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Evidence of a tipping point in a southern African savanna?

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ABSTRACT

Many ecosystems exhibit threshold behaviour, where periods of relative stability are punctuated by rapid transitions between alternate stable states when an ecological threshold, or tipping point, is reached. This is of concern in grass-dominated habitats, many of which appear to be on the point of conversion to more wooded vegetation assemblages. However, changes in grass-dominated ecosystems are often difficult to interpret, because it is not always clear whether grasslands are ancient or are anthropogenically derived from past deforestation. As a result, the conservation, maintenance and restoration of ancient grasslands are sometimes neglected.

In this study, the history of vegetation change in the savannas of the Hluhluwe-iMfolozi Park, KwaZulu-Natal, South Africa, are investigated by analysing stable carbon isotopes ($\delta^{13}C$) from soil profiles. Without exception, the data show that C_3 dominated thicket, forest, and densely wooded savanna now occur on sites that were previously C_4 grassland or open savanna. Although the drivers of this change are not clear, there is potential for management intervention because tree density can be manipulated through fire, a natural part of this dynamic landscape. The study identified two sites which are at a threshold between C_4 and C_3 dominance, and highlighted them as priorities for conservation management intervention.

1. Introduction

Many ecosystems exhibit threshold behaviour, in that periods of relative stability are punctuated by a transition between alternate stable states when an ecological threshold, or "tipping point", is crossed (Holling, 1973; Petraitis and Latham, 1999; Gunderson and Holling, 2001; Beisner et al., 2003; Scheffer and Carpenter, 2003; Folke et al., 2004; Schröder et al., 2005). This is true of savanna–forest ecosystems, which have been described in terms of alternate stable states, where feedbacks between fire and vegetation maintain mutually exclusive assemblages of fire and shade tolerant plant communities (Gillson and Ekblom, 2009; Warman and Moles, 2009; Hirota et al., 2011; Mayer and Khalyani, 2011; Staver et al., 2011a,b; Higgins and Scheiter, 2012; Parr et al., 2012).

Predicting threshold behaviour is important for biodiversity conservation and the management of ecosystems, because rapid change affects ecological function, biodiversity and the provision of ecosystem services. However, long-term data are needed to distinguish unprecedented changes between alternate stable states, from normal, background variability, or from cyclical change. The question of vegetation history is especially relevant in African savannas, where the impact of iron-age communities and European settlers is poorly understood (e.g. Feely, 1980; McKenzie, 1989). Scrub encroachment has been observed in many savanna areas and is of concern where grassland habitats may lose their unique array of species. For example, aerial photographs indicate a widespread thickening of woody vegetation in many areas of KwaZulu Natal (KZN), South Africa, in recent decades (Balfour and Midgley, 2008; Wigley et al., 2009, 2010). Furthermore, a previous pilot isotopic study from the Hluhluwe-iMfolozi Game Reserve showed that an area that is currently under forest was previously dominated by a C_4 grassland (West et al., 2000).

Long-term data are needed if appropriate management intervention is to be decided, since it is difficult to distinguish whether increasing woody plant cover is simply part of the natural variability of savannas, is a recovery of more wooded conditions after deforestation and bush clearance in the past (Hall, 1984; Bond, 2008; Runyan et al., 2012), or is an unprecedented shift to an alternate, more wooded stable state (Beisner et al., 2003; Warman and Moles, 2009; Staver et al., 2011a; Higgins and Scheiter, 2012). Further, some savannas are shifting mosaics in which patches of vegetation undergo regular cycles from C_4 to C_3 dominance so that on a broader scale the landscape can remain meta-stable despite

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the internal, cyclical dynamics of individual patches (Olff et al., 1999; Gillson, 2004a). Knowledge of past landscapes and the drivers that cause transitions between alternate stables states is important in setting ecologically realistic conservation goals and in identifying appropriate management interventions.

The grasslands and savannas of Hluhluwe-iMfolozi Park in Kwa Zulu Natal provide a case study of changing grass and woody plant abundance and a testing ground for distinguishing cyclical shifting mosaic/patch dynamics from biome-wide shifts between alternate stable states. These savannas are composed of a heterogeneous mosaic of tree/shrub and grass dominated vegetation patches. The grass-dominated components comprise grazing lawns (dominated by bunchgrasses), savanna grassland dominated by tallgrass, and wooded savannas with a continuous grass matrix and scattered trees and shrubs. The tree/shrub-dominated elements are thicket (shade tolerant C_3 trees with a dense, shrubby understory and little or no ground cover), afromontane forests, containing large trees with little or no understory, and gallery forest adapted to specific hydrological conditions along river corridors (Archibald et al., 2005; Waldram et al., 2007; Parr et al., 2012). Not all of the abrupt boundaries between these components represent steep gradients in physical environmental variables (such as topography or hydrology), suggesting instead that threshold responses to disturbance variables like fire and herbivory are more likely. Furthermore, some boundaries are diffuse, suggesting instability, possibly linked with gradual responses to a continuous variable or a gradual change in vegetation over time.

