



Using palaeoecology to explore the resilience of southern African savannas



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Savannas are dynamic and heterogeneous environments with highly variable vegetation that responds to a multitude of interacting drivers. Rainfall, soils, herbivory, fire and land use all effect land cover in savannas. In addition, savannas have a long history of human use. Setting management goals is therefore complex. Understanding long-term variability in savannas using palaeoecology provides a context for interpretation of recent changes in vegetation and can help to inform management based on acceptable or historical ranges of variability. In this article, we review and synthesise palaeoecological data from southern African savannas and use resilience theory as a framework for structuring and understanding of vegetation dynamics in savannas. We identify thresholds between alternate stable states, which have different ecological properties, suites of species and ecosystem services. Multi-proxy palaeoecological records can assist in identifying alternate states in savanna vegetation, as well as showing how different drivers (fire, herbivory, nutrients and climate) interact to drive transitions between states.

Conservation implications: The ecological thresholds identified from palaeoecological data can be used to inform the development of management thresholds, known as thresholds of potential concern. Thresholds of potential concern are designed to facilitate or impede transitions between states by manipulation of those variables (e.g. fire and herbivory) that can be controlled at the landscape scale.

Keywords: resilience; thresholds; thresholds of potential concern; palaeoecology; alternate stable states.

Introduction

In savannas, interactions between fire, herbivory and climate can alter ecosystem structure and function, potentially resulting in shifts between grass- and tree-dominated states (Hempson et al. 2019; Sankaran, Ratnam & Hanan 2008). These transitions may occur on any spatial scale from local (hundreds of metres) to regional (subcontinental) and timescales of decades to centuries. The heterogeneity and dynamism of savanna vegetation and the complexity of drivers and scales raise challenges both theoretically and practically, especially in view of climate change and possible vegetation responses. Resilience theory provides a framework for integrating the knowledge of savanna dynamics that can be applied in biodiversity conservation and ecosystem management, as will be explored in this article. Two aspects of resilience are commonly described in the literature: (1) ecological resilience – which is defined as the capacity of an ecosystem to withstand disturbance without changing structure and function and (2) engineering resilience – which is defined as the capacity of an ecosystem to recover from a disturbance that causes change in structure and function (Holling 1996; Oliver et al. 2015; Sundstrom et al. 2016).

Understanding of Holocene vegetation dynamics can elucidate how interactions between fire, herbivory and climate alter ecosystem structure and function over different timescales (Venter, Hawkins & Cramer 2017) – knowledge that is fundamental for the formulation of management strategies today and in the future. In addition, studies of areas with different management histories illustrate possible effects of different combinations of fire and herbivory over time. Here we will focus on palaeoecological sequences from three protected areas – Kruger National Park (KNP) and Hluhluwe-iMfolozi Parks (HiP) in South Africa and Limpopo National Park (PNL) in Mozambique – to analyse how different drivers (e.g. fire, herbivory, nutrients and climate) interact to drive transitions between alternate states in savanna vegetation.

The focus on protected areas is motivated by the specific challenges of conservation management, in defining the range of variability that can sustain biodiversity without leading to irreversible or

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undesirable shifts in vegetation with changing environmental parameters (Rogers 2003). Non-equilibrium ecology and resilience thinking have led to innovations in savanna management and conservation, with the emergence of thresholds of potential concern (TPCs) as operational goals that define the upper and lower limits of acceptable change in ecosystem parameters (Rogers 1997, 2003; Rogers & O'Keeffe 2003). The formulation of TPCs in defining spatiotemporal heterogeneity raises both ecological and social questions (Biggs et al. 2011). Most of Africa's parks and protected areas were founded under atypical conditions that nevertheless continue to shape expectations to this day. Hunting of large herbivores and carnivores, as well as policies of fire suppression and outbreaks of disease such as rinderpest during the 18th–19th century, likely transformed ecosystem structure and function, yet we have limited knowledge of how ecosystems looked prior to this time. Stakeholder preferences are informed also by how they perceive current changes in ecosystem state relative to their own personal baselines. We have argued elsewhere (Forbes et al. 2018) that baselines shift depending on personal experience and the lifespan of projects, and highlight the valuable role of long-term data in contextualising change that has occurred over recent decades. Palaeoecological data may therefore help managers and ecologists to envisage scenarios to help that are outside of their personal experience (Gillson & Marchant 2014; Gillson 2015a).

In this article, we interpret changes in vegetation structure inferred from palaeoecological data in terms of resilience and thresholds, and attempt to identify the range of factors that drive transitions between alternate stable states, or which promote resistance and stability of vegetation, despite environmental variability. To translate the palaeoecological data into a form that can be utilised in ecosystem management, we then compare long-term (palaeo) ecological thresholds with management thresholds (TPCs). We anticipate that such a framework could inform future quantitative analysis and modelling that could allow savanna managers and conservationists to explore the effects of manipulating fire and herbivory under various scenarios of future rainfall, temperature and carbon dioxide (CO_2).

Methods

The basis for our discussion is data generated from multiple palaeoecological records from KNP and HiP in South Africa, and Limpopo National Park in Mozambique (PNL [see Figure 1 and Table 1–A1]) (Eklom & Gillson 2010a, 2010b, 2010c; Eklom, Gillson & Notelid 2011; Eklom et al. 2012; Gillson 2015b; Gillson & Duffin 2007; Gillson & Eklom 2009, 2009b). The period discussed here, the last ca. 6000 years, has experienced both periods of warming and cooling combined with shifts in rainfall (Scott 2016; Scott et al. 2012). The time period covers the end of the mid-Holocene warming 4000 years ago when there was an increase in rainfall in the summer rainfall region. This was followed by a period of variable but overall cooler and drier conditions. Overall wetter conditions took place ca. 1200–800 years ago associated with globally

