Ecohydrological interactions in a degraded two-phase mosaic dryland: implications for regime shifts, resilience, and restoration

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ABSTRACT

In the semi-arid rangelands of north central Kenya, the abundance of grasses has declined over recent decades. Concomitantly, the native succulent herb *Sansevieria volkensii* has greatly proliferated in many areas. Landscape structure has thus shifted from contiguous herbaceous cover to large, dense stands of *S. volkensii* with interpatches of bare or sparsely vegetated ground. Local pastoralists view this transition as highly undesirable; understanding the mechanisms and reversibility of the transition is necessary to develop management options. Because water availability is a key driver in this dryland ecosystem, we assessed the ecohydrological dynamics that may govern the vegetative spread of *S. volkensii* patches in a communal landholding in Laikipia District, Kenya. We assessed surface water flow patterns, soil moisture, *S. volkensii* proliferation, and adjacent vegetation density along the margins of dense patches of *S. volkensii*. We found that run-on zones along patch margins had greater soil moisture than runoff zones following a rain event. These run-on zones also had significantly higher *S. volkensii* ramet density, more new ramets, and greater leaf water content. New ramet density was negatively affected by the density of adjacent interpatch vegetation. We interpret these findings in the context of scale-dependent feedbacks and the cusp catastrophe model of ecosystem transitions. We hypothesize that the amount and spatial heterogeneity of plant available moisture governs the reversibility of transitions in this system and discuss the implications of this finding for management and restoration. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS   semi-arid rangeland; degradation; scale-dependent feedback; pattern formation; cusp catastrophe model; threshold; *Sansevieria volkensii*; Kenya

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INTRODUCTION

Dryland ecosystems cover about 40% of the earth's land surface (Reynolds *et al.*, 2007). In Sub-Saharan Africa, they provide the resource base for over 40 million traditional pastoralists, whose livelihoods derive solely or predominantly from livestock production (Thornton *et al.*, 2002). Drylands are characterized by not only limited water availability but also high spatial and temporal variability in rainfall, conditions to which pastoralists have adapted with mobile, flexible, responsive land use practices (Niamir-Fuller, 1998; Homewood, 2008). However, these coupled human–environment systems have undergone drastic changes in the last century. Shifts in governance and rapid human population growth in many regions have led to denser and less mobile populations of pastoralists and livestock, which have intensified pressure on rangeland resources. These changes are often associated with widespread degradation of ecosystem function, including reduced productivity of fodder species, increased erosion, deteriorating quantity and quality of water resources, and loss of both plant and animal species diversity (Millennium

Ecosystem Assessment, 2005). Degradation of ecosystem function now threatens the ability of pastoralists to meet their basic livelihood needs (Scoones, 1995). Increased rainfall variability due to climate change (Hulme *et al.*, 2001) threatens to further exacerbate the stresses on pastoralist systems (Weltzin *et al.*, 2003).

A particularly troubling aspect of rangeland degradation is that ecosystem structure and function often change drastically, rapidly, and nonlinearly, and these changes can be extremely difficult to reverse even when disturbance is removed (Westoby *et al.*, 1989; Folke *et al.*, 2004). Such threshold phenomena have become central to understanding responses to environmental changes in numerous ecosystems (Norberg and Cumming, 2008; Scheffer, 2009; Suding and Hobbs, 2009), with semi-arid rangelands providing many of the classic examples (Anderies *et al.*, 2002; Foley *et al.*, 2003; Briske *et al.*, 2006). The challenge remains to apply our growing understanding of threshold phenomena to the objective of limiting and potentially reversing cases of land degradation in African rangelands or other dryland systems around the globe. To do so entails the coupling of two different research avenues: (1) using generalized knowledge of dryland ecohydrology to understand site-specific mechanisms, interactions, and feedbacks that are driving ecosystem change and (2) evaluating the implications of those feedbacks for broader patterns and trajectories of regime shifts in the

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system. After introducing the background for the first avenue, we offer a novel synthesis of catastrophe models as a framework for the second avenue of understanding the broader implications of threshold behaviour in drylands.

Dryland dynamics

On a mechanistic level, structural transformations in drylands are often driven by feedbacks among rainfall, soil moisture, and vegetation (Rietkerk *et al*., 2002; Zeng *et al*., 2004; D'Odorico *et al*., 2007), and spatial and temporal heterogeneity are central to understanding them (Tongway and Ludwig, 1994; Wilcox *et al*., 2003; Wainwright *et al*., 2011). Dryland vegetation is typically patchy or non-uniform in its spatial distribution, often appearing as a two-phase mosaic of vegetated patches and bare or less-vegetated interpatch areas (Aguiar and Sala, 1999; HilleRisLambers *et al*., 2001; Ludwig *et al*., 2005). The key limiting resource, rainfall, arrives in characteristic temporal pulses, and its effects on soil moisture and vegetation dynamics differ between vegetation patches and interpatches, as depicted in Figure 1. Interpatches tend to have lower infiltration rates because they are more prone to soil surface sealing and have fewer obstructions to slow runoff (Cammeraat, 2004; Mayor *et al*., 2009). Limited infiltration and greater evaporative exposure result in lower soil moisture in interpatches, which in turn limits vegetation growth. More heavily vegetated patches, on the other hand, tend to maintain more permeable soil surfaces due to biotic activity and attenuated impact velocity of raindrops (Tongway and Ludwig, 2001; Bhark and Small, 2003; Assouline, 2004). This allows higher infiltration, resulting in higher soil moisture availability for plant growth (Loik *et al*., 2004; Zeng *et al*., 2004). During rainfall pulses, surface flow redistributes water from interpatch to patch areas, thereby linking the two contrasting sets of localized interactions (Ludwig *et al*., 2005; Puigdefábregas, 2005). Both sets of localized interactions can form positive feedback loops (a resource-concentrating feedback in patches and a resource-losing feedback in interpatch areas), with horizontal resource redistribution reinforcing the site-specific resource-retention and resource-loss feedbacks (Figure 1) (Wilson and Agnew, 1992; Rietkerk *et al*., 2002; Saco *et al*., 2007).

This system of feedbacks is often called scale-dependent, because resource-growth feedbacks are positive locally, within each patch type, but effects are negative at larger scales between patches and interpatches (Rietkerk and van de Koppel, 2008). When the localized feedbacks are of comparable strength, they drive and maintain the self-organization of spatial heterogeneity in landscape structure and function (Tongway and Ludwig, 2001). However, if the component interactions that comprise the localized feedbacks or redistribution dynamics are altered, the balance between resource-concentrating and resource-losing interactions can also shift, resulting in changes in landscape-scale ecosystem structure as either vegetation patches or interpatches expand (Ludwig and Tongway, 1996; Rietkerk *et al*., 2004; Briske *et al*., 2006).

Disturbance and climate can drive the emergence and disappearance of two-phase mosaics as transitions between fully vegetated and fully degraded landscapes (Aguiar and Sala, 1999; Lechmere-Oertel *et al*., 2005; Kefi *et al*., 2007b; Bisigato *et al*., 2009); thus, spatial patterning has been widely studied as a potential indicator of desertification (Schlesinger *et al*., 1990; Von Hardenberg *et al*., 2001; Kefi *et al*., 2007a; Maestre and Escudero, 2009; Okin *et al*., 2009). This process occurs not only in drylands but in other patterned landscapes as well. For example, in a two-phase salt marsh zone in the Netherlands, scale-dependent positive feedbacks were found to generate and maintain spatial patterning at seasonal time scales, but over yearly to decadal time scales, that zone was found to be in transition from fully bare to fully vegetated because of relatively stronger within-patch feedbacks permitting patch expansion (van Wesenbeeck *et al*., 2008).

