Savanna dynamics under extreme conditions

Insights from a mathematical model

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Summary

Savannas cover a broad geographical range across continents and are a biome best described by a mix of herbaceous and woody plants. The former create a more or less continuous layer while the latter should be sparse enough to leave an open canopy. What has long intrigued ecologists is how these two competing plant life forms of vegetation coexist.

Initially attributed to resource competition, coexistence was considered the stable outcome of a root niche differentiation between trees and grasses. The importance of environmental factors became evident later, when data from moister environments demonstrated that tree cover was often lower than what the rainfall conditions would allow for. Our current understanding relies on the interaction of competition and disturbances in space and time. Hence, the influence of grazing and fire and the corresponding feedbacks they generate have been keenly investigated. Grazing removes grass cover, initiating a self-reinforcing process propagating tree cover expansion. This is known as the encroachment phenomenon. Fire, on the other hand, imposes a bottleneck on the tree population by halting the recruitment of young trees into adulthood. Since grasses fuel fires, a feedback linking grazing, grass cover, fire, and tree cover is created. In African savannas, which are the focus of this dissertation, these feedbacks play a major role in the dynamics.

The importance of these feedbacks came into sharp focus when the notion of alternative states began to be applied to savannas. Alternative states in ecology arise when different states of an ecosystem can occur under the same conditions. According to this an open savanna and a tree-dominated savanna can be classified as alternative states, since they can both occur under the same climatic conditions. The aforementioned feedbacks are critical in the creation of alternative states. The grass-fire feedback can preserve an open canopy as long as fire intensity and frequency remain above a certain threshold. Conversely, crossing a grazing threshold can force an open savanna to shift to a tree-dominated state. Critically, transitions between such alternative states can produce hysteresis, where a return to pre-transition conditions will not suffice to restore the ecosystem to its original state.

In the chapters that follow, I will cover aspects relating to the coexistence mechanisms and the role of feedbacks in tree-grass interactions. Coming back to the coexistence question, due to the overwhelming focus on competition and disturbance another important ecological process was neglected: facilitation. Therefore, in the first study within this dissertation I examine how facilitation can expand the tree-grass coexistence range into drier conditions. For the second study I focus on another aspect of savanna dynamics which remains underrepresented in the literature: the impacts of inter-annual rainfall variability upon savanna trees and the resilience of the savanna state. In the third and final study within this dissertation I approach the well-researched encroachment phenomenon from a new perspective: I search for an early warning indicator of the process to be used as a prevention tool for savanna conservation. In order to perform all this work I developed a mathematical ecohydrological model of Ordinary Differential Equations (ODEs) with three variables: soil moisture content, grass cover and tree cover.

Facilitation: Results showed that the removal of grass cover through grazing was detrimental to trees under arid conditions, contrary to expectation based on resource competition. The reason was that grasses preserved moisture in the soil through infiltration and shading, thus ameliorating the harsh conditions for trees in accordance with the Stress Gradient Hypothesis. The exclusion of grasses from the model further demonstrated this: tree cover was lower in the absence of grasses, indicating that the benefits of grass facilitation outweighed the costs of grass competition for trees. Thus, facilitation expanded the climatic range where savannas persisted into drier conditions.

Rainfall variability: By adjusting the model to current rainfall patterns in East Africa, I simulated conditions of increasing inter-annual rainfall variability for two distinct mean rainfall scenarios: semi-arid and mesic. Alternative states of tree-less grassland and tree-dominated savanna emerged in both cases. Increasing variability reduced semi-arid savanna tree cover to the point that at high variability the savanna state was eliminated, because variability intensified resource competition and strengthened the fire disturbance during high rainfall years. Mesic savannas, on the other hand, became more resilient along the variability gradient: increasing rainfall variability created more opportunities for the rapid growth of trees to overcome the fire disturbance, boosting the chances of savannas persisting and thus increasing mesic savanna resilience.

Preventing encroachment: The breakdown in the grass-fire feedback caused by heavy grazing promoted the expansion of woody cover. This could be irreversible due to the presence of alternative states of encroached and open savanna, which I found along a simulated grazing gradient. When I simulated different short term heavy grazing treatments followed by a reduction to the original grazing conditions, certain cases converged to the encroached state. Utilising woody cover changes only during the heavy grazing treatment, I developed an early warning indicator which identified these cases with a high risk of such hysteresis and successfully distinguished them from those with a low risk. Furthermore, after validating the indicator on encroachment data, I demonstrated that it appeared early enough for encroachment to be prevented through realistic grazing-reduction treatments.

Though this dissertation is rooted in the theory of savanna dynamics, its results can have significant applications in savanna conservation. Facilitation has only recently become a topic of interest within savanna literature. Given the threat of increasing droughts and a general anticipation of drier conditions in parts of Africa, insights stemming from this research may provide clues for preserving arid savannas. The impacts of rainfall variability on savannas have not yet been thoroughly studied, either. Conflicting results appear as a result of the lack of a robust theoretical understanding of plant interactions under variable conditions. . My work and other recent studies argue that such conditions may increase the importance of fast resource acquisition creating a 'temporal niche'. Woody encroachment has been extensively studied as phenomenon, though not from the perspective of its early identification and prevention. The development of an encroachment forecasting tool, as the one presented in this work, could protect both the savanna biome and societies dependent upon it for (economic) survival. All studies which follow are bound by the attempt to broaden the horizons of savanna-related research in order to deal with extreme conditions and phenomena; be it through the enhancement of the coexistence debate or the study of an imminent external threat or the development of a management-oriented tool for the conservation of savannas.

Allgemeinverständliche Zusammenfassung

Savannen sind gekennzeichnet durch die Koexistenz von Gräsern und Bäumen. Sie bedecken circa 20% der globalen Landfläche und Millionen Menschen hängen von ihrer Intaktheit ab. Allerdings bedrohen sowohl der Klimawandel als auch Landnutzung dieses Biom. In dieser Studie werden die Existenz von Savannen unter sehr trockenen Bedingungen, ihre Reaktionen auf steigende Fluktuationen des Niederschlags und die Quantifizierung ihrer Resilienz untersucht.

Die Ergebnisse zeigen, dass unter extrem trockenen Bedingungen der positive Einfluss von Gräsern auf Bäume eine wichtige Rolle für das Überleben der Bäume spielt. Kommt es hingegen zu einer Erhöhung der Niederschlagsvariabilität, wird dadurch eine starke Konkurrenz zwischen den beiden Lebensformen verursacht. Die Resilienz der Savannen und ihre Veränderungen lassen sich quantifizieren und mit dem im letzten Teil dieser Dissertation präsentierten Werkzeug erkennen.

Meine Arbeit demonstriert, dass sich der Fokus der aktuellen Savannenforschung weiten muss, um die Reaktionen von Savannen auf sich ändernde Umweltbedingungen vorherzusagen. Um Savannen langfristig zu erhalten, müssen jedoch die bereits vorhandenen Grundlagen in einem soliden Framework zusammen gebracht werden.

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1 General Introduction

1.1 Motivation and theoretical background

Savanna biomes cover around 20% of the global land surface, spread primarily across the tropics, and comprise of a broad range of ecosystems (Lehmann et al., 2014). Common to all these is the coexistence of woody (trees and/or shrubs) and herbaceous (grasses) vegetation (Scholes and Archer, 1997). The former must be scattered enough to allow for an open canopy, thus distinguishing savannas from forest. Grasses, on the other hand, span the landscape, filling the space between the trees and shrubs. Similarly to previous studies (e.g. Bond and Midgley, 2012; Sankaran et al., 2004) for reasons of simplicity, I will refer to all woody vegetation as trees and the two terms will be interchangeable, while grasses will stand for all herbaceous vegetation.

Even though light competition may play a role during early tree establishment and soil nutrients are important for any plant, water is the common resource plants compete most strongly for. However, contrary to what 'competitive exclusion' would predict, savanna trees and grasses coexist and have done so for thousands of years (Gillson and Ekblom, 2009). This turned out to be the big mystery, also known as the 'savanna question' (Sarmiento, 1984), ecologist were after solving for many years.

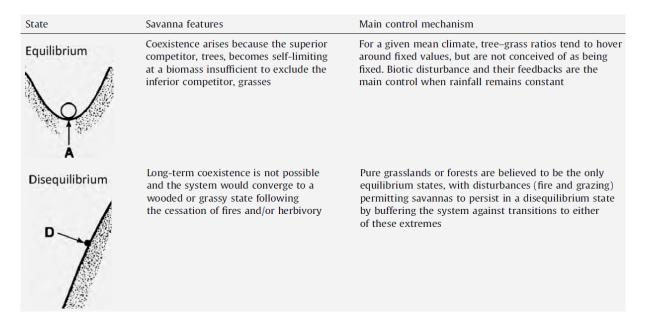


Figure 1.1 Overview of the equilibrium and disequilibrium theories. Source: Gil-Romera et al. (2010).

The first major breakthrough was Walter's 'two-layer hypothesis', which explained coexistence through root niche differentiation (Walter, 1972). The two plant types, according to the hypothesis, accessed water from different soil layers and were thus able to coexist in the long term. This hypothesis described savannas as essentially stable systems in equilibrium (Walker et al., 1981). This deterministic interpretation of coexistence came under scrutiny as more data became available. Savanna sites were studied where the stable competition model did not fit observations (Sankaran et al., 2004; Scholes and Archer, 1997). In particular, these were sites with more rainfall and surprisingly low tree cover. The response to this was a new wave of theories which were based on stochastic disturbances, turning the equilibrium notion on its head. According to these theories, either trees or grasses would dominate the landscape but for the stochastic occurrence of disturbances such as grazing or fires (Higgins et al., 2000). The former, for example, removes grass cover releasing trees from competition, while fires reduce the likelihood of tree recruitment and thus create a bottleneck in the adult tree population growth. This so called dis-equilibrium approach was best described by (Jeltsch et al., 2000) with the concept of 'buffering mechanisms': with grassland and forest at either end of the biome spectrum, savannas depend on stochastic buffering mechanisms, such as grazing and fire, to maintain the balance between trees and grasses.

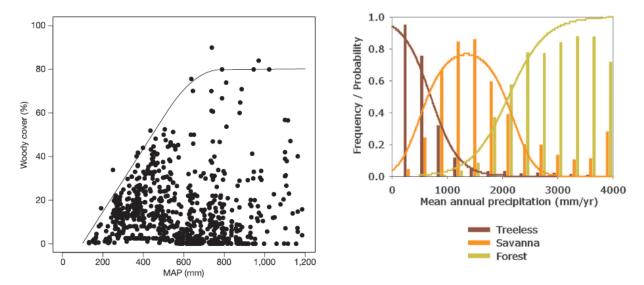


Figure 1.2 (Left) Tree cover data from African savannas along the mean annual precipitation gradient. Source: Sankaran et al. (2005). (Right) The global frequency distributions of treeless, savanna and forest biomes along the mean annual precipitation gradient showing the coexistence of alternative states for the same amount of rainfall. Source: Hirota et al. (2011).

A more complete picture emerged once the competition- and disturbance-based theories were merged: coexistence in savannas was found to be primarily due to resource competition, but also dependent on stochastic disturbance (Sankaran et al., 2005). In African savannas in particular, there appeared to be a clear cut-off between climate- and the disturbancedependent savannas along the rainfall gradient. Below a certain amount of annual rainfall (~650mm/year, see Fig. 1.2, left), tree cover increased linearly with rainfall and coexistence was deemed to occur as a result of resource competition. Disturbances in these conditions were assumed to impact the vegetation ratios rather than coexistence itself (Higgins et al., 2010). Under moister conditions, however, tree cover did not respond to the rainfall gradient (Fig. 1.2, left) due to fires which suppress the development of young trees into adults (Sankaran et al., 2008). Fires, though, require grasses as fuel (Bond et al., 2005) so their success in limiting the expansion of tree cover depends on the availability of flammable grass cover, and thus a positive grass-fire feedback is established. As long as tree cover remains below a certain threshold, the fire feedback can maintain an open landscape (Staver et al., 2011a). However, a weakening of the grass-fire feedback will initiate a reverse positive feedback: tree cover expands at the expense of grass cover, reducing fuel for fires and providing ever improving tree recruitment opportunities. Given that rainfall is the primary determinant of maximum tree cover (see Fig. 1.2 left), tree cover would then expand unhindered to reach this climatically-determined maximum, in many cases leading to a closed-canopy forest (Staver et al., 2011b).

Answering the coexistence conundrum, or else the 'savanna question', by relying on stochastically occurring positive feedbacks opened up the door to another topic: the existence of alternative states (Beisner et al., 2003). As the data which led to the formulation of the combined competition-disturbance coexistence theory showed, tree cover in African savannas had a multimodal distribution (Xu et al., 2016). This means that sites with the same climatic conditions can either form a grassland, a savanna with scattered trees or something closer to a forest (Fig. 1.2, right). Theory has shown that positive feedbacks are essential for the existence of these alternative states and for preserving the system within one of them (Kéfi et al., 2015). If the grass-fire feedback, to use the same example, is strong enough, trees can almost be excluded from the biome even under moist conditions (Calabrese et al., 2010). However, the same site under the same climatic conditions could have been dominated by trees if fires were less potent or frequent (Staver et al., 2011a). Thus, fire as a tree recruitment

bottleneck - and positive feedbacks in general - took on a new significance by inducing alternative savanna states (van Langevelde et al., 2003).

Regarding savannas as states within inherently bistable systems (systems with two alternative states) has significant implications for the transition between states as well. As mentioned above, a positive feedback can maintain the system in its current state. Weakening one such feedback can release a different one, which pushes the system towards the alternative state (D'Odorico et al., 2006). Grazing, which removes grass cover, weakens fire, and thus promotes tree cover expansion, creating a positive grazing-tree cover feedback (Lohmann et al., 2012). Once a threshold is crossed, the grazing-tree cover feedback takes over, forcing the transition to a tree-dominated savanna in the absence of significant management interventions. This increase in tree (or woody) cover at the expense of grass cover is known as 'woody encroachment' (or shrub encroachment) (Graz, 2008). The issue with such transitions is that they are not reversible by a simple return to the originally prevailing conditions (e.g. lowering grazing intensity) (D'Odorico et al., 2012). The inability of a system to return to its original state despite the conditions doing so is known as 'hysteresis' and is intertwined with the existence of alternative states (see Fig. 1.3 below, taken from Beisner et al., 2003). This phenomenon is not simply the result of a theoretical model, but has been observed in a wide range of ecosystems (e.g. spruce budworm outbreak (Ludwig et al., 1978), lake eutrophication (Carpenter et al., 2011)) and even shapes our current understanding regarding greenhouse gas emissions and climate change (Lenton et al., 2008).

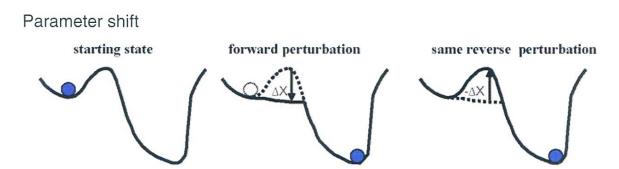


Figure 1.3 Hysteresis caused by parameter changes: the landscape changes and forces the ball to move to the alternative state. An equal parameter change in the opposite direction is then not sufficient to return the ball to the original state. Source: Beisner et al. (2003).

1.2 Open questions

As is normally the case with research - and human curiosity in general - reaching one answer is rarely the end of the road. Even more so when one regards how the aforementioned answers indicate that savannas are biomes with complex underlying dynamics which can be sensitive to external forcing. In light of climate change and more direct human impacts, savannas may respond in unexpected ways. Thus questions such as the following arise: what coexistence processes dominate under extreme environmental or climatic conditions? Will climate change alter the competitive interactions and impact coexistence? What will be the impact of increased stochasticity on savannas, both as a biome and a bistable system? Does hysteresis manifest itself in savanna transitions such as woody encroachment? Are there ways to prevent irreversible transitions?

1.2.1 Facilitation theory missing from the savanna debate

Throughout the discussion on savanna coexistence mechanisms, nowhere did facilitation appear. Competition-oriented studies set the tone early. When the debate expanded to also include stochastically occurring disturbances, their impact was regarded with respect to the competitive balance between the different plant types. Facilitation theory was slow to develop in relation to competition, even more so in relation to the savanna debate. The Stress Gradient Hypothesis (SGH) (Bertness and Callaway, 1994), which claims that facilitation in plant-plant interactions becomes stronger with increasing environmental stress, was formulated in the mid-1990s but remained on the side-lines for some time. Plant-plant interactions under extreme conditions became relevant more recently due to the impacts of climate change (Brooker et al., 2008). The SGH re-emerged as a hot topic among ecologists who initially worked toward validating (Lortie and Callaway, 2006) or quashing it (Maestre et al., 2005), and later to refine and improve it (Holmgren and Scheffer, 2010; Malkinson and Tielboerger, 2010). This work spilled over into tree-grass interactions within savannas, but only in the limited context of local interactions tested in the field (Anthelme and Michalet, 2009; Moustakas et al., 2013). Even so, some interesting results demonstrated how facilitation between otherwise competing species guaranteed their coexistence.

Plants can facilitate their neighbours either through creating a more favourable microenvironment around them (Iacona et al., 2012) or by providing physical refuge from

predators, such as herbivores (Smit et al., 2009). In arid environments, ameliorating the harsh conditions could be vital for the survival of neighbouring plants. Shade, for example, can help maintain moisture in the soil (Vadigi and Ward, 2013). As such, a plant providing shade can facilitate the survival of its neighbours. In savannas, adult trees could take such a role of a 'nurse' plant (Soliveres et al., 2015), providing shade for grasses without restricting their access to sunlight (Dohn et al., 2013; Moustakas et al., 2013). Similarly, grass tufts create more humid microenvironments for young tree seedlings to benefit (Anthelme and Michalet, 2009). A different facilitation path in arid environments comes in the form of the welldocumented positive vegetation-moisture feedback, such as rainfall infiltration (Gilad et al., 2007). Vegetated patches create pores which allow rainfall to infiltrate and minimise water loss due to run off. This leads to increased soil moisture, which allows for more vegetation, creating a vegetation-sustaining positive feedback. This facilitation pathway has been much studied with respect to vegetation pattern formation in arid environments (Meron, 2012), however, it has barely featured within the 'savanna question' context (Baudena and Rietkerk, 2013). Unfortunately a systematic effort to test such results at the biome level is missing to date.

1.2.2 Climatic variability

Aspects of climate change such as rising temperatures, increasing atmospheric CO₂ concentrations, changing rainfall patterns, or the fluctuations in the onset of seasons will have, and actually already do have, significant ramifications for ecosystems and the species within (IPCC 2013): whole ecosystems are expected to collapse (e.g. coral reefs (Hoegh-Guldberg et al., 2007)), species (including certain humans) already migrate to survive (e.g. Andean trees (Feeley et al., 2011)), while others look set to benefit (e.g. invasive plants (Hellmann et al., 2008)). Clearly, climate change will impact savannas too. Most studies suggest that woody vegetation stands to benefit from an increase in atmospheric CO₂ because it will narrow the competition gap with C4 grasses (Bond et al., 2003; Bond and Midgley, 2012).

Climate change is predicted to affect rainfall patterns as well (Easterling et al., 2000; Fischer et al., 2013) with variability of rainfall between years as well intensity of individual rainfall events expected to increase (O'Gorman and Schneider, 2009). The two-layer hypothesis relies on a competitive niche relating to water availability in different soil depths: grasses dominate the top soil layer, while trees rely on accessing water from deeper soils. Following from the

two-layer hypothesis, it would be reasonable to assume that the intensity of individual rainfall events could shift the balance in the favour of trees (Kulmatiski and Beard, 2013). However, this has been disputed by studies that show the rise in importance of the temporal niche: increasingly variable conditions, the argument goes, will require temporally aggressive strategies for resource acquisition (Hoover et al., 2014; Xu et al., 2015). Unfortunately, though, not many savanna-related studies have focused on this changing rainfall patters until now (Aleman et al., 2016).

Also intriguing is the link between bistability and increased variability. Theoretical work has shown that increasing variability tends to act against bistability (Sharma et al., 2014). Similarly, in studies specifically focused on drylands, stochasticity was found to have a stabilising impact. In one case it created an intermediate steady state between the two alternatives (D'Odorico et al., 2005) while in a different study, high levels of variability eliminated bistability altogether (Guttal and Jayaprakash, 2007). Unfortunately, though, our understanding with respect to the possible impact of high inter-annual rainfall variability on the alternative states present in savannas is still lacking, as no such studies exist.

1.2.3 Woody encroachment: why wait to act?

Woody encroachment is the phenomenon where woody cover expands at the expense of grass cover and in some cases at the expense of overall vegetation cover (Graz, 2008). This essentially breaks up the savanna into a grid of vegetated patches and bare soil. Encroachment, thus, degrades the whole ecosystem and threatens the livelihoods of millions of people who rely on healthy savannas (D'Odorico et al., 2013). The latter of course, may be the cause of the problem in the first place. Heavy grazing has been strongly linked to woody encroachment, since it is a process which removes grass cover (D'Odorico et al., 2012). In this way fires become less effective in suppressing tree cover (Lohmann et al., 2014), a strong competitor is taken out of the picture and a positive feedback of grazing-tree cover expansion is initiated (van Langevelde et al., 2003).

The dynamics of woody encroachment have been much studied and so have its negative impacts on the ecosystem. Interestingly it has also been demonstrated that encroachment can be abrupt (Ratajczak et al., 2014) and irreversible (D'Odorico et al., 2012). This means that once we are faced with signs of encroachment it is too late to reverse the process without

applying extreme management measures. Irreversible, or catastrophic, transitions are linked to bistable systems: a jump to the alternative state cannot be undone by a simple return to the original conditions (hysteresis, see Fig. 1.3). Examples of such transitions have been found in multiple natural systems (e.g. fisheries collapse (Jackson et al., 2001), desertification of drylands (Kéfi et al., 2007)). A consequence of investigating catastrophic transitions was the development of methods to anticipate them (Scheffer et al., 2001). Such early warning signals, as they are referred to, are behavioural patterns exhibited by the systems as they approach a transition (Scheffer et al., 2009).

Early warning signals can warn of a loss of resilience, represented by a slowing response to perturbations ('critical slowing down') (Lenton et al., 2012), or of an impending shift induced by stochasticity, witnessed as rapid transitions between the alternative states ('flickering') (Dakos et al., 2013), among others. Critical slowing down, in particular, has received much attention because it presents itself in multiple ways which are easy to pick up either in theoretical studies (Scheffer et al., 2009) or in data (Dakos et al., 2008). Two typical manifestations of critical slowing down are increasing variability and autocorrelation (the correlation between consecutive states) in a leading variable (Dakos et al., 2012). Examples thereof have been found in whole ecosystem experiments (lake eutrophication (Carpenter et al., 2011)) or lab microcosms (e.g. cyanobacteria populations (Veraart et al., 2012)) and even in climate data (Lenton, 2011). One would think that a well-understood transition such as woody encroachment and a much-studied tool for the early identification of this kind of transition would have long been combined into an extremely useful field of research. However, to this point, there have been no studies for the early identification of woody encroachment in savannas.

