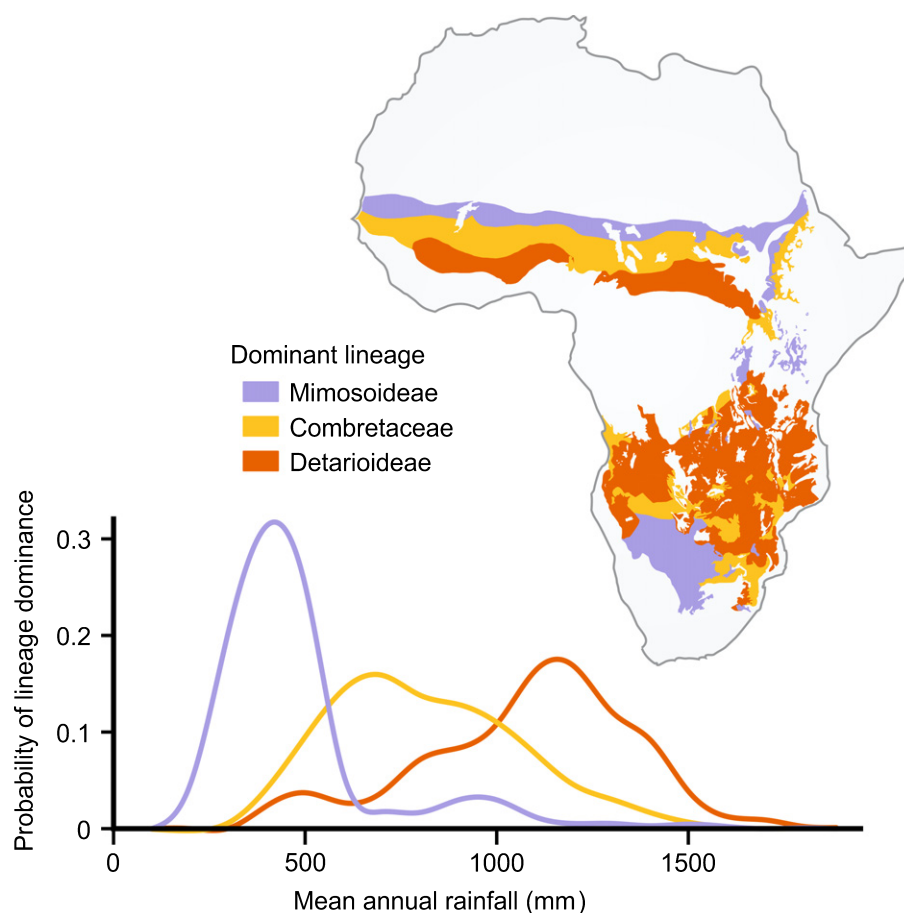


Fig. 5 Distribution of savannas in Africa. African savannas, defined by a continuous ground cover of C_4 grasses and discontinuous woody plant cover, and classified by floristic 'functional types' of savanna tree lineages. Graph shows the probability of occurrence for these savanna functional types in relation to climate, as illustrated by mean annual rainfall (mm). The importance of drought, soil nutrients, herbivores and fire in controlling woody plant cover also changes along this continental rainfall gradient (discussed in text). Briefly, the vegetation map of White (1983) was used to map savannas following the approach used by Lehmann *et al.* (2011). Savannas were defined as vegetation units with a continuous ground cover of C_4 grasses and a discontinuous tree cover. This definition excluded closed woody formations spanning heaths, shrublands, thickets and forests, and treeless C_4 grasslands or vegetation where the ground cover is dominated by C_3 grasses. A number of other vegetation units were also excluded, including edaphic grasslands, croplands, montane ecosystems and deserts. In combination, these conditions exclude a number of vegetation units in South Africa and the Horn of Africa that may be classified as savannas according to less stringent criteria. Each vegetation unit description for these savannas contains a species list of dominant woody plants derived from plot data collated by White (1983). Using the species lists, we classified dominant species into legume subfamilies (Mimosoideae, Combretaceae and Detarioideae) and classified each vegetation unit according to the dominant subfamily. Further details are provided in Supporting Information Methods S1.