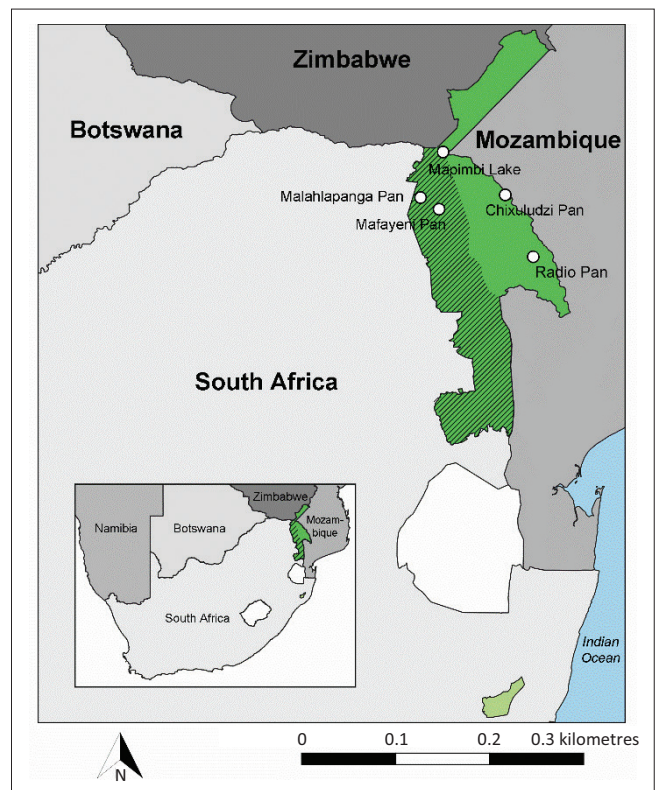


FIGURE 1: Map showing location of sediment cores and protected areas mentioned in the text.

warmer climate (sometimes referred to as the medieval warming) (Holmgren et al. 2003; Humphries, Green & Finch 2016; Lee-Thorp et al. 2001; Neumann, Botha & Scott 2014; Scott & Lee-Thorp 2004; Scott et al. 2012; Scott 2016). Shorter cool-dry events took place in AD 1100, 1350, 1450 and 1500 interspersed with periods of higher rainfall. A prolonged trend of cool-dry conditions took place after AD 1600, especially severe at AD 1700, with a return of more rainfall only 200 years ago (Holmgren et al. 2003, 2012; Lee-Thorp et al. 2001; Scott et al. 2012; Sundqvist et al. 2013; Woodborne et al. 2015, 2016). Although the dynamics of these changes, and if these climate shifts are analogous to future climate shifts, are still debated (Fitchett et al. 2017), the knowledge of the scale and rate of vegetation changes are important to understand for informed management decisions.

Changes in vegetation are here reconstructed using the relative changes of pollen types in dated sediments. Transitions from grass-dominated to woody vegetation are studied using pollen from sediments and stable carbon isotopes in soil profiles. The pollen record is compared with the amount of charcoal as an indicator of fire frequency/intensity and dung loving spores as a possible indicator of herbivore abundance, while nitrogen availability is also reconstructed based on $\delta^{15}\text{N}$ isotopes. Transitions from grass-dominated to woody vegetation can also be studied using stable carbon isotopes in soil profiles. Grasses and trees in savannas use different photosynthetic pathways, resulting in distinctive isotopic signatures, where grasses are enriched in heavier carbon. By analysing $\delta^{13}\text{C}$ in soil profiles, changes in the relative abundance of grasses and trees over time can be estimated,

with more recent vegetation reflected in the uppermost soil or sediment profiles. Although the palaeoecological records from small wetlands, pans and swamps presented here reflect local changes, and sampling has been limited by suitable sediment deposits and available proxies, we are still able to construct a general understanding of vegetation dynamic in terms of the factors that might drive transitions between stable states, or that promote resistance or resilience.

Ethical considerations

This article followed all ethical standards for a research without direct contact with human or animal subjects.

Results: Alternate stable states in Savannas

Water-limited grassland

The most stable vegetation states identified in our pollen records are water-limited grasslands. Although annual rainfall (600 mm/year) is presently sufficient for supporting a more dense woody cover, trees are scarce or absent because of water limitations imposed by local hydrology (i.e. lack of connection to ground water fed by perennial rivers). Such a landscape is exemplified by Radio Pan in PNL (Eklom & Gillson 2010c). The resistance or resilience of this vegetation state is demonstrated by the lack of response of tree cover (represented

by arboreal pollen) to climate, fire and nutrients. On the basis of the time series data, we did simple regression analyses between tree cover, charcoal (fire influence), dung loving spores (possible grazing influence) and $\delta^{15}\text{N}$ isotopes (nitrogen availability). We expected arboreal pollen abundance to have a significant negative relationship with spores and charcoal, reflecting the negative impact of herbivory and fire on tree recruitment. We expected to find a positive correlation between nitrogen availability and tree abundance, reflecting a positive relationship between tree abundance and nitrogen. However, at Radio Pan, there was no significant correlation between arboreal pollen and nitrogen availability (based on $\delta^{15}\text{N}$), fire (based on charcoal abundance) or herbivory (based on dung fungal spore abundance) (Figure 2a) (Eklom & Gillson 2010c). In contrast, a nearby site, Chixuludzi, with connections to perennial water, that is, Limpopo River, showed significant correlations between tree abundance, fire and nitrogen availability (Figure 2b) (Eklom & Gillson 2010c).

The complete dominance of grassland surrounding Radio Pan persisted throughout a 600-year history, despite changes in rainfall and in contrast to Chixuludzi, which showed variations in tree cover over time (Figures 2a and 2b). We suggest that at Radio Pan, water is the limiting factor that constrains tree recruitment, meaning that changes in fire and herbivory had no effect on tree abundance. It is not clear from the pollen data whether the resistance of grassland around