Catastrophe models: scale dependence and varying hysteresis

To address the second research avenue of broader ecosystem shifts, the two-dimensional fold catastrophe model is commonly used to characterize drastic system-level reorganizations. The model represents the equilibrium ecosystem state as an S-shaped function of a single environmental variable, such

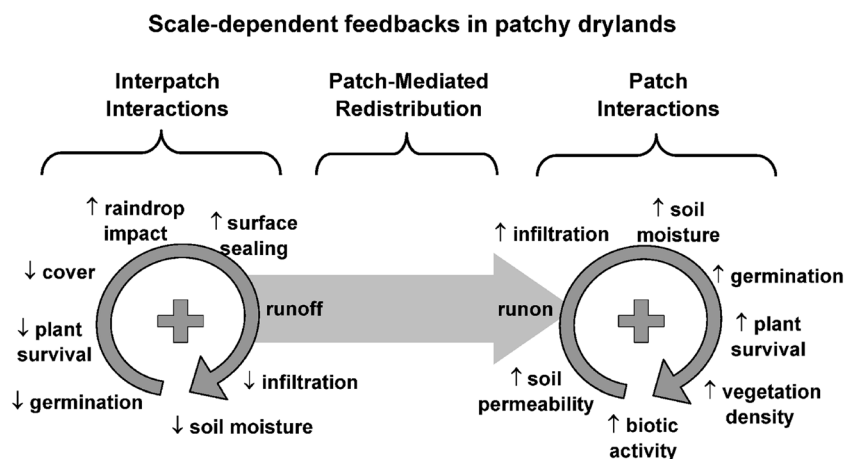**Scale-dependent feedbacks in patchy drylands**

Figure 1. Conceptual diagram showing key components of ecohydrologically driven scale-dependent feedbacks in patchy drylands: localized interpatch and patch interactions and resource (water) redistribution from interpatch to patch areas. When interpatch and patch interactions form positive feedback loops, reinforced by patch-mediated redistribution of water, scale-dependent feedbacks drive landscape spatial organization and pattern formation.

that within the 'folded' environmental variable range, there are two alternative attractors and an unstable equilibrium point between them (Figure 2A) (Rietkerk and van de Koppel, 1997; Scheffer *et al.*, 2001). For ecosystem states such as 'grass-dominated' or 'shrub-dominated', the attractors are multivariate equilibria, representing configurations of species, densities, trophic relationships, and so forth, toward which the interactions and feedbacks among components tend to impel the system (Walker *et al.*, 2004).

The folded response function explains how gradual environmental change results in discontinuous and hysteretic shifts in ecosystem state. To illustrate, consider an ecosystem situated on the upper left stability contour in Figure 2A. As the environmental variable gradually increases, its state would follow the contour to the point where it folds back. Any further increase in the environmental variable will result in a 'jump' to the lower stable contour. If the environmental variable is then decreased, the system does not jump back up at that same point; rather the system will continue to exist in the lower state until reaching the lower end of the fold. This difference in forward and reverse pathways is called hysteresis. The term bistability

describes the folded region, where the ecosystem can tend toward either of the two attractors, depending on its initial condition.

Despite the model's simplicity, it has been successfully applied to explain a number of observed ecosystem shifts (Scheffer and Carpenter, 2003). There are, however, two extensions or elaborations of this standard catastrophe model, which are particularly relevant to drylands because they capture characteristic forms of complexity shown by these ecosystems and thereby offer additional insights into ecosystem shifts. Here we describe first the inclusion of spatial patterning, second the inclusion of variable degrees of hysteresis in catastrophe models, and lastly how these two extensions can be synthesized via the relation of scale-dependent feedbacks to each of them.

The extension of the two-dimensional catastrophe model to include spatial patterning is based on the following reasoning. In threshold models, systems move toward attractors because of impelling and stabilizing feedbacks among ecological interactions (Scheffer *et al.*, 2001). When the feedbacks impelling the system toward different local basins of attraction are *scale-dependent* feedbacks, a two-phase mosaic
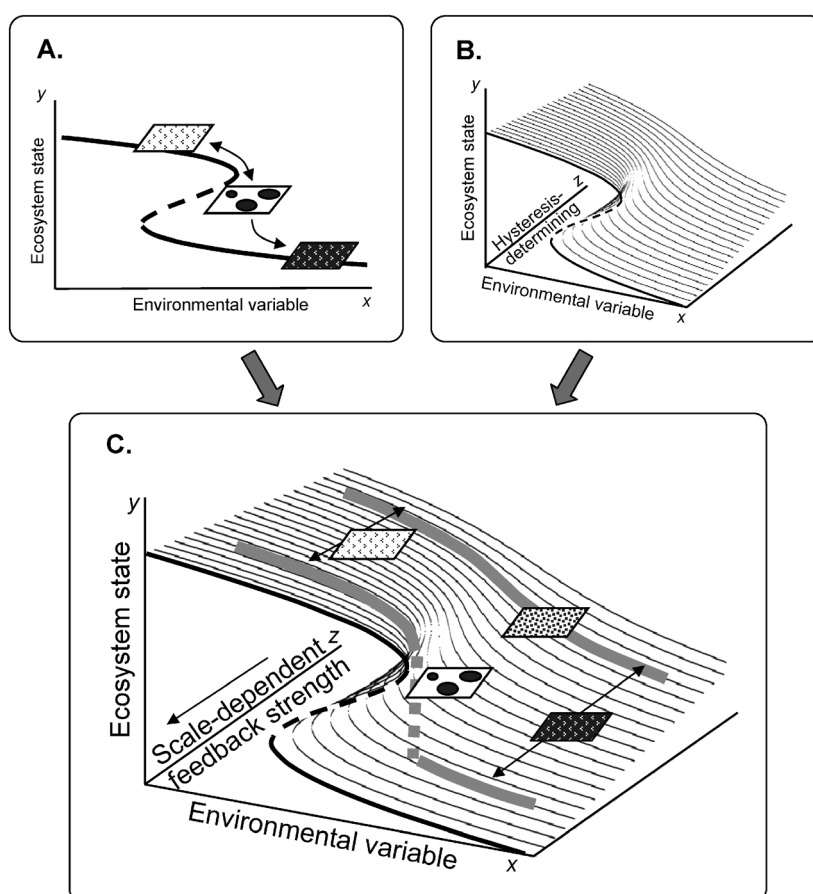

Figure 2. (A) Two-dimensional catastrophe model extended to the case of patchy landscapes. Solid portions of the curve indicate stable equilibria, and dashed portion indicates unstable equilibria and region of bistability. Extending the model to incorporate patchy landscapes, the light-filled and dark-filled boxes on upper and lower curves represent single-phase states; the spotted box represents a two-phase mosaic as a transitional state. (B) Three-dimensional cusp catastrophe model, with a hysteresis-determining axis (*z*) that determines whether a region of bistability exists. The foreground of the diagram is the same as the two-dimensional model in (A), while the background represents a domain of continuous change between ecosystem states with no hysteresis or bistability region. (C) Three-dimensional cusp catastrophe model extended to the case of patchy landscapes. The hysteresis-determining axis indicates the strength of scale-dependent feedbacks. In the fore, scale-dependent feedbacks are strong, creating a region of bistability and reinforcing regular spatial patterning. With weak scale-dependent feedbacks, toward the back of the stability surface, transitions are not hysteretic, and regular spatial patterns are less likely or evident as ecosystems change between the upper and lower states.

landscape can occur in the 'folded' domain. In the mosaic, each attractor state is being represented simultaneously but in spatially discrete patches, so the mosaic itself can be a direct manifestation of bistability (Figure 2A) (Rietkerk *et al.*, 2004; Kefi *et al.*, 2007b). The theoretical linkages between scale-dependent feedbacks, two-phase mosaics, and catastrophic regime shifts have been demonstrated in several modelling studies and are consistent with empirical studies of two-phase ecosystems (Rietkerk and van de Koppel, 2008; van Wesenbeeck *et al.*, 2008; Kéfi *et al.*, 2010). The development of two-dimensional catastrophe models to address spatial patterning is particularly valuable and relevant to semi-arid rangelands because the emergence of regular patterning may signal that a system is near or has crossed a threshold, rendering it vulnerable to catastrophic reorganizations that threaten ecosystem services upon which humans depend (Rietkerk *et al.*, 2004).