(e.g. dynamic global vegetation models; Higgins & Scheiter, 2012; Scheiter *et al.*, 2012). Advances in model development and functional ecology must be complementary and iterative: improved knowledge of ecological mechanisms should inform model development, while the requirements for model parameterization must guide ecological data collection.

Felling and cutting

African savanna trees are resilient to stem and branch damage compared with their counterparts in tropical forests, probably because they have coevolved with indigenous megaherbivores (e.g. Fig. 1, node 1, Fig. 3e). Large-bodied mammals such as elephants directly damage trees by stripping bark, pulling off branches and toppling trunks (Malhi *et al.*, 2016). When this damage is chronic it may kill trees outright or cause topkill, where the stem is killed but

the tree resprouts from the base, as may happen after fires (Morrison *et al.*, 2016). In combination with the consumption of seedlings, damage caused by large mammals can reduce woody plant cover in African savannas more than 10-fold (Asner *et al.*, 2009, 2016). Adaptations of woody plants to this damage include resprouting and clonal recruitment (Table 1). Especially noteworthy in this context are the Detarioideae species dominating Miombo savannas (Fig. 5; *Brachystegia* spp. and *Julbernardia* spp.), which tolerate high degrees of disturbance from felling (Fig. 3c,d; Chidumayo, 1993; McNicol *et al.*, 2015). Here, biomass and biodiversity can rapidly recover after short periods under cultivation (Figs 1, node 1, 3c,d; Tredennick & Hanan, 2015). This is important because the fastest net losses of woody plant cover in African savannas are occurring in the Miombo savannas distributed in wet subtropical climates south of the equator (Mitchard & Flintrop, 2013; Ryan *et al.*, 2016).

Table 1 Functional traits of savanna plants that mediate their environmental responses

Functional trait	Mechanism	Influence on ecosystem structure	Species differences	References
<i>Trees</i>				
Bud position in bark	<i>Fire-related traits</i> Buds protected by bark have greater survival after fire, increasing epicormic resprouting	Greater survival after fires and recruitment into large size classes	Bud depth within bark; presence of accessory buds; bud bank underground (root suckers/underground trees) (M?, C?, D?)	Maurin <i>et al.</i> (2014), Charles-Dominique <i>et al.</i> (2015a)
Bark thickness : stem diameter	Greater bark thickness for a given size class reduces topkill after fire	Greater survival after fires and recruitment into large size classes Trees with better-protected buds and faster bark growth inhabit fire prone environments	Bark growth rate (M–, C+, D+)	Balfour & Midgley (2006), Hoffmann <i>et al.</i> (2012), Lawes <i>et al.</i> (2013), Charles-Dominique <i>et al.</i> (2017)
<i>Trees</i>				
Cage architecture	<i>Herbivore-related traits</i> Saplings with intricate branching prevent herbivore access to their leaves and buds	Greater survival in herbivore-controlled vegetation	Higher branching density and spinescence (M+, C+, D–)	Archibald & Bond (2003), Staver <i>et al.</i> (2012), Charles-Dominique <i>et al.</i> (2016)
Spinescence	Reduces the bite size and biting rate of mammals	Greater survival in herbivore-controlled vegetation	Presence of thorns, hooks, prickles (M+, C–, D–)	Grubb (1992), Cooper & Owen-Smith (1986), Charles-Dominique <i>et al.</i> (2015b, 2016)
Chemical defences	Reduces the digestibility of browse or increases toxicity	Influences the preference of mammalian herbivores	Nitrogen availability reduced by lower digestibility (M–, C+, D+) Flavonoid/terpenoid/alkaloids (M–, C+, D–)	Cooper & Owen-Smith (1986), Owen-Smith (2002)
<i>Trees</i>				
CO ₂ responsiveness of height growth	<i>CO₂-related traits</i> Enables trees to more rapidly escape fire or browse traps Stronger responses expected in species with greater leaf sugar export, larger sink capacity (via storage or mutualisms) or ability to obtain other limiting nutrients via mutualisms	Increased tree recruitment into large size classes Tree encroachment	Leaf sugar export capacity (M?, C?, D?) Mycorrhizal associations (M = AM, C = AM, D = EM) Nodulating vs nonnodulating (M+, C–, D–) Potential size of storage sinks, e.g. lignotubers (M?, C?, D?)	Höglberg, 1986; Bond & Midgley (2000, 2012), Ainsworth <i>et al.</i> (2002), Bond <i>et al.</i> (2003), Kgope <i>et al.</i> (2010), Terrer <i>et al.</i> (2016), Ainsworth & Lemonnier (2018)
CO ₂ responsiveness of leaf area	Increased carbon supply and improved water status leads to greater canopy development Stronger responses expected in more open canopies	Shading of understorey, C ₄ grass exclusion and fire suppression Tree encroachment	Ratio of canopy diameter to stem diameter (M++, C+, D+) and canopy openness depend on shoot architecture	Norby & Zak (2011), Lehmann <i>et al.</i> (2014), Moncreiff <i>et al.</i> (2015)
CO ₂ responsiveness of recruitment	Increased density of seedlings or new ramets (in clonal species) Greater population size if the probability of survival after drought, herbivory or fire remains unchanged Strong closure response protects hydraulic system from failure during droughts.	Increased tree population densities in small size classes Reduces seedling visibility and predation risk from herbivores Reduced mortality during drought Higher potential tree cover in a given rainfall regime	Capacity to increase sexual reproduction in response to greater carbon supply (M?, C?, D?) Development of new ramets through clonal reproduction (M–, C–, D+) Response varies among tree species from +4% to –24% (M?, C?, D?)	Smit & Prins (2015) Curtis & Wang (1998) Quirk <i>et al.</i> (2013) Stevens <i>et al.</i> (2016a)
<i>Grasses</i>				
Resprouting rate (and its CO ₂ response)	Faster resprouting after fire is enabled by high photosynthetic rate, nitrogen-use efficiency (NUE) and specific leaf area	Mediates competition after fire, which determines grass community composition	Grass lineages differ in resprouting rates and NUE	Forrestel <i>et al.</i> (2014), Ripley <i>et al.</i> (2015)