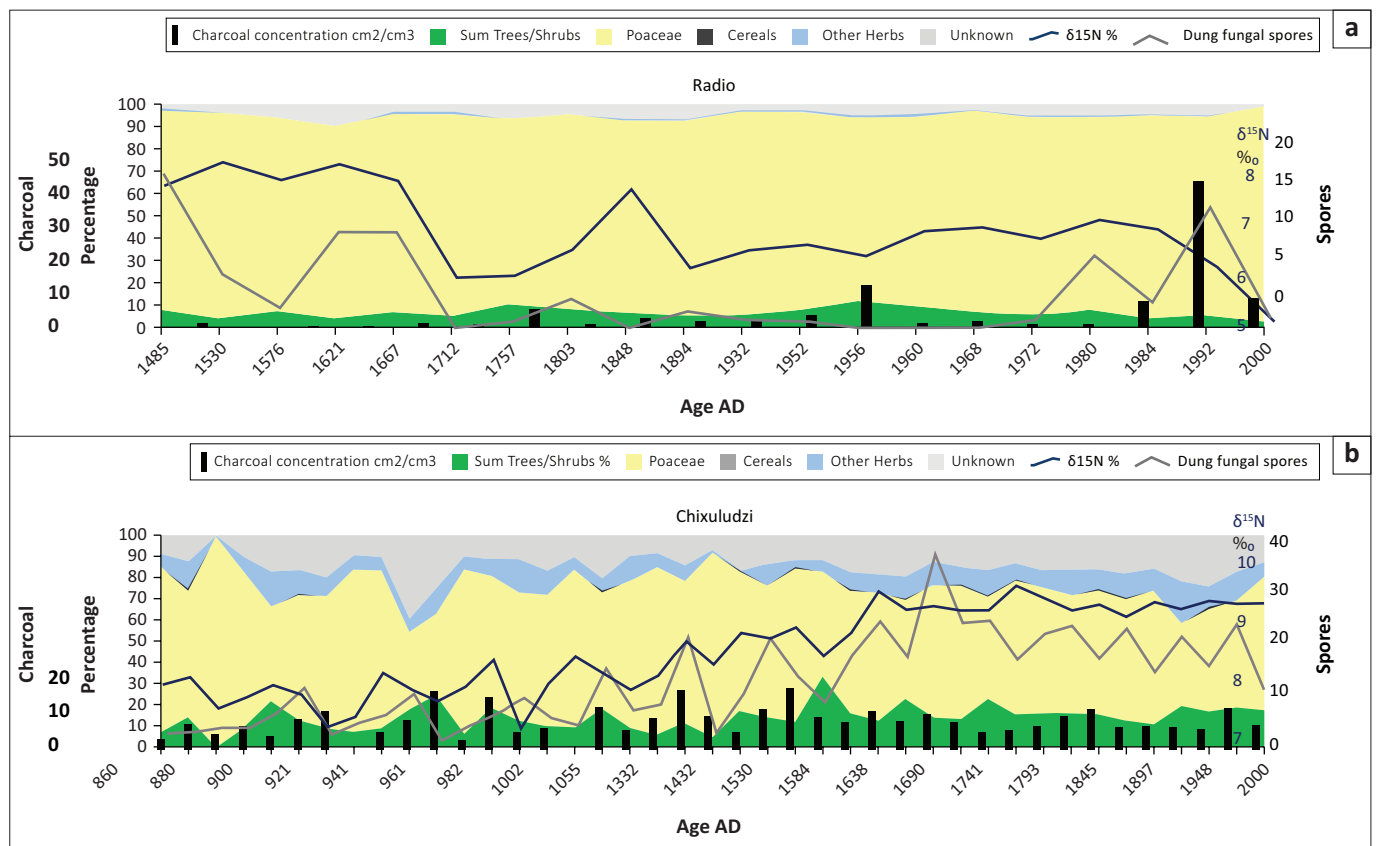


FIGURE 2: Summary diagrams of the Radio (a) and Chixuludzi (b) sedimentary sequences. Colored silhouettes show distribution of the main vegetation groups in percentages based on terrestrial pollen (c. 300–500 pollen); Black bars show charcoal concentration (estimated as concentration cm^2/cm^3). In the Radio diagram (a) the red lines shows the distribution of coprophilous dung fungal spores (converted in percentages in relation to the pollen sum) and the blue lines changes in the $\delta^{15}\text{N}$ values. The blue line shown in the Chixuludzi diagram (b) shows changes in the $\delta^{15}\text{N}$ values and the grey line the distribution of coprophilous dung fungal spores (converted in percentages in relation to the pollen sum).

Radio Pan is conferred by persistence of grassland composition or by internal dynamism (i.e. turnover of grass species within the grass community). Recent work from highland grasslands Mpumalanga (Bremen et al. 2019), based on phytoliths, suggests that resilience of grasslands might be enhanced through internal turnover within the grassland community, which can buffer the effects of changing climate, thereby enhancing resistance. Further analysis of phytoliths and biomarkers from water-limited grasslands such as Radio Pan might help to resolve this question.

Herbivore-limited grassland (grazing lawn) transitioning to wooded savanna

Grazing lawns are maintained by high levels of herbivory, especially by mega-herbivores such as white rhino, which limit tree recruitment and also prevent fire by reducing grass biomass levels below those which can support fire (Waldram, Bond & Stock 2007). Herbivores can contribute to fast nutrient cycling through addition of faeces and urine to the soil, although they may also promote competition for nitrogen by removal of biomass. Competition for nitrogen can also help maintain grazing lawns as grasses grow quickly and the rapid uptake of nitrogen makes them the superior competitor, able to exclude trees. These grazing lawns can persist over long time periods but might be de-stabilised by sudden losses of herbivory (e.g. because of drought, disease or over-hunting) (Staver & Bond 2014; Waldram et al. 2007).

Decreased herbivory in combination with increased water availability could therefore facilitate transitions from grazing lawns to wooded (open-canopy) savannas, especially if increased water in the landscape allowed dispersal of water-dependent herbivores, reducing pressure on vegetation around water sources (Redfern et al. 2005). We observed this phenomenon in the pollen record from Malahlapanga (KNP), our oldest record covering a long period of climate variability. Here, an open grassland (indicated by very scarce tree pollen and absence of charcoal abundance) transitioned to fire-prone wooded savanna during the period of increasing rainfall around 800 years ago (Figure 3a) (Gillson & Ekblom 2009a).