1.3 Objectives

The sections, above, describe three interesting topics which are related to savanna theory but have so far been either underrepresented in or are absent from the savanna literature. With a focus on coexistence processes and mechanisms, I study tree-grass interactions under extreme aridity; savanna tree cover and savanna resilience under increasing rainfall variability; and the early identification and prevention of woody encroachment in savannas. To this end, I develop a model of coupled soil moisture vegetation dynamics and investigate the appropriate environmental and climatic conditions for each question. The principle aim of this dissertation is to relate important and well-studied aspects of ecological theory, which have been developed in their own right, to savanna dynamics and thus extend the scope of savanna research.

1.3.1 Research questions

The limited amount of studies on facilitative tree-grass interactions within savannas had only began to demonstrate how important facilitation may well be (Anthelme and Michalet, 2009; Moustakas et al., 2013). However, such is the nature of empirical studies relating to whole ecosystems, that generalisations are hard to make unless sufficient evidence is in place. Given my modelling approach I aim to provide the first study to discuss facilitation as a possible coexistence mechanism at the biome level. As the Stress Gradient Hypothesis postulates, facilitation ought to dominate under extreme conditions. Therefore I ask whether facilitation can be a process which leads to coexistence under conditions of extreme aridity. More specifically, under the assumption that grasses are superior competitors in these conditions (Ward et al., 2013), I investigate whether their indirect impact on trees via shading and infiltration outweighs resource competition to extend the coexistence range.

I then move onto the question of stochasticity's impact on the vegetation itself and on the alternative states. Expected increases in inter-annual rainfall variability will impact not only the competitive balance between trees and grasses, but also the indirect feedbacks which maintain a system in its given state. Since the roles of competition and disturbance vary along the rainfall gradient I choose two systems (semi-arid and mesic) and subject them to simulated increases in inter-annual rainfall variability. In these two mean rainfall scenarios I ask what the effect of increasing rainfall variability will be on the vegetation composition

(tree cover in particular), how savanna resilience will be impacted and which processes are responsible for any observable effects.

In the last study within this dissertation I seek to apply early warning signal theory to the phenomenon of woody encroachment. Since it is considered an irreversible process, I ask whether the related theory of early warning signals can successfully predict its onset. To this end, I simulate scenarios of heavy grazing which can lead to a transition from an open to an encroached savanna, with encroachment having a different likelihood of being irreversible in each scenario. I ask whether a warning appears prior to the onset of encroachment and whether this warning can distinguish between the reversible and irreversible cases. Ultimately, the success of any possible encroachment indicator will depend on how early it shows up so that the process can be prevented before it unfolds. I, therefore, ask whether realistic management actions at the end of the heavy grazing treatments suffice to prevent encroachment from unfolding.

1.3.2 Modelling approach

Models of savanna dynamics allow for the exhaustive testing of a range of scenarios and are extremely useful in investigating questions of scale (spatial or temporal). Over the years, multiple savanna models have been developed using different modelling approaches: state and transition (Bestelmeyer et al., 2004), rule-based (Jeltsch et al., 1996), or differential equations (van Langevelde et al., 2003) models. Each approach has its benefits and limitations, but the choice of the most appropriate one depends on the research question. Mathematical models of differential equations are a natural choice for questions that regard the underlying dynamics and processes of the system, in other words, its qualitative properties (Tietjen and Jeltsch, 2007). Such models have facilitated the advancement of our understanding in science for centuries, from Verhulst's logistic growth to the famous Lotka-Volterra equations. These types of models provide a solid framework within which more intricate interactions can be researched.

Differential equations models of savanna dynamics have allowed for a systematic testing of our ecological assumptions (e.g. de Knegt et al., 2008; van Langevelde et al., 2003). The models involve certain variables which represent an aspect of savannas (e.g. tree cover) and parameters which make up the various processes. Each equation represents the dynamics one

variable and all equations are coupled with each other, which means there are interactions between all variables. The equations themselves describe the rate of change of the corresponding variable for each time step (e.g. one year). Crudely described, the rate of change increases with 'growth' or 'births' and is slowed down by 'mortality'. In this simple and simplified way, individual processes can be included in the model in a manner that reflects our understanding of the interactions they form.

For these reasons, this dissertation utilises a mathematical ecohydrological model of savanna dynamics: the research questions evolve around understanding plant interactions with respect to climatic and environmental conditions. I modify an existing model of Ordinary Differential Equations (ODEs) (Accatino et al., 2010; De Michele et al., 2011) with three variables: soil moisture content, grass cover and tree cover. The model incorporates the key assumptions regarding resource competition, positive vegetation-soil moisture feedbacks and disturbances (grazing, browsing and fire). The modifications to the original involve the inclusion of infiltration, altering the role of fire and representing grazing, browsing and fire as non-linear functions. Rainfall infiltration was not included in the original model, but it has been demonstrated to play an important role for coexistence, particularly in dry environments (Baudena and Rietkerk, 2013). Infiltration increases with the amount of vegetation cover, providing soil with more water, which can in turn support more vegetation. Another important change with respect to the savanna dynamics in the model is the representation of fire as a limitation of tree growth rather than a morality of adult trees. It has been repeatedly shown and strongly argued for that savanna trees are fire tolerant and that fire limits tree cover by top-killing young saplings or seedlings (Higgins et al., 2000), which ought to be reflected in the model assumptions (Hanan et al., 2008). Since the model does not include an age structure, the role of fire in the tree equation is to restrict further colonisation. Moreover, fire is represented as a sigmoidal function of grass cover (Staver et al., 2011a), which acts as fuel. Grazing and browsing, which cause a reduction in grass and tree cover respectively, are also non-linear, increasing saturating functions (du Toit and Olff, 2014). For the first study I apply a deterministic version of this model, while in the next two studies I include stochasticity both in the rainfall amount between years and the occurrence of fires within years.

1.4 Structure of the dissertation

1.4.1 Dissertation outline

'Facilitation in drylands: modelling a neglected driver of savanna dynamics' (Chapter 2) focuses on the role of facilitation as a coexistence mechanism in savannas. In it I expand on how savanna research and facilitation theory developed in parallel with very little overlap. Given that savannas do exist under extreme climatic conditions I test the Stress Gradient Hypothesis (SGH) with respect to savanna dynamics and I pose the question of whether facilitation can be a stronger driver of coexistence than resource competition. For this I apply my model of ODEs which is validated on data of African savanna sites. The work focuses on conditions which, according to the SGH, could induce facilitative interactions. Different grazing and browsing regimes are also included in the simulations, providing an interaction between biotic and abiotic stressors.

The next chapter, 'Inter-annual rainfall variability impacts plant interactions and fire to produce contrasting responses of savannas along a rainfall gradient' (Chapter 3), studies how inter-annual rainfall variability alters the importance of plant interactions and environmental processes. In order to investigate this topic the model is amended accordingly: the deterministic rainfall parameter becomes a time series based on current conditions in Kenya. This is then adjusted for two mean rainfall conditions: semi-arid and mesic and different levels of inter-annual variability compared to current levels are simulated for both mean rainfall scenarios. Fire also switches from a continuous (yearly) process to a stochastic one, based on the grass-fire feedback. Having established the methodological framework for the study I investigate how increasing inter-annual rainfall variability impacts tree cover and the resilience of savannas, whilst attempting to uncover the mechanisms responsible for these responses.

The last study within the dissertation, 'Forecasting and preventing irreversible encroachment in savannas' (Chapter 4), deals with the phenomenon of woody encroachment under mesic conditions. The irreversibility of this process makes it an ideal candidate for the application of early warning signals. Using the stochastic version of the model I apply heavy grazing treatments of a fixed duration but of different intensities and test standard metrics of early warning signals, attempting to answer the questions outlined above: does a signal appear and

will it be able to distinguish between the cases with a high likelihood of irreversibility and the rest; does the signal show up early enough?

In the final chapter (Chapter 5, General discussion) I bring together the major findings of the three studies. As I have already mentioned, all three studies focus on gaps in the current literature: each one links savanna ecology to a well-researched topic which has not been satisfactorily investigated within or integrated into the savanna framework. Therefore, the general discussion expands on this 'bridging' of the different research questions. Moreover, in light of climate change projections, all three studies describe phenomena and conditions which are likely to affect savannas in the near future. The overarching idea, therefore, is to understand how savannas and their continued existence can be impacted by such external forcing. The work starts from the purely theoretical (facilitation hypothesis), shifts to the applied (rainfall variability and resilience) and reaches the strongly practical (prevention of encroachment) in order to emphasise short- and long-term climate-related savanna conservation issues.

1.4.2 Cumulative dissertation specifics

This is a cumulative dissertation so it consists of a general introduction (current chapter), three research articles (Chapters 2-4) and a general discussion (Chapter 5). The three articles are thematically related yet independent since they are published in or are in the review process at international peer-reviewed, ISI-listed scientific journals. These chapters can be read independently as they focus on specific topics and, thus, constitute stand-alone contributions to scientific literature. As such, the references relating to each chapter can be found at the end of the corresponding chapter. Nevertheless, to facilitate the reader, at the end of Chapters 2 and 3, a short transitional text links each study to the following one. Certain parts of the three articles may be similar, the model description in particular, since all were written independently and were submitted as stand-alone studies for publication. Unlike the general introduction (Chapter 1) and discussion (Chapter 5), the research articles within the dissertation (Chapters 2-4) are written in first-person plural because they have been coauthored. I should note that having been the lead author in all articles I performed the majority of the work: formulating the research questions, designing the model, running the simulations, and writing the text. Moreover, the views expressed throughout these and the dissertation in general are my own. I do, however, acknowledge the contribution of my coauthors in the development of the model and the related methodologies as well as their feedback during the writing process. Finally, I want to emphasise that all the work and results presented herein are original and stem from work that I have performed independently during my time working toward this dissertation.

1.4.3 Regarding the studies presented in the following chapters

Chapter 2, 'Facilitation in drylands: modelling a neglected driver of savanna dynamics' has been published as: Synodinos AD, Tietjen B, Jeltsch F (2015) Facilitation in drylands: Modeling a neglected driver of savanna dynamics. Ecological Modelling 304:11–21. doi: 10.1016/j.ecolmodel.2015.02.015.

The study in Chapter 3 is the product of major revisions following a review by the American Naturalist and will be resubmitted the journal in its current form as: Synodinos AD, Lohmann D, Tietjen B, Jeltsch F. 'Inter-annual rainfall variability impacts plant interactions and fire to produce contrasting responses of savannas along a rainfall gradient'.

The study in Chapter 4 will be submitted to the Journal of Ecology as: Synodinos AD, Blaum N, Jeltsch F, Tietjen B. 'Forecasting and preventing irreversible encroachment in savannas'.

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2 Facilitation in drylands: modelling a neglected driver of savanna dynamics

Our current understanding regarding the functioning of the savanna ecosystem describes savannas as either competition- or disturbance-dependent. Within this generalized view, the role and importance of facilitation has been mostly neglected. This study presents a mathematical model of savannas with coupled soil moisture-vegetation dynamics, which includes interspecific competition and environmental disturbance. We find that there exist environmental and climatic conditions where grass facilitation toward trees plays an important role in supporting tree cover and by extension preserving the savanna biome. We, therefore, argue that our theoretical results in combination with the first empirical studies on the subject should stimulate further research into the role of facilitation in the savanna ecosystem, particularly when analysing the impact of past and projected climatic changes on it.

2.1 Introduction

Savannas have been generally defined as ecosystems with a more or less continuous grass layer and scattered trees, distinct in function from grassland, forest and desert biomes (e.g. Scholes and Archer 1997). Here, we refer to all woody plants as trees, while grasses encompass all the herbaceous vegetation. Given that these two life forms would normally be regarded as either mutually exclusive or unequal competitors, savanna research has focused on understanding the mechanisms that allow for their continued coexistence (Baudena et al., 2010; Bond and Midgley, 2012; Bond, 2008; Bond et al., 2003; Gillson, 2004; Gil-Romera et al., 2010; Jeltsch et al., 1998, 1996; Scheiter and Higgins, 2007; Tietjen et al., 2010; Van Langevelde et al., 2003). This research has led to the identification of two principal coexistence mechanisms: competition for resources (water) and environmental disturbance. Competition-based theories started with Walter's two-layer hypothesis, which predicted stable tree-grass coexistence via a resource niche differentiation (Walter 1972; Walker et al. 1981; Walker and Noy-Meir 1982; Belsky 1990). However, the general validity of the original twolayer hypothesis was questioned (Higgins et al., 2000; Sankaran et al., 2004; Scholes and Archer, 1997), leading to refinements proposing that grasses dominate the 'topsoil' layer and regulate the amount of water that infiltrates deeper into the soil, from where trees access their resources (Kulmatiski et al., 2010; Ward et al., 2013). In the meantime, alternative coexistence theories surfaced, in which water availability ceases to be the sole driving force. These postulate that the savanna ecosystem is not necessarily stable and, lying in the middle of a continuous spectrum of vegetation starting from open grasslands and ending at a closedcanopy forest, it requires environmental disturbances to preserve it from shifting to either end of the vegetation spectrum (Augustine and Mcnaughton, 2004; Bond et al., 2005; D'Odorico et al., 2006; Higgins et al., 2000; Scholes and Archer, 1997). A different formulation, ot hinging on defining savannas as an equilibrium or a non-equilibrium system, focused on how such disturbances act as 'buffering mechanisms' to preserve the savanna ecosystem (Jeltsch et al., 2000).

Sankaran et al. (2004) proposed an aggregation of the different theories to best describe savanna dynamics, with later studies demonstrating how incorporating both competition and disturbances into models can yield more realistic results for a broad range of rainfall regimes (Justin M Calabrese et al., 2010; De Michele et al., 2011; Higgins et al., 2010; Sankaran et al.,

2005; Staver et al., 2011). This has led to the current widely accepted perception that competition becomes the primary coexistence mechanism under strong resource limitation (rainfall below ~650 [mm/year]), while disturbances stop the ecosystem from shifting to a different biome when water is theoretically sufficient for trees to form a closed canopy.

Facilitation has been largely absent from the aforementioned savanna debate, even though some recent empirical studies have investigated the impact of a facilitative relationship between grasses and trees at small spatial scales. Some studies found evidence of grass facilitation toward tree seedlings through the amelioration of harsh conditions or through the protection from grazers (Anthelme and Michalet, 2009a; Good et al., 2014a; Iacona et al., 2012a; F. T. Maestre and Cortina, 2004). Others observed how trees facilitated grasses by improving moisture conditions in their vicinity (Dohn et al., 2013a; Holzapfel et al., 2006; Moustakas et al., 2013a). Nevertheless, there has been no systematic effort to study facilitation as a possible tree-grass coexistence mechanism in savannas at the ecosystem level until now, despite some first signs of its possible significance (Baudena and Rietkerk, 2013). Due to this lack of facilitation studies at the savanna level, we are not in a position to assess its possible impact as a coexistence mechanism nor are we able to identify certain climatic and environmental patterns which may cause facilitative tree-grass interactions to support savannas.

In this study we use a new deterministic mathematical model of coupled soil moisture-vegetation cover dynamics to investigate the role of facilitation as a mechanism preserving arid and semi-arid savannas. In these climatic conditions where tree cover is low and savannas can potentially be replaced by grasslands (Bond, 2008), we focus on the notion of grass facilitation toward trees only. Our model includes inter- and intra-specific competition for resources and space, as well as environmental disturbances such as fire, grazing and browsing. We realized positive feedbacks that allow for facilitation among growth types by a positive impact of vegetation cover on infiltration and shading. We apply the model to evaluate, under which conditions grasses can facilitate trees and to assess the impact of grass facilitation on the vegetation composition at the ecosystem level. We finally discuss how our theoretical results, combined with existing empirical studies, should stimulate further investigation into the role of facilitation in savannas.

2.2 Methods

Previous Ordinary Differential Equation (ODE) models of grassland and savanna dynamics focused on the roles of competition (Tilman, 1994), herbivory (De Knegt et al., 2008), fire (Beckage et al., 2009) or on a combination thereof (Van Langevelde et al., 2003). We used the ecohydrological ODE model of Accatino et al. (2010) as our starting point to simultaneously model interactions between the two vegetation types (grasses and trees) and between the vegetation cover and soil moisture. This model of coupled vegetation-soil moisture includes competitive interactions (resource competition), environmental disturbance (fire) and herbivory (grazing and browsing). We have also included positive vegetation-soil moisture feedbacks (infiltration and shading). In this section we first present the model design and its assumptions as well as the model parameterisation. Afterwards, we describe the simulated scenarios and the methods used to evaluate the results.

2.2.1 Model Design

We designed a deterministic ecohydrological model of Ordinary Differential Equations (ODEs) to describe the dynamics of soil moisture (M), grasses (G) and trees (T) based on the model of Accatino et al. (2010). Soil moisture content is given by the rate of change in the saturation of the soil which is determined by infiltrated rainfall, evaporation and transpiration:

$$\frac{dM}{dt} = \delta(G, T) \left(\frac{p}{v_1}\right) (1 - M) - \varepsilon M (1 - T - G) - w_G M G - w_T M T \qquad (1)$$

We assume that trees and grasses extract water from the same depth (Kulmatiski et al., 2010) and that the water table is so deep that it does not affect the water dynamics in the root zone (Accatino et al., 2010). Then M, defined as the water volume present in the root zone relative to the maximum volume of water that can be held in this zone, increases with rainfall p[l/t], which is normalized by the unitary volume porosity, $v_1[l]$, and controlled by infiltration $\delta(G,T)=(1-a)(G+T)+a$. The unitary volume porosity, $v_1[l]$, is the product of the soil depth, z[l], and soil porosity, n[-]. Parameter a[-] from the infiltration function represents the proportion of infiltrated water in a bare landscape. A fraction of infiltrated rainfall is lost through percolation into deeper soil layers, $-\delta(G,T)\frac{p}{v_1}M$ (Accatino et al., 2010). Additional

soil moisture losses occur via evaporation over bare ground at a rate ε [1/t], and through grass and tree transpiration, at respective rates w_G [1/t] and w_T [1/t].

The rate of change of grass cover G is determined by the expansion of grass cover minus losses:

$$\frac{dG}{dt} = c_G MG(1 - T - G) - d_G G - \gamma(G)$$
(2)

Here, we assume that grasses only colonize empty space (1-T-G) at rate c_G [1/t] and that grass cover growth is linearly dependent on soil moisture content, M. Grass cover is lost due to a constant natural mortality rate d_G [1/t] and grazing, $\gamma(G) = a_G G^{b(1-G)}$ [1/t]. Grazing is defined as a non-linear, increasing saturating function of grass cover (details are given in section 'Modelling Assumptions').

The rate of tree cover change follows the same principle as that of grass cover, colonisation minus mortality:

$$\frac{dT}{dt} = c_T MT (1 - f(G) - T) - d_T T - \beta(T)$$
(3)

Tree cover, T, dynamics (eq. 3) are similar to those of grass cover with different rates for colonisation, c_T [1/t], and natural mortality, d_T [1/t], and a non-linear function $\beta(T) = a_T T^{b(1-T)}$ [1/t] for browsing rather than grazing. The density-regulating term of trees in the growth term, (1-f(G)-T), includes the impact of fire, $f(G) = a_S G^{b(1-G)}$ [-]. Because our model does not explicitly describe the age structure of trees, we represent the demographic bottleneck principle (Higgins et al., 2000; Jeltsch et al., 2000; Sankaran et al., 2005) as a hindrance on the establishment of new trees, which impacts the overall growth of tree cover, following the proposal of Hanan et al. (2008).

2.2.2 Model Assumptions

Competition: Inter-specific competition for resources occurs via transpiration (eq. 1), where both vegetation types remove moisture from the soil. In addition, intra-specific competition for space is represented by a density-regulating term (eqs. 2 & 3). Trees are additionally able to displace grasses (Accatino et al., 2010; De Michele et al., 2011), whereas grasses can only establish in unoccupied space.

Environmental disturbance: The environmental disturbance in the establishment of trees is represented by fire, which is fuelled by existing grasses cover (Bond, 2008; D'Odorico et al., 2012). Furthermore, we assumed that fire intensity has a sigmoidal response to increasing grass cover (Staver et al., 2011). Grazing and browsing have a direct negative impact on grass and tree cover, respectively. Losses by grazing impact grass cover additionally to the natural mortality rate and are defined as a non-linear, increasing saturating function of grass cover. We assume that the presence of herbivores will increase with the available amount of forage based on the concept of grazing lawns (McNaughton, 1979). Even though the grazers do not remove the fire-fuelling bunchgrasses, the existence of grazing lawns can have a negative impact on the bunchgrasses (Cromsigt and Olff, 2008) and has been found to be linked to weaker fire regimes (Archibald, 2008). Thus we have assumed a negative grazing-fire intensity feedback in the model. Browsing only affects tree cover and has been defined similarly to grazing by applying the same reasoning ('browsing hedges', du Toit and Olff 2014). It should be noted, that though browsers remove tree cover, in reality this does not always translate into an actual reduction in transpiration. However, we have not made such a distinction in our approach as we assume that tree cover is directly related to transpiration. Since this may be overestimating the impact of browsing, low browsing values are likely to better apply to our approach.

Facilitation: There are two positive vegetation-soil moisture feedbacks in the model: infiltration and shading (Baudena and Rietkerk, 2013; Gilad et al., 2007). Rainfall infiltration is assumed to increase linearly with existing vegetation cover (Franz et al., 2011; Gilad et al., 2007; Rietkerk et al., 2000). The impact of shading is represented by a reduction in moisture losses through evaporation because of the presence of vegetation cover.

2.2.3 Parameter Values

To determine the parameter values (Table 2.1) we followed the process applied by Accatino et al. (2010). The idea is to measure how quickly each parameter in isolation shifts the system from one steady state to another. By assessing the resulting time-scales, the most appropriate parameter values were selected. For growth parameters (colonisation rates) this represented the necessary time for vegetation to fully colonize an initially empty landscape. For mortality rates (natural mortality, grazing, browsing) or moisture-loss parameters (evaporation, transpiration), this translated into the time it took to reach a bare landscape from a vegetated state or dry soil starting from saturated conditions, respectively.

For the grass and tree colonisation rates (c_G, c_T) and the grass natural mortality rate (d_G) we used conservative values from the ranges proposed by Accatino et al. (2010), where grasses require half a year to fully colonize an initially empty landscape in the absence of any trees and given unlimited resources. Similarly, trees need 50 years for a corresponding colonisation of a bare landscape. Conversely, we assumed that grasses become extinct in 5 years in the absence of any new colonisation. We used a conservative value for tree mortality (d_T) based on Patrut et al. (2007) and Hanan et al. (2008), so trees die out after 200 years without any colonisation.