Table 1 (Continued)

Functional trait	Mechanism	Influence on ecosystem structure	Species differences	References
Dry-season biomass (and its CO ₂ response)	High-biomass fuel load results in more intense combustion that is sustained longer	Increases likelihood of killing trees or grass neighbours	Grass species differ in dry-season biomass	Ripley <i>et al.</i> (2015), Simpson <i>et al.</i> (2016)
Canopy curing rate	Rapid canopy senescence and curing leads to dry fuel that ignites more readily and burns more rapidly, whereas green leaves extinguish fires	Changes likelihood of fire and tree recruitment	Invasive species (<i>Cenchrus setaceus</i>) remains green in the dry fire season	Simpson <i>et al.</i> (2016)
Stomatal closure under rising CO ₂	May enable longer growing season and greater productivity	Increased fuel load? Greater chance of green fuel?	Response varies among grass species from –20% to –60%	Ward <i>et al.</i> (1999)
Tolerance of repeated defoliation	Improved shoot water relations	Mediates survival after herbivory	Grass species differ in tolerance	Archibald & Hempson (2016), Forrester <i>et al.</i> (2015)
Tolerance of shading	Enables persistence in communities that experience sustained herbivory	Fire suppression allows fire-intolerant forest trees to invade	Grass species differ in tolerance	Hoffmann <i>et al.</i> (2012)
	Shade intolerance means that savanna grasses are excluded by tree canopy closure			

Functional traits, the mechanism by which they operate, their influence on savanna vegetation structure, literature-based hypotheses about how they differ among species, and supporting references. Predictions for CO₂-related traits are untested for most savanna species, whereas fire- and herbivore-related traits are better established. AM, arbuscular mycorrhizal; EM, ectomycorrhizal. In the 'Species differences' column: M (Mimosoideae), C (Combretaceae) and D (Detarioideae) indicate the three lineages of trees that define African savannas, as shown in Fig. 5. Based on assessments of the literature, traits are either present (+), absent (–) or unknown (?) for these lineages. We list data on the hypothesized predictors of CO₂ responsiveness (e.g. mycorrhizal status), but lack direct evidence about whether these actually translate into different CO₂ effects. There is insufficient information on the grass species to confidently assign most of the trait responses at a lineage level.