As mega-herbivores such as rhino continue to decline in African savannas because of illegal hunting (Bennett 2014; Lubbe et al. 2017; Wittemyer et al. 2014), we might expect the number of grazing lawns to decrease (Archibald et al. 2005; Waldram et al. 2007). Beyond a threshold of woody plant density, densely wooded areas may also create barriers for fire by shading out grass biomass and creating discontinuities in the fuel layer, which would further enhance recruitment of woody taxa (Higgins & Scheiter 2012). If the atmospheric forcing resulting from global warming is analogous to the past, we would expect more rainfall with higher temperatures. However, current climate models suggest overall drier conditions with higher incidence of extreme rainfall events (Engelbrecht, Engelbrecht & Dyson 2013; Engelbrecht, McGregor & Engelbrecht 2009; Pinto, Jack & Hewitson 2018) and/or more unpredictability (Haensler 2010; Haensler, Hagemann & Jacob 2011a; Pinto et al. 2016). Regardless of rainfall changes, the added effects of CO₂

fertilisation (see below) might further enhance the competitiveness of trees, shifting the balance away from open grassland habitats (Bond & Midgley 2012).

Unstable wooded savannas

The above examples are savannas where open grass cover is persistent as trees are constrained either by water availability, herbivory and/or nitrogen availability. Below we will describe savannas that are potentially unstable and that can change from open grassland to wooded savanna because of one or the combination of drivers. On a landscape scale, savannas are constituted by patches of dense or lightly wooded areas interspersed with grasslands. Overall, the stability of grass or woody cover is maintained when the number of dense and lightly wooded patches remains constant at the landscape scale, although each patch will go through asynchronous cycles of tree recruitment, thickening and senescence, a process known as patch dynamics (see Gillson 2004a). However, drivers such as dramatic, region-wide changes in herbivore density might lead to mass tree recruitment, as occurred at the end of the 19th century during the rinderpest pandemic (Staver & Bond 2014). Furthermore, policies of fire suppression might also facilitate tree recruitment, as was the case with the fire suppression policy implemented in South Africa during the early 20th century (e.g. Carruthers 1995; Van Wilgen et al. 2004). In both of these examples, the decline in herbivory and fire suppression resulted in a mass recruitment of woody cover, which led to an overall loss of patch structure through the development of even-aged tree or shrub stands. The increase in woody cover could limit the effects of fire by creating discontinuity in the fuel (grass biomass) layer, further enhancing the possibilities for woody recruitment.

We see evidence for mass closure of savanna tree canopies, for example, in stable isotope data from soil profiles in HiP, where $\delta^{13}\text{C}$ consistently decreases in the upper layers of the soil profile, indicating a transition from mixed C₃–C₄ vegetation to C₃-dominated vegetation over time (Gillson 2015b). Furthermore, when the frequency distribution of $\delta^{13}\text{C}$ is analysed, the stable isotope data show some evidence of bimodal distribution, clustered around $\delta^{13}\text{C}$ values typical of grasses and trees. This bimodality is a possible signature of transition between alternate stable states; if woody cover was a continuum between more and less grassy landscapes, we would expect the stable isotope data to be normally distributed and not bimodally distributed as here (Gillson 2015b). Similarly, analysis of aerial photographs covering the period from the 1930s to the 21st century shows consistent increase in tree canopy cover across different land-use types that differ in grazing and fire management history (conservation area, communally managed farm and commercial farm), providing evidence for a global rather than a local driver (Wigley, Bond & Hoffman 2009, 2010).

Wooded savanna transitioning to closed canopy forest

While savanna trees are able to persist in fire-prone environments through re-seeding or re-sprouting, forest trees

cannot tolerate fire. Closure of tree canopies in savannas will shade out the herbaceous layer, potentially excluding fire and allowing fire-sensitive, shade-tolerant forest trees to penetrate (Charles-Dominique et al. 2015; Higgins & Scheiter 2012; Hoffmann et al. 2012). Once these trees have established, they would eventually replace the shade-intolerant savanna species and would continue to exclude fire through shading out of the herbaceous layer. This feedback between vegetation and fire exclusion will continuously promote forest trees and associated taxa into an alternate stable state (see Figure 5). Because perennial rivers in savannas are typically bordered by riverine forests, and patches of true forest can co-exist alongside wooded savanna, we might expect the closure of tree canopies in savannas to lead to transitions to forest vegetation that are difficult to reverse. Such a hysteretic mechanism has been modelled using an adaptive dynamic global vegetation model (aDGVM) and is predicted to lead to an expansion of forest biomes at the expense of savanna and grassland biomes by 2100 (Higgins & Scheiter 2012).

Forest transitions would be difficult to reverse because forest ecosystems maintain themselves through the feedback mechanism of shading and fire exclusion, as described above (Staver, Archibald & Levin 2011). A transition back to open savanna might be expected only in the case of severe fire-storms, which are rare events where intense fires spread to the forest canopy (Archibald et al. 2017; Charles-Dominique et al. 2015). Another situation is in case of very extreme and prolonged or repeated droughts which may kill off trees. At Mapimbi, in the extreme north of KNP, forest taxa declined during the 18th century, which has been connected with the extreme droughts in this period (Figure 3b) (Ekblom et al. 2012; Holmgren et al. 2003, 2012; Lee-Thorp et al. 2001; Scott et al. 2012; Sundqvist et al. 2013; Woodborne et al. 2015, 2016). An analogous situation is where humans clear patches of forest, for example, for crop cultivation, which may interact with drought effects; however, there is little evidence of historical forest clearing on a larger scale (Ekblom et al. 2012; Gillson & Ekblom 2009b). Riverine forest recovered within a century from these climatically induced disturbances. Riverine forest also showed relatively rapid recovery over a few decades following the extreme flood events in the 20th century (O'Connor 2010; Rountree, Rogers & Heritage 2000). Even though riverine forests in Mapimbi recovered, the centennial scale of recovery from droughts is problematic from a managerial point of view and may have far reaching consequences that are difficult to predict because of the uncertainty in the climate model projections. Again, negative effects on forest vegetation from more droughts or more catastrophic events may be countered by CO₂ fertilisation, but more data are needed to assess this.