The evaporation rate (ε) was derived by combining the data of Wythers et al. (1999) and Mellouli et al. (2000). Our parameter value means that the soil dries out after half a year if there is no rainfall and no vegetation cover. The transpiration rates (w_G , w_T) were determined by the assumption that loss of moisture via transpiration occurs slower than via evaporation (Cavanaugh et al., 2011) and that grasses take up water faster than trees per unit area (Graz, 2008; Van Langevelde et al., 2003). To estimate the transpiration rates we excluded the impact of evaporation and assumed only one vegetation type was present. As a result, grasses dry out the soil after one year and trees after one and a half years. The unitary volume porosity v_1 is the product of the soil depth, z = 0.4 [I], and soil porosity, n = 0.4[-], referring to sandy soils. We fixed rainfall losses through run-off to (1-a) = 0.25 (Mwendera and Saleem, 1997), hence a = 0.75 [-].

Grazing and browsing are defined as non-linearly increasing, saturating functions, where the parameters, $a_G[1/t]$ and $a_T[1/t]$, determine the maximum value of the respective function. Their ranges were determined similarly to the natural mortality rates by measuring the time to extinction caused by a combination of the herbivory-induced and the natural mortalities in the absence of colonisation. In this way, the highest value for grazing leads to grass extinction after 2 years and similarly for browsing and trees after 125 years. The exponential parameter b[-] determines the shape (i.e. the slope) of the non-linear functions. Therefore it is a very theoretical parameter which cannot be easily related to empirical data. As a result, our choice for b was based on its qualitative impact on the non-linear functions. The choice of b = 1.5 provides us with a smoothly increasing sigmoidal response pattern of grazing and browsing to grass and tree cover respectively. A lower value would make the shape more linear, while a larger value would make the function behave as an on-off response.

The fire-related parameter, a_s [-], represents the maximum proportion of grass cover that is burned as fuel, so it varies within the interval [0,1] with no further calibration required. Similarly to the other non-linear functions, b [-] was selected to provide a smooth sigmoidal response of fire intensity to grass cover, as proposed by Staver et al. (2011). This led to the same choice, b = 1.5, as with grazing and browsing. Given the purely theoretical nature of the parameter, and following a parsimonious principle, we decided not to add another parameter without empirical support. As we demonstrate in the sensitivity analysis (2.7 Appendix A) the model's dynamics are not sensitive to perturbations in this parameter. Grass and tree cover are only sensitive to a large decrease (i.e. the functions become more linear) in b when either vegetation type is vulnerable (high and low rainfall respectively). The impact of facilitation is also only mildly sensitive to this parameter.

Table 2.1 A list of all parameters in the model with their symbols, meaning and the values used as 'defaults' where applicable or ranges otherwise.

Parameter symbols	Description	Range	Default value
and dimensions			
a [-]	Proportion of infiltrating rainfall over bare ground	-	0.75
p[l/t]	Annual rainfall	150-1200	-
v_1 [I]	Unitary volume soil porosity	-	0.16
$\mathcal{E}\left[1/t\right]$	Annual evaporation rate	-	8
$W_G[1/t]$	Annual rate of grass transpiration	-	6
W_T [1/t]	Annual rate of tree transpiration	-	4
c_G [1/t]	Annual colonisation rate of grasses	-	20
$c_T [1/t]$	Annual colonisation rate of trees	-	0.2
$d_G[1/t]$	Annual natural mortality rate of grasses	-	1
$d_T [1/t]$	Annual natural mortality rate of trees	-	0.023
$a_G[1/t]$	Maximum annual grazing rate	0-4	Low: 0.5
			Medium: 1
			High: 4
a_s [-]	Maximum Fire intensity	0-1	Low: 0.2
			Medium: 0.5
			High: 0.8
$a_T [1/t]$	Maximum annual browsing rate	-	Low: 0.01
			High: 0.03
<i>b</i> [-]	Non-linear function exponent	-	1.5

2.2.4 Model Evaluation

2.2.4.1 Comparison of Simulated Tree Cover to Empirical Data

In the first part of the results we compare tree cover from African savanna sites to our simulated tree cover. The dataset of 854 sites (Sankaran et al., 2005) contains information

such as grazing and browsing densities and fire frequencies, though not all are available for each site. To simulate each individual data-point we use its information on grazing density, browsing density and fire frequency in determining the corresponding parameter values. For grazing and browsing, we linearly downscale the density values to our parameter ranges (Table 2.1). The original fire information describes recurrence intervals of which we use the reciprocal value, since our corresponding parameter indicates fire intensity. We then follow the same procedure of linearly scaling these values down to our parameter range. All missing values for grazing and browsing, there were none for fire, are replaced by the average scaled values of the respective parameter. To run the simulation, we use the given rainfall value of each data point. All remaining parameters, such as evaporation, colonisation, etc. are set to their default values as determined in the previous section (Table 2.1). Each simulation is run for 2000 simulation years, at which point the steady state has been reached.

2.2.4.2 Quantifying Grass-Tree Interactions

To understand the relationship between trees and grasses we evaluate four scenarios along the rainfall gradient covering combinations of low and high grazing and browsing. We select a weak fire disturbance for each of the four scenarios, allowing for the presence of sufficient tree cover to make the impact of grazing and browsing observable. We compare the effect of grazing on tree cover for low and high browsing and calculate the difference in tree cover between the low- and high-grazing scenarios: $T_d = T_{Low Grazing} - T_{High Grazing}$.

We use these simulations to further investigate how grasses affect trees. There exist indices that quantify various aspects of plant interactions (Weigelt and Jolliffe, 2003) out of which we use an altered version of the Relative Neighbour Effect (RNE). The original RNE (Markham and Chanway 1996) compares the performance of one plant in the presence of a neighbouring plant to its performance in the absence of this neighbour, normalized by the maximum value of the two. We alter the original index, renaming it RNE_C (eq. 4) and apply it to the plant community level rather than to individual plants. Our measure of performance is vegetation cover. The following definition of the RNE_C equation measures the effect of grass cover on tree cover:

$$RNE_C = \frac{T_{+G} - T_{-G}}{\max(T_{+G}, T_{-G})}$$
 (4)

Hence, we have tree cover with grasses present in the model (T_{+G}) minus tree cover in the absence of grasses (T_{-G}) , normalized by the highest value of the two. This normalisation produces an index of the overall importance of interactions rather than its intensity (Brooker et al., 2005; Brooker and Kikvidze, 2008). A positive RNE_C value means that tree cover is higher in the presence of grasses, which implies that grasses facilitate trees, while a negative RNE_C indicates that competition dominates. We apply this index in the second part of our analysis in the Results.

2.2.4.3 Facilitation-less Model Configuration

To demonstrate the impact of grass facilitation on the results, we create a facilitation-less model configuration and compare its outputs to those of the original model. For this, we remove grass cover from all facilitative processes which we assumed in our model, namely infiltration and shading. Originally, infiltration was a linearly increasing function of the sum of grass and tree cover. Here, we remove the impact of grass cover on infiltration, leading to the function $\delta(G,T) = (1-a)T + a$. Equation 1 also includes the reduction of evaporation through the presence of grass and tree cover, which we modify to $\varepsilon M(1-T)$ for the facilitation-less model. As a result the positive vegetation-soil moisture feedbacks are only dependent on tree cover in this model configuration.

2.2.4.4 Biome definitions

To evaluate the impact of facilitation on the ecosystem level, we analyse the resulting biome after 2000 simulation years. Our biome definitions are determined by tree cover at a primary level and grass cover at the secondary level (Fig. 2.1) based on Higgins and Scheiter (2012), leading to six broad biomes: desert, grassland, woodland, savanna-grassland, savanna-woodland and forest.

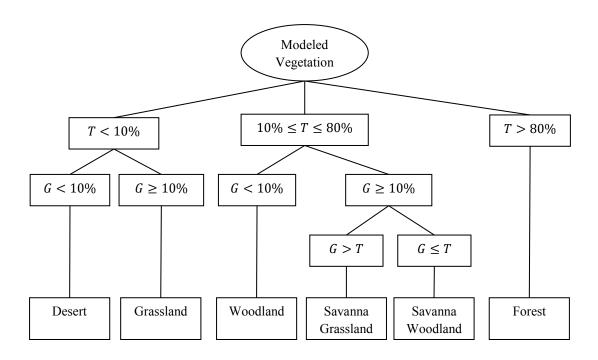


Figure 2.1 Biome definitions based on Higgins and Scheiter (2012). Classifications are based on the individual and combined grass cover, G, and tree cover, T, values.

2.2.5 Sensitivity Analysis

We performed an analysis (2.7.1 Appendix A.1) to test the sensitivity of the three variables towards parameter changes and to test if model results regarding the impact of facilitation are robust towards parameter shifts. All analyses were performed by shifting a single parameter at a time, with all other model parameters remaining at their default values (Table 2.1). In the first part of the sensitivity analysis, where we examined the sensitivity of soil moisture content (M), grass cover (G) and tree cover (T), we perturbed each parameter by -20%, -10%, +10% and +20%. All parameters were investigated, one at a time, apart from grazing, browsing and fire. This was repeated for three different rainfall (p) values, p = 400,800,1200 [mm/year]. Perturbations in the maximum grazing (a_G) and browsing (a_T) rates, and the maximum fire intensity (a_S), were not tested since these parameters are evaluated in our scenarios. For the purpose of the sensitivity analysis, grazing and fire were set to 'intermediate' and browsing to 'low' values as defined in Table 2.1.

In the second part we investigated how the impact of facilitation is affected by parameter perturbations (2.7.2 Appendix A.2). For this, we focused on the conditions with a low

maximum fire disturbance $(a_S=0.2)$ and a low maximum browsing rate $(a_T=0.01)$, as in the biome distribution analysis presented in the results. We analysed the impact of the parameter shifts for rainfall between 200 and 500 [mm/year] and grazing for $a_G \in [0,2]$ [1/year]. We evaluated the resulting vegetation composition (i.e. the biomes) for 20 points within this parameter space for both the original and the facilitation-less model configurations. We compared the savanna area increase due to facilitation in the default parameter setting to the increase occurring under each parameter shift. In this way we were able to quantify the effect of parameter perturbations on the impact of facilitation within the rainfall - grazing parameter space.

2.3 Results

2.3.1 Comparison to Empirical Data

First we compare simulated tree cover to tree cover in the dataset compiled by Sankaran et al. (2005) (Fig. 2.2a). The outputs demonstrate the model's ability to produce realistic results, apart from the 9 outliers at around 400 to 500 [mm/year] of rainfall. These occur because the scaling of the browsing densities produced certain extremely low browsing values for our simulation. In some cases this was compounded by a similarly weak fire disturbance. Based on our model design, browsing has a direct negative impact on tree cover. Fire, on the other hand, is defined as a negative grass-tree feedback, meaning that fire's impact on tree cover depends on grass cover. Other simulated sites with the same amount of rainfall as the outliers, have lower tree cover because browsing is higher. These simulated sites are well within the range determined by the empirical data. Finally, there is a pattern of certain sigmoidal curves forming around the mid-range of our tree cover outputs due to our replacement of missing parameter values by the average value.

To better quantify the model's performance, we compare a subset of the original data and the corresponding simulated tree cover (Fig. 2.2b). This subset only includes sites with a sand content of 75% or higher, since we set our soil-related parameter to a default value which corresponds to sandy soils. The fit between the data and the simulation proved satisfying. The simulation's polynomial regression lies within the 90% confidence interval of the original data polynomial regression, despite the fact that rainfall alone predicts only a small part of the variance of tree cover (Sankaran et al., 2008, 2005).

Our sensitivity analysis (2.7.1 Appendix A.1) supports our results. Soil moisture is only sensitive to a strong reduction of soil porosity at low rainfall. Grass and tree cover become more sensitive towards parameter changes where their respective cover is low. At low rainfall, the low tree cover is sensitive to tree colonisation and mortality as well as the strongest drivers of soil moisture (soil porosity) and grass cover (grass colonisation). Conversely, grass cover becomes sensitive to the tree-dominant parameters (colonisation and natural mortality) under moister conditions.

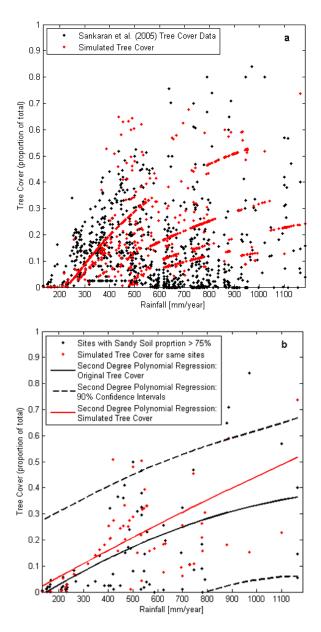


Figure 2.2 a) Tree cover from African savanna sites along the rainfall gradient from Sankaran et al. (2005). (black) compared to simulated tree cover, (red) each simulated tree cover corresponds to an original data point. The model outputs have been produced using the original rainfall value of the corresponding original data point, while the original grazing, browsing and fire values have been scaled to the model's parameter ranges. All other parameters are set to their default value. Model outputs correspond to the steady state attained after 2000 simulation-years with and initial conditions M_0 , G_0 , $T_0 = [0.1,0.3,0.3]$ b) A comparison between the sites with sandy soil concentration equal or greater than 75% performed in the same way as in Fig. 2.2a. Both regressions (black line for original data and red one for simulation outputs) are second degree polynomial regressions. The regression of the original data has a confidence interval of 90%.

2.3.2 Grass-Tree Interactions

When we compare the impact different grazing regimes on tree cover (Fig. 2.3), we observe the following pattern: under dry conditions, grazing has a negative impact on tree cover, even though grazing is modelled by solely removing grass cover. As a result we find higher tree cover with lower grazing ($T_d > 0$), indicating a facilitative effect of grasses on trees. In contrast, under moister conditions, trees are positively impacted by grazing and we get higher tree cover with increasing grazing ($T_d < 0$). The different browsing rates do not qualitatively alter the pattern of the results, though the shift from a negative effect of grazing on tree cover to a positive effect ('switch point') occurs at lower rainfall if browsing is low.

All four simulations have positive RNE_C values at low rainfall, albeit with varying magnitude (Fig. 2.3b), which verifies the domination of grass facilitation under dry conditions. Furthermore, simulations with low grazing have a higher RNE_C value than the ones with high grazing, confirming that lower grazing benefits trees more. As rainfall, and thus soil moisture availability, increase, the RNE_C decreases and eventually becomes negative. Based on the two plots of Fig. 2.3 we postulate that grass cover has a positive impact on tree cover in dry conditions when the fire disturbance is weak.

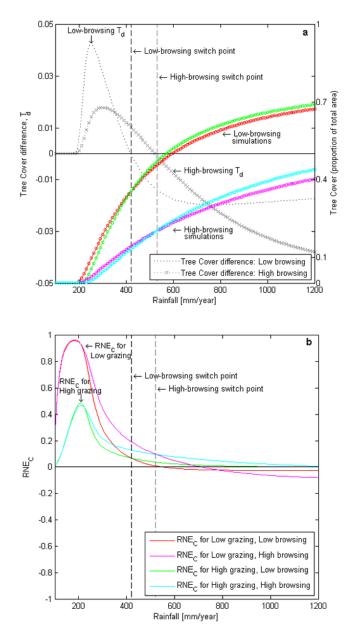


Figure 2.3 a) Four low-fire intensity scenarios with combinations of low and high grazing and browsing (low grazing/low browsing in red, low grazing/high browsing in purple, high grazing/low browsing in green, high grazing/high browsing in blue). The difference in tree cover between low- and high-grazing simulations, T_d (dashed lines), is plotted against the left y-axis and tree cover, T (circles), against the right y-axis. Vertical lines identify the point along the rainfall gradient at which T_d crosses zero and the effect of grazing on tree cover switches from positive to negative. b) RNE_C curves for the four simulations in Fig. 2.3a along the rainfall gradient. $RNE_C > 0$ means a positive grass-to-tree effect (grass facilitation) and $RNE_C < 0$ a negative one (competition).

2.3.3 Grass Facilitation at the Biome Level

To understand the impact of grass facilitation at the ecosystem level, we compared simulation outputs of the original model to those of the facilitation-less version (see 2.2.4.3 'Facilitation-less Model Configuration') under dry conditions with a weak fire disturbance (Fig. 2.4).

The original model (Fig. 2.4a) produces two different thresholds: (i) a rainfall threshold (250-280 [mm/year]) below which trees cannot persist and where we thus find a desert or grassland biome depending on the grazing regime, and (ii) a grazing threshold that increases with rainfall. If the grazing threshold is exceeded, grass is reduced substantially (G<10%) leading either to a classification as desert for low rainfall or woodland for moister conditions. If we have low enough grazing and moist conditions, trees and grasses may coexist, each with a cover above 10% (savanna). Within the savanna domain, grasses dominate under low grazing and rainfall conditions (savanna-grassland), while there is a shift to a tree-dominated savanna with increasing grazing and/or rainfall (savanna-woodland).

In the absence of grass facilitation (Fig. 2.4b) both thresholds have shifted. The rainfall threshold has moved up by approximately 50 [mm/year], while the grazing threshold is exceeded at a lower grazing rate than originally. As a result, the savanna biome parameter range is reduced through the expansion of grasslands into moister conditions at low and intermediated grazing values, while the desert and woodland biomes expand (Fig. 2.4c). The desert appears in regions of higher rainfall and lower grazing than before, while woodlands occupy space previously taken up by savanna-woodland.

By removing grasses from the positive soil moisture-vegetation feedbacks we did not only create overall drier conditions, which shift the vegetated biomes higher up the rainfall gradient. The lack of grass facilitation additionally makes grasslands more vulnerable to desertification at a lower grazing rate. Most importantly, however, the absence of grass facilitation hinders the establishment of trees over a wide rainfall range (approx. 300-550 [mm/year]) if grazing is low enough. Therefore savanna-grassland is to a large part replaced by grassland, because trees require more rainfall and a stronger grazing disturbance to establish a significant cover. Thus, we can see how grass facilitation increases the range of climatic and environmental conditions under which savannas occur.

In our sensitivity analysis (2.7.2 Appendix A.2) we find that the impact of facilitation depends most strongly on water availability and is sensitive to parameters related to soil moisture (infiltration, soil porosity, or evaporation). Additionally, as tree colonisation or mortality rates change to positively affect tree cover, the importance of facilitation decreases.

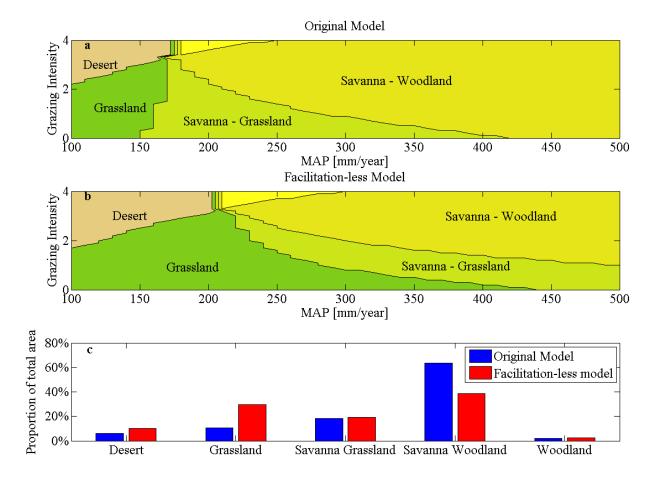


Figure 2.4 a) Biome distributions for the original model configuration. Model outputs correspond to the steady state after 2000 simulation years with initial conditions M_0 , G_0 , T_0 = [0.1,0.3,0.3]. Fire and browsing are set to 'low' and the remaining parameter values set to 'default' (Table 2.1). Biomes are defined based on the combinations of grass and tree cover (Fig. 2.1). b) The biome distributions for the facilitation-less model configuration for the steady states given the same initial conditions and parameter values as in Fig. 2.4a. In this model configuration grass cover is not included in the positive vegetation cover-soil moisture feedbacks (infiltration and shading). c) The biomes from Figures 2.4a. and 2.4b. are represented by bars (blue for the original model and red for the facilitation-less model)demonstrating the proportion of the total parameter space which they cover.

2.4 Discussion

The ecological debate regarding the long-term persistence of savannas has evolved around the concepts of tree-grass competition for resources (Van Langevelde et al., 2003; Ward et al., 2013) and stochastic disturbances that control the relative abundance of these two life-forms (e.g. Higgins et al. 2000; Jeltsch et al. 2000). We presented a deterministic spatially implicit ecohydrological savanna model of Ordinary Differential Equations (ODE) with positive and negative feedbacks between soil moisture, grasses and trees, including both competition and disturbances. Our results demonstrated the importance of the overlooked process of facilitation and in particular the impact that grass facilitation can have on supporting tree cover and the savanna biome by extension.

In simulating tree cover along a rainfall gradient, our outputs were realistic, spanning the values of observed tree covers (meta-analysis in Sankaran et al. 2005). Moreover, in agreement with existing studies, tree cover responded in a sigmoidal pattern to increasing rainfall, which Bucini and Hanan (2007) argued provides the best fit to data from Africa. Browsing pushed tree cover to lower values, a phenomenon often attributed to large browsers in savannas (Augustine and Mcnaughton, 2004; Sankaran et al., 2008), while fire suppressed tree cover given sufficient fuel, as in the studies of (Justin M. Calabrese et al., 2010; D'Odorico et al., 2006).

Interestingly, grazing, modelled as a grass-removal process, had an impact on tree cover and this changed with moisture availability. Under moist conditions grazing and tree cover were positively correlated. Such a relationship has been observed in previous studies and is regarded as one of the key drivers of shrub encroachment when rainfall is not a limiting factor (D'Odorico et al., 2012; Jeltsch et al., 1997; Lohmann et al., 2012). The reasoning is that, given these favourable climatic conditions, the removal of grasses allows trees and shrubs to colonize the empty space without any strong competition from grasses. In dry conditions, however, we observed a negative impact of grazing on tree cover. A similar result was reported by Lohmann et al. (2012), who found that overgrazing in these conditions lead to the expansion of bare ground and resulted in soil degradation. Sankaran et al. (2008) also found a negative correlation between grazing and woody vegetation. However, this occurred below a grazer biomass threshold. Their study did not investigate this relationship further and there was no link established between this threshold and rainfall conditions. Thus when interpreting

this result, the authors simply referred to the 'grazing optimisation hypothesis' (McNaughton, 1979), according to which the strongest competition from grasses occurs under intermediate grazing. Though our work and the studies of (Lohmann et al., 2012) and (Sankaran et al., 2008) do not focus on the same issues, they all provide evidence that the removal of grasses through grazing can be detrimental to trees. We interpret our finding as an indication of a positive effect of grasses on trees with increasing aridity.