Herbivory

Woody plants in savannas resist browsing via a range of physical and chemical defences. 'Cage architecture', spinescence and small leaves restrict or prevent mammalian herbivores from accessing foliage (Fig. 1, node 2; Table 1; Archibald & Bond, 2003; Staver *et al.*, 2012; Charles-Dominique *et al.*, 2016, 2017), chemical defences reduce leaf digestibility or make foliage toxic (Table 1; Cooper & Owen-Smith, 1986; du Toit, 1995), while nutritional quality depends upon plant secondary metabolites, the concentrations of nutrients such as protein, and digestible energy (Table 1; Owen-Smith, 2002; Bedoya-Pérez *et al.*, 2014). Across the African continent, the proportion of spiny species (especially Mimosoideae; Table 1) increases in open dry savannas, on fertile soils, when mesoherbivores and large-bodied browsers are present, and when fires are infrequent (Charles-Dominique *et al.*, 2016). The quality of forage for browsers is also expected to vary along environmental gradients, being significantly higher in low-rainfall, eutrophic savanna ecosystems dominated by Mimosoideae than in high-rainfall, dystrophic savannas dominated by Combretaceae and Detarioideae (Table 1; Fig. 5; du Toit, 1995). However, while the palatability of woody plants is assumed to play a major role in regulating animal densities, virtually no information is available at the community scale (DeGabriel *et al.*, 2014). This knowledge gap hinders prediction of global change impacts on plant–herbivore interactions.

Large-bodied mammals also have transformative effects on the ground flora, reducing grass sward height and promoting 'grazing lawns' dominated by grasses with a prostrate growth form (Hempson *et al.*, 2015b). These grass species tolerate grazing under dry conditions, invest more in leaves relative to stems, and tend to be palatable and nutrient rich, with high rates of photosynthesis and growth in the wet season (Table 1; Hempson *et al.*, 2015b). In African savannas, grazing lawns are most commonly established in regions of intermediate rainfall, where grass productivity is sufficient to sustain repeated defoliation, but not so high that herbivores cannot maintain a short sward (Hempson *et al.*, 2015b). However, in high-rainfall regions the greater productivity of grasses favours tall bunchgrass species that invest heavily in stems and that have a low nutritional value and palatability (Table 1). These species accumulate a high fuel load, supporting frequent fires (Archibald & Hempson, 2016). The associated differences among grass species in fire and grazing tolerance mean that the management of ignitions and grazing pressure within a particular climate and soil regime causes predictable shifts in the grass community composition (Tainton, 1999). As a consequence of these interactions between plant traits and the biotic and abiotic environments, patterns of fire and herbivory show contrasting patterns across the continental rainfall gradient (Hempson *et al.* 2015a; Archibald & Hempson, 2016). Savanna vegetation structure is controlled primarily by herbivory and rainfall where mean annual precipitation is lower than *c.* 600 mm, and by fire in wetter regions (based on the proportion of biomass consumed by each process; Archibald & Hempson, 2016). This climatic break-point leads to geographical patterns in the mechanisms

controlling savanna woody plant cover across the African continent, corresponding approximately to the boundary between eutrophic and dystrophic savannas identified previously (du Toit, 1995). Consequently, herbivory and drought are most important in the Mimosoideae savannas, whereas fire dominates in the Combretaceae and Detarioideae types (Fig. 5b; Greve *et al.*, 2012; Maurin *et al.*, 2014; Charles-Dominique *et al.*, 2017).

Fire

The flammability of plants and their regeneration strategy after fires are strongly determined by plant functional traits (Fig. 1, node 3; Table 1). Savanna fires are fuelled by grasses in the ground layer, and characterized by frequent, cool and rapid combustion (Archibald *et al.*, 2013). The fast flammability of grass species depends on a number of leaf canopy traits (Table 1; Pausas *et al.*, 2017). For example, diversity among South African grass species in leaf moisture content causes fourfold variation in ignition time, while diversity in canopy biomass leads to twofold differences in combustion rate (Simpson *et al.*, 2016). Grasses generally resprout rapidly after fires, and their regrowth rate varies threefold among the phylogenetic lineages found in South Africa, with a relationship between biomass before fire and regrowth afterwards (Table 1; Ripley *et al.*, 2015). For example, *Heteropogon contortus* accumulates a large, dry, canopy fuel load before fire and resprouts rapidly afterwards, whereas *Aristida diffusa* retains green leaves during the fire season and resprouts slowly after being burned (Ripley *et al.*, 2015). Rapid resprouting is an adaptation to frequent fire (Ripley *et al.*, 2015).