The second extension deals with variability in threshold behaviour. Recalcitrant regime shifts, such as woody encroachment or the replacement of perennial bunchgrasses with annual grasses, have been observed in various rangeland systems around the world. But such responses are not ubiquitous to *all* systems, nor within a given system do changes in a particular environmental variable always elicit catastrophic shifts. Instead, changes in ecosystem structure can show varying degrees of irreversibility and hysteresis (Briske *et al.*, 2003). Interactions that comprise feedbacks are often multivariate and nonlinear, and most ecological interactions are also environmentally dependent. Accordingly, the nature of feedbacks may depend not just on a single controlling variable but also on the state of another variable or on an exogenous condition (Lockwood and Lockwood, 1993; Briske *et al.*, 2006). Thus, rather than asking if a transition is irreversible, it may be more fruitful to ask *when*, under what multivariate conditions, a transition is more likely to be irreversible. Recognizing the likelihood of context-dependent hysteresis in drylands, Loehle (1985), Lockwood and Lockwood (1993), and Rietkerk *et al.* (1996) proposed using the three-dimensional cusp catastrophe model (Figure 2B) to understand threshold behaviours in rangelands.

The cusp catastrophe model extends the standard two-dimensional model by including a third variable (z-axis) that governs the degree to which changes in equilibrial ecosystem state are discontinuous (Figure 2B) (Loehle, 1985). Because tight cause-and-effect coupling among variables (i.e. strong feedbacks) are responsible for creating alternate attractors that lead to different ecosystem states (Walker *et al.*, 2004; Briske *et al.*, 2006), it follows that, functionally, the z-axis variable is an indicator of the strength or weakness of feedbacks. We therefore expect the hysteresis-governing variable to act as a proxy for the strength of the feedbacks that govern ecosystem organization, indicating whether feedbacks are strong enough to create alternate attractors. The z-axis variable may be a direct causal driver that governs the strength of feedbacks but may also be a landscape-scale metric that indicates when suites of component interactions are more or less likely to generate strong feedbacks. An arguable strength of the model is that it allows a 'black box' approach to the control variables: one can model the emergent system behaviour

without knowing all the inextricably complex interactions that generate it (Saunders, 1980). Yet our identification of this one attribute of the z-axis, its relationship to feedback strength, helps to conceptually link the cusp catastrophe model to the other salient characteristic of drylands – spatial structure.

If the z-axis characterizes the strength of feedbacks that generate alternate attractors, then it follows that for two-phase mosaic landscapes, the z-axis variable would be a proxy for the strength of scale-dependent feedbacks (Figure 2C). Thus, when scale-dependent feedbacks are strong, the landscape is more likely to exhibit distinct, regular spatial patterning and a stronger tendency for hysteresis, reflecting bistability. But under conditions that weaken scale-dependent feedbacks, regular spatial patterning is not reinforced, and we also expect less hysteresis in ecosystem structure in response to change in the primary controlling (x) variable. Indeed, Kéfi *et al.* (2010) arrived at this same conclusion but from a different analytical approach – a mechanistic modelling study that explored the role of resource-concentrating feedbacks in the generation and maintenance of regular spatial patterning.

While the cusp catastrophe model's most common ecological application has indeed been to rangeland systems, it has only recently been considered in relation to spatial patterning (Turnbull *et al.*, 2008) but has not previously been utilized as a context to address two-phase mosaics and scale-dependent feedbacks. Furthermore, the cusp catastrophe model's putative utility in land management is to generate testable hypotheses about the conditions under which degradation may be reversible. That utility can only be realized when empirical cases of rangeland dynamics are fitted and contextualized with the model.

Objectives

In East Africa, a particular syndrome of degradation is becoming increasingly common: in areas where grasses have been depleted due to intense grazing pressure, the native succulent plant *Sansevieria volkensii* has proliferated, resulting in a distinct two-phase mosaic with dense *S. volkensii* patches and sparsely vegetated interpatch areas. In this study, we seek to identify the ecohydrological mechanisms underlying this form of degradation and contextualize those dynamics in broader frameworks of ecosystem change to develop hypotheses of future system trajectories.

We seek to validate the hypothesis that scale-dependent feedbacks are involved in the dynamics and proliferation of *S. volkensii* patches at one such site by examining four key contributing interactions: (1) Do patches affect surface water redistribution? (2) Does patch-mediated water redistribution lead to differences in soil moisture? (3) Does *S. volkensii* plant growth respond to those differences in soil moisture? (4) Does the abundance of adjacent interpatch vegetation attenuate within-patch positive feedbacks by modulating *S. volkensii*'s response to soil moisture heterogeneity? Our findings are consistent with scale-dependent feedbacks; they indicate strong positive feedbacks among surface flow, soil moisture,

and *S. volkensii* growth, with weak negative effects of adjacent interpatch conditions on *S. volkensii* spread.

We use the scale-dependent version of the cusp catastrophe model (Figure 2C) to organize our current understanding of dynamics in the study system and deduce an appropriate putative hysteresis-determining variable. Then we examine the implications of this qualitative model fitting for future system behaviour, thereby developing new hypotheses regarding the potential reversibility of the observed transition-in-progress. We conclude that the cusp catastrophe model is a useful tool to contextualize two-phase mosaic dynamics: it highlights the conceptual linkages between the model's third axis and the strength of scale-dependent feedbacks and can help identify testable hypotheses of system function and appropriate manipulation strategies for restoration in degraded drylands.

METHODS

Site description

The study was conducted on Koija Group Ranch, a 7600 ha landholding in Laikipia District, Kenya (0°31′ 57″N, 36°54′ 30″E, 1700 m elev.), owned communally by resident Laikipia Maasai pastoralists. Koija receives about 450-mm mean annual precipitation (35–40% coefficient of variation (CV)); the average daily rainfall total on days with rain is 8 mm (Franz, 2010). The vegetation is predominantly bushland and savanna, with 5% to 25% woody canopy cover, mostly *Acacia mellifera*, *Acacia tortilis*, and *Acacia etbaica*. Koija residents reported that the abundance of herbaceous vegetation has decreased substantially in recent decades, while a previously occasional species, *S. volkensii* Gurke (Dracaenaceae), has proliferated dramatically (King, 2008). This native, rhizomatous herb, with acaulescent ramets of 1–12 erect, spear-like succulent leaves 40–120 cm tall (Mwachala and Mbugua, 2007), typically forms dense patches (20–100 ramets/m^2) with distinct margins, ranging in size from 1–2 m in diameter, to continuous cover for 1 km or more.