2.4.1 Grass facilitation in savannas: community-wide effects

Our result agrees with the principle of the Stress Gradient Hypothesis (SGH) (Bertness and Callaway, 1994), a theory predicting that facilitation will dominate plant-plant interactions with increasing environmental stress. Though its general validity has come under scrutiny (Lortie and Callaway, 2006; Maestre et al., 2005; Fernando T Maestre and Cortina, 2004), leading to various proposed refinements (Graff and Aguiar, 2011; He and Bertness, 2014; Holmgren and Scheffer, 2010; Maestre et al., 2009; Malkinson and Tielboerger, 2010), the dynamics postulated in the SGH have been well established in multiple studies (see (Brooker et al., 2008; Bruno et al., 2003; He et al., 2013). Anthelme and Michalet (2009) investigated the impact of grass patches on tree height in an arid grazed ecosystem and found a strong positive effect of grasses on tree seedlings. The authors argued that this was the result of below-ground interactions and that it became more important with grazing. The increased effectiveness of facilitation under grazing was the result of a process known as 'associational resistance' (Smit et al., 2009), where the grass patches act as refuges from biotic stress (herbivory) for the seedlings. (Maestre et al., 2003) studied the effect of grasses on shrubs in a semi-arid grassland to find that facilitation took place throughout the duration of the experiment. In this case, grass facilitation was attributed to the improvement of microclimatic conditions and the increase in soil moisture rather than through any impact on soil fertility. Good et al. (2014) tested how grasses affected tree seedling growth and survival in a semiarid savanna. Similarly to the aforementioned studies, they found competitive and facilitative interactions occurring simultaneously, with the latter dominating through the amelioration of harsh conditions and the protection from herbivores. Similarly to the pattern observed in these studies, our results showed that as rainfall decreased, the overall impact of grass cover on soil moisture became positive, thus ameliorating the arid conditions and facilitating trees.

The mechanisms that facilitate tree seedling establishment are not always clear, though. Iacona et al. (2012) found increased seedling recruitment in response to reduced soil moisture stress in a long-leaf pine savanna. However, shading was not responsible for this facilitative effect. On the contrary, it had a negative effect on seedlings, possibly because the strength of the negative impact of light limitation exceeded that of the positive impact of soil moisture retention. Such an outcome seems reasonable in savannas where water is not a limiting factor (Vadigi and Ward, 2013). Nevertheless, Iacona et al. (2012) found that the microsites in the vicinity of grass patches were cooler and moister. They, thus, proposed that the facilitative impact of grasses may be obvious at the community level rather than within these microsites. Interestingly, our model, which functions at the aggregated community scale, produced an overall positive effect of grasses on trees under dry conditions, through increased rainfall infiltration and retention of soil moisture.

Grass facilitation also extended the parameter range where savannas established in our model. Excluding grasses from the facilitative processes (infiltration and shading) had a negative impact on soil moisture, which caused a shift of vegetated states to moister conditions. However, savannas also became limited by grazing, as demonstrated by the expansion of grasslands in our model without grass facilitation. This occurred due to the interaction of a biotic disturbance (grazing) with abiotic stress (aridity). As highlighted by (Smit et al., 2009), considering multiple factors that act simultaneously can impact our predictions. In this case, grazing switched from being a disturbance hindering facilitation in the original model, to a disturbance that released trees from the competitive influence of grasses in the facilitation-less configuration. Thus, it was only under higher grazing pressure that savannas established in the latter case, squeezing the savanna domain. This demonstrates how our inclusion of a simple positive grass cover-soil moisture feedback in the modelling assumptions (Gilad et al., 2007) has a huge impact on the modelled ecosystem's processes and dynamics. The importance of these positive feedbacks will vary depending on the savanna in question. In a heterogeneous landscape, for example with more complex topography, the impact of grass-dependent infiltration could be greater (Baudena and Rietkerk, 2013). We therefore argue that facilitative interactions ought to be given serious consideration when we debate the mechanisms that lead to tree-grass coexistence in savannas.

2.4.2 On investigating facilitation in savannas

We used a simplified representation of savanna dynamics within specific environmental conditions to investigate the facilitation of grass cover toward trees. Our analyses focus on grass facilitation since under low rainfall conditions tree cover is low and savannas can potentially be replaced by grasslands. However, there also exists evidence for tree facilitation toward grasses. Moustakas et al. (2013) demonstrated how the overall effect of trees on grasses shifted from negative to positive with increasing aridity, through increased subcanopy soil moisture availability. Other studies showed tree facilitation toward grasses took place via the increase of nutrients availability (Dohn et al., 2013b; Ludwig et al., 2001), even though results do not always agree (Ludwig et al., 2004). To include such detailed local interactions would certainly increase the realism and complexity of any model. Nevertheless, it is important that future studies investigate aspects of the interplay between grass-to-tree and tree-to-grass facilitation and competition. Under moister conditions for example, a positive effect of trees on grasses (Riginos et al., 2009) could help maintain savannas either by promoting direct competition from grasses (Riginos, 2009) or because of grass-fuelled fires (Sankaran et al., 2005).

The role of the spatial scale in determining the outcome between grass-tree interactions has generated interesting results, but has lacked consistent attention (Riginos et al., 2009). Depending on the ecosystem in question, the life-forms under investigation and the environmental stress being considered this outcome may vary. In a study of cobble beaches, (van de Koppel et al., 2006) found that though grasses facilitated forbs along an intertidal stress gradient through the large-scale modification of the shoreline environment, local interactions were competitive. In arid ecosystems, on the other hand, the combination of local facilitation and long-range competition lead to large-scale spatial patterns and long-term coexistence of different species (Rietkerk and van de Koppel, 2008). In a recent analysis of data from South African savannas, (Moustakas, 2015) found that tree-tree interactions vary from positive to negative when shifting from the local to the larger spatial scale given fire as the stressor. This confirmed the conclusions of two stochastic modeling studies, which found positive local tree-tree interactions as a response to adverse effects of fire (Bacelar et al., 2014; Martínez-García et al., 2013).

Other processes not included in this model would conceivably magnify the impact of grass facilitation. (de Dios et al., 2014) found that passive grass facilitation alleviated drought stress in a desert shrub savanna. The authors showed how dead grass cover acted as buffer against extreme aridity for tree seedlings. Considering that dead grass biomass plays a key role in savannas as a fuel for fires (Bond, 2008; D'Odorico et al., 2012), its positive impact should also be given more attention. Finally, our model did not include another well-established path of grass facilitation: associational resistance. As studies mentioned above demonstrate (Anthelme and Michalet, 2009b; Brooker et al., 2008), grass patches can provide refuge from grazers for tree seedlings further supporting the notion of grass facilitation being an important factor.

We used a mean-field approach to demonstrate the notion of grass facilitation toward trees maintaining arid and semi-arid savannas. Our discussion of these results in connection to related studies aims to bring attention to the lack of a systematic investigation of facilitation in savannas. It is telling how the findings of studies based on such different methods not only do not contradict each other, but together they move to further consolidate our call to rigorously investigate the role of facilitation in savannas.

2.5 Conclusion

We believe our work demonstrates there is room for a debate that merges facilitation and savanna research. Our study did not only focus on competition and disturbances so we were able to demonstrate the possible significance of facilitation in preserving the savanna ecosystem. The next step would be to create a model including plant-plant interactions in a spatial context in order to assess the impact of facilitation in a more detailed manner. Our results showed how grasses can exert a facilitative effect on trees via soil moisture and how this facilitation extends the parameter space in which arid and semi-arid savannas can establish. Whether facilitation occurred was primarily determined by limited soil moisture availability. Such conditions prevail in many African savanna sites and it is critical to understand how facilitation mechanisms will evolve under a changing climate. Given projections regarding future rainfall patterns, we may find that facilitation becomes even more vital for the persistence of savannas. Similarly, predicted changes in temperature can also impact facilitative interactions. Increased temperature leads to faster rates of evaporation, making soil moisture retention more essential still. The inclusion of facilitation in the study of dryland ecosystems such as savannas could prove invaluable in our attempt to reconstruct the past and predict their future.

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2.7 Appendix

Here we present a sensitivity analysis in two parts. First we test the model's robustness to parameter perturbations in terms of its three output variables, soil moisture content (M), grass cover (G) and tree cover (T). In the second part we investigate whether such parameter perturbations affect the key finding of our results, namely the impact of facilitation in preserving arid and semi-arid savannas with a low fire disturbance. All analyses were performed by perturbing a single parameter at a time, with all other parameters set to their default values (Table 2.1 of main manuscript). Four different levels of perturbation were considered: -10%, -5%, +5% and +10% compared to the default parameter value.

2.7.1 Appendix A.1 Sensitivity of soil moisture content, grass cover and tree cover to parameter perturbations

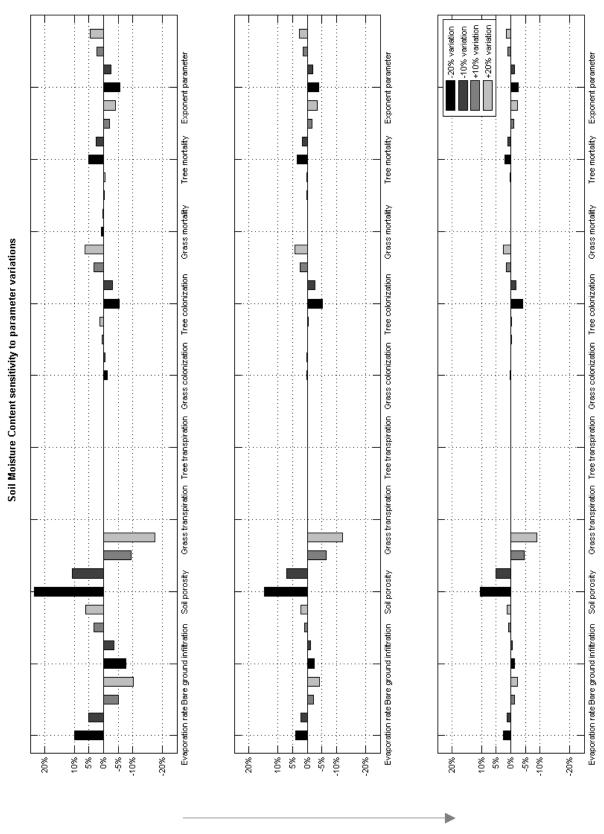
In the first part of the sensitivity analysis, the grazing (a_G), browsing (a_T) and fire intensity (a_S) parameters were not perturbed, because the results section of the manuscript essentially deals with this issue, namely how the variables and biomes are affected by changes in grazing, browsing and fire regimes. For the purpose of the sensitivity analysis, grazing and fire were set to 'intermediate' and browsing to 'low' values (Table 2.1). Hence, the first part of the sensitivity analysis was performed with respect to the following parameters: minimum rainfall infiltration proportion over bare ground a, unitary volume soil porosity v_1 , evaporation rate ε , grass transpiration rate w_G , tree transpiration rate w_T , grass colonisation rate ε_G , tree colonisation rate ε_T , grass natural mortality rate d_G , tree natural mortality rate d_T and the exponent of the non-linear functions δ . Each set of parameter perturbations was repeated for three different mean annual rainfall (p) values (p = 400,800,1200 [mm/year]).

The results are presented in three figures, one per variable, with each figure including three subplots, one per rainfall value. We define the relative sensitivity (RS) as the output variable's value given the parameter perturbation (V_p) minus the output variable's value given the default parameter (V_d) , normalized by V_d , $RS = \frac{V_p - V_d}{V_d}$ (Reineking et al., 2006). A negative

sensitivity corresponds to a decreased variable value compared to the default scenario, RS < 0 and a positive sensitivity refers to the cases where RS > 0. A variable is sensitive to a parameter if the magnitude of RS exceeds the magnitude of the perturbation.

2.7.1.1 Appendix A1.1 Soil moisture content (*M*) sensitivity analysis results

Soil moisture content, M, is mostly unaffected by parameter perturbations (SF1). Only under the drier conditions ($p = 400 \, [\text{mm/year}]$) is it sensitive to soil porosity. Soil porosity normalizes the rainfall (eq. (1)) and as a result has a direct impact on the amount of rainfall added to soil moisture. Therefore, it is expected to have a strong impact on the soil moisture content. This observed sensitivity, however, does not translate into a significant change in terms of soil moisture values. As a result of the largest (+/- 20%) soil porosity perturbations, M varies from 19% in the default scenario, to 21.5% and 17.6% respectively.



(MAM) notiestigional Precipitation (MAP)

Figure 2.5 Relative sensitivity of soil moisture content (M). Soil moisture content (M) sensitivity to parameter perturbations measured in terms of relative change, i.e. $RS = \frac{M_p - M_d}{M_d} \text{ where } M_p \text{ and } M_d \text{ are the soil moisture contents for the perturbed and the}$

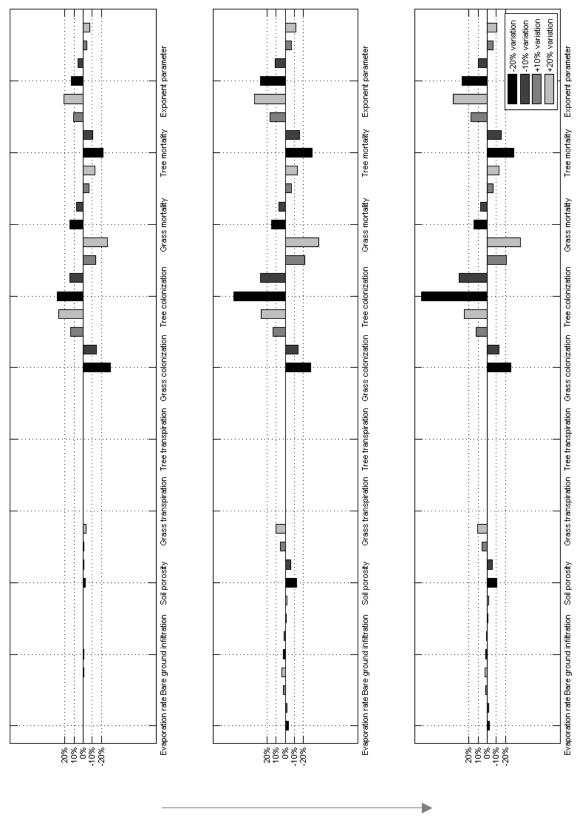
default parameter values respectively. Parameters are listed along the x-axis, with each having four perturbations from the default value: -20%, -10%, +10% and +20%. Rainfall increases with each subplot from top to bottom (p = 400,800,1200 [mm/year]). The dots on the x-axis signify when the variable exceeds the sensitivity threshold, i.e. where the magnitude of RS is greater than the magnitude of the perturbation.

2.7.1.2 Appendix A.1.2 Grass cover (*G*) sensitivity analysis results

Grass cover is above the relative sensitivity threshold for the following parameters: grass colonisation, tree colonisation. tree natural mortality and the exponent of the non-linear functions. c_G is the only parameter which directly impacts grass cover growth, hence the dependence of grass cover on it is logical. In dry conditions, we have a shift of grass cover between G=27.82% and G=50.24% when c_G changes by -20% to +20% respectively, with G=39.64% being the default value. As rainfall increases, the relative sensitivity of G to grass colonisation remains stable. At 1200 [mm/year] of rainfall, this translates to a maximum change from G=24.86% to either G=18.49% or, G=31.05% depending on the direction of the perturbation.

With increasing rainfall trees become increasingly dominant and we observe a stronger effect of the tree colonisation and natural mortality rates on grass cover. Tree colonisation has the most pronounced effect on grass cover in the wettest scenario. Here, grass cover moves from the from G=24.86% to G=42.76% given a -20% change in c_T , and to G=15.84% for a +20% perturbation. The first change also corresponds to a shift from a tree-dominated savanna (savanna-woodland) to a grass-dominated one (savanna-grassland). Sensitivity of grass cover to tree natural mortality is much weaker though still above the relative sensitivity threshold. The strongest shift, for instance, occurs in the wet conditions, when tree mortality is increased by 20%. There G moves up to G=34.15% from G=24.86%, but trees remain the dominant vegetation type at T=48.22%.

Finally, grass cover is just over the sensitivity threshold for the -20% perturbation of the exponent of the non-linear functions. Grass cover shifts from G=24.86% to G=31.74%, but trees remain dominant at T=48.62%.



Grass Cover sensitivity to parameter variations

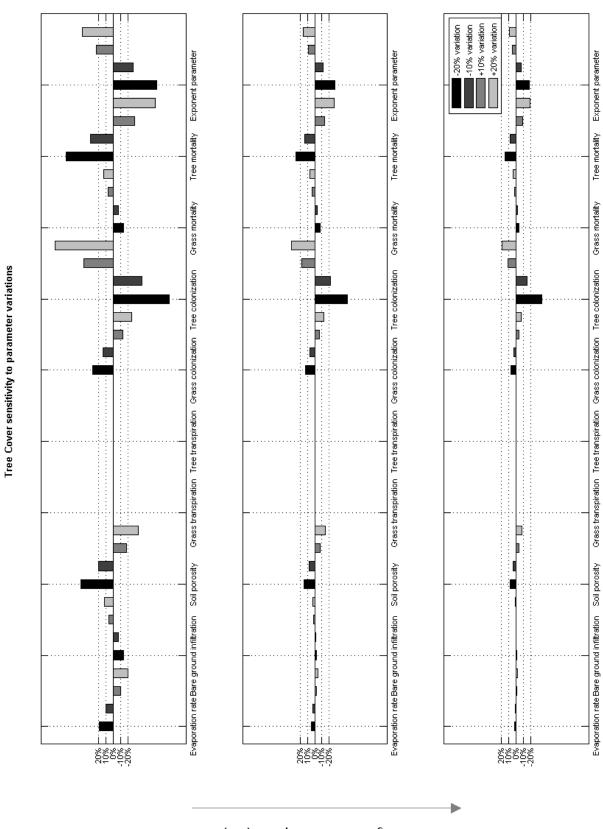
(MAM) notesting Mean Annual Precipitation (MAP)

Figure 2.6 Relative sensitivity of grass cover (G). Grass cover (G) sensitivity to parameter perturbations measured in terms of relative change, i.e. $RS = \frac{G_p - G_d}{G_d}$ where G_p and G_d are the soil moisture contents for the perturbed and the default parameter values respectively. Parameters are listed along the x-axis, with each having four perturbations from the default value: -20%, -10%, +10%. Rainfall increases with each subplot from top to bottom (p = 400,800,1200 [mm/year]). The dots on the x-axis signify when the variable exceeds the sensitivity threshold, i.e. where the magnitude of RS is greater than the magnitude of the

2.7.1.3 Appendix A.1.3 Tree cover (*T*) sensitivity analysis results

perturbation.

Tree cover is the most sensitive variable. In the driest case T responds strongly to changes in soil porosity, grass colonisation, tree colonisation, tree mortality and the non-linear functions' exponent. This is partly due to the water limitation making trees more strongly dependent on grasses and partly because tree cover is fairly low (T=20.12%). Hence, even small shifts in absolute value can cause large relative changes. Under moister conditions (rainfall=800 [mm/year]), tree cover is dominant. As a result it becomes less sensitive to parameter perturbations. The only parameters above the sensitivity threshold are tree colonisation and mortality rates, and the exponent parameter. The later demonstrates there is still some dependence of tree cover on its relationship to grass cover, though indirect and much weaker. The impact of the colonisation and natural mortality rates is expected, given that these parameters have a direct influence in tree cover growth and loss. As we move to the highest rainfall conditions, the only parameter above the threshold is tree colonisation, only when it is reduced by 20%.



(MAM) noisstigical Precipitation (MAP)

Figure 2.7 Relative sensitivity of tree cover (T). Tree cover (T) sensitivity to parameter perturbations measured in terms of relative change, i.e. $RS = \frac{T_p - T_d}{T_d}$, where T_p and T_d are

the soil moisture contents for the perturbed and the default parameter values respectively. Parameters are listed along the x-axis, with each having four perturbations from the default value: -20%, -10%, +10%. Rainfall increases with each subplot from top to bottom (p = 400,800,1200 [mm/year]). The dots on the x-axis signify when the variable exceeds the sensitivity threshold, i.e. where the magnitude of RS is greater than the magnitude of the perturbation.

2.7.2 Appendix A.2. Sensitivity of the impact of facilitation on preserving arid and semi-arid savannas

In this section we demonstrate how the impact of facilitation in preserving arid and semi-arid savannas remains largely unaffected by the same parameter perturbations as above. We focused on savannas with low fire intensity ($a_S = 0.2$) and browsing rate ($a_T = 0.01$), conditions where the impact of facilitation is strongest and easiest to compare between the original and facilitation-less model configurations (Fig. 4). We, then, selected a region within the rainfall-grazing parameter space (Fig. 4) which includes both grassland and savanna and where we observed that facilitation extended the savanna boundaries: rainfall \in [200,500] [mm/year] and maximum grazing rate, $a_G \in$ [0,2] [1/year]. We then simulated the vegetation composition (i.e. the biomes) for 20 points within this region, each point corresponding to a different rainfall-grazing combination. The coordinates of these 20 points were determined by rainfall and grazing rate intervals along the x- and y-axis respectively: at every 100 [mm/year] for the former and every 0.5 for the latter. As a result our analysis was performed on arid and semi-arid conditions with a low fire disturbance, low to intermediate grazing rate and low browsing rate.

We present the results in Table 2.7.1. The table demonstrates the percentage of the total parameter space covered by savannas for the original and the facilitation-less model configurations. This percentage is derived by simulating the 20 points within the parameter space as analysed above and calculating how many of these points represent savannas. The comparison of the savanna area percentage between the original and the facilitation-less

configurations is thus performed and shown for all parameter perturbations. For simplicity we combine savanna grassland and savanna woodland (see Fig. 1 for biome definitions) into a single biome, namely savanna.

The area comprises of 20 points determined by the combinations of the rainfall and grazing intensity values: p = 300, 400, 500, 1000 [mm/year], $a_G = 0, 0.5, 1, 1.5, 2$ [1/year]. The parameters in the first and fourth columns were perturbed each one at a time, while the remaining parameters were given their default values (see Table 1). Fire and browsing intensities were set to low ($a_S = 0.2, a_T = 0.01$,). The columns of the original and facilitation-less model configurations show the percentage of the total area covered by savanna. Small changes within the same configuration caused by perturbations are coloured green and larger ones are coloured red.

The objective of this analysis is to demonstrate that the impact of facilitation in preserving savannas remains unaffected by parameter perturbations. The table compares how the area occupied by the savanna biome increases with the inclusion of grass facilitation processes in the model. For example, in the default scenario of the facilitation-less configuration, savannas cover 35% of the total area; with the inclusion of facilitation this rises to 75%. We then compared how this relationship is affected by parameter perturbations. For all parameters and their perturbations, the proportion of savanna area remains the same for the original model configuration, thus making comparisons even simpler. For four parameters (grass transpiration rate (w_G) , tree transpiration rate (w_T) , grass colonisation rate (c_G) , grass natural mortality rate (d_G) there is no change in the facilitation-less configuration either, thus preserving the exact same impact of facilitation despite the perturbations.