In frequently burned savannas, woody plants typically adopt a nonflammable strategy (Pausas *et al.*, 2017), using thick, corky bark to protect vascular cambium and epicormic buds (Balfour & Midgley, 2006; Hoffmann *et al.*, 2012; Lawes *et al.*, 2013; Charles-Dominique *et al.*, 2015a). This trait is most prevalent in Combretaceae and Detarioideae (Table 1) and enables resprouting after grassy surface fires. Survival of woody species is also promoted by belowground energy stores (e.g. in lignotubers) and root suckers, which promote vegetative spread and resprouting (Table 1; Charles-Dominique *et al.*, 2015a). This strategy is pursued to the extreme by 'underground trees' (geoxyles), whose underground network of woody stems and roots enables herbaceous shoots to resprout above ground after fires (Maurin *et al.*, 2014). However, there is significant diversity among South African savanna trees in these fire adaptations. For example, at Hluhluwe-iMfolozi (South Africa), higher bark growth rate, better-protected buds and root suckers dominate in wetter, frequently burned areas, whereas in drier areas with infrequent fires the bark growth rate is slow, buds are less well protected and structural defences against mesoherbivores become more important (Charles-Dominique *et al.*, 2015a,b, 2016, 2017). Such herbivore defences require densely branching 'cage architecture', which is incompatible with the infrequently branching 'pole architecture' needed for trees to increase height rapidly and escape topkill by fires (Fig. 2; Staver *et al.*, 2012). However, we have less information about continental-scale

differences in fire adaptations across the major floristic regions of African savanna.

Drought

Savanna tree dieback has been attributed in several instances to droughts caused by extended rainless periods and heatwaves (reviewed by Allen *et al.*, 2010; Anderegg *et al.*, 2016) (Fig. 1, node 4). Woody plants are typically killed during droughts because the vascular system fails at extremely low water potentials (reviewed by Anderegg *et al.*, 2016).

Drought avoidance is achieved in some savanna trees by accessing water during the dry season with deep roots (Fan *et al.*, 2017), especially in dry regions (Ward *et al.*, 2013). However, drought is most effectively avoided via deciduousness, a trait common among African savanna trees (Stevens *et al.*, 2016b). In deciduous species, leaf shedding is associated with soil drying (De Bie *et al.*, 1998), whereas leaf emergence ('green-up') typically precedes the rainy season to an extent that varies significantly between and within the major savanna types on the continent (Ryan *et al.*, 2017).

Rising carbon dioxide

Atmospheric CO₂ influences vegetation structure and function via direct effects on photosynthesis and indirect effects on plant water relations (Fig. 1, node 5). Experiments with two African Mimosoideae savanna tree species (*Acacia karroo* and *Acacia nilotica*) supplied with ample soil nutrients demonstrated strong positive effects of increased atmospheric CO₂ on leaf photosynthesis, which led to faster shoot growth and the accumulation of larger energy stores in root systems (Kgope *et al.*, 2010). In combination, these responses are expected to drive faster resprouting after fire or herbivory, increasing the likelihood of sapling trees escaping a fire or browse trap (Fig. 2; Bond & Midgley, 2000, 2012; Buitenwerf *et al.*, 2012). An alternative model predicts that rising CO₂ changes the outcome of competition between trees and grasses for limiting soil resources (Kambatuku *et al.*, 2013), by increasing tree growth and survival (Ward, 2010). However, the evidence for both models is limited by the paucity of experiments measuring CO₂-fertilization effects for most of the common woody species occupying African savannas (Fig. 5; Leakey *et al.*, 2012), although the effects on grasses are better known (Ward *et al.*, 1999). Furthermore, no CO₂ enrichment experiments with savanna species have yet considered environmental circumstances (e.g. soil infertility or drought; Leakey *et al.*, 2012), or the diversity of plant functional traits that may either damp or stimulate growth responses.