Field measurements were conducted at a 300×300-m site on Koija Group Ranch, with gently sloping terrain (0·5–1·5%), red lateritic sandy clay loam soils, and 9% tree cover. The site was characterized by two different predominant forms of ground cover, *S. volkensii* patches and interpatches of bare soil with sparse grass, which together formed a mosaic at spatial scales of 10^0 to 10^1 m. The *S. volkensii* patches were dense (average 30 ramets/m^2), 3–60 m wide and covered 22% of the site. A diverse array of grasses, forbs, and subshrubs were found in patches but not outside *S. volkensii* patches at the site. The sparse interpatch vegetation ranged from 0% to 35% cover/m^2 during peak growing season, but <10 cm in height due to herbivory, and was dominated by two grasses, *Eragrostis tenuifolia* and *Cynodon plectostachys*. The hard, sealed soil surfaces in interpatches showed clear evidence of sheet and/or rill erosion with channels and fans indicating surface water flow patterns and with a layer of depositional sand 0·2–2·0 cm deep in some places.

Measurement protocols

In April 2008, we selected four *S. volkensii* patches >12 m wide, with varying amounts of interpatch vegetation cover abutting their margins. Every 2 m along concentric loops within the patch perimeter, 2, 4, and 6 m (where possible) inward, we placed a 50×100-cm frame and counted *S. volkensii* ramets and new leaves. Every 2 m along the patch margins, we placed a 100×100-cm frame so that the patch margin bisected the frame, giving a sampling area of 50×100 cm that lay inside the patch. Within the frame, we counted the number of *S. volkensii* ramets and newly emerged leaves. In the portion of the frame lying outside the patch margin, we visually estimated % cover of herbaceous vegetation. We mapped the position of quadrats along patch boundaries, allowing quadrats to be associated with run-on and runoff zones identified in June 2009. New leaves, which emerged in response to the last substantial period of rainfall, were easily distinguished by the colour and texture of the leaf base.

In June 2009, we added four additional patches to the ones selected in April 2008 using the same criteria. On the basis of visible flow paths on the soil surface, all patch margins were divided into segments characterized as run-on (flow into patches) or runoff/neutral (flow out of or adjacent to patches, called 'runoff' hereafter) zones (Figure 3). All identified zones were longer than 8 m. The patch margins and
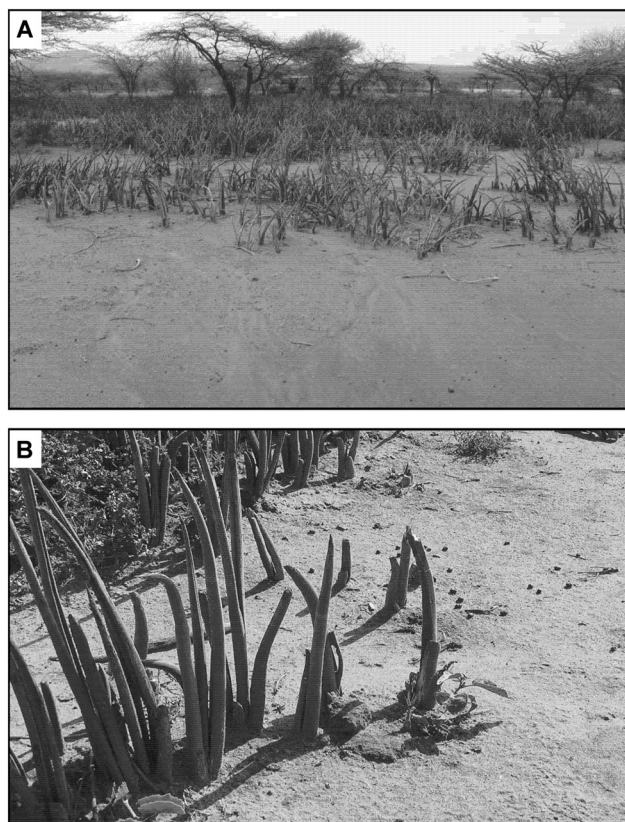

Figure 3. *Sansevieria volkensii* patches and bare interpatch areas at Koija Group Ranch, Kenya. (A) Visible flowpath on soil surface indicates run-on into *S. volkensii* patch. (B) Along patch margins, rhizomes spread into interpatch areas, and new ramets break up the compacted, sealed interpatch soil surface as they emerge.

zone segments were mapped using a Trimble Pro-XRS global position sensor (Seiler Instrument and Manufacturing Company, Inc., St. Louis, Missouri). Every 2·5 m along margins of all eight patches, we placed a 50×50-cm frame, with one edge aligned with the patch margin, and the rest of the frame inside the patch. We counted *S. volkensii* ramets, total leaves, and new leaves in the frame. We also cut the mature, undamaged leaf located nearest to a midpoint mark on the sampling frame, sliced leaves into 1-cm-thick discs, and weighed them before and after drying for several days at 60 °C to a constant dry weight. We did not measure cover of herbaceous vegetation adjacent to patch margins in 2009; because of severe drought conditions, herbaceous vegetation was largely absent.

To map changes in soil moisture in and around each patch, we used a Dualem 1-S sensor (Dualem Inc., Milton, Ontario), which uses electromagnetic induction to measure and integrate the bulk electrical conductivity (EC_a) of approximately $1 m^3$ of soil above which the instrument is passed. The device recorded conductivity every second and was coupled to the Trimble GPS unit that simultaneously recorded the location of each measurement. We carried the device by hand while walking in 1·5-m-spaced concentric perimeters, from 4·5 m outside patch margins to 4·5 m inside patch margins. EC_a is a function of cation abundance (Sheets and Hendrickx, 1995), so is affected by soil moisture, pH, and clay fraction. By taking repeated measurements days before and after wetting events, differences in EC_a indicate changes due to soil moisture, because soil pH and texture do not vary on such short time scales (Abdu *et al.*, 2008). Beginning on 24 July 2009, we performed five conductivity surveys, at 3-day intervals, beginning 1 day before a 6-mm rain event on 24–25 July 2009.

Statistical analyses

We used analyses of variance (ANOVAs) to test the effect of distance from patch margin on density of new *S. volkensii* leaves/m^2 and total ramets/m^2 in April 2008. We tested and found that these variables had no spatial autocorrelation between the sampled quadrats, which were spaced 2 m apart. Models included distance from edge as a discrete variable and patch as a block effect. New leaf density required $\log(Y+1)$ transformation to meet assumptions of normality and homoscedasticity.

To analyse changes in soil moisture along margins of patches in July 2009, we first used quality assurance and quality control procedures to eliminate outliers in the EC_a datasets and correct for soil temperature variation (Franz *et al.*, 2011). Following a normal score transform, a semivariogram was fit to each dataset. By using block kriging and the local variogram method, each day's survey data were interpolated to the same 1-m^2 grid. We then extracted the kriged EC_a data for all 1-m^2 cells that coincided with run-on and runoff zones of patch margins. For each of those cells, we then calculated differences between the pre-rain EC_a and each of the post-rain event surveys [d(EC_a)$_i$ where i = days after rain]. For each zone type in each plot, we averaged d(EC_a)$_i$ values. We used ANOVA to test whether average d(EC_a)$_i$ varied with zone type (run-on or runoff), with patch included as a block effect.

To determine whether *S. volkensii* ramet density, new leaf density, and leaf water content were correlated with zone types, we averaged the response variables for quadrats of each zone type in each patch run-on zones in June 2009. All variables met the assumptions of normality and homoscedasticity. We performed ANOVAs for each response variable, with zone type as a main effect and patch as a block effect.