For three parameters (minimum rainfall infiltration proportion over bare ground (a), evaporation rate (ε) , the exponent of the non-linear functions (b)) we only have 'small' changes as a result of the strongest perturbations $(\pm 10\%)$. We define a change as small when the order of magnitude of change in savanna cover is close to the magnitude of the perturbation. As the proportion of infiltrated rainfall (a) decreases, the impact of facilitation becomes stronger, while when a increases the opposite occurs. This is easily explained by the fact that a controls the amount of rainfall that is added to the soil. As we have already observed, facilitation becomes more important under drier conditions. Consequently this

pattern re-emerges due to perturbations in the infiltration parameter. The same dynamic occurs as a result of the evaporation rate perturbations, whereby a decreased evaporation rate weakens the impact of facilitation and vice versa. Interpreting the impact of changes in the exponent parameter is complex. The non-linear functions represent both grass (grazing) and tree (browsing) mortalities as well as a negative grass-tree feedback (fire), with the exponent affecting their curvature. Therefore, understanding and analyzing how simultaneous changes in all three functions affect the dynamics becomes extremely difficult. At this stage, however, it suffices to know that the impact of facilitation is only a little sensitive to the model's feedbacks.

The remaining three parameters (unitary volume soil porosity (v_1) , tree (c_T) and natural mortality rates (d_T)) have a larger impact on facilitation. Unitary volume soil porosity is used to normalize the rainfall value in the moisture equation. Thus it acts similarly to infiltration, but in the opposite direction; increasing v_1 essentially reduces the amount of rainfall in the soil and vice versa. In the first case, when v_1 increases by 10%, the impact of facilitation becomes slightly stronger. When v_1 drops by the same amount, facilitation becomes weaker: the difference in the proportion covered by savannas between the original and facilitation-less configurations drops from 40% to 25%. A drop in v_1 could either mean slightly less porous sandy soils or a shallower soil depth. In either case, such variations would be expected to have some impact on processes such as.

Given the impact of the two tree-related parameters (c_T and d_T) on the variables in the previous analysis, it is hardly unexpected to find that facilitation is also sensitive to these. These two variables act as major controls on tree cover. As a result, their perturbations have an effect on both trees and grasses. This is exactly what we observe in our latest results (Table 2.2). As we mentioned above, the difference in the area covered by savannas between the original and the facilitation-less configurations in the default setting is 40%. By increasing tree colonization this difference drops to 20% as trees become less reliant on grasses for their growth. Equivalently, reducing c_T can increase the difference to 55%, as grasslands expand into areas where trees with a slower colonization rate are unable to establish. The natural mortality rate of trees (d_T) has a similar, though opposite, impact: increasing the mortality rate strengthens facilitation (the difference becomes 50%) and decreasing it weakens facilitation (the difference drops to 25%). Though the impact of facilitation shows some

sensitivity toward these two parameters, its overall importance in preserving savannas and extending the savanna biome remains undisputed throughout. Therefore, we find that our key result regarding the presence and impact of facilitation in arid and semi-arid savannas with a low fire disturbance is robust to parameter perturbations.

Table 2.2 Comparison between the original and facilitation-less model configurations with respect to the savanna area as percentage of the total rainfall-grazing parameter space. * and ** denote a 'small' and a 'large' impact of the parameter on facilitation respectively.

Parameter	Perturbation level	Savanna cover (% of total area)	
		Original configuration	Facilitation-less configuration
<i>a</i> [-],	-10%	75	30
proportion of	-5%	75	35
infiltrating rainfall	Default	75	35
over bare ground *	+5%	75	35
	+10%	75	40
	-10%	75	50
v₁ [m],unitary volumesoil porosity **	-5%	75	35
	Default	75	35
	+5%	75	35
	+10%	75	30
	-10%	75	40
ε [1/year],	-5%	75	35
annual evaporation	Default	75	35
rate *	+5%	75	35
	+10%	75	30
	-10%	75	35
W_G [1/ year],	-5%	75	35
annual rate of	Default	75	35
grass transpiration	+5%	75	35
grass transpiration	+10%	75	35
	-10%	75	35
w_T [1/ year],	-5%	75	35
annual rate of	Default	75	35
tree transpiration	+5%	75	35
	+10%	75	35
	-10%	75	35
C_G [1/ year],	-5%	75	35
annual rate of grass colonisation	Default	75	35
	+5%	75	35
	+10%	75	35
	-10%	75	20
c_T [1/ year], annual rate of tree colonisation **	-5%	75	30
	Default	75	35
	+5%	75	40
	+10%	75	55
	-10%	75	35
d_G [1/ year],	-5%	75	35
annual rate of grass natural mortality	Default	75	35
	+5%	75	35
	+10%	75	35
d_T [1/ year],	-10%	75	50
	-5%	75	40

2. Facilitation in drylands

annual rate of	Default	75	35
tree natural mortality **	+5%	75	30
	+10%	75	25
b [-], non-linear function exponent *	-10%	75	30
	-5%	75	35
	Default	75	35
	+5%	75	35
	+10%	75	40

2.7.3 Appendix A.3 References

Reineking, B., Veste, M., Wissel, C., Huth, A., 2006. Environmental variability and allocation trade-offs maintain species diversity in a process-based model of succulent plant communities. Ecol. Model. 199, 486–504. doi:10.1016/j.ecolmodel.2006.03.038

Link to following chapter

The work in Chapter 2 demonstrated that the existence of grasses was beneficial to trees under arid conditions. Grasses, which were the dominant vegetation type, helped ameliorate the harshness of these conditions by preserving more moisture in the system via two pathways: increased rainfall infiltration and shading. As such, tree cover was higher in the presence of grasses that it was in their absence. These results were in agreement with the idea described by the Stress Gradient Hypothesis, namely that facilitative interactions become increasingly important with environmental stress. It is also encouraging that similar results have been produced by empirical studies. Even though these applied at the local scale, the facilitation pathways and impacts thereof were closely related to those from the modelling study presented above. The chapter, thus, concluded that facilitation can act as a coexistence mechanism by expanding the range within which trees and grasses coexist toward the arid end of the rainfall gradient.

Chapter 2 dealt with an idealised scenario of constant environmental and climatic conditions within which it was shown that facilitation outweighed competition as a coexistence mechanism at the arid end of the rainfall gradient. Temporal variability in savanna processes, however, is also important to consider in savannas. This becomes the main focus of the following study. In Chapter 3 the model is adjusted to include inter-annual rainfall variability. To increase the realism in the simulated conditions, fire also becomes a stochastic process whose occurrence depends on grass cover, and thus indirectly on the inter-annual rainfall variability. The questions I aim to answer are how savanna trees and savanna resilience will be impacted by increasing rainfall variability and through which processes this will occur.

3 Inter-annual rainfall variability impacts plant interactions and fire to produce contrasting responses of savannas along a rainfall gradient

Tree-grass coexistence in African savannas is the result of resource competition and stochastic disturbances such as fires, which can produce alternative states of open landscapes and tree-dominated biomes. Within this mechanistic framework we are currently lacking a good understanding of the impact of inter-annual rainfall variability on savanna vegetation and resilience. Using a stochastic ordinary differential equations model of soil moisture, grass cover and tree cover, we simulated a gradient of inter-annual rainfall variabilities for two different mean rainfall conditions. The system exhibited bistability with savanna and grassland as alternative states under both semi-arid and mesic conditions but variability had contrasting effects on the two. In the former, it gradually reduced savanna tree cover, until a variability threshold was crossed and the savanna state collapsed, while under mesic conditions, it expanded the basin of attraction and hence the resilience of the savanna state. The reasons for this contrasting response related to competition, fires and the response speed of the different plant types. Under semi-arid conditions trees were unable to compensate during wet years for the negative impact of droughts due to increased grass competition, stronger and more frequent fires. Under moist conditions, though, variability provided more opportunities for rapid tree growth episodes. Our study suggests that increasing inter-annual rainfall variability, as expected under climate change, can impact plant interactions by shifting the importance toward their responsiveness to climatic variability and thus creating a temporal niche.

3.1 Introduction

Savannas, biomes with a more or less continuous grass layer and scattered trees (Scholes and Archer, 1997), can be found across a broad range of climatic, edaphic and environmental conditions around the tropics (Lehmann et al., 2011). Rainfall is the primary determinant of maximum tree cover (Sankaran et al., 2005), with disturbances such as fire and grazing restricting it to lower values (Bucini and Hanan, 2007; Sankaran et al., 2008). A consequence of disturbances is that the realized biomes do not always correspond to the prevailing climatic conditions and we can find savannas where grassland or forest could have established (Bond, 2008; Lehmann et al., 2014). These climatically overlapping biomes can be described as alternative states (Hirota et al., 2011; Staver et al., 2011a), with positive feedbacks critical in preserving a given state (D'Odorico and Bhattachan, 2012; Scheffer and Carpenter, 2003).

The grass-fire feedback is a case in point: grasses provide the fuel for fires (Bond et al., 2005; Higgins et al., 2000), which hinder the recruitment of young trees into adult ones (Bond and Midgley, 2012; Hanan et al., 2008). Thus, the fire disturbance will maintain an open landscape even if the climatic conditions favour forest or woodland establishment (Calabrese et al., 2010; Staver and Levin, 2012) subject to a threshold in flammable grass cover and, by extension, tree cover (Archibald et al., 2009; Staver et al., 2011a): with tree cover below this threshold, the strong positive grass-fire feedback will keep pulling the system back to the grassland state, whereas high tree cover will suppress the positive feedback, preserving a treedominant savanna. In terms of the dynamics of the alternative states, this threshold determines each state's basin of attraction (Nolting and Abbott, 2016). The basin of attraction reflects how far we can move from a state without causing a catastrophic transition to the alternative state (Scheffer et al., 2001), the mathematical equivalent to ecological resilience (Holling, 1973). What follows from all of the above is that an external forcing causing changes in the vegetation composition can trigger or suppress a positive feedback with huge implications on the resulting ecosystem and biome (Colombaroli et al., 2014; Scheffer et al., 2009).

Climate change is such an external forcing which is predicted to alter rainfall patterns including inter-annual variability (Fischer et al., 2013; O'Gorman and Schneider, 2009; Wetherald, 2009). Though drylands are expected to be vulnerable to variable rainfall patterns (Ma et al. 2015), we are lacking sufficient studies on this (Seddon et al., 2016). Trees and shrubs could benefit from increasing inter-annual rainfall variability, either due to their deeper

roots buffering against droughts (Gherardi and Sala, 2015) or via rapid growth episodes in wet years (Holmgren et al., 2006, 2001). However, deeper roots can become less effective under increasingly variable conditions, where a 'temporal niche' may dominate competitive interactions (Xu et al., 2015). The impacts of disturbances further muddle the picture. In Africa, where fires play a major role in driving savanna dynamics (Staver et al., 2011b), savanna tree cover does not respond to increased inter-annual rainfall variability (Holmgren et al., 2013), while it has recently been argued that the impacts of disturbances, in the form of land use, will outweigh those of climate change (Aleman et al., 2016). Meanwhile, theoretical studies predict that increasing variability will enhance the resilience of bistable ecological systems in general (Sharma et al., 2014a) and drylands in particular (D'Odorico and Bhattachan, 2012). The lack of a consistent pattern across the aforementioned findings starkly demonstrates the need to improve our understanding regarding the drivers of vegetation responses to climatic variability.

With this in mind, we use a theoretical model of savanna dynamics not only to investigate the impacts of inter-annual rainfall variability on savanna vegetation and resilience, but to understand how tree-grass interactions and the underlying ecological mechanisms shape this response. Our mathematical model is based on the prevailing assumptions on the ecohydrological processes governing African savannas and as such incorporates tree-grass competition, environmental disturbances and feedbacks between trees and grasses as well as between vegetation and soil moisture. Using this model, we simulate savanna responses to conditions of increasing inter-annual rainfall variability for two different mean rainfall scenarios (semi-arid and mesic) and look to answer the following questions: i) how does tree cover respond to increasing inter-annual rainfall variability, ii) how does variability impact savanna resilience, and iii) what drives these responses?

3.2 Methods

3.2.1 Model description

We use the ordinary differential equations (ODE) model of coupled soil moisture (M), grass cover (G) and tree cover (T) dynamics of (Synodinos et al., 2015) with the following equations as our basis:

$$\frac{dM}{dt} = \delta(G, T) \left(\frac{p}{v_1}\right) (1 - M) - \varepsilon M (1 - T - G) - w_G MG - w_T MT$$
 (1)

$$\frac{dG}{dt} = c_G MG(1 - T - G) - d_G G - \gamma(G)$$
 (2)

$$\frac{dT}{dt} = c_T MT (1 - f(G) - T) - d_T T - \beta(T) \tag{3}$$

All three variables (M, G, and T) are proportions, with M as relative saturation and G and T as fractional cover. The total vegetation cover is limited to 100% $(G+T \le I)$.

Soil moisture dynamics (eq. 1): Rainfall, p, infiltrates the soil depending on existing vegetation cover, $\delta(G,T) = (1-a)(G+T) + a$. Moisture is homogeneously distributed within the unitary volume soil, V_1 , which is the product of soil porosity and soil depth. Moisture is lost through percolation beyond the point of saturation, -M, evaporation over bare ground, $-\varepsilon M(1-T-G)$, and transpiration from grasses and trees, $-w_GMG-w_TMT$ respectively.

Grass cover dynamics (eq.2): Grass cover colonises empty space proportionally to existing cover and soil moisture, $c_GMG(1-T-G)$ and it drops due to naturally occurring mortality, $-d_GG$, and grazing, which is an increasing saturating function of grass cover, $\gamma(G) = a_GG^{b(1-G)}$. We assume a positive correlation between herbivores and grass cover based on the concept of grazing lawns (McNaughton, 1979). Even though grazers do not remove fire-fuelling bunchgrasses, grazing lawns have been found to be linked to weaker fire regimes (Archibald, 2008). Therefore, we have assumed a negative grazing-fire intensity feedback in the model.

Tree cover dynamics (eq.3): Existing tree cover and fire restrict tree cover expansion, with colonisation being proportional to existing moisture and tree cover, $c_T MT(1-f(G)-T)$. Fire, $f(G) = \varphi a_S G^{b(1-G)}$, is an increasing saturating function of grass cover (Staver et al., 2011a), which serves as fuel load (Higgins et al., 2000). Trees die naturally, $-d_T T$, and additional cover is lost due to browsing, $\beta(T) = a_T T^{b(1-T)}$. Browsing only affects tree cover and has been defined similarly to grazing by applying the same reasoning ('browsing hedges', du Toit and Olff 2014).

3.2.2 Parameters

The default parameter values (Table 3.1) used in all simulations are those used in (Synodinos et al., 2015). We assume a maximum rainfall runoff of 25% in determining the infiltration parameter a (Mwendera and Saleem, 1997), over sandy soils with a depth of 40 cm, since trees and grasses extract most water from the same depth (Kulmatiski et al., 2010) in fairly shallow soils (Kulmatiski and Beard, 2013). Evaporation and transpiration rates are based on the amount of time required by each process in isolation to drain the soil of all moisture and assume that loss of moisture via transpiration occurs slower than via evaporation (Cavanaugh et al., 2011) and that grasses take up water faster than trees per unit area (Graz, 2008). Evaporation in a bare landscape requires half a year (Mellouli et al., 2000; Wythers et al., 1999), while grass and tree transpiration remove soil moisture in one year and one-and-a-half years respectively, in the absence of any other processes. Colonisation and mortality rates reflect the time required for each vegetation type to fully colonise the landscape uninhibited and the time from full vegetation cover to extinction if mortality is the only process taking place, respectively. Grasses require half a year to expand to full cover, then becoming extinct after five years in the absence of any colonisation (Accatino et al., 2010). Similarly, trees require sixty and two hundred years, respectively (Accatino et al., 2010; Patrut et al., 2007). Grazing, fire and browsing are sigmoidal functions of either grass (the first two) or tree (the latter) cover. Here we determine their maximum intensity, i.e. the value of the function when the respective vegetation cover is 100%. During the simulations, though, the value of these functions will be determined by vegetation cover at each time step, in accordance to the scaling of the sigmoidal function based on its maximum intensity. We selected maximum grazing and browsing intensities to reflect an intermediate disturbance as compared to the equivalent natural mortality rates, while maximum fire intensity has not been scaled and is set to 100%. The exponent of these non-linear functions is selected to define a smooth sigmoidal response.

Table 3.1 Parameter values used as the default parameter set in all simulations (Synodinos et al., 2015).

Parameter symbols and units	Description	Range	Default value
<i>a</i> [-]	Proportion of rainfall infiltrating bare ground	-	0.75
p [m/year]	Annual rainfall	0.520-0.780	-
V_1 [m]	Unitary volume soil porosity	-	0.16
& [1/year]	Evaporation (annual rate)	-	8
$W_G[1/year]$	Grass transpiration (annual rate)	-	6
W_T [1/year]	Tree transpiration (annual rate)	-	4
C_G [1/year]	Grass colonisation (annual rate)	-	20
C_T [1/year]	Tree colonisation (annual rate)	-	0.2
d_G [1/year]	Grass natural mortality (annual rate)	-	1
d_T [1/year]	Tree natural mortality (annual rate)	-	0.023
a_G [1/year]	Maximum grazing (annual rate)	-	0.7
a_{S} [-]	Maximum Fire intensity	-	1
arphi [-]	Fire Occurrence	Binary 0,1	
a_T [1/year]	Maximum browsing (annual rate)	-	0.01
<i>b</i> [-]	Non-linear function exponent	-	1.5

3.2.3 Rainfall Variability

Rainfall p (eq. 1) is applied as a time series based on the Kenya CRU CY v. 3.20 annual rainfall record (Harris et al., 2014), with a mean value of 650 mm/year and a standard deviation of σ =12%. To create a rainfall gradient, we alter the mean rainfall amount of the Kenyan time series by -/+ 20% (520 mm/year and 780 mm/year respectively) and thus produce clearly distinct semi-arid and mesic conditions, with the possibility of different underlying savanna dynamics between the two (Sankaran et al., 2005).

The Kenyan time series has a standard deviation of σ =12%, which we define as 'current' variability. We use this as the basis variability scenario and investigate variability changes from 0.5σ to 2σ , with an increment of 0.25σ . We extend the variability gradient more toward higher values, because they produce qualitative changes in the model's dynamics, while it is also a more plausible scenario for East Africa (Nicholson, 2000).

3.2.4 Fire stochasticity

In order to simulate the occurrence of fires, f(G) (eq. 3), stochastically, we introduce a fire occurrence factor, φ , which is binary, taking the value 1 when a fire occurs and 0 otherwise. The resulting, stochastic function is $f(G) = \varphi a_S G^{b(1-G)}$. The driving principle determining the occurrence of fire is based on the positive grass-fire feedback (Higgins et al., 2000), according to which higher grass cover increases the probability of fire occurring in a given year. At each simulation time step, a random number, $r \in [0,1]$, is picked from a uniform distribution; if r is less than the value of grass cover, r < G, then $\varphi = 1$, otherwise $\varphi = 0$.

3.2.5 Bistability simulations

We simulate the steady states for each combination of mean rainfall and variability. To determine the model's sensitivity to initial conditions, we tested for multiple values of initial tree and grass cover. Bistability, the convergence to different steady states depending on initial conditions, was only induced via initial tree cover changes. In this study, we use two initial tree cover values, $T_0 = 5\%$ and $T_0 = 50\%$, to demonstrate the existence of bistability. Initial soil moisture and grass cover are the same for all simulations ($M_0 = 10\%$, $G_0 = 10\%$).

Each simulation is repeated 50 times, with a different rainfall time series generated per iteration. The length of the simulations is not constant for all scenarios due to certain climatic conditions requiring longer time scales to converge (3.7.6 Appendix F, Table 3.2). Based on various test runs we can tell whether a simulation has attained a steady state if its value is indeed one of the two possible outcomes. At the end of the simulations we confirmed that all simulations reached their steady state. To minimize the noise induced by the stochasticity, the steady state values we use are the mean value over the last 100 simulation years.

3.2.6 Bistability threshold range

Since initial tree cover determines which of the two steady states the system converges to, there exists a threshold initial tree cover value splitting the two outcomes. Given the stochasticity in the model, this threshold is a range rather than a single value with the initial values within this range not leading to the same outcome 100% of the time. To determine this range, we perform multiple test runs and search for its upper and lower limits for both mean rainfall scenarios. Once the appropriate range is established we assess the impact of rainfall variability on this threshold range for semi-arid and mesic conditions. We perform 100 simulation iterations per variability and initial tree cover combination. To minimize the impact of stochasticity-induced fluctuations, we use the mean tree and grass cover values over the last 100 simulation years. At the end of each simulation, we classify the resulting biomes as grassland, if tree cover is below 10% and grass cover above 10%, or as savanna, if both vegetation types have a cover above 10% as in (Synodinos et al., 2015). We then calculate the relative frequency of simulations reaching the savanna state which we define as the savanna occurrence probability.

3.2.7 Analysis of mechanisms

To investigate the mechanisms leading to the patterns observed in the results we perform a final set of simulations for semi-arid and mesic conditions under current (σ =12%) and maximum rainfall variability (2 σ). For this set of simulations we use initial tree cover values for which the impact of increased variability is evident. For semi-arid conditions this means initial tree cover above the tree cover threshold (for current variability); for mesic, within the threshold (for current variability). A value satisfying both conditions is T_0 =16%. We perform 36 iterations and aggregate all data-points in a single dataset. We use part of the full

length of the simulation to focus on the transient dynamics in order to understand the processes leading to final outcome. The reason is that we are looking for response patterns of tree cover to inter-annual rainfall variations. Including points after the steady state has been reached, where tree cover is stable and not responsive, would obscure the impact of rainfall changes.

3.2.8 Sensitivity analysis: parameters and modelling assumptions

We perform an analysis to test the sensitivity of the three variables towards parameter changes by shifting a single parameter at a time, with all other model parameters remaining at their default values. In the first part of the sensitivity analysis, we perturb each parameter by -20%, -10%, +10% and +20% (3.7.1 Appendix A). We apply this to the full parameter set, apart from fire intensity which is tested separately (3.7.2 Appendix B). We also perform an additional analysis to assess whether trees accessing moisture from deeper soil layers changes the results (3.7.3 Appendix C). Furthermore, we compare simulation outputs to tree cover data from (Sankaran et al., 2005) (3.7.4 Appendix D) and test a the coexistence mechanisms by running a model without fire and one with half the fire intensity (3.7.5 Appendix E).

All simulations were performed using Matlab version R2007b.

3.3 Results

We simulated tree cover steady states along an inter-annual rainfall variability gradient for two mean annual rainfall conditions: semi-arid (~520 mm/year) and mesic (~780 mm/year). Under current rainfall variability levels, both mean rainfall scenarios induced alternative treeless grassland and tree-dominant savanna states (Fig. 3.1).

3.3.1 Bistability

Under semi-arid conditions (Fig. 3.1a), there was a gradual reduction of the savanna state tree cover along the variability gradient for values between 0.5σ and 1.5σ , starting at 36% and dropping to 35%, 34%, 32%, and finally 30%. Once variability increased to 1.75σ , the savanna steady state collapsed, producing a single, thus eliminating bistability. The impact of variability on the savanna tree cover steady state was negligible under mesic conditions (Fig. 3.1b). From one end of the variability gradient to the other $(0.5 \sigma-2 \sigma)$ tree cover only dropped by 2% (from 58% to 56% respectively).