Discussion and Conclusions: Implications for ecosystem services and management options

The palaeoecological record shows evidence of different alternate stable states and mechanisms of resilience and

resistance in the vegetation of southern African savannas (Figure 4a). The most resistant form of vegetation that we encountered in our data is water-scarce open grasslands. These are maintained by a combination of local hydrology and fire despite climate variability. Water scarcity overrides other factors such as fire, herbivory and nutrients (Beckage et al. 2019) that we would normally expect to correlate with tree abundance in landscapes that are less water limited (e.g. see Gillson & Ekblom 2009a). The effects of global warming on rainfall patterns currently are debated (Fitchett et al. 2017) and there is no consensus here other than that conditions will become more unpredictable (see above). Thus, we will leave open the question of effects of rainfall changes to look at other dynamics in this discussion. However, the managerial decisions discussed below will be relevant also for observed effects of rainfall changes.

Grazing lawns are open habitats similar to water-scarce grasslands, but they are maintained by mega-herbivores, particularly white rhino. Their continued existence will therefore be threatened by the ongoing illegal killing of rhino (Lubbe et al. 2017; Waldram et al. 2007). The loss of open, grassy landscapes has implications for grazers and other flora and fauna adapted to these environments (Higgins & Scheiter 2012; Parr et al. 2014). Reduction in open grazing lawns may also be detrimental to wildlife tourism as it will decrease game viewing potential. Management would need to focus on monitoring of open areas, through on the ground and remotely sensed data, and rapid management action where tree encroachment reaches a TPC (Gillson & Duffin 2007; Rogers & Biggs 1999) (Figure 4b). For example, intense fires have been shown to effectively control shrub encroachment (Van Wilgen et al. 2014) and could be used alongside increased herbivore density in an attempt to curb tree recruitment. Furthermore, the capacity to support mega-herbivores may increase under conditions of high CO₂ (Scheiter & Higgins 2012).

The most variable and unstable type of vegetation that we found in the palaeoecological record is the wooded, heterogeneous savannas that typify most of the savanna biome. These landscapes can exist in a multitude of forms with varying levels of tree cover (e.g. see Sankaran et al. 2005, 2008). From a conservation management perspective, there are many ecologically possible options, and decisions about the desirable state of these landscapes will have different trade-offs, for example, between carbon storage and game viewing and/or grazing mentioned above. Decisions will therefore need to consider the perspectives of multiple stakeholder groups (Biggs et al. 2011). In this context, it is also important to consider the landscape history of individual sites and the acceptance of landscape transformation (Gillson 2015a; Gillson & Marchant 2014). Woody plant thickening may be seen as undesirable in ancient grassland sites (Parr et al. 2014), but may be tolerated in sites that have been historically cleared but which are recovering because of changing land uses, for example, land abandonment. Therefore, site-specific TPCs would be needed, where stakeholders decide on the acceptable limits of change in woody cover, depending on the landscape history and their land-use needs.