We first used analysis of covariance (ANCOVA) to test the effects of zone type and adjacent herbaceous cover on (log-transformed) new leaf density and total ramet density in patch margins in April 2008. Adjacent herbaceous cover required log(%cover +1) transformation to meet ANCOVA assumptions. The model with log(%cover + 1), zone type, their interaction, and patch as a blocking factor yielded significant effects of cover, zone type, and patch on new leaf density (cover $p = 0.032$, zone $p < 0.0001$, patch $p < 0.001$) and on total ramet density (cover $p < 0.0001$, zone $p = 0.043$, patch $p = 0.002$). However, because of the data transformations, the results were difficult to conceptualize biologically. To better illustrate the trends, adjacent herbaceous cover estimates were combined to yield three fairly evenly populated cover classes, 0–5%, 10–20%, and 25+%, and used as a discrete independent variable along with zone type, cover class by zone interaction, and patch in a three-way ANOVA. Although categorizing the cover estimates entailed a loss of information and statistical power, the resulting analyses identified the same set of factors as significant. We used Tukey's pairwise contrasts (corrected for multiple post-hoc comparisons) to understand specific patterns of main effect variation. All analyses were performed using JMP Statistical Software (JMP, 2007).

RESULTS

S. volkensii patch expansion

We measured spatial variability in the density of ramets and new leaves in *S. volkensii* patches and found that the patterns were consistent with the widely held perception of continuing patch expansion. The density of new leaves varied significantly with distance from patch margins ($p < 0.0001$). New leaves were most abundant immediately (0 to 0·5 m) inside patch margins, averaging 5·0 new leaves/m^2, and decreased significantly with 2-m increments toward the interior in the patch (Figure 4a). Even in the patch interiors, new leaves were still frequently encountered, with an average of 2·6 new leaves/m^2 at 6 m within patch margins. Ramet density also varied significantly with distance from patch margins ($p = 0.002$) but showed the opposite trend: ramet density was significantly lower at 0 and 2 m from patch margins than at 4 or 6 m (Figure 4b). The patterns of new and existing growth imply a trend of ongoing outward patch expansion via new leaf emergence, while patch interiors maintain or increase leaf density with lower rates of new leaf growth.
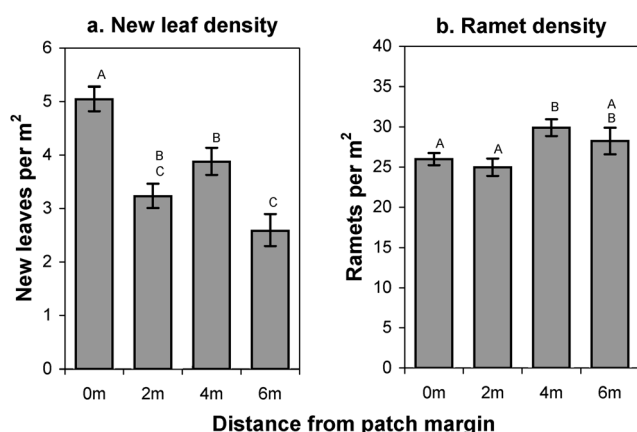
Figure 4. Means ± 1 s.e. of *Sansevieria volkensii* newly emerged leaf density (a) and ramet density (b) at varying distances inward from patch margins. New leaf density was log transformed for analysis; back-transformed means and s.e. are shown. Distances sharing the same superscripted letter did not differ significantly in Tukey post-hoc pairwise comparisons.

Surface water flow and soil moisture

In general, patches at this site tend to show greater soil moisture response to rainfall than interpatch areas (Franz *et al.*, 2011). So to specifically target the contribution that *patch interception* of surface flow makes to increased soil moisture, we compared soil moisture along patch margins that received direct run-on versus patch margins that did not.

At 2, 5, 8, and 11 days after a 6-mm rain event, we calculated differences in electrical conductivity $d(EC_a)$. In both zone types, $d(EC_a)$ was greatest 2 days after the rain event, then soil moisture decayed toward the baseline EC_a values. By using site-specific empirical calibrations (Franz, 2010), the initial jump in EC_a represents an increase in saturation of about 10%. We found that in all four post-rain surveys, $d(EC_a)$ values were consistently and significantly greater in run-on zones than in runoff zones (Figure 5, Table I), indicating that soil moisture increases were greater in the upper 1 m of soil in patch margins that received run-on than in patch margins that did not intercept surface water flow.
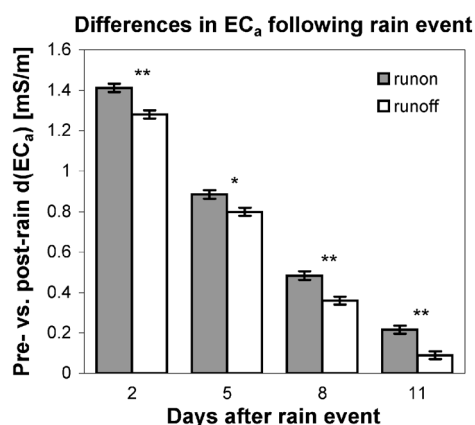

Figure 5. Means ± 1 s.e. of $d(EC_a)$ calculated 2, 5, 8, and 11 days after a 6-mm rainfall event in July 2009, by subtracting EC_a measured 1 day before the rain event, from post-rain EC_a values. Differences between run-on and runoff zones were significant for each post-rain census ($*p = 0.003$, $**p > 0.0001$).

This analysis served to confirm that our visually delineated run-on and runoff zones indeed reflected differences in interception and infiltration of surface water flow. Here we present the soil moisture response to one below-average (6 mm) rainfall event, but we also conducted the same measurements around two of the patches before and following an above-average 15-mm event in April 2009. That event generated about 10 times greater increases in soil moisture along patch margins and about 10 times larger differences between run-on and runoff zones (Franz *et al.*, 2011). However, because of the limited sample size ($n = 2$ patches), the soil moisture findings from the larger rain event could not be evaluated statistically, but the trend further supports that run-on and runoff zones are associated with different localized soil moisture dynamics.

Sansevieria responses to surface water flow

Mature leaf water content and mean number of new *S. volkensii* leaves/m² were significantly greater in run-on zones than in runoff zones (p = 0·037 and 0·034, respectively). Ramet density showed a similar trend but was not statistically significant (p = 0·133, Figure 6). Power analysis indicated that for the observed differences in ramet density means to differ significantly, a sample size of 12 zones of each type, instead of eight, would have been required to detect a significant effect. Thus, both *S. volkensii* leaf water content and new growth were greater in the same zones that had greater increases in soil moisture following rain events, suggesting a preferential upslope expansion of *S. volkensii* patches.

S. volkensii response to adjacent vegetation

We found no correlation between density of total or new ramets and the density of other vegetation within *S. volkensii* patches (data not shown). We did find, however, that *S. volkensii* density near patch margins varied with the herbaceous vegetation cover adjacent to (0–0·5 m outside) patch margins. We found that the density of both total ramets and new *S. volkensii* leaves decreased significantly with increasing adjacent vegetation (Figure 7, Table II).

Although the interaction terms in both analyses were non-significant, post-hoc contrasts indicated zone-specific differences in the way new leaf density changed with increasing adjacent vegetation cover. New leaf density in run-on quadrats was elevated in both the 0–5% and 10–20% adjacent cover classes then decreased when adjacent cover was greater than 25%. In contrast, in runoff quadrats, new leaf density responded negatively when adjacent vegetation cover increased from 0–5% to 10–20%. Summarized, in run-on zones, it took more adjacent vegetation (25% cover or more) to lead to a decrease in *S. volkensii* proliferation, while in runoff areas, lower levels of adjacent vegetation cover (10–20%) were associated with decreased proliferation (Figure 7a). The density of total *S. volkensii* ramets did not show zone-specific differences; in both zone types, a significant decrease in ramet density was

Table I. Effects of zone type and patch on d(EC_a) at four post-rain surveys.