Increasing rainfall variability also impacted the basins of attraction of the two states and hence their resilience (Holling, 1973). In the semi-arid case the savanna basin of attraction contracted until it completely vanished at variability 1.75σ (Fig. 3.2a). In mesic savannas the effect was the opposite but also subtler: increasing variability extended the basin of attraction of the savanna state (Fig. 3.2b). Given a constant initial tree cover, savanna establishment likelihood increased with variability. Taking T_0 =15%, there was a 10% savanna establishment probability under current variability, whereas the probability more than doubled to 23% for double the variability (2σ). The same pattern held for other values of T_0 . Thus, the basin of attraction of the savanna state expanded to lower initial tree cover values (full results tables are available in the 3.7.6 Appendix F).

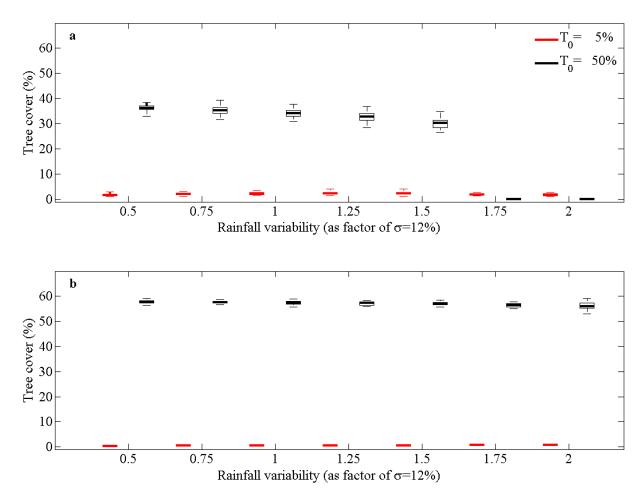


Figure 3.1 Tree cover steady states along the inter-annual rainfall variability gradient for two mean rainfall scenarios: (a) semi-arid (520 mm/year); (b) mesic (780 mm/year). The alternative steady states occur as a result of the different initial conditions: T_0 =5% and T_0 =50%. Each box represents the steady states of 50 iterations with different rainfall time series. All simulations were performed using the default parameter set (Table 3.1). Linear regression equations: (a) y= -1.5x + 38.3; (b) y= -0.25 + 58.1.

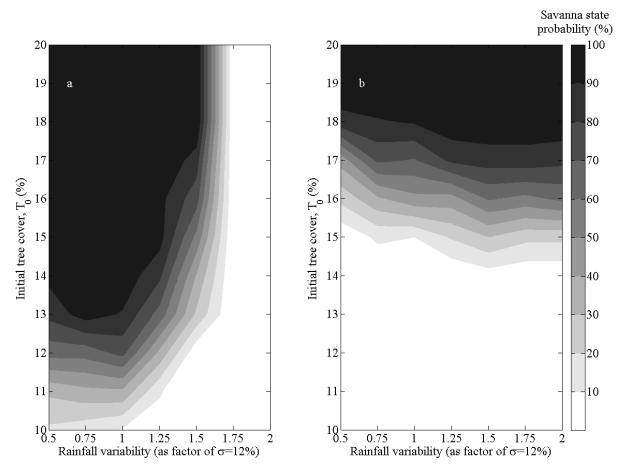


Figure 3.2 Likelihood of savanna occurrence under (a) semi-arid and (b) mesic conditions in the inter-annual rainfall variability and initial tree cover value parameter space. The likelihood of savanna occurrence is the proportion of simulations out of a total of 100 converging to the savanna. All simulations were performed using the default parameter set (Table 3.1).

3.3.2 Underlying dynamics

In the semi-arid case tree cover was positively correlated to rainfall, though this levelled off at the higher end of the rainfall distribution (Fig. 3.3a). At the dry extremes, the two large values are not reliable due to the lack of sufficient cases, indicated by the large error bars. For high variability the negative impact of the dry years was stronger, while the levelling off during wet extremes was more pronounced. In the mesic case there was a clearer difference between current and high variability levels (Fig. 3.3b). In the former case, tree cover responded negatively in the mid-rainfall range, with spikes at either end of the gradient which could be caused by the small number of cases (see large error bar). This result probably reflected the tree extinction outcome rather than shedding light on the causality. For high variability the response pattern of trees resembled that of the semi-arid case. Critically, though, the negative

impact during the low rainfall years was weaker and the positive effect of the high rainfall years stronger without levelling off. By isolating the extreme dry (1st quartile) and wet (3rd quartile) years, we observed the impact of variability on soil moisture, grass cover and fire frequency (Fig. 3.3c, d, e). As expected, high variability caused larger shifts away from the mean values due to the increased frequency of extreme events. This was not the case only for the mesic wet extremes with respect to grass cover and fire frequency, where increased variability had a negative effect on both.

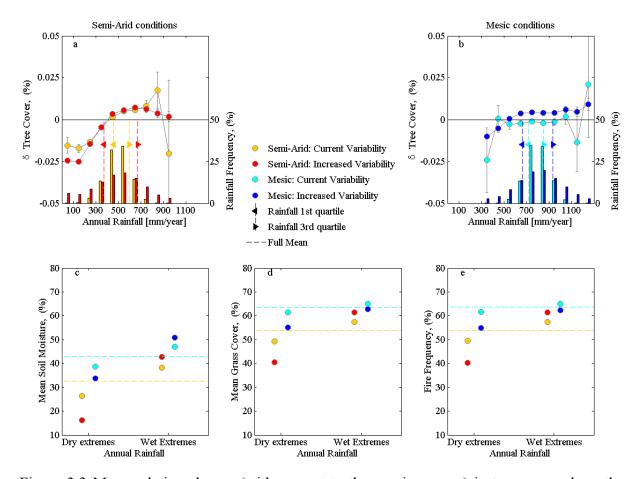


Figure 3.3 Mean relative change (with respect to the previous year) in tree cover along the rainfall gradient for (a) semi-arid and (b) mesic conditions for two levels of variability (current and high). Points represent mean values with error bars from 36 simulations. Rainfall distributions plotted against the right y-axis. Bottom panel: (c) mean soil moisture, (d) mean grass cover and (e) relative fire frequency for the bottom and top quartiles of the rainfall distributions. Dashed horizontal lines: mean values under current variability levels for semi-arid (yellow) and mesic (light blue) conditions.

3.4 Discussion

Our ecohydrological model of African savannas produced alternative states of tree-dominated savanna and a tree-less grassland under both semi-arid (520 mm/year) and mesic (780 mm/year) conditions (Fig. 3.1). In savannas, competition alone sufficed to guarantee coexistence, with fire limiting tree cover below the rainfall-determined maximum (3.7.5 Appendix E), consistent with our understanding of savanna dynamics (Bucini and Hanan, 2007; Higgins et al., 2010; Sankaran et al., 2008). At the same time, the positive grass-fire feedback created a threshold in tree cover which determined whether the biome would converge to the savanna or the grassland state (Fig. 3.2). This threshold, which split the two basins of attraction and determined each state's resilience (Holling, 1973), was similar in the semi-arid and mesic conditions under current rainfall variability levels. Increasing variability, however, shifted the threshold weakening bistability, albeit in opposite directions for the two mean rainfall scenarios. The stabilizing effect of variability on bistable ecological systems has consistently showed up in theoretical studies (Ai et al., 2003; Rong et al., 2012), particularly when the noise was uncorrelated (Sharma et al., 2014b), as in our simulations. The same phenomenon persisted in studies specific to dryland dynamics, with bistability becoming weaker to the point that in some cases it was eliminated altogether (D'Odorico et al., 2005; D'Odorico and Bhattachan, 2012; Guttal and Jayaprakash, 2007), as in our semi-arid scenario.

3.4.1 Rainfall variability interacts with fire and mean rainfall

While in the semi-arid case increasing variability negatively affected savanna trees and the savanna state overall, it boosted savanna resilience under mesic conditions. The combination of soil moisture fluctuations and fires was the key behind these contrasting patterns. In the semi-arid case, tree cover dropped and increased during extremes of dry and wet years respectively (Fig. 3.3a). Even though it has been argued that the deeper tree roots would shield them against variability (Gherardi and Sala, 2015), when we accounted for trees being able to access soil moisture from depths beyond the reach of grasses, the negative impact of rainfall variability on trees persisted (3.7.3 Appendix C). Moreover, there exists evidence that trees cannot always withstand droughts, particularly when these are extreme (Fensham et al., 2015, 2009), as in the bottom rainfall quartile of our simulations. Compounding this, was the inability of trees to compensate with sufficient growth during extreme wet years and grasses were the main reason for this. Their rapid response speed meant that competition was

strongest during years of high resource availability, a common phenomenon in savannas (February et al., 2013; Riginos, 2009). Apart from grasses limiting tree access to water, high grass cover also resulted in more frequent and potent fires (Fig. 3.3e), a positive feedback that hampered tree recruitment (Bond, 2008; Staver et al., 2011b). Tellingly, in a study where tropical savanna trees responded overall positively to increasing rainfall variability, African sites did not follow this pattern, with fire being touted as a possible reason for this (Holmgren et al., 2013). Crucially, the increase in rainfall variability meant that these dry and wet extremes, in which trees lost out on average, became more frequent causing the extinction of savannas in the long term.

On the other hand, mesic savannas became more resilient with increasing rainfall variability (Fig. 3.2b), driven by the positive response of tree cover to wet extremes (Fig. 3.3b). In our model, moisture availability was coupled to colonisation, with fires limiting tree cover expansion. The years of high rainfall promoted colonisation pulses which overcame the fireinduced limitation. As Harrington (1991) argued, such pulses, where the balance between moisture availability and the fire disturbance favours tree establishment, are essential for tree survival. Increasing rainfall variability produced more such 'windows of opportunity' (Holmgren and Scheffer, 2001) in two ways: increased frequency of wet extremes and higher stochasticity in fire occurrence. The former promoted fast growth episodes, known to promote tree cover expansion (Holmgren et al., 2013), while the importance of the latter in preserving savanna tree populations has been previously demonstrated (Higgins et al., 2000).

3.4.2 The temporal niche

Our results highlighted how increasing rainfall variability can shift plant-plant interactions away from the well-established resource competition (Ward et al., 2013) and disturbance (e.g. Staver et al. 2011a) mechanisms toward the trait of responding fast. Bond et al. (2003) had shown how post-burn tree growth rates were a major factor in determining whether savanna trees would survive or not, albeit with atmospheric CO₂ driving these rates. Hence, it is possible that responding fast to variable conditions will become the defining aspect of plant interactions under increasingly variable conditions, making temporal processes and corresponding plant traits the major driver of dynamics (Hoover et al., 2014). Xu et al. (2015) demonstrated this quite elegantly in a study of increasing rainfall intensities in savannas.

Despite the general expectation that trees would benefit from more intense rainfall events due to increased percolation (Kulmatiski and Beard, 2013; Mazzacavallo and Kulmatiski, 2015; Ward et al., 2013), Xu et al. (2015) showed how grasses would actually be the beneficiaries due to their aggressive water use strategy. Response speed was the defining factor in our results too: grasses were too fast for trees in semi-arid conditions, competing stronger and fuelling more fires in years of high rainfall, but this advantage was reversed in the mesic case, where fast tree growth during wet extremes increased savanna resilience.

3.4.3 Open questions

We modelled rainfall variability without correlation between years. Theoretical studies show that this can impact how bistable systems respond to variability (Ai et al., 2003; Sharma et al., 2014b), which is relevant due to the link between rainfall patterns and the El Nino Southern Oscillation cycle (Holmgren and Scheffer, 2001). Furthermore, high rainfall variability could be linked to more intense individual rainfall events (Easterling et al., 2000; O'Gorman and Schneider, 2009). Both our work and that of Xu et al. (2015) demonstrated that the tree advantages due to root niche separation (Gherardi and Sala, 2015; Kulmatiski and Beard, 2013), may fail under high rainfall variability and intensity. Future studies of higher complexity would be required to address this and enhance our understanding. Fire could also be affected by climatic and environmental variability, particularly with respect to the timing of fires within a year (Nelson et al., 2012). Even though our analysis (3.7.2 Appendix B) demonstrated that stochasticity in the timing of fire within a year did not counteract the impacts of increasing variability, more targeted studies should address the specifics of fire dynamics.

3.5 Conclusions

We showed how rainfall variability interacted with resource availability, competition and fires, to produce contrasting tree responses in dry and moist savannas. While tree cover dropped and savannas were eliminated in the former case, high variability enhanced savanna resilience in the latter. These diverging outcomes were determined by the varying response speeds of two plant types to changing conditions. Future studies should aim to further test how variability impacts plant interactions, using existing insights provided here and in other studies as building blocks where appropriate. The idea of the temporal niche deserves a thorough investigation, as it may provide a solid conceptual framework for studying plant responses to climatic variability.

3.6 References

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3.7 Appendix

3.7.1 Appendix A. General sensitivity analysis.

A sensitivity analysis was performed by perturbing a single parameter at a time, with all other parameters set to their default values (see Table 3.1 for default parameter set). Four different levels of perturbation were considered: -20%, -10%, +10% and +20% compared to the default parameter value. The analysis was performed with respect to the following parameters: minimum rainfall infiltration proportion over bare ground a, soil porosity (where unitary volume soil porosity V_1 is the product of soil porosity and unitary volume soil depth), evaporation rate \mathcal{E} , grass transpiration rate W_G , tree transpiration rate W_T , grass colonisation rate \mathcal{E}_G , tree colonisation rate \mathcal{E}_G , maximal grazing rate, \mathcal{E}_G , maximal browsing rate, \mathcal{E}_G , and the exponent of the nonlinear functions \mathcal{E}_G , \mathcal{E}_G , for grazing, browsing and fire respectively. Fire intensity perturbations were investigated separately in 3.7.2 Appendix B.

The analysis was produced for semi-arid (520 mm/year) and mesic (780 mm/year) conditions, for low (T_0 =5%) and high (T_0 =50%) initial tree cover under current rainfall variability levels (σ =12%). Each simulation ran for t=1,000 simulation years. The steady state was taken to be the mean variable value over the last 100 simulation years. The mean of the steady states of 20 iterations was used for the analysis.

We define the relative sensitivity (RS) as the output variable's value given the parameter perturbation (V_p) minus the output variable's value given the default parameter (V_d) , normalized by V_d , $RS = \frac{V_p - V_d}{V_d}$ (Reineking et al., 2006). A negative sensitivity corresponds to a decreased variable value compared to the default scenario, RS < 0, and a positive sensitivity refers to the cases where RS > 0. A variable is sensitive to a parameter if the absolute value of RS exceeds the magnitude of the perturbation. In the subsequent figures we demonstrate relative and absolute change of the output variables in response to parameter perturbations.

3.7.1.1 Appendix A.1 Soil moisture content, *M*

Soil moisture content was not sensitive to changes in any of the parameters under either mean rainfall conditions or initial tree cover scenario (Fig. 3.4a, b; Fig. 3.5a, b).

3.7.1.2 Appendix A.2 Grass cover, *G*

Under semi-arid conditions grass cover was sensitive to grass and tree colonisation and natural mortality, as well as grazing, browsing and the exponents of the non-linear functions (Fig. 3.4 c, d). In the case of low initial tree cover, where the original biome was a tree-less grassland, grass cover showed negative sensitivity to parameters which caused a shift to a savanna biome: decreasing grass colonisation, increasing grass mortality, increasing tree colonisation, decreasing tree mortality, increasing grazing, a steeper increase in the grazing function and, conversely, a slower response of browsing and fire (Fig. 3.4c). Given high initial tree cover the sensitivity of grass cover to perturbations in the opposite direction (e.g. faster grass colonisation) switched to positive and led to an increase in grass cover at the expense of trees (Fig. 3.4d).

Under mesic conditions, grass cover was much more robust to parameter perturbations (Fig. 3.5c, d). Only grass colonisation and tree mortality caused a shift above the relative sensitivity threshold. Depending on the initial tree cover, grass cover was either negatively (Fig. 3.5c) or positively (Fig. 3.5d) sensitive to these two parameters.

3.7.1.3 Appendix A.3 Tree cover, T

Similarly to grass cover, tree cover was particularly sensitive under semi-arid conditions (Fig. 3.4e, f). Given a low initial tree cover (Fig. 3.4e), trees were positively sensitive to decreasing grass colonisation, increasing tree colonisation, increasing grass mortality, decreasing tree mortality, increasing maximal grazing, a steeper grazing function and a slower response of browsing and fire. Conversely, trees were always negatively sensitive to changes in the opposite direction of these parameters for the high initial tree cover scenario (Fig. 3.4f). In this case, parameters benefiting grasses (e.g. higher grass colonisation) caused a drop in tree cover, to the extent that in most cases the biome shifted from savanna to grassland.

Under mesic conditions, tree cover was only sensitive to two parameters per scenario (Fig. 3.5). Given a low initial tree cover, trees were positively sensitive to a decrease in grass

colonisation and tree mortality, leading to a savanna biome instead of grassland (Fig. 3.5e). For high initial tree cover, trees were negatively sensitive to lower tree colonisation and higher tree mortality (Fig. 3.5f). In the former case trees died out, while in the latter we observed a shift from tree- to grass-dominated savanna.

3.7.1.4 Appendix A.4 Summary

Tree-grass coexistence in savannas is the result of competition under dry conditions and environmental disturbance in moister conditions (Bond, 2008; Sankaran et al., 2004). Hence, access to resources is the key process regulating semi-arid savannas (Ward et al., 2013), while fire, grazing or other disturbances determine mesic biomes' vegetation composition (Staver et al., 2011b; Veldhuis et al., 2014). Our sensitivity analysis results demonstrated this: semi-arid savannas were sensitive to parameter determining the competitive balance between trees and grasses, whereas mesic savannas were much more robust to these parameter perturbations.

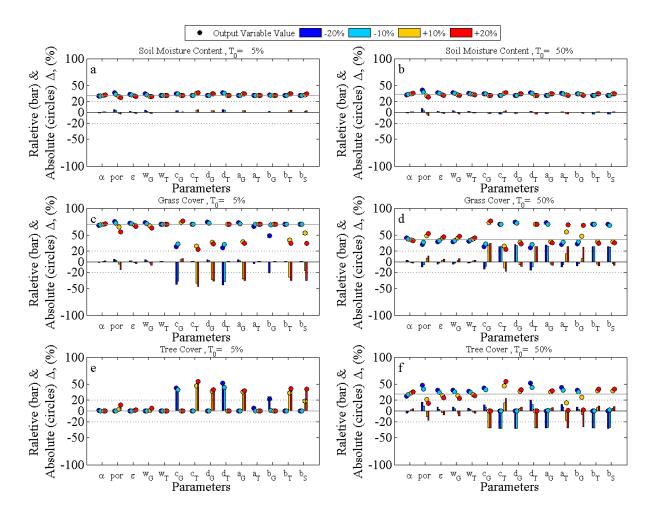


Figure 3.4 Sensitivity analysis of moisture content (a, b), grass cover (c, d) and tree cover (e, f) under semi-arid conditions. Parameters along the x-axis in order of appearance: minimum rainfall infiltration proportion over bare ground a, soil porosity, evaporation rate ε , grass transpiration rate w_G , tree transpiration rate w_T , grass colonisation rate c_G , tree colonisation rate c_T , grass natural mortality rate d_G , tree natural mortality rate d_T , maximal grazing rate, a_G , maximal browsing rate, a_T , grazing function exponent b_G , browsing function exponent b_T , and fire function exponent, b_S . Bars represent relative sensitivity, while circles show the actual variable value for each perturbation. The grey horizontal line shows the steady state value of the variable for the original parameter set. Initial tree cover differs between the left and right plots: T_0 =5% and T_0 =50% respectively.

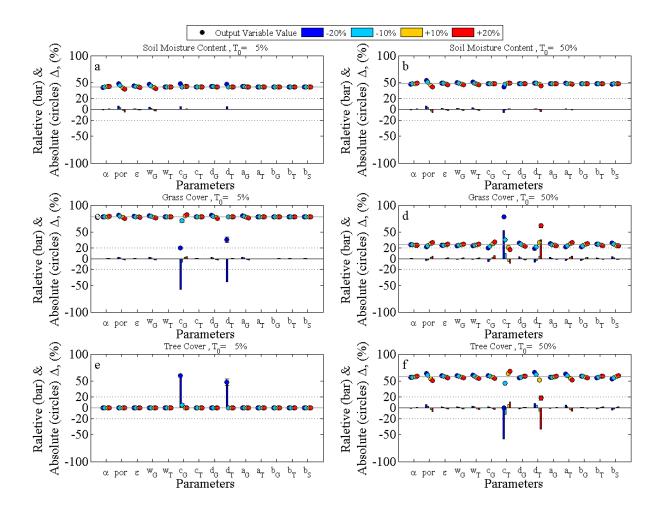


Figure 3.5 Sensitivity analysis of moisture content (a, b), grass cover (c, d) and tree cover (e, f) under mesic conditions. Parameters along the x-axis in order of appearance: minimum rainfall infiltration proportion over bare ground a, soil porosity, evaporation rate ε , grass transpiration rate w_G , tree transpiration rate w_T , grass colonisation rate c_G , tree colonisation rate c_T , grass natural mortality rate d_G , tree natural mortality rate d_T , maximal grazing rate, a_G , maximal browsing rate, a_T , grazing function exponent b_G , browsing function exponent b_T , and fire function exponent, b_S . Bars represent relative sensitivity, while circles show the actual variable value for each perturbation. The grey horizontal line shows the steady state value of the variable for the original parameter set. Initial tree cover differs between the left and right plots: T_0 =5% and T_0 =50% respectively.

3.7.2 Appendix B. Sensitivity of results to fire intensity stochasticity.

In this section we investigated whether stochastic fluctuations in the intensity of fires altered the impact of increasing rainfall variability on semi-arid and mesic savannas. Our original fire function, $f(G) = \varphi \, a_S G^{b_S(1-G)}$, was applied using a constant maximum fire intensity $a_S = 1$. As a proxy for variability in the timing of fire events from year to year, we created a normal distribution around this intensity value and investigated three levels of variability: $\sigma=10\%$, 20% and 30%. We ran simulations for low $(T_0=5\%)$ and high $(T_0=50\%)$ initial tree cover under current $(\sigma=12\%)$ and high $(\sigma=24\%)$ rainfall variability levels with 20 iterations per scenario.

The duration of the simulations differed depending on the amount of time required for each configuration to produce its steady state. For the mesic conditions steady states were attained within t=1,000 simulation years. For semi-arid conditions with the lowest fire variability (σ =10%), t=10,000 simulation years were sufficient for all simulations to attain their steady state. For the intermediate scenario of fire variability (σ =20%) we simulated t=30,000 years under current variability levels. For the high rainfall variability scenario, we used two different simulation lengths depending on the initial condition: for T_0 =5%, t=30,000 sufficed, while for T_0 =50%, t=50,000 where required for all simulations to converge. Finally, for the highest fire intensity variability scenario tested (σ =30%), we simulated t=15,000 years under current rainfall variability levels. The same simulation time sufficed for high rainfall variability in the high initial tree cover case. For the low initial value T_0 =5% a simulation time t=30,000 was necessary.