In recent decades, there has been an increase in woody vegetation in many areas of Hluhluwe-iMfolozi (Balfour and Midgley, 2008; Wigley et al., 2009, 2010; Parr et al., 2012), while other vegetation boundaries have remained stable. In general, there seems to be an expansion of C_3 vegetation into open savanna and grassland. Furthermore, some savannas are also expanding into open grassy areas, and aerial photographs indicate a widespread thickening of woody vegetation (Wigley et al., 2009, 2010). This is of conservation concern because open grassland areas harbour a unique suite of species, and are also important habitats for grazers and for other small herbivores that are less vulnerable to predators in open spaces (Inamdar, 1996; Archibald et al., 2005, Parr et al., 2014).

Intriguing ecological questions are raised by the heterogeneous nature of vegetation change in Hluhluwe-iMfolozi. What is driving the expansion of woody vegetation? If a global driver is responsible for this expansion, why do some C_3–C_4 boundaries remain stable while others are dynamic? How dense was woody vegetation prior to major anthropogenic impact? And what is the role of feedbacks in maintaining stability and at what thresholds do boundaries become unstable?

In this study, the spatial and temporal patterns of vegetation change in a mosaic landscape of woody, (C_3) and grassy (C_4) dominated vegetation is investigated. Using stable isotopes of $\delta^{13}C$ from soil profiles, the history of C_3 and C_4 plant abundance in areas that are presently vegetated with grasslands, savanna, thicket and forest is investigated. This is possible because C_4 plants are enriched in ^{13}C compared with C_3 plants, and this signature persists in soil organic carbon in soil profiles (Balesdent and Mariotti, 1996; Wynn et al., 2005). The isotopic profiles are used to test whether the heterogeneous landscapes of Hluhluwe are (H1) recovering from past deforestation (H2) shifting mosaics that undergo cyclical changes in the dominance of C_3 and C_4 plants at the local scale, thereby remaining meta-stable at larger spatial scales (Watt, 1947; Dublin et al., 1990; Rietkerk and Koppel, 1997; Beisner et al., 2003; Gillson, 2004a), or (H3) whether increases in C_3 dominance is an unprecedented shift from less grass-dominated to woody-dominated vegetation, implying a shift between alternate stable states at the landscape – regional scale (Table 1). Furthermore, possible management interventions are highlighted, focusing on C_4 grass-dominated patches as conservation targets.

2. Study area

2.1. Vegetation, climate and geology

Hluhluwe-iMfolozi Park is situated in KwaZulu-Natal, eastern South Africa (28°00′–28°26′ S and 31°43′–32°09′ E, see Fig. 1). Occupied by Iron Age communities from approximately 300 AD, the area has a long history of human activity, including harvesting of wood for charcoal and iron smelting from approximately 2000–1600 years ago (Hall, 1984; Neumann et al., 2010) and the establishment of a hunting preserve at Hluhluwe by the influential Zulu leader Shaka, who wanted to restrict access to game animals

Table 1
Summary of hypotheses under test, rationale for the hypothesis and expected isotopic profile.

Hypothesis	Rationale	Expected isotopic profile	References
(H1) Current increases in woody plants is a recovery after past land clearance	Past human activity (e.g. harvesting of wood for iron smelting) may have caused wide-scale clearance of woody plants. Recovery of woody vegetation may have begun in the 19th century, after abandonment of agricultural land, depopulation due to political instability, and the designation of reserve areas	The isotopic profile should show a period of C_3 dominance (low $\delta^{13}C$) in deeper layers, followed by an increase in $\delta^{13}C$ when trees were cleared and C_4 grasses became dominant, then declining $\delta^{13}C$ as C_3 woody plants recover	Acocks (1953), van der Merwe and Killick (1979), Feely (1980), Hall (1984), Neumann et al. (2010)
(H2) Meta-stable patch dynamic landscape	Woodland-grassland cycles occur at the patch scale due to localised fires, herbivory or recruitment/senescence of trees, but over a large enough area, however, the vegetation composition remains meta-stable because the cycles are out of phase	Oscillations between high and low $\delta^{13}C$ throughout the soil profile (C_3 and C_4 dominance), reflecting transitions from wooded to grassland phases. C_3 and C_4 dominance out of phase at different sites	Pickett and Thompson (1978), Wu and Loucks (1995), Olff et al. (1999), Gillson (2004a,b), Moustakas et al. (2009), Riginos et al. (2009), Hanan et al. (2010)
Widespread encroachment of woody plants: a tipping point between a grass dominated and a tree-dominated ecosystem	Unprecedented increases in woody plants have been observed in many savanna ecosystems. Possible causes include changes in grazing and fire management and/or CO_2 fertilisation, which benefits C_3 plants more than C_4 plants	High $\delta^{13}C$ in deeper/older soil levels, indicating C_4 plant abundance. A transition to lower $\delta^{13}C$ in newer soil layers that are nearer the surface, indicating C_3 plant dominance	Ward (2005), Wigley et al. (2009), Barger et al. (2011), Eldridge et al. (2011)