General knowledge from other biomes does show how plant species differ in their growth and allocation responses to enhanced atmospheric CO₂ (Curtis & Wang, 1998), with a number of plant traits predicting CO₂-fertilization effects (Fig. 1, node 5). First, the CO₂ responsiveness of growth depends on the capacity of a plant to export carbon from leaves and sequester it in developing sinks (Table 1; Ainsworth & Lemmonier, 2018). Leaf capacities for carbon export differ significantly among species according to

physiological mechanisms of phloem loading (Table 1; Ainsworth & Lemonnier, 2018), while species differences in sink development may arise from the capacity to produce storage organs, the determinacy of growth, and the ability to reproduce clonally (Table 1). However, carbon-sink development may be limited by the availability of soil nitrogen or phosphorus, such that CO₂ fertilization is damped in plants growing on infertile soils or as nutrients are depleted over time (Table 1; Norby *et al.*, 2010; Reich *et al.*, 2014; Ellsworth *et al.*, 2017). Mutualistic symbioses are important in these interactions, with mycorrhizal association mediating plant responses to CO₂ (Table 1), as outlined in the earlier example. The CO₂ fertilization of photosynthesis and growth is further modulated by nitrogen-fixing root nodules, which reduce nitrogen limitation and provide additional carbon sinks (Table 1; Ainsworth *et al.*, 2002). These causal factors that determine responsiveness to CO₂ fertilization differ among the lineages of tree species that dominate the major floristic assemblages of African savannas (Fig. 5; Table 1). Marked variation in CO₂ responses is therefore predicted among savanna ecosystems, but has never been investigated experimentally.

The hypothesized effect of CO₂ on woody plant recruitment could be partially offset by any CO₂ fertilization of C₄ grasses, in which faster growth may be mediated via stomatal closure and improved water relations (Morgan *et al.*, 2011). This mechanism has the potential to change fuel characteristics and competition for water and nutrients, with implications for tree growth (Wand *et al.*, 1999; Table 1) and disturbance regimes.

Designing management and mitigation strategies

Atmospheric CO₂ accumulation over the past 25 yr has tracked the worst-case Intergovernmental Panel on Climate Change scenario, and driven marked global changes in vegetation structure (Zhu *et al.*, 2016). However, management solutions must be actionable at local scales. Which parts of African savannas can be managed and for what purposes, and which are beyond our control? What steps can be taken to manage and mitigate woody plant encroachment or the loss of herbivores? What are the tipping points in vegetation change that should be averted? Which parts of the continent are most vulnerable to changes that have negative impacts on livelihoods and biodiversity? And how can landscapes be managed to accommodate agriculture whilst conserving biodiversity and maintaining savanna ecosystem services?

These questions may be addressed using models that simulate how biotic and abiotic factors control savanna structure, function and ecosystem services. Models need to be adapted to local circumstances by using functional trait data to parameterize the diverse responses of woody plants and grasses to herbivory, fire, drought and rising CO₂. Locally adapted models may then be used to explore the impacts of alternative scenarios of global change via changes in community assembly. These will provide a better scientific basis for the development of management strategies for mitigation or adaptation.

Three potential interventions may be particularly useful for managing woody plant cover in African savannas by manipulating fire and herbivory (Figs 1, 2). The first involves managing fire

regimes by manipulating the frequency and timing of ignitions (Archibald, 2016). Woody encroachment can be reversed using prescribed burns. For this strategy to be effective, however, managers must increase fire frequency or intensity in comparison with historical fire regimes, or change the timing of burns (Smit *et al.*, 2016; Twidwell *et al.*, 2016; Case & Staver, 2017). Fires and grazing must be managed concurrently because grazers consume grass biomass, which increases woody plant recruitment by reducing grass competition, fuel load and fire intensity (Case & Staver, 2017). Conversely, mammalian browsers may act synergistically with fire, enhancing the fire suppression of woody plant growth (Staver *et al.*, 2009). A historical example corroborates the effectiveness of this management regime: bush encroachment seems to have been uncommon in heavily populated communal land areas established during the early 1900s in South Africa, where woody plants were browsed heavily by goats, burned frequently, and cut for fuel and construction (Hoffman, 2013).

However, frequent fires do not always reduce the density of woody plants in low-rainfall savannas (Devine *et al.*, 2015), and increasing fire frequency may not be possible in these ecosystems because grass fuel accumulates too slowly (Smit *et al.*, 2016), or grasses are not flammable (Ripley *et al.*, 2015; Simpson *et al.*, 2016). In low-rainfall savannas it may be more effective to increase fire intensity by delaying burns until late in the dry season (Smit *et al.*, 2016), countering the tendency of African land managers to set early fires (Archibald, 2016). Long-term fire trials show that this strategy is an effective way to reduce the density of trees in African savannas when applied regularly (Laris & Wardell, 2006).