The results for the mesic conditions were identical to the original model (Fig. 3.6d, e, f): depending on the initial tree cover the outcome was either savanna (T_0 =50%) or grassland (T_0 =5%) for both current and high rainfall variability levels irrespective of fire intensity stochasticity. Likewise for the lowest scenario of fire intensity variability (σ =10%) under semi-arid conditions (Fig. 3.6a): increasing rainfall variability eliminated savanna-grassland bistability in favor of grasslands. In the second case of fire intensity variability (σ =20%, Fig. 3.6b), the basin of attraction of savannas under current rainfall variability was extended. Thus, given initial tree cover T_0 =5% the grassland outcome was not a certainty and savanna established in approximately 50% of the simulations. When rainfall variability was doubled,

though, savannas became extinct once more. Under the highest fire intensity variability scenario tested (σ =30%, Fig. 3.6c) savannas were the only steady state for both initial tree cover values (T_0 =5%, 50%), a result which persisted under increased rainfall variability as well.

These results clearly demonstrate the persistence of the negative impact of increasing rainfall variability on semi-arid savannas, despite additional stochasticity in the intensity of fires. Only in one case (σ =30%) did it counter-act this negative impact by drastically weakening the strength of fires. Even in this case, though, savanna establishment required extremely long time scales (t=30,000), which underlines the difficulty of tree survival under high rainfall variability in semi-arid savannas.

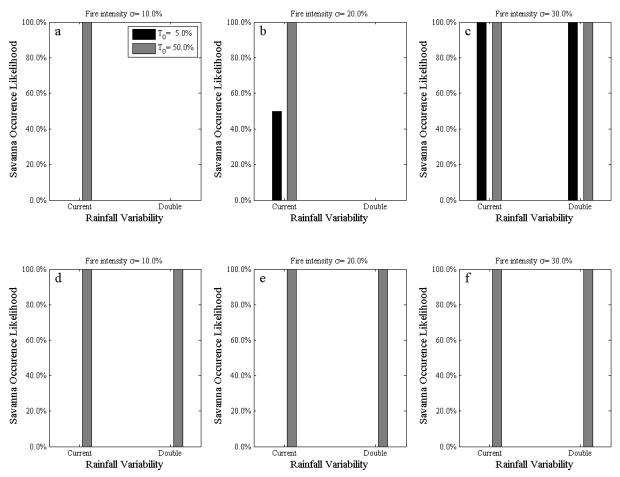


Figure 3.6 The relative frequency of savanna state outcomes out of 20 simulation iterations for semi-arid (top panel) and mesic (bottom panel). Increasing from left to right: different fire intensity variability scenarios. Each scenario was simulated for current and high rainfall variability conditions with both a low (black bars) and a high (grey bars) initial tree cover.

3.7.3 Appendix C. Sensitivity of results to additional water uptake by trees.

Our model did not account for trees and grasses accessing water from different soil depths as in Walter's two layer hypothesis(Ward et al., 2013). Rather than include this root niche we selected to represent the different water uptake strategies by having different rates for trees and grasses, thus creating a temporal niche (Xu et al., 2015). Given that competition for resources is a critical aspect of tree-grass interactions, we tested whether adding a proxy for deeper tree roots would alter the impact of rainfall variability on dry savannas.

We simulated two mean rainfall scenarios, arid (330 mm/year) and semi-arid (520 mm/year). For each scenario we modelled low (T_0 =5%) and high (T_0 =50%) initial tree cover under current (σ =12%) and high (σ =24%) rainfall variability levels with 20 iterations per scenario. The simulation length was t=10,000 years. Steady states were evaluated as the mean of the last 100 years.

Tree root depth could not be represented explicitly due to the model having no spatial dimension. Instead, we altered the tree equation to include an additional water uptake factor:

$$\frac{dT}{dt} = c_T (\underbrace{M}_{\substack{\text{existing} \\ \text{moisture}}} + \underbrace{u}_{\substack{\text{additional water} \\ \text{uptake proposition}}} \underbrace{\delta(G, T) \frac{p}{v_1} M}_{\substack{\text{percolating moisture} \\ \text{from moisture}}}) T (1 - f(G) - T) - d_T T - \beta(T)$$

In this way trees accessed water which percolated from the soil layer represented in the model. We modelled two different values for the water uptake parameter: u=10%, 50%.

Based on the process of parametrization of the model, we had to alter the tree colonisation parameter for each value of u and mean rainfall amount, p. The colonisation parameter was originally determined by assuming that trees fully colonised an initially empty landscape with unlimited resources after 60 years (Accatino et al., 2010). In this altered model version both the additional water uptake factor, u, and annual rainfall, p, impacted this. Hence we selected the following values of tree colonisation to keep in line with the original criterion:

Arid conditions,
$$p = 330 \, mm / year$$
, $u = 10 \, \%$, $c_T = 0.2$, and $u = 50 \, \%$, $c_T = 0.12$;
Semi-arid conditions, $p = 520 \, mm / year$, $u = 10 \, \%$, $c_T = 0.18$, and $u = 50 \, \%$, $c_T = 0.1$.

Simulations for arid conditions produced a similar pattern to the semi-arid conditions in the original model (Fig. 3.7a,b): increasing rainfall variability eliminated the savanna state. In this case, however, there was no bistability: both choices of u led to the absence of alternative states. For current variability the steady state was savanna, for high variability grassland. Interestingly, for u=50% the savanna tree cover steady state was lower than for u=10%, which suggests that the temporal niche continued to play a major role in grass-tree interactions. Under semi-arid conditions, the inclusion of the tree water uptake factor u, produced the same pattern as the original model under mesic conditions: a bistable grassland-savanna system whose steady states were not significantly impacted by increasing rainfall variability (Fig. 3.7c, d).

The inclusion of a proxy for tree root depth caused a shift of the observed pattern to drier conditions: tree extinction due to high rainfall variability occurred under arid (330 mm/year) rather than semi-arid (520 mm/year) conditions.

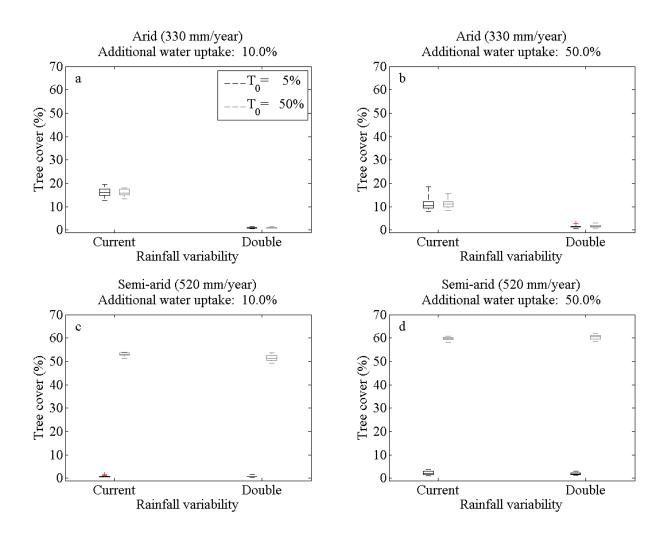


Figure 3.7 Tree cover steady states for arid (a, b) and semi-arid (c, d) conditions for different additional tree water uptake scenarios: u=10% (a, c) and u=50% (b, d). Two rainfall variability scenarios are on the x-axis axis: current ($\sigma=12\%$) and double ($\sigma=24\%$). Two initial tree cover values per variability scenario: $T_0=5\%$, $T_0=50\%$. Tree cover boxes represent steady states of 20 simulation iterations.

3.7.4 Appendix D. Comparison between tree cover data from East Africa and simulated tree cover.

We compared our model outputs to East African tree cover data from the dataset of African savannas from (Sankaran et al., 2005). This study had found that tree cover responses to rainfall showed two distinct patterns depending on the rainfall amount. For this reason, we created a distinction between dry and mesic conditions in our validation exercise. Therefore, from the total of 514 sites we created two subsets, one for dry (200-550 mm/year) and one for mesic (650-1000 mm/year) conditions, with 110 and 261 sites, respectively. For each site we used the rainfall amount in order to simulate comparable conditions. Rainfall variability was set to the basis scenario (σ =12%) and we used a high initial tree cover (T_0 =50%) apart from specific cases in the last plot where we use the low initial value (T_0 =5%). Simulations reached their steady states within t=1,000 years and the mean of the final 100 years was used as the steady state value. We performed 20 iterations per site and used the mean of the steady states thereof. We used the default parameter set (Table 3.1 from main manuscript) and did not parameterize the model for each individual site (the dataset contained information on fire return intervals, soil type, grazer biomass, etc.).

First we compared the data to our simulated tree cover for the two subsets (Fig. 3.8a). Then we selected only included sites with a fire return interval of up to 3 years (Fig. 3.8b), since we modelled conditions of high fire frequency. In the first analysis (no fire condition), simulated tree cover slightly underestimated actual tree cover in the dry case, but greatly overestimated it under moist conditions. Nevertheless, simulated tree cover was within the range of maximum actual tree cover. Moreover, our model reproduce the steep positive response of trees to increasing rainfall under dry conditions and the levelling off of this trend under moister conditions. Our model parameterization did not include site-specific information (e.g. grazing regime, land use, etc.), so the difference in the individual values ought to be expected. The reason for the poor fit with the mesic dataset was the multiple cases of extremely low

actual tree cover despite the high amount of rainfall. We could not have accounted for these cases in a conceptual model which was designed to reproduce savanna dynamics, even less so when we did not alter the parameter set for each simulated site. Once the fire return interval criterion was applied we found an improved fit with the data (Fig. 3.8b). Moreover, a bimodal distribution of tree cover appears in the data with either high or very low tree cover present. To emphasize how site-specific information would have improved our predicted tree cover, we produced a final plot (Fig. 3.8c), where we included outputs of mesic simulations with a low initial tree cover (T_0 =5%) corresponding to the sites with almost no tree cover in the data (T<2%), which greatly improved the fit with the data.

This validation exercise demonstrated that our general savanna model, both in terms of processes represented and parameter choices, produced realistic tree cover values, but most importantly reproduced the tree cover responses patterns along the rainfall gradient. Without using site-specific information to parameterize the model, it performed satisfactorily under semi-arid conditions, but less so under mesic conditions. The reason was the large amount of sites with very low cover despite the high amount of rainfall. Including simulations with comparable fire scenarios (Fig. 3.8b) and then simulations which produced both alternative states in mesic conditions (Fig. 3.8c) produced significantly improved results, which should add support for our model's ability to reproduce tree cover patterns.

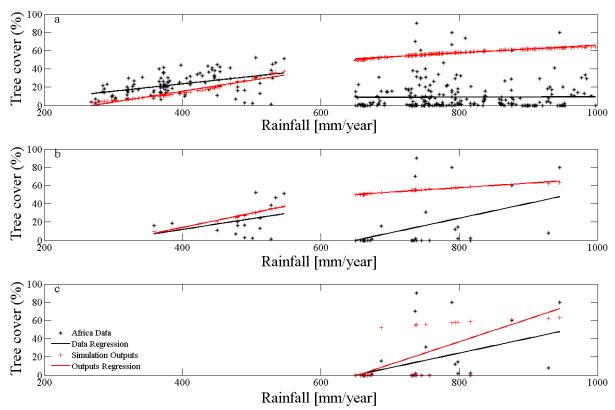


Figure 3.8 Tree cover from East Africa (black) and simulation outputs (red) for dry (200-550 mm/year) and mesic (650-1000 mm/year) conditions. a) all sites, b) sites with a fire return interval 3 years or more, c) including simulation with low initial tree cover value. The regression line equations: a) dry, data: y=0.8x-9.1, simulation: y=1.2x-32.7, mesic, data: y=0.02x+7.7, simulation: y=0.4x+23; b) dry, data: y=1.2x-34.8, simulation: y=1.6x-105.4, simulation: y=0.5x-18.1; c) mesic, data: y=1.6x-105.4, simulation:

3.7.5 Appendix E. Model versions without fire and weaker fire intensity

We created two alternative model versions to test what the impact of fire was with respect to tree-grass coexistence, which has previously been distinguished between resource-depending and disturbance controlled along the rainfall gradient (Sankaran et al., 2005). By running a model without fire we could test whether fire was necessary to maintain coexistence in either mean rainfall scenario. We also simulated conditions with lower fire intensity (50%) for the same reasons. The analysis was performed following the same principles as the first analysis in the main manuscript: for each rainfall variability value (σ =6, 9, 12, 15, 18, 24%), 50 iterations were performed for two different initial values, T_0 =5% and T_0 =50%. Having determined the time required for the simulations with fire intensity a_S = 0 and a_S = 0.5 to reach the steady state, a simulation length of t=1,000 years was deemed sufficient. The mean

value of the variables over the final 100 simulation years was taken as the steady state value each simulation.

The results showed that coexistence in our model was achieved irrespective of fire and that high fire intensity created alternative states (Fig. 3.9). Both results are consistent with the literature. Resource competition has been repeatedly demonstrated to lead to coexistence, particularly in the mean rainfall conditions that we applied (Holdo, 2013; Ward et al., 2013). Likewise with fire as a positive feedback which creates alternative states (Higgins et al., 2010; Staver et al., 2011a; van Langevelde et al., 2003).

We found a single steady state of high tree cover in the absence of fire or even with weak maximum fire intensity for both semi-arid and mesic scenarios. Tree cover in the absence of fire was slightly above 50% (Fig. 3.9a) while with weak fire intensity (Fig. 3.9b) it dropped o slightly below that. Interestingly, variability had a negative impact on tree cover even without fire in the model. The pattern observed here (tree cover reduction along the variability gradient) is the result of resource competition, since fire is absent. These results support our interpretation of our main results with respect to the temporal niche: more rainfall fluctuations and increased frequency of extreme events due to higher variability had a negative impact on trees because grasses responded faster and competed strongly during the wet extremes. The reason an alternative tree-less state did not exist and trees did not die out under high variability was that the positive fire feedback was either absent (Fig. 3.9a) or too weak (Fig. 3.9b) to impose the population-level bottleneck in tree-recruitment.

In the mesic case the impact of fire on the steady states was weaker (Fig. 3.9c, d). Tree cover without fire was just below 65% whereas with weak fire it dropped 2-3%. Tree cover along the variability also remained fairly stable for both cases, demonstrating that resource competition in these conditions does not significantly impact tree cover

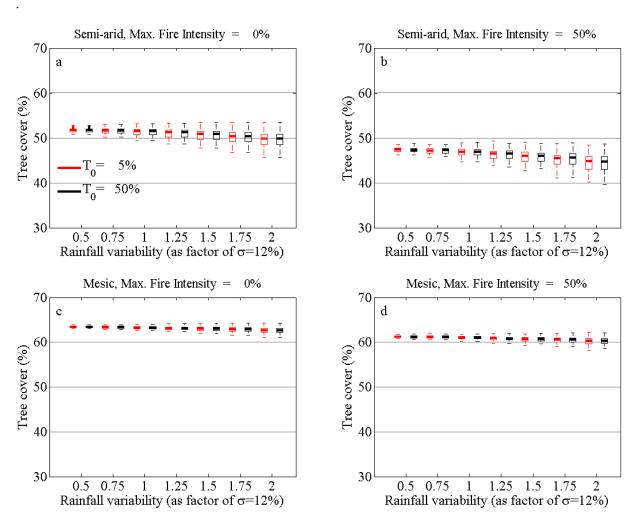


Figure 3.9 Tree cover steady states along the inter-annual rainfall variability gradient. Two mean rainfall scenarios (upper and botton panels) and two model configurations: without fire (left column) and with maximum fire intensity $a_S = 0.5$ (right column). The use of different initial conditions ($T_0=5\%$ and $T_0=50\%$) was aimed at testing for alternative states. Each box corresponds to the steady states of 50 iterations with different rainfall time series. All simulations were performed using the default parameter apart from the fire value (Table 3.1).

3.7.6 Appendix F. Tables of simulation details.

Table 3.2 Simulation times required to reach steady state for each combination of mean annual rainfall and rainfall variability.

Mean Rainfall [mm/year]	520		780	
Initial tree cover (%)	5	50	5	50
Variability as factor of basis scenario	Simulati	on time [year	rs]	
0.5 σ [6%]	8,000	1,000	1,000	1,000
0.75 σ [9%]	8,000	1,000	1,000	1,000
σ [12%]	8,000	1,000	1,000	1,000
1.25 σ [15%]	8,000	1,000	1,000	1,000
1.5 σ [18%]	8,000	1,000	1,000	1,000
1.75 σ [21%]	8,000	30,000	1,000	1,000
2 σ [24%]	8,000	30,000	1,000	1,000

Table 3.3 Simulated tree cover (%) at the savanna steady state for semi-arid and mesic conditions and the full variability gradient.

Mear	n Rainfa	all	520				780			
			Mean		Min.	Max.	Mean		Min.	Max.
			Tree		Tree	Tree	Tree		Tree	Tree
			Cover	SD	Cover	Cover	Cover	SD	Cover	Cover
			(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
nal		0.5	36	1.2	33	38	58	0.5	56	59
origii		0.75	35	1.5	31	38	58	0.5	57	59
r of (ρ	1	34	1.4	31	37	57	0.6	56	59
facto	variability	1.25	32	1.6	29	35	57	0.6	56	58
ty as	varië	1.5	30	1.7	27	33	57	0.8	55	58
Variability as factor of original		1.75	0.08	0	0.60	0.09	57	0.8	55	58
Vari		2	0.08	0	0.05	0.09	56	0.9	54	58

Table 3.4 Simulated likelihood (%) of a savanna steady state for a range of initial tree cover and inter-annual rainfall variability under mesic mean rainfall conditions.

		Variability as factor of original variability σ						
		0.5	0.75	1	1.25	1.5	1.75	2
Initial Tree Cover (%)	13	0	0	0	0	0	0	0
	14	1	1	3	1	5	2	2
	15	2	12	10	21	30	23	23
	16	23	38	47	46	61	57	62
al Tro	17	44	72	69	82	85	86	83
Initi	18	86	89	91	97	97	96	97
	19	99	99	99	100	98	100	100
	20	100	100	100	100	100	100	100

3.7.7 Appendix G. References

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Link to following chapter

The inclusion of stochasticity in the model produced alternative states of grass- and tree-dominated biomes, with increasing inter-annual rainfall variability having contrasting effects between semi-arid and mesic conditions. In the former case, faster-responding grasses dominated good rainfall years via direct resource competition and through the increased potency of fires. Thus, grasses recovered from the drought stress imposed by the dry years, unlike trees which gradually lost out, becoming extinct in scenarios of very high variability. Under mesic conditions, the impact of variability on the dynamics was the opposite. Water stress was not too severe in the poor rainfall years and trees suffered less in comparison to the droughts of the semi-arid case. In the wet extremes, despite the higher likelihood and increased strength of fires, moisture was so abundantly available that it allowed trees to grow fast enough to escape the fire trap. Thus, trees in mesic savannas were more likely to survive under higher variability which presented them with more frequent rapid growth opportunities, increasing savanna resilience as a result.

Within this framework of alternative tree-less and tree-dominated states, it is possible to investigate grazing-induced shifts between these states. However, my focus will not be the dynamics of encroachment, which have been much studied and well understood. Instead, I will search for an early warning of encroachment. The key here will be to prevent the process from unfolding because once the biome transitions to the alternative state, restoration may be tough due to hysteresis. Early warning signals prior to such so-called irreversible transitions between alternative states often appear in the system's behaviour and have been found in multiple ecological systems (e.g. fisheries collapse, lake eutrophication), but not yet for encroachment in savannas. In the following chapter I seek for such signals as I simulate various scenarios of a grazing-induced transition from open to woodland savanna. Critically, I will search for an early indicator of encroachment which successfully distinguishes between cases with a high likelihood of being irreversible and those with a low such risk. Ultimately, this indicator's success will depend on whether it shows up early enough to prevent encroachment altogether.

4 Forecasting and preventing irreversible woody encroachment in savannas

Grazing-induced woody encroachment in African savannas can be abrupt and irreversible, making encroachment a serious threat for the ecosystem. Early warning signals have been developed for the timely identification of precisely such transitions, but have yet to be applied to encroachment in savannas. After demonstrating that our modelled system exhibited alternative states of open and encroached savanna, we found that short-term heavy grazing could lead to irreversible encroachment, despite a return to the original grazing conditions. We applied standard deviation of woody cover, a signal typically used to demonstrate the loss of a system's resilience, on the short-term heavy grazing time series. Without any prior knowledge regarding the cessation of heavy grazing, the warning signal distinguished the scenarios which led to irreversible encroachment from the ones which returned to the open savanna state. We validated the temporal warning signal on shrub encroachment data and demonstrated its usefulness by simulating hypothetical prevention treatments in cases where the encroachment warning appeared. Though temporal warning signals have been much studied, we demonstrated how a simple indicator can be applied in the short term not only to successfully identify the risk of catastrophic encroachment but also in time to prevent it.

4.1 Introduction

Within the context of savanna research, encroachment describes the phenomenon where woody species suppress the herbaceous vegetation (Gil-Romera et al., 2010), degrading the savanna to woody patches surrounded by bare soil (D'Odorico et al., 2012). Non-degraded savannas rely on the balancing of tree-grass competition through multiple environmentally and climatically controlled biotic and abiotic interactions (Higgins et al., 2000; Lehmann et al., 2014; Sankaran et al., 2008), such as the positive grass-fire (D'Odorico et al., 2006; Staver et al., 2011a) or grazing-tree cover (De Michele et al., 2011; van Langevelde et al., 2003) feedbacks. The former controls tree recruitment, allowing grasses to survive under treefavouring, moist climatic conditions (Bond, 2008; Maurin et al., 2014; Wakeling et al., 2011), while the latter works in the opposite direction: grazers remove flammable grass cover, reducing the frequency and potency of fires, thus improving tree establishment opportunities (Graz, 2008; Lohmann et al., 2012). Altering the strength of such feedbacks can cause a chain reaction, pushing the system beyond a threshold (Dakos and Hastings, 2013) and leading to abrupt regime shifts (D'Odorico et al., 2012). Encroachment is a typical example of this process: heavy grazing causes an abrupt increase in woody cover and tips the savanna into an encroached state (Ratajczak et al., 2014). Since encroachment can often be irreversible (D'Odorico et al., 2012; Ratajczak et al., 2014), there lies great value in finding early warning indicators to prevent this process from unfolding.

The research field of early warning signals has developed the theory for such indicators (Scheffer et al., 2009, 2001; Scheffer and Carpenter, 2003) with examples ranging from lake eutrophication (Carpenter et al., 2011) and the collapse of fish populations (Jackson et al., 2001) to laboratory yeast populations (Dai et al., 2012), but it has yet to be applied on encroachment in mesic savannas. One of the better studied early warning signals is Critical Slowing Down (CSD), which describes the system's slowing responsiveness to perturbations as it approaches a tipping point (Boettiger et al., 2013; Dakos et al., 2015). CSD manifests itself in various ways in models and in data: eigenvalues approach zero (Lade and Gross, 2012), autocorrelation (Dai et al., 2012; Veraart et al., 2012) and variance (Carpenter et al., 2014; Carpenter and Brock, 2006) increase to name just a few (Dakos et al., 2012). Woody encroachment in mesic savannas represents a scenario where one would expect to find indicators of CSD (Dakos et al., 2015): alternative states of open and woody-dominated

savanna exist (Hirota et al., 2011) with grazing as the threshold-inducing driver (D'Odorico et al., 2012; Gil-Romera et al., 2010; Lohmann et al., 2012). Critically, identifying CSD patterns that precede encroachment would only be meaningful if they could be applied to prevent an irreversible regime shift (Contamin and Ellison, 2009).