		Post-rain survey							
		Day 2		Day 5		Day 8		Day 11	
Source	d.f.	F	p	F	p	F	p	F	p
Zone type	1	21·41	<0·0001	8·74	0·003	18·29	<0·0001	20·59	<0·0001
Patch	7	31·20	<0·0001	63·97	<0·0001	136·50	<0·0001	111·12	<0·0001

Results of two-way ANOVAs testing the effects of run-on versus runoff zone types and patch on d(EC_a) calculated following surveys performed 2, 5, 8, and 11 days after a 6-mm rainfall event in July 2009.

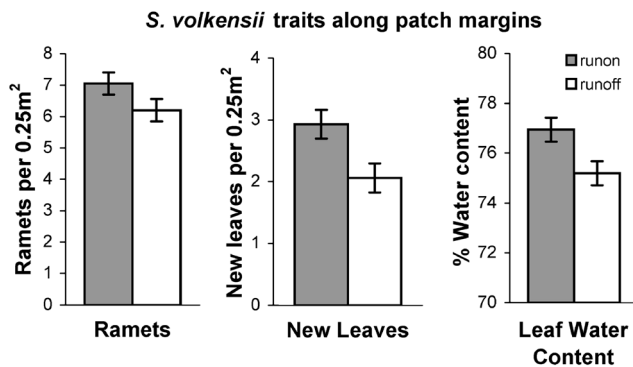**S. volkensii traits along patch margins**

Figure 6. Comparison of ramet density, new leaf density, and leaf water content of *Sansevieria volkensii* in run-on and runoff zones along patch margins. Differences between zone types were significant for each response variable.

observed when adjacent vegetation cover was greater than 25% (Figure 7b).

If run-on zones were associated with denser adjacent vegetation, the negative effect of adjacent vegetation could potentially attenuate the upslope proliferation of *S. volkensii* patches. However, contingency analysis indicated the opposite trend: the majority of low-cover quadrats (60%) occurred in run-on zones, while 59% of high vegetation cover quadrats were in runoff zones ($n = 333$, d.f. = 2, $\chi^2 = 8.51$, $p = 0.014$). Associated vegetation tended to be sparser adjacent to the upslope margins, weakening the potential effect of adjacent vegetation on the preferentially upslope proliferation of *S. volkensii*.

DISCUSSION

Mechanisms underlying the two-phase mosaic

In drylands with patchy two-phase vegetation structure, scale-dependent feedbacks arise that result in (1) limited resource accumulation and productivity in interpatch areas, (2) interpatch-to-patch resource redistribution, and (3) increased resource concentration and productivity in patches (Figure 1). In this study, we did not assess interpatch dynamics, but our results are consistent with the two other components, patch-mediated redistribution and within-patch feedbacks. Soil moisture increased more along run-on zones than along patch margins that did not intercept surface water flows. The greater abundance of new *S. volkensii* leaves along those margins indicated that the plants respond positively to the increased resource capture. Total ramet density was also greater in run-on zones, which may indicate a positive feedback, as denser vegetation may further obstruct surface water flows and further increase infiltration in run-on zones. In recent modelling studies, redistribution and within-patch dynamics (parts 2 and 3 of full scale-dependent feedbacks) have proven sufficient to generate resource-concentrating feedbacks and pattern formation (Kefi *et al.*, 2007b; Kéfi *et al.*, 2010). We therefore infer that the redistribution and within-patch interactions are creating positive feedbacks that reinforce a two-phase vegetation structure and impel the proliferation of *S. volkensii*.

Furthermore, we found that run-on zones tended to have less associated vegetation, which would favour the
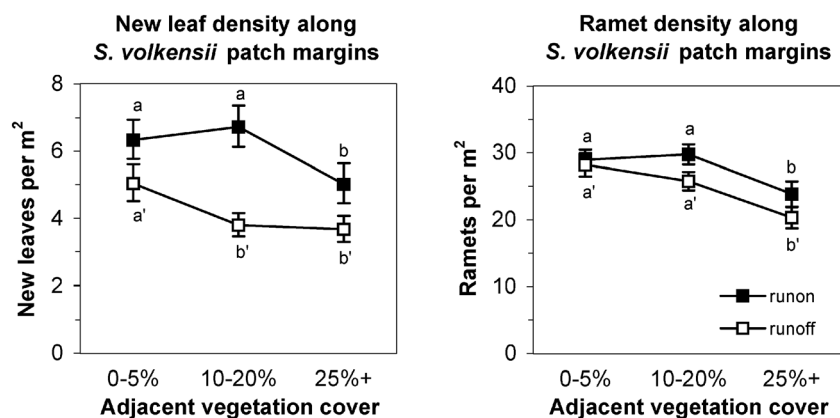

Figure 7. New leaf density and ramet density of *Sansevieria volkensii* in quadrats with differing densities of adjacent vegetation cover. Filled squares represent quadrats in run-on zones, and unfilled squares represent quadrats in runoff zones. Filled squares with different superscripts were significantly different, and unfilled squares with different primed superscripts were significantly different (corrected Tukey post-hoc comparisons, $p < 0.05$).

Table II. Effects of zone type, adjacent vegetation, and patch on *Sansevieria volkensii* plant traits.

Source	d.f.	New leaf density		Ramet density	
		F	*p*	*F*	*p*
Zone type	1	20·855	<0·0001	4·602	0·033
Adjacent vegetation cover	2	3·211	0·042	8·483	0·0003
Zone × adjacent vegetation	2	1·758	0·174	0·652	0·522
Patch	3	15·267	<0·0001	6·113	0·0005

Results of three-way ANOVAs testing the effects of run-on versus runoff zone type, adjacent vegetation cover class, their interaction, and patch, on *S. volkensii* new leaf density (log-transformed) and total ramet density in quadrats along patch margins in April 2008.

preferential upslope expansion of *S. volkensii* through the aforementioned positive feedbacks. It is at first counter-intuitive that herbaceous vegetation is less abundant adjacent to run-on zones, where soil moisture is higher following rain pulses. However, many of the run-on zones have large, unimpeded contributing areas that generate high-velocity surface water flow, which can cause scoured hard soil surfaces that inhibit grass establishment or can carry away seeds to be deposited where flows are slower or more tortuous (Ludwig *et al*., 1997). If surface hardness and disturbance are more influential in limiting grass establishment than soil moisture, then we would indeed expect greater abundance of adjacent vegetation downslope from patches, where observations of the soil surface typically indicated slower, winding flow patterns and litter deposition.

Beyond these findings, our current knowledge of the patterns and mechanisms of ecosystem change is limited by the lack of long-term quantitative monitoring in the communal rangelands experiencing *S. volkensii* proliferation. In such instances, local ecological knowledge is recognized as a valuable resource for identifying relevant variables and qualitative trends and for refining hypotheses (Oba and Kotile, 2001; Huntington *et al*., 2004; Roba and Oba, 2008). In our study area, analysis of residents' knowledge and perceptions of environmental change indicated temporal correlations between *S. volkensii* expansion, decreases in perennial grass cover, and livestock grazing pressure (King, 2008). From these trends, we infer that some stabilizing interaction associated with grass abundance, such as plant–plant competition, historically limited *S. volkensii* proliferation and now has been altered or lost from the system.