A new development in this area is to intentionally create intense crown-fires, of the kind occurring naturally during extremely hot, dry, windy weather (Archibald *et al.*, 2017). These 'firestorms' may locally clear badly encroached vegetation and are followed by frequent grass fires after the woody plants have been thinned. Evidence from North America shows that this strategy is most successful if fires reach sufficient intensities to topkill established trees (Twidwell *et al.*, 2013) and if fires occur during drought events (Twidwell *et al.*, 2016). However, firestorms are potentially hazardous for local people and property, and pose risks to neighbouring land-cover types, such as indigenous forests with high conservation value (Archibald *et al.*, 2017).

A second potential point of leverage is the management of large-bodied mammal communities, including both wild animals and domestic livestock (Fig. 3e,f). Grazing mammals consume grass fuel, while trampling and browsing limit tree growth. Changes in the local population sizes of animals, such as elephants, may have profound effects on savanna structure (Asner *et al.*, 2009, 2016; but see Kalwij *et al.*, 2010) and may prevent woody encroachment in low-rainfall regions (Stevens *et al.*, 2016a). Conservation management has the potential to strongly influence the populations of these megaherbivores (Fynn *et al.*, 2016), although wild animals may compete for (Odadi *et al.*, 2017), or partition (Charles *et al.*, 2017), resources with domestic cattle, sheep and goats.

A third potential point of leverage is the maintenance of savanna landscapes that are sufficiently connected and unfragmented to sustain suitable fire and herbivore regimes. The area

burned each year by fires declines strongly with increasing human population density (Archibald *et al.*, 2009), because livestock reduce amounts of grassy fuel, while croplands and roads fragment landscapes (Archibald, 2016). Once landscapes are fragmented beyond a sharp threshold, fires will not spread. Fires become smaller and less frequent as common land is used increasingly for agriculture, and rapid changes happen under low private ownership, as indicated by *per capita* gross domestic product (Andela *et al.*, 2017). However, the development of strategies to manage encroachment by avoiding the fragmentation of fire and herbivory regimes must involve engagement with local people. This is essential to understand how land management decisions are made and the consequences these decisions have for people's livelihoods.

Population growth in Africa over the coming century will result in population densities across the continent that are equivalent to those in China today (Gerland *et al.*, 2014). Although more than half of the African population is expected to live in cities by 2035 (AfDB/OECD/UNDP, 2016), rural population growth, coupled with infrastructure investment (e.g. in road building) for sustainable development, will increasingly fragment savanna landscapes. Greater understanding of what determines the thresholds for fire spread, animal movements, and ecosystem health contingent on fire and herbivory would enable national and international agencies to make better-informed planning decisions. Such decisions are currently being made in the context of African forest and landscape restoration programmes (Bonn Challenge, 2016; World Resources Institute, 2016). However, if these programmes fail to recognize the functional characteristics that define savannas as a unique ecological entity, they will degrade rather than restore ecosystem functions and services (Fig. 4).

Research agenda

The effective management and mitigation of global change impacts in African savannas will require a programme of research to meet five goals.

Goal 1. Ecological processes

Improve understanding of plant functional strategies in relation to CO₂, climate, fire and herbivory, the main controllers of woody plant cover in savannas. Elucidate both the effects of plant traits on these processes (flammability and palatability) and the responses of plants to fire and herbivore consumption (survival and tolerance). Use this knowledge to develop better process-based models of savanna structure and function.

Goal 2. Geographical diversity

Based on knowledge of plant functional strategies (goal 1), develop conceptual models for rapidly assessing these strategies in the field, and identifying the relevant functional traits (i.e. an extension of the approach proposed by Ratnam *et al.*, 2011). Using this methodology, map how the functional traits of woody plants and grasses differ regionally among and within savannas across the African

continent, using floristic regions as a starting point (Fig. 5). Parameterize the process-based ecological models of woody plant cover using this spatially explicit trait dataset.