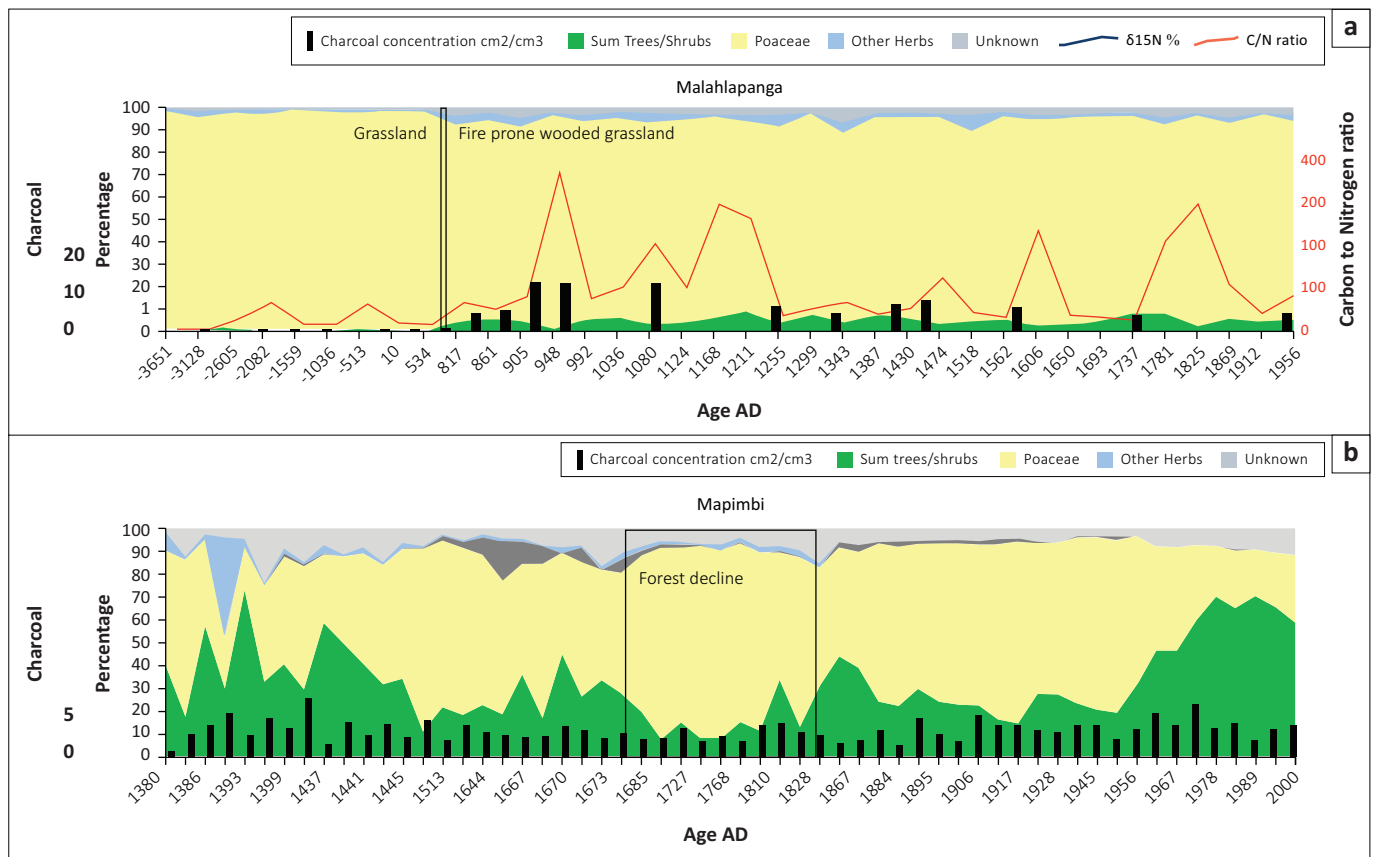
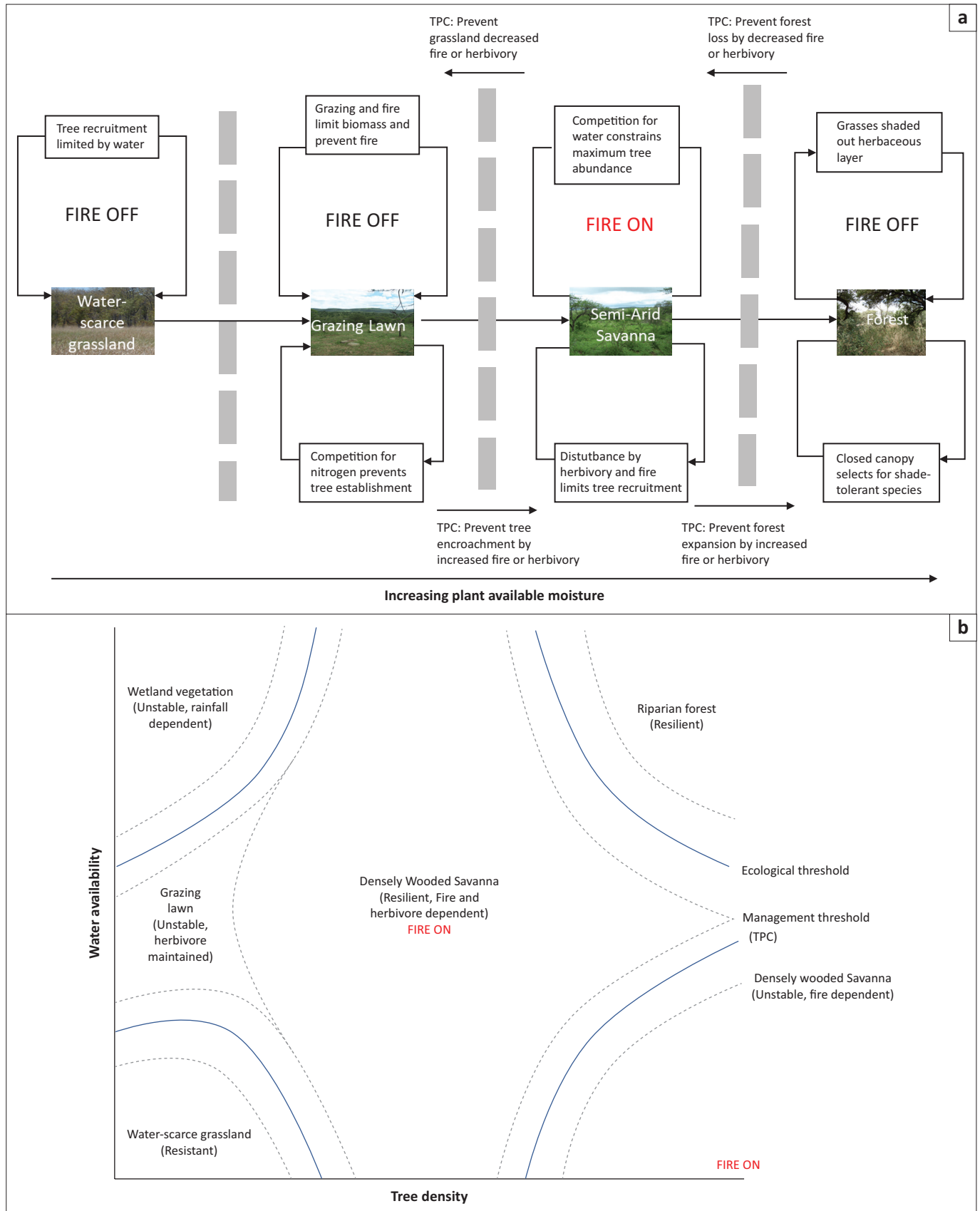


FIGURE 3: Summary diagrams of the Malahlapanga (a) and the Mapimbi (b) sedimentary sequences. Colored silhouettes show distribution of the main vegetation groups in percentages based on terrestrial pollen (c. 300–500 pollen); Black bars show charcoal concentration (estimated as concentration cm²/cm³). The blue lines in the Malahlapanga sequence (a) show the $\delta^{15}N$ values and the red lines the C/N (eg. Carbon to Nitrogen) ratio.

The degree of change in vegetation cover in savannas over decadal to millennial timescales is poorly understood. Yet, in deciding management thresholds, it is important to understand how the vegetation cover has changed before, during and after the main environmental and historical events that have shaped the southern African region since the mid-Holocene. These include changes in human land use, including the arrival of pastoralists from ca. 2000 years ago and increased management of fire, as also warmer conditions of the Mediaeval Warm period, the Little Ice Age. More recent changes that may have influenced vegetation changes are the growth of the international trade in ivory as well as the rise of the use of firearms in hunting for sport and trade, colonial settlement and associated changes in faunal assemblages (e.g. extermination of predators, local extirpation of elephants) and land management (e.g. replacement of traditional fire management with policies of fire suppression) (Carruthers 1995; Holmgren et al. 2001, 2003, Van Wilgen et al. 2004). In addition to this, there are 20th-century changes in warming temperatures, changing rainfall patterns, CO₂ fertilisation, which interact with the effects of past and present land-use changes, including the effects of urbanisation, land abandonment and the growth of the private conservation sector. By examining the historical range of variability under different climatic and land-use scenarios, stakeholders can decide on the acceptable range of variability and thereby better define the TPCs in tree cover, which is appropriate to their local context (Figure 4b) (Biggs et al. 2011; Gillson & Duffin 2007).