The finding that greater adjacent vegetation cover decreased new *S. volkensii* leaf emergence is consistent with a competitive release hypothesis, but we did not observe conditions that effectively halted *S. volkensii* expansion. Unfortunately, because of logistical circumstances and repeated drought, we have as yet been unable to test whether higher-than-ambient adjacent vegetation densities can more strongly inhibit *S. volkensii* growth. Instead, in the following sections, we utilize the spatial version of the cusp catastrophe framework developed in the Introduction section (Figure 2C) to conceptually explore the possibility of limiting or reversing the spread of *S. volkensii*. From this exercise, we gain insights and testable hypotheses regarding system behaviour and identify promising directions for future research.

Applying the cusp catastrophe model to S. volkensii dynamics. The spatial version of the cusp catastrophe framework offers an appropriate and potentially helpful model to organize our current understanding of *S. volkensii* proliferation. Furthermore, the exercise of fitting the study system to the model illustrates how this qualitative model can be used to educe further hypotheses about system function. We begin the exploratory exercise by using accumulated information about the system to infer plausible variables for the model axes. We believe that the historical condition was fairly continuous cover of perennial and annual grasses. Today, the system state is a two-phase mosaic of *S. volkensii* patches with largely bare interpatch areas. The findings of this study, and nearby swaths of *S. volkensii* >1 km long, suggest a potential third state: continuous *S. volkensii* cover. Thus, we label the vertical (y) axis 'proportion of grass patch cover' and describe the ecosystem state and basin of attraction on the upper plateau as 'grass-dominated', the lower plateau as '*S. volkensii*-dominated', and the current mosaic as a transitional state between the two. Our analyses indicate that resource-concentrating feedbacks are reinforcing the maintenance and the spread of *S. volkensii* patches. Thus, the two-phase mosaic may be transitory as the landscape continues toward greater *S. volkensii* domination. The threshold-bearing environmental variable (x-axis) most parsimoniously associated with the observed shift is grazing intensity.

The variable for the z-axis should meet four criteria in order to align with the model and in order to yield relevant and testable hypotheses. First, on the basis of the reasoning laid out in the Introduction section, it must be relevant to the state variables and feedbacks that govern the system, such that it reflects the strengths of scale-dependent feedbacks involved in landscape organization. Second, it should be measurable and conceptually scalable from patch to landscape scales (Wilcox *et al*., 2003; Bautista *et al*., 2007). Third, it should, if possible, collapse a suite of interrelated variables into a single variable, thereby reducing the dimensionality of the complex dynamics under consideration (Stafford Smith and Reynolds, 2002). Lastly, to give the cusp catastrophe model applied utility, the variable should have some relevance to management.

Rietkerk *et al*. (1996) proposed effective rainfall or plant available moisture (PAM) as the hysteresis-determining variable in their application of the cusp catastrophe model to Sahelian vegetation transitions. We concur that soil moisture is the key link between water redistribution and vegetation response feedbacks. In order to incorporate the spatial

element of scale-dependent feedbacks, we propose a measure of patch–interpatch soil moisture heterogeneity, d(PAM), as a z-axis variable that meets the criteria outlined earlier. Calculated as the difference between the mean PAM in patches and the mean PAM in interpatch areas, d(PAM) would be an indicator, rather than a driver, of scale-dependent feedback strength. When interpatch feedbacks of poor infiltration and limited plant growth are strong, runoff is generated and redistributed to drive the within-patch positive feedbacks. Under those conditions $PAM_{interpatch}$ would be low and PAM_{patch} high, leading to high d(PAM). Conversely, d(PAM) would only be low when interpatch infiltration was adequate and runoff redistribution limited, conditions under which scale-dependent feedbacks would be weak. In terms of scalability, a random, regular, or stratified array of point measurements of PAM is scaled up to the landscape level directly through the difference of averages. This metric also effectively integrates the effects of spatial patterning and other water input-related processes because PAM at a given point will already reflect surface flow contributing area, degree of obstruction, surface infiltration characteristics, and so on. Thus, for example, in a landscape with 30% patch cover, vegetation arranged in a few large patches would have higher d(PAM) than a pattern of many small patches because the former would have long unobstructed flowpaths and harsh interpatch conditions, while the latter pattern would slow runoff and dampen the interpatch-to-patch redistribution. Finally, d(PAM) is relevant to management issues because there are numerous ways to both monitor and manipulate it for management and restoration.

With putative variables identified for the model axes, we now map observed and projected trajectories of ecosystem change onto the stability surface (Figure 8A). Because the x-axis and z-axis variables are both involved in the feedbacks and thus not independent of one another, not all points on the stability surface are ecologically plausible; rather, trajectories are expected to follow certain 'paths' across the stability surface (Rietkerk et al., 1996).

Historically, we believe that the landscape had more uniform grass cover, allowing high soil infiltration rates and little overland flow in interpatch areas, resulting in low d(PAM) and locating the system in the upper, far corner of the stability surface (Figure 8A, stage I).
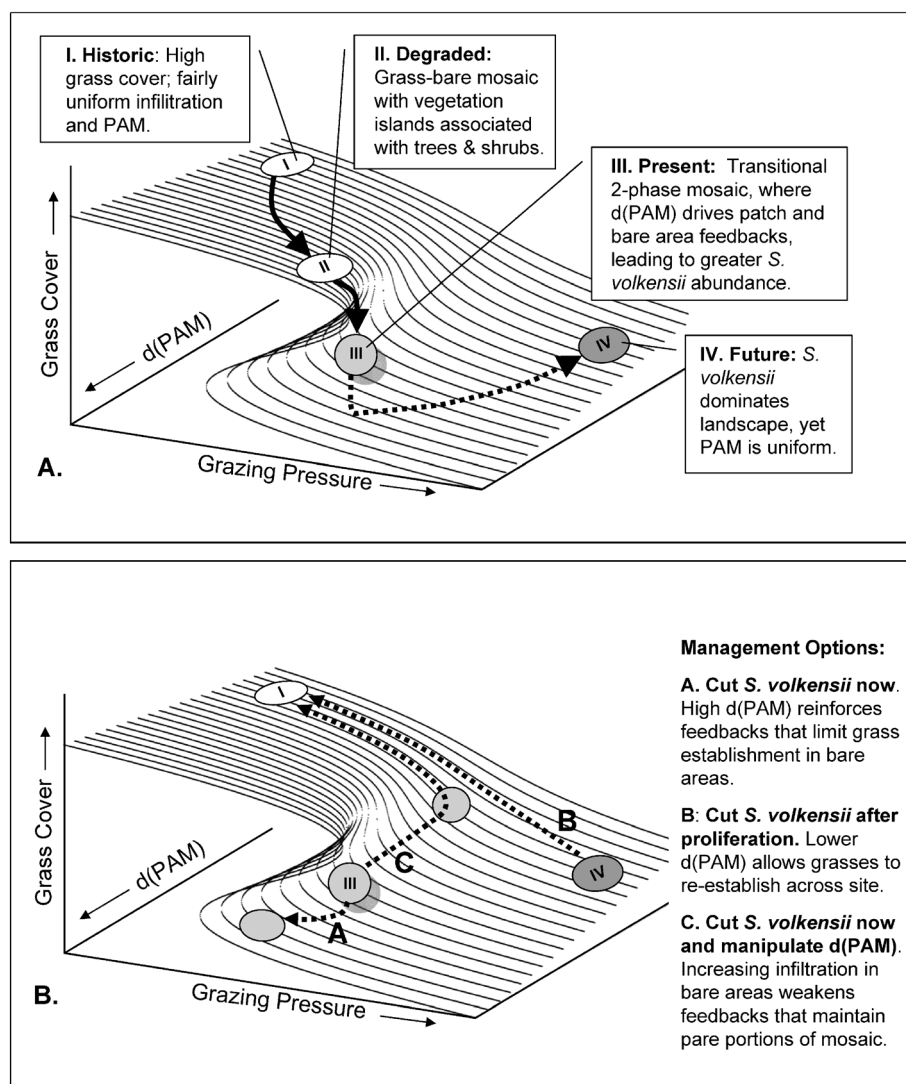

Figure 8. Mapping study site states and trajectories of change onto cusp catastrophe stability surface. (A) Past, present, and projected future states. (B) Projected outcomes of management options. The description of each state and trajectories are given, and the reasoning is more fully described in the text.