Goal 3. Landscape disturbance regimes

Scale up from ground-based measurements of functional traits to remote measurements that can be made from aircraft or satellites (e.g. lidar), to establish large-scale metrics of vegetation flammability and palatability. Combine Earth observations of land cover, vegetation properties and fires to quantify the relationships between savanna vegetation properties, landscape fragmentation by croplands and urbanization, and the size of fires. Use this information to empirically define the thresholds across the continent beyond which fragmentation dramatically reduces fire size.

Goal 4. Ecosystem services

Combine field campaigns with models to establish how functional trait diversity in African savanna floras influences ecosystem functions and services. Work with local, national, regional and international stakeholders to understand the values placed upon each function and service. Compare ecosystem functions and services of savanna ecosystems with alternative stable states of forest and thicket. Develop databases to quantify how functions and services vary with woody plant cover, and how these relationships differ among savanna floristic regions.

Goal 5. Adaptation and mitigation

Work with stakeholders to better understand the governance structure and chain of decisions involved in savanna management, and the decisions most likely to impact savanna integrity and functioning in the medium- and long-term futures. Take lessons learned in one region and apply in other regions (Beale *et al.*, 2013). Integrate ecological models (goal 2) and Earth observation inferences (goal 3) to evaluate the sensitivity of savanna ecosystems to these decisions and their impacts on ecosystem services (goal 4).

Conclusions

African savannas are undergoing rapid changes at the continental scale but, unlike in forested biomes, ongoing woody plant encroachment in savannas is detrimental to the ecosystem services provided to local people. Efforts to avert a crisis in savannas are impeded by inadequate understanding of the ecological mechanisms driving observed changes, and of the diversity among savanna types in their resistance and resilience to change. These knowledge gaps hamper the development of sound management strategies at the local and regional scales. With the population of Africa expected to at least double by 2050 and the need for food security in a changing climate, conservation and livelihoods must be balanced to embrace the diverse services that African savannas provide, and their unique biodiversity that is nearing extinction (Searchinger

et al., 2015; Estes *et al.*, 2016). Careful consideration must be given to policies for agricultural development, where industrial agriculture and silviculture may be abandoned not long after land clearing, with long-term costs to carbon storage, biodiversity and hydrology (Searchinger *et al.*, 2015; Estes *et al.*, 2016). If the aim is to support the integrity of ecosystems and their resilience in a changing world, strategies that are actionable at local scales must support communities and conservation within multifunctional landscapes. Here, a new understanding of the diverse ecologies of African savannas will provide crucial guidance for management.

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ORCID

Colin P. Osborne  <http://orcid.org/0000-0002-7423-3718>







Tristan Charles-Dominique  <http://orcid.org/0000-0002-5767-0406>

Nicola Stevens  <http://orcid.org/0000-0002-0693-8409>

William J. Bond  <http://orcid.org/0000-0002-3441-2084>

Guy Midgley  <http://orcid.org/0000-0001-8264-0869>

Caroline E. R. Lehmann  <http://orcid.org/0000-0002-6825-124X>

**Colin P. Osborne^{1,2*} , Tristan Charles-Dominique³ ,
Nicola Stevens⁴ , William J. Bond^{5,6} , Guy Midgley⁴ ,
and Caroline E. R. Lehmann^{7*} **

¹Grantham Centre for Sustainable Futures, University of Sheffield, Sheffield, S10 2TN, UK;

²Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK;

³Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, 666303 Yunnan, China;

⁴Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa;

⁵South African Environmental Observation Network (SAEON), Private Bag X7, Claremont 7735, South Africa;

⁶Department of Biological Sciences, University of Cape Town, Rondebosch 7701, South Africa;

⁷School of GeoSciences, University of Edinburgh, Edinburgh, EH9 3FF, UK

(*Authors for correspondence: tel +44 (0) 114 222 0146, email c.p.osborne@sheffield.ac.uk (C.P.O.);

tel +44 (0) 131 650 6025, email Caroline.Lehmann@ed.ac.uk (C.E.R.L.))

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article:

Methods S1 Methods used to construct Fig. 5.

Notes S1 Attendees at a meeting of UK and South African scientists in Edinburgh, September 2015 during which the ideas behind this paper were discussed.

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Key words: C₄ grass, climate change, degradation, ecosystem services, rising atmospheric CO₂, savanna, woody encroachment.