In the future, the resistance of these landscapes might be compromised by the effects of CO₂ fertilisation, which will increase the growth rates of trees, allowing more rapid access to water in deep soil layers and enhancing the water use efficiency of C₃ savanna trees to the detriment of the grasses (Bond & Midgley 2012; Midgley & Bond 2015). From the mid-20th century, increasing CO₂ has had a fertilising effect on savanna trees, causing them to grow more rapidly, making them (1) less vulnerable to drought, as roots reach moist soil layers more quickly and (2) more able to escape the fire trap – that is, they can quickly reach a height that is higher than the flame zone, allowing them to recruit to larger size classes (Midgley & Bond 2015). In the absence of CO₂ fertilisation, savanna tree seedlings can become trapped in the herbaceous layer, being repeatedly burned to the ground and re-sprouting only from their root stock (Bond & Midgley 2012). With faster growth under higher CO₂ conditions, trees can grow more rapidly, escape the fire trap and join the ranks of adult tree classes (Midgley & Bond 2015). This effect is currently being exacerbated by escalating illegal hunting of mega-herbivores, historically important in keeping tree canopies open (Bennett 2014; Lubbe et al. 2017; Wittemyer et al. 2014).

Riverine forest responds to changing climatic and disturbance drivers but, as suggested from the Mapimbi record discussed above, recovers from disturbance over decades (e.g. Ekblom et al. 2012; Gillson & Ekblom 2009b). Although more records are needed to analyse this process in detail, similar



Source: Photos courtesy of A. Ekblom; Purdon, Parr & Somers 2019

FIGURE 4: (a) Hypothetical model showing transitions between alternate states with increasing plant available moisture, showing the role of vegetation-fire feedbacks in maintaining alternate stable states. (b) Alternate stable states in savanna landscapes as a function of tree density and water availability, indicating both ecological and management thresholds. Ecological states are bounded by solid lines. Dotted lines represent management thresholds (TPC) where tree density could be manipulated through changes in fire or ivory. Three grassland states are possible, depending on levels of water availability. They could transition to fire-maintained wooded savannas if water availability increased and/or herbivory decreased. Wooded savannas could transition to forest ecosystems if canopies closed leading to the exclusion of fire. Management intervention in the form of manipulation of fire and herbivory could be triggered when ecosystems reach the TPC.

observations have been made in connection recovery of riverine forest after the 20th-century flood events as discussed above. This resilience is likely to be further enhanced by CO₂ fertilisation, which will facilitate rapid colonisation by trees. These gallery forests and other forest patches could act as a reservoir of forest species that could colonise closed canopy savannas, leading to hysteretic transitions to forest cover, as predicted by Higgins and Scheiter (2012) (Figure 5). However, the effects of increasingly severe drought and/or more seasonal rainfall (Davis-Reddy & Vincent 2017; Engelbrecht & Engelbrecht 2016; Haensler, Hagemann & Jacob 2011b; Pinto et al. 2016) might act in opposition by hampering the recolonisation of fire- and drought-sensitive forest taxa. Forest expansion would again lead to loss of grazing adapted suites of species, loss of grazing resources and game-viewing activities. Remotely sensed data will be critical in monitoring forest expansion, but more detailed palaeoecological studies assessing rate of change in forest communities will be needed to put recent changes into context. Decisions as to whether this transition should be permitted or prevented must be negotiated based on the trade-offs between ecosystem services, such as carbon storage, grazing, game viewing and

biodiversity (Biggs et al. 2011). In this respect, it is important that carbon storage potential of open ecosystems is not underestimated (Veldman et al. 2019) and that the urgent need to increase carbon storage does not overwhelm other concerns such as the biodiversity and ecosystem services provided by open ecosystems (Midgley 2018). Therefore, where the extent of riverine forests is changing, site-specific TPCs will be needed depending on what is ecologically possible and socially preferable.

Transitions between stable states have consequences for biodiversity and the provision of ecosystem services (e.g. see Figure 4). Savanna vegetation responds to a range of factors that operate over a range of spatial and temporal scales, and their heterogeneous and patchy nature means that local-scale changes may not reflect overall vegetation dynamics at landscape or regional scales (e.g. see Gillson 2004a, Ekblom & Gillson 2009; 2010c). Although global drivers such as CO₂ and regional effects such as rinderpest have had major effects on the composition of southern African savannas, the palaeoecological record also shows the importance of local factors, specifically fire and herbivory, in maintaining