Grazing pressure would decrease grass cover, resulting in bare interpatches with lower infiltration rates and surface flow obstruction than patches. This would increase d(PAM) and bring the system to the fore of the stability surface, near the grazing threshold (Figure 8A, stage II). With continued grazing pressure, the scale-dependent positive feedbacks emerge: reinforcing resource loss from interpatches, interpatch-to-patch redistribution, and resource capture in *S. volkensii* patches. With our findings, we believe that the two-phase mosaic observed today is likely to be transitory, because the strong resource-concentrating feedbacks in patches are promoting the continued expansion of *S. volkensii* into bare areas (stage III). However, with fuller cover of *S. volkensii* patches (stage IV), the landscape will have fewer, smaller bare interpatches, with smaller contributing areas and slower surface flow velocities, allowing higher infiltration and thus higher PAM in bare areas. This would result in a lower overall d(PAM) for the landscape, moving the system toward the back of the stability surface.

Implications for management and resilience. On the basis of the variables and system behaviour hypothesized for the cusp catastrophe model, we explore potential implications of different restoration strategies on future trajectories of change. Because we have not yet identified conditions that halt patch expansion, we adopt the conservative premise that, in addition to reducing grazing pressure, cutting *S. volkensii* patches may be a necessary precondition for restoring a grassy state. We compare predicted trajectories of system response to cutting *S. volkensii* patches now at their current transitional mosaic state versus cutting them later, when they dominate the landscape (Figure 8B, starting stage III vs IV).

If *S. volkensii* patches are cut now (Figure 8B, option A), the system will still have high d(PAM), which means that the scale-dependent feedbacks will be able to persist. If the vegetation remaining in *S. volkensii* patches after they are cut has a smaller obstructive effect on surface water flow, we may even expect resource-losing feedbacks to become stronger and bare patches to increase across the landscape. In the diagram, the hysteresis-indicating fold in the stability surface represents this barrier to recovery (Figure 8B, arrow A). However, with fuller *S. volkensii* domination (Figure 8B, option B), the landscape will have fewer bare patches and, as reasoned previously, lower overall d(PAM). We expect this to attenuate the scale-dependent feedbacks. Thus, following *S. volkensii* clearing and reduced grazing, herbaceous vegetation may be able to persist and develop further throughout the landscape, returning to a grass-dominated state (Figure 8B, arrow B).

Another management option (Figure 8B, option C) arises from our analysis of the cusp catastrophe framework. If one were to cut *S. volkensii* now, we surmise that simultaneous physical manipulation of the low infiltration areas via soil ripping might help recreate the landscape-wide infiltration that we hypothesize is necessary for recovery. This is labour or machinery-intensive but would

also achieve the goal of reducing d(PAM) to a point that restoration becomes possible (Pueyo *et al.*, 2009).

These insights regarding potential future ecosystem changes are counter to the commonly held notion that ecosystems become increasingly difficult to restore as threshold transitions are crossed. By including a third dimension that characterizes when a threshold is reversible, we draw a much richer, and we believe more mechanistically valid, set of inferences about restoration potential in the system. Our mechanistic understanding about the importance of scale-dependent feedbacks shows us that *S. volkensii* proliferation, although odious to local pastoralists, may actually be performing an essential restorative role as it expands: it is recreating soil permeability in otherwise bare, encrusted areas, reducing resource loss and redistribution. By doing so, it is in fact enabling, rather than preventing, the future potential for ecosystem recovery.

Ecosystem resilience can be defined as the ability of a system to maintain or recover its functionality in the face of disturbance (Walker *et al.*, 2004). In this landscape, resilience depends not only on the extent of disturbance (grazing pressure) but also on the spatial distribution of water resource availability. Our conceptual analysis suggests that the current state has particularly low resilience, because grass cover is severely reduced, and recovery is prevented by the high contrast in soil moisture between patches, which reinforces degradation in interpatch areas. Interestingly, the continued proliferation of *S. volkensii* may in fact serve as a mechanism to restore the system's resilience because their habit of growth actually creates the soil surface and moisture conditions necessary for grasses to re-establish. The application of the cusp catastrophe model highlights the notion that management options can target either a land use variable, such as grazing pressure, or a resource variable, such as d(PAM), in strategies to enhance or restore ecosystem resilience.

Future research directions. By coupling and corroborating empirical study of ecohydrological mechanisms with theoretical understanding of system-wide behaviour, we have gained novel insights into the potential trajectories of ecosystem change. These inferences can now serve as strong hypotheses to guide further experimental field research in order to hone the development of effective restoration strategies. The inferences also motivate additional modelling research to broaden the utility of the work to other dryland research agendas. Large field manipulations of patch structure and interpatch soil conditions are underway to test whether the system responds as predicted by the proposed trajectories (Figure 8B). Further attention to temporal heterogeneity in water availability is also warranted; we expect that temporal explicitness will be critical in order to effectively quantify the key interactions driving ecosystem organization. Sensitivity to temporal dynamics is one of many dimensions of the study system being explored using a recently developed cellular automata model, with horizontal and vertical water redistribution and plant growth feedbacks (Franz, 2010).

Although we have posited that d(PAM), a difference in arithmetic means, will integrate spatial variation in PAM to

yield a metric that is proportional to the strength of scale-dependent feedbacks, we recognize that the function may be nonlinear or that different ways of calculating variance in PAM due to patch type may prove to be better metrics. With their model of water redistribution and concentration, Kéfi *et al.* (2010) proposed using the ratio of infiltration rates in bare and vegetated patches as a metric for scale-dependent feedback strengths. That metric is also conceptually valid and is in keeping with their model's focus on infiltration, whereas a metric based on PAM would integrate the effects of infiltration plus root uptake and shading on resource-concentrating dynamics. In ongoing work, we are exploring different mathematical expressions for patch–interpatch heterogeneity in PAM by using both the aforementioned cellular automata model and field measurements.

Because the cusp catastrophe model conceptually links processes at the levels of specific interactions, feedback loops, and ecosystem resilience, it can be useful as a source of testable hypotheses that can be pursued with parallel, complementary lines of inquiry using observational and manipulative empirical studies, formal models and simulations, and conceptual analyses. Recent commentaries on the state of ecohydrology have stressed that the integration of empirical hypothesis testing with theoretical analyses is essential for developing our understanding of ecosystem change, as well as for providing scientific products that are useful to land management (Hannah *et al.*, 2007; King and Caylor, 2011). In the case of *S. volkensii* proliferation in East Africa, we are continuing to couple different modes of analysis across different ecological scales. The same multifaceted approach is likely to lead to deeper understanding and novel insights into other dryland systems as well.

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