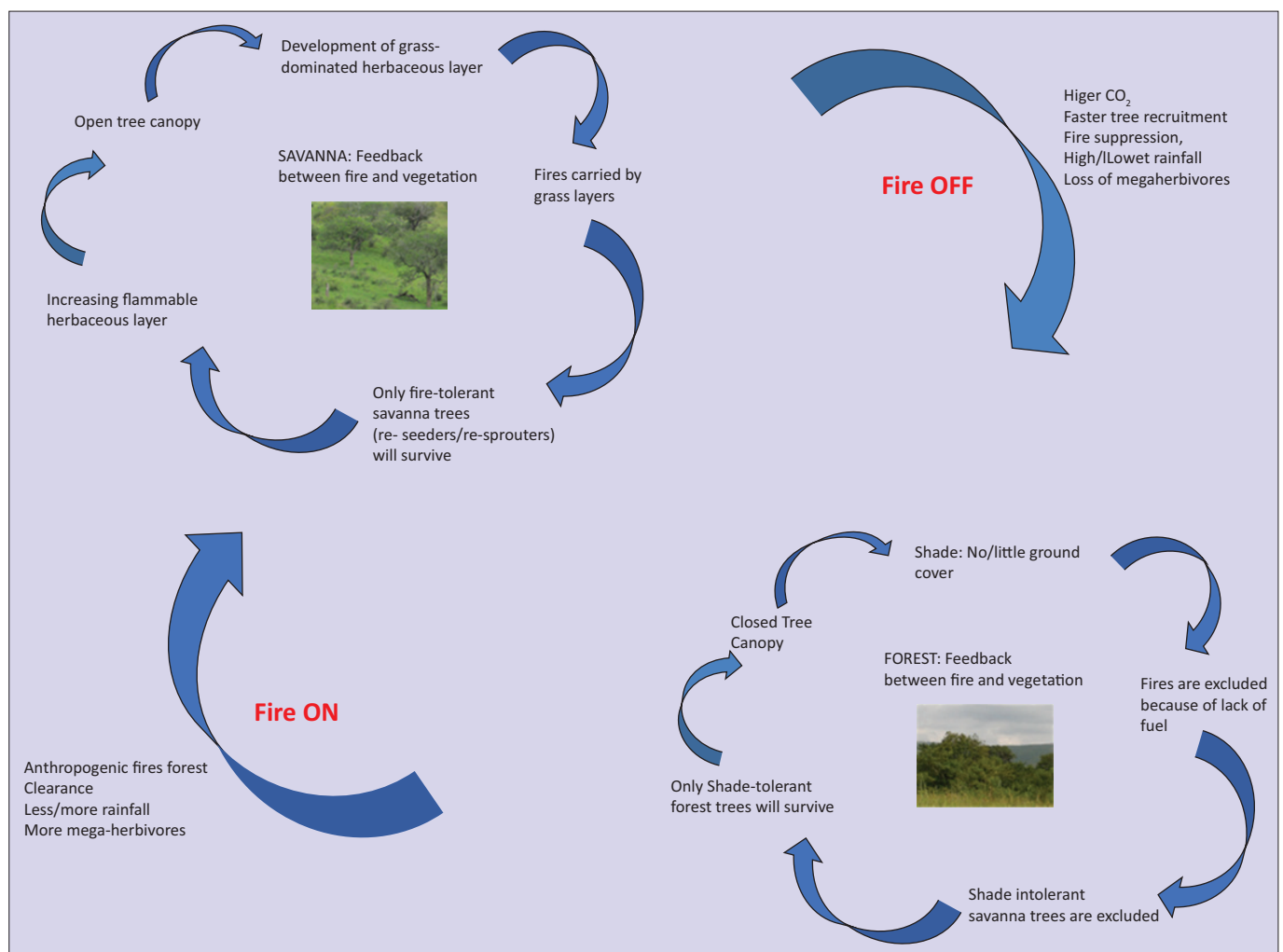


FIGURE 5: Possible feedback mechanisms that maintain savanna and forests as alternate stable states. The grass layer in savannas supports fires, perpetuating an open canopy of fire-tolerant savanna trees. Forest trees shade out understory and prevent fires, perpetuating the recruitment of shade-tolerant, fire-sensitive forest trees. Transitions from savanna to forest can be facilitated by the fertilising effects of CO₂, fire suppression, changes in rainfall, loss of megaherbivores, or interactions between any or all of these factors.

alternate stable states and in driving transitions between them (e.g. Gillson 2004a, 2004b; Gillson & Ekblom 2009a). This knowledge is of great significance for biodiversity conservation because local factors can be manipulated by conservation managers to maintain desirable states, prevent transitions to undesirable states and even in some cases attempt to reverse transitions. Informed local management can thus have major effects on the future of biodiversity and ecosystem services. Greater understanding of the mechanisms that drive transitions between stable states is needed to identify leverage points where managers can manipulate local drivers, such as fire and herbivory, to develop appropriate TPCs and maintain favoured vegetation states. Such analyses could lead to the development of co-designed models that allow managers to test the effects of different fire and herbivory regimes under varying future scenarios of climate and CO₂, possibly utilising palaeoecological records from past warm periods such as the Medieval Warm Period and mid-Holocene altithermal to provide clues of how savannas change in warmer climates and linked rainfall changes. As has been briefly discussed here, there is still plenty of work needed to refine climate models using palaeoecological data (see the discussion in Fitchett et al. 2017). The decision as to what constitutes a desirable state is to some extent subjective, and we argue here that the knowledge of palaeoecology and the impacts of interacting environmental and social drivers can help stakeholders to develop TPCs for current use, as well as to explore future scenarios of vegetation change under different scenarios of rainfall, drought, fire and herbivory. The complexity of savanna ecology and the feedbacks between climate, disturbance and vegetation mean that various future states are possible. For example, increasing drought may reduce fire occurrence because of reduced grass biomass (Van Wilgen et al. 2004) and could also reduce the population of herbivores, reducing grazing pressure. Processes such as system dynamics modelling will assist stakeholders in exploring these feedback loops, helping them to make informed decisions about desirable outcomes and the best management practices to achieve them, both now and in the future.

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Author's contributions

Both authors were involved in generating and interpreting data, and in drafting of the manuscript.

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Data availability statement

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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Appendix 1

TABLE 1-A1: Site locations, ecology and sampling details for sites presented in the article.

Site name (location): Coordinates	Ecology/substrate: Basin size	Core depth/analysis resolution: Date AD/BC
Chixuludzi (PNL): S22°51'37.1"; E31°56'33.5"	Mopane shrubveld/Limpopo palaeofloodplain (recent alluvial soils), responsive to the Limpopo River: 100 metres/diameter	80 cm from surface (2 cm analysis resolution): AD 690–900
Mahlapanga (KNP): S22°53'20.0"; E31°02'25.8"	Mopane-Combretum shrubveld/Granite bedrock and coarse sand, tributary to Shingwedzi River: 50 metres/diameter	80 cm from surface (2–8 cm analysis resolution): 3950–3350 BC with a possible hiatus until AD 760–890
Mapimbi lake (KNP): S22°53'20.0"; E31°02'25.8"	Riparian-Mopane shrubveld/Limpopo palaeofloodplain (recent alluvial soils), responsive to the Limpopo River: 75 metres/diameter	80 cm from surface (2 cm analysis resolution): AD 1300
Radio (PNL): S23°30'40.3"; E32°18'09.2"	Mopane shrubveld/Deep sandy soil: 50 metres/diameter	80 cm from surface (2 cm analysis resolution): AD 1287–1394

PNL, Limpopo National Park; KNP, Kruger National Park.