Despite, our ever increasing understanding of the phenomenon of CSD, little progress has been made in the application of CSD as a management forecasting tool in order to avert catastrophic transitions (Biggs et al., 2009; Carpenter et al., 2014; Contamin and Ellison, 2009). Identifying CSD indicators requires long continuous time series which are hard to find (Dakos et al., 2015; Kéfi et al., 2014; Wang et al., 2014). Moreover, the discovery of these signals can be too close to the point of transition in relation to the management options available in order to avert catastrophe (Contamin and Ellison, 2009). Spatial rather than temporal patterns could have overcome this limitation if a clear link between pattern and the proximity to critical transition were found (Dakos et al., 2011; Kéfi et al., 2007), which itself has proved challenging [36–38].

In this study we seek temporal indicators of CSD preceding woody encroachment which can be identified in time to prevent irreversible encroachment. For this purpose we use a stochastic Ordinary Differential Equations model of coupled soil moisture and vegetation dynamics and simulate scenarios of short-term heavy grazing treatments followed by a return to the original grazing conditions. Based on the resulting dynamics, we ask: is there a distinct pattern in the temporal dynamics of the CSD indicator for the cases where long-term encroachment has been locked in despite the return to the original grazing conditions? Does this pattern emerge in field data of shrub encroachment? Finally, we produce grazing reduction scenarios to test whether the warning signal appears early enough to allow for the prevention of the transition to an encroached savanna.

4.2 Methods

4.2.1 Model description

We simulate the African savanna applying a stochastic version of an existing Ordinary Differential Equations (ODE) model of coupled soil moisture and vegetation dynamics of three variables: soil moisture content (M), grass cover (G) and tree cover (T) (Synodinos et al., 2015), where tree cover represents all woody vegetation. The three equations are:

$$\frac{dM}{dt} = \frac{p}{v_1} \delta(G, T) (1 - M) - \varepsilon M (1 - T - G) - w_G M G - w_T M T \tag{1}$$

$$\frac{dG}{dt} = c_G MG(1 - T - G) - d_G G - \gamma(G)$$
(2)

$$\frac{dT}{dt} = c_T MT (1 - f(G) - T) - d_T T - \beta(T) \tag{3}$$

The model assumes that rainfall infiltration depends linearly on existing vegetation (Gilad et al., 2007). Infiltrating rainfall is then homogeneously distributed within the soil, with moisture above the saturation level percolating into deeper soils (Accatino et al., 2010). Soil moisture evaporates in the absence of shading, while grasses and trees both extract moisture for transpiration. Grasses only colonise free space and die out due to natural mortality. In addition, grass cover is reduced by grazers. The impact of grazing increases non-linearly with grass cover following the principle of grazing lawns whereby more productive patches attract more herbivores (Mcnaughton, 1984). Trees can colonise free space and can displace grasses, but tree cover growth is limited by fire (Hanan et al., 2008). Apart from loss of tree cover due to natural mortality, browsing also reduces tree cover and is defined similarly to grazing by applying the same reasoning ('browsing hedges' (du Toit and Olff, 2014)).

4.2.2 Parameters

Rainfall, p, is a time series with a mean value of 780 mm/year and a standard deviation of 12%, based on the Kenya CRU CY v. 3.20 annual rainfall record (Harris et al., 2014). The mean rainfall value has been adjusted to represent mesic conditions (Sankaran et al., 2005).

Soil, represented by v_1 as the unitary volume porosity, is determined as sandy soil porosity with a depth of 40 cm (Kulmatiski et al., 2010; Kulmatiski and Beard, 2012). Infiltration, $\delta(G,T) = (1-a)(G+T) + a$, is assumed to start at a minimum rate of a = 75% (Mwendera and Saleem, 1997). In the absence of any rainfall and vegetation, evaporation, ε , causes the loss of all soil moisture after half a year (Mellouli et al., 2000; Wythers et al., 1999). Similarly, in the presence of only one vegetation type, the loss of all soil moisture solely due to transpiration occurs after one year for grasses (W_G) (Cavanaugh et al., 2011) and one-anda-half years for trees (w_T) (Graz, 2008). Grasses colonise (c_G) an initially empty landscape after half a year given no competition, no mortality and unlimited resources, while an equivalent tree colonisation (c_T) requires fifty years (Accatino et al., 2010). Natural mortality rates represent a maximum life span of five years for grasses (d_G) (Accatino et al., 2010) and two hundred years for trees (d_T) (Patrut et al., 2007). In this study, grazing, $\gamma(G) = a_G G^{b(1-G)}$, ranges from no grazing to a maximum intensity, a_G , equal to the natural mortality. Browsing, $\beta(T) = a_{\tau} T^{b(1-T)}$, is set to approximately half the natural mortality rate. Fire, $f(G) = \varphi a_s G^{b(1-G)}$, occurs stochastically depending on grass cover (Higgins et al., 2000), while fire intensity is a sigmoidal increasing function of grass cover (Staver et al., 2011b), which acts as fuel load (Bond et al., 2005). The maximum intensity, a_s , is set to one. Hence, intensity is determined by grass cover alone. At each simulation time step, a random number, $r \in [0,1]$, is picked from a uniform distribution that reflects the dependence of fire occurrence on grass cover: if r is less than the value of grass cover, r < G, then $\varphi = 1$, otherwise $\varphi = 0$. All parameter values are provided in Table 4.1.

Table 4.1 Parameter values used in simulations

Parameter symbols and units	Description	Range	Default value
<i>a</i> [-]	Proportion of rainfall in filtrating bare ground	-	0.75
p [m/year]	Annual rainfall	-	0.780
$V_1 [m]$	Unitary volume soil porosity	-	0.16
\mathcal{E} [1/year]	Evaporation (annual rate)	-	8
$W_G[1/year]$	Grass transpiration (annual rate)	-	6
W_T [1/year]	Tree transpiration (annual rate)	-	4
C_G [1/year]	Grass colonisation (annual rate)	-	20
C_T [1/year]	Tree colonisation (annual rate)	-	0.2
d_G [1/year]	Grass natural mortality (annual rate)	-	1
d_{T} [1/year]	Tree natural mortality (annual rate)	-	0.023
$a_G[1/year]$	Maximum grazing (annual rate)	0-1	-
a_S [-]	Maximum Fire intensity	-	1
φ [-]	Fire Occurrence	Binary 0,1	
a_T [1/year]	Maximum browsing (annual rate)	-	0.01
b [-]	Non-linear function exponent	-	1.5

4.2.3 Simulations

Simulations are performed in four separate analyses. We first determine the possible steady states along the grazing gradient, $a_G = 0$ -1. Then, within the grazing range where alternative states appear, we determine a tree cover threshold distinguishing between the alternative states. Following this, we perform simulations of different short-term heavy grazing treatments in the proximity of this threshold. Finally, we simulate encroachment prevention scenarios focusing on reducing the grazing intensity. All simulations were performed using Matlab version R2007b.

4.2.4 Possible steady states

We simulate the steady states along a grazing gradient, $a_G = 0-1$. Each scenario is replicated 50 times, each time with a different rainfall time series. Each simulation runs for t=2,000 time

steps. To ensure simulations reach a steady state and in order to select the initial values so that alternative states were not excluded, we performed multiple test runs. A steady state has been attained if tree and grass cover values agree with values at which they stabilised during the corresponding test runs. Simulation durations were selected accordingly and the results presented in the manuscript are only based on simulations that reach equilibrium. To minimise the noise induced by the stochasticity, the steady states are calculated as the mean value over the last 100 simulation years. Bistability, the existence of alternative steady states, is induced via differences in initial tree cover. For our grazing scenarios, the initial values of $T_0 = 5\%$ and $T_0 = 50\%$ suffice to demonstrate the existence of alternative states. Initial soil moisture and grass cover are the same for all simulations ($M_0 = 10\%$, $G_0 = 10\%$).

4.2.5 Bistability threshold range

Since initial tree cover determines to which of the two steady states the system converges, there exists a threshold initial tree cover value, above which the simulations converge to one steady state (encroached state) and below which they converge to the other (grassland). Given the stochasticity in the model, this threshold is a range rather than a single value: the initial values within this threshold range do not lead to the same state 100% of the time. Multiple test runs were performed to determine appropriate initial tree cover values which span the threshold range for each baseline grazing scenario ($a_G = 0.3$, 0.4, 0.5, 0.6, 0.7, 0.8) (Table 4.4). All simulations run for t=2,000 time steps and converge to either one of the steady states. Each scenario is repeated 50 times.

4.2.6 Grazing treatments

We simulate the long-term impact of short-term (30 years) grazing increases in the proximity of the bistability threshold for six baseline values of grazing intensity ($a_G = 0.3$, 0.4, 0.5, 0.6, 0.7, 0.8) (Table 4.2). For each grazing value we use an initial tree cover at 95% of the minimum threshold range value, i.e. initial cover that always led to a grassland state in the simulations for the bistability threshold range. We test 10 heavy grazing scenarios that are applied to each of the baseline values of grazing intensity for 30 years: an increase of 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100%. At the end of the heavy grazing period, grazing intensity returns to the baseline value. Each simulation, then, converges to a steady state after a total

simulation time of t=2,000 years. Each grazing combination (6 baseline and 10 heavy grazing scenarios) is replicated 50 times. The risk of long-term encroachment is calculated as the proportion of simulation iterations which converge to the encroached state.

Table 4.2 Baseline grazing and corresponding initial tree cover values used in short-term overgrazing scenarios.

Baseline grazing value	Initial tree cover T_0 (95% T_{c_min})	Bistability threshold range, T_c
0.3	35.5%	37%-40%
0.4	29.45%	31%-39%
0.5	23.75%	25%-31%
0.6	19%	20%-23%
0.7	13.3%	14%-18%
0.8	8.55%	9%-12%

4.2.7 Early warning signals

Increased variance and autocorrelation at-lag-1 (the correlation between consecutive time steps, referred to as autocorrelation from here on) prior to tipping points are considered standard early warning indicators of critical slowing down (Dakos et al., 2012; Scheffer et al., 2009). For a measure of variance we use standard deviation (Carpenter and Brock, 2006). For the steady state simulations along the full grazing gradient, we calculate the standard deviation and autocorrelation of the full tree cover time series of each iteration. We use the median over all iterations as the value of the corresponding early warning signal.

For the heavy grazing treatments, we test three rolling window early warning indicators (Dakos et al., 2012). The indicators are tree cover change, standard deviation and autocorrelation with a 5-year rolling window. This creates a 25-year time series for each indicator, which allows us to observe its temporal dynamics. We first calculate the mean value of each rolling window warning to create an indicator value for each grazing scenario. Since the rolling window temporal dynamics are smooth, the mean is an appropriate metric. We then take the mean over the 50 iterations. To account for the variability between the iterations we also calculate the standard error of the mean (SEM). In the end we are left with a

mean rolling window early warning indicator value for each baseline grazing and heavy grazing combination. In the next analysis, where we establish the encroachment warning signal, we make use of the temporal dynamics of the warning indicators observed in the rolling window time series. We focus on standard deviation and compare its value at the beginning and the end of the heavy grazing period. In particular we calculate the difference in tree cover standard deviation (Δ SD) between the last and first 5 years as our primary indicator and between the last and first 10 years as a secondary indicator. We select these Δ SDs as they provide a good indication of the temporal patterns of standard deviation. The 5- and 10-year Δ SDs are calculated for each simulation and the mean over all 50 iterations is then used as the warning indicator's value. The SEM is calculated to account for the variability between simulation iterations.

4.2.8 Data validation

We use the data of Ratajczak et al. (2014) for validation. This consists of six 31-year time series of shrub cover in a tallgrass prairie in the US, with each time series corresponding to a different treatment: grazed and un-grazed plots with a fire return interval (FRI) of 1, 4 and 20 years. For the encroachment warning (Δ SD), we ignore data beyond year 15 in of the time series, because shrub encroachment occurs beyond this point. We calculate the difference between the standard deviation of the last and first 5 years of the relevant data as our encroachment warning.

4.2.9 Prevention scenarios

We select four cases from the heavy grazing treatments with basis grazing a_G =0.5, 0.6, 0.7 and 0.8, each with a 30-year increase of grazing intensity by 90%. All cases exhibit the encroachment warning and all have a high likelihood (>90%) of converging to the encroached state in the absence of prevention treatments. We use the soil moisture content, grass cover and tree cover values at the end of the 30-year heavy grazing period as the initial values of the prevention simulations. All four cases undergo a grazing reduction compared to the baseline grazing by 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, or 90% for a duration of 10, 20, 30, 40 or 50 years. Once the treatment duration is over, grazing returns to the respective baseline value and the simulation converges to a steady state after a total of t=2,000 years. Each scenario is replicated 50 times with different rainfall time series.

4.2.10 Sensitivity analysis

We perform sensitivity analyses of the model parameterisation and the encroachment warning. For the former, we separately vary each model parameter value by -20% and +20% and measure the effect of the perturbation on the output variables (4.7.1 Appendix A). To test the sensitivity of the warning signal to simulated scenarios, we investigate the impact of different initial tree cover values and heavy grazing durations (4.7.2 Appendix B). To test the warning signal's ability to identify encroachment in the data we apply Δ SD intervals of different lengths (4.7.2 Appendix C).

4.3 Results

4.3.1 Alternative states

We simulated tree cover along a grazing gradient for mesic East African savanna conditions under current inter-annual rainfall variability levels (Harris et al., 2014). At each end of the grazing gradient we found a single steady state of either no woody cover (grassland: low grazing) or high woody cover, T=60% (encroached state: high grazing) (Fig. 4.1a). In the mid grazing range ($a_G=0.3-0.85$), depending on initial tree cover, the system converged to either the grassland state ($T_0=5\%$) or the encroached state ($T_0=50\%$). In the latter case, the steady state value increased with grazing from T=52% to T=60% within this grazing range.

For each tree cover steady state we measured the standard deviation (Fig. 4.1b) and autocorrelation (Fig. 4.1c) of the corresponding time series. For an initial tree cover of T_0 =50%, both increased with grazing as we moved from the single grassland state to the establishment of the alternative encroached state (bifurcation point). At the highest value of grazing still leading to a grassland state (i.e. prior to bifurcation), a_G = 0.25, standard deviation and autocorrelation peaked at just under 20% and 0.999 respectively. Similarly, standard deviation and autocorrelation increased prior to the other bifurcation point, as grazing dropped from the top end of the gradient and approached the establishment of the grassland for initial tree cover T_0 =5%. Exactly prior to the bifurcation, at a_G = 0.9, standard deviation peaked at 25% and autocorrelation reached the maximum value of 0.999.

Within the bistability range along the grazing gradient ($a_G = 0.3$ -0.8), we calculated the bistability threshold (T_c): the initial tree cover values (T_0) which separated the two alternative basins of attraction. Any simulation with T_0 within this range had an uncertain outcome, whereas simulations starting above ($T_0 > T_c$) or below ($T_0 < T_c$) the threshold range always converged to the encroached and grassland states respectively. This threshold range dropped with increasing grazing (Fig. 4.2 and Table 4.4): as grazing increased the encroached state's basin of attraction expanded, and biomes with lower initial tree cover converged to this state.

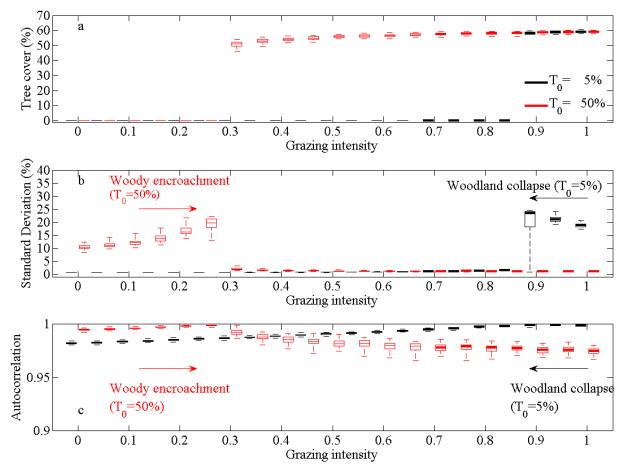


Figure 4.1 (a) Tree cover steady states along a grazing intensity gradient for simulations with low (T_0 =5%, black) and high (T_0 =50%, red) initial tree cover.). Standard deviation (b) and autocorrelation (c) values of the corresponding tree cover time series. The alternative steady states occurred as a result of the different initial conditions. Each box corresponds to the median steady state value of 50 simulation iterations. All simulations were performed using the default parameter set (Table 4.1).

4.3.2 Early warning of encrohment likelihood

We simulated the impact of 10 different short-term (30 years) heavy grazing intensities in the proximity of the bistability threshold for six baseline grazing cases. At the end of the heavy grazing period, grazing intensity returned to its respective baseline. For each grazing scenario (60 cases in total) we calculated three different early warning indicators from the tree cover time series: 5-year rolling intervals of tree cover change, standard deviation and autocorrelation. We plotted these against the proportion of simulation iterations converging to

the encroached state (Fig. 4.3). With all simulations initiated within the grassland basin of attraction, this quantified the risk that a short-term grazing increase had forced a change of steady state in the long term. All three indicators increased with the likelihood of switching to the encroached state: fitted to a linear regression, autocorrelation Fig. 4.3c) provided the best result with an R² of 64%. Standard deviation (Fig. 4.3b) and tree cover change (Fig. 4.3a) R² were 62% and 57%, respectively. The fact that the reduction of grazing at the end of the heavy grazing period did not return certain cases to the grassland basin of attraction represented a typical case of hysteresis (B. E. Beisner et al., 2003).

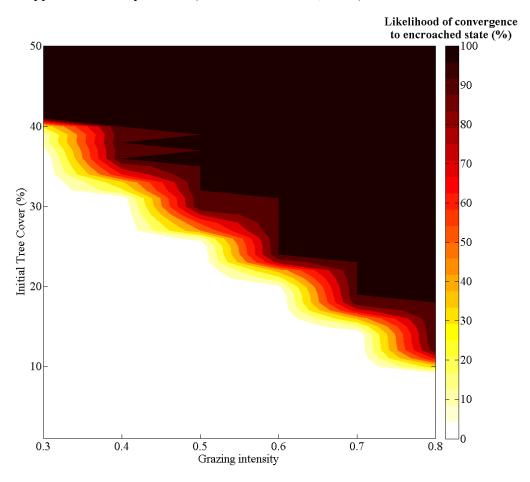


Figure 4.2 The grassland (0% likelihood) and encroached (100% likelihood) states' basins of attraction with the bistability threshold range in between. The contours depict the proportion of simulations which converged to the encroached state out of a total of 50 iterations. All simulations were performed using the default parameter set (Table 4.1). Extended simulation results are provided in Table 4.7.4.2.

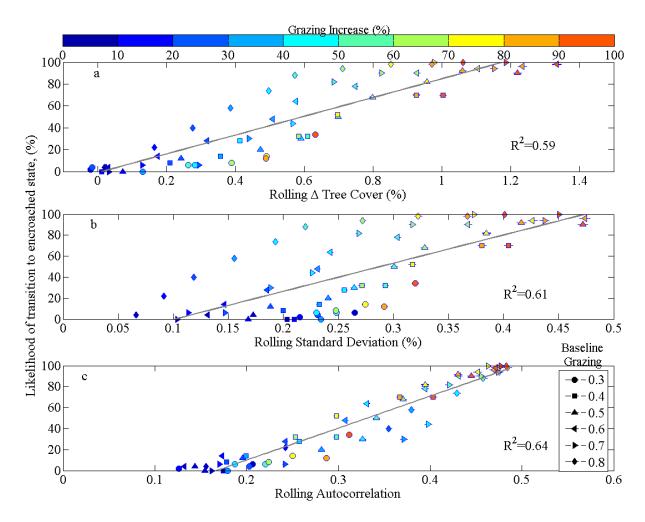


Figure 4.3 Warning indicators of transition to the encroached state. Mean values of the 5-year rolling window time series of (a) tree cover difference, (b) standard deviation and (c) autocorrelation. The rolling window time series was generated only for the duration of the heavy grazing treatment (30 years). The steady state transition likelihood refers to the proportion of simulations (out of 50) converging to the encroached steady state after the heavy grazing had ceased and the simulations were allowed to attain their steady state. Each point in the plots represents a different baseline grazing (markers) and heavy grazing treatment (colour bar) combination. Each indicator has been fitted with a linear regression with the R² value given in each plot.

The difference between the last and first 5-year standard deviations (5-year Δ SD) proved a good predictor of high (>75%) encroachment likelihood: 5-year Δ SD was positive only for these (Fig. 4.4), correctly predicting 13 of 18 total cases. The 5 cases the 5-year Δ SD did not successfully identify were detected by the 10-year Δ SD: the difference in 10-year SD between the last and first decades. In total, the combined indicators of 5- and 10-year Δ SD predicted

100% of the high risk cases, and 5 out of 7 of cases with 50-75% encroachment likelihood, and thus missed only 8% of cases with transition likelihood greater than 50%. With respect to this risk range, the combined indicators produced 8 false positives out of a total of 35 cases (22%).

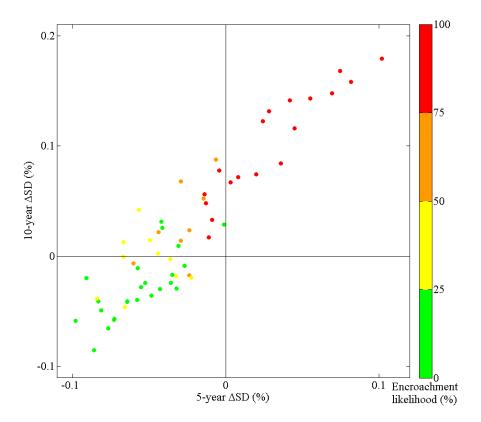


Figure 4.4 The combined encroachment likelihood indicator (5- and 10-year ΔSD) for all baseline grazing and heavy grazing treatment combinations (6 baseline grazing intensities, 10 heavy grazing treatments, Fig. 4.3). ΔSD : the SD of the first 5 or 10 years is subtracted from the SD of the last 5 or 10 years, respectively. Each point represents the mean ΔSD value of 50 iterations. The encroachment likelihood is calculated as the proportion of simulation iterations which converge to the encroached state once the heavy grazing has ceased and despite the grazing intensity having been reduced to the baseline value (i.e. irreversible encroachment). The colour map splits the encroachment likelihood into 4 ranges: 0-25% (green), 25-50% (yellow), 50-75% (orange) and 75-100% (red).

4.3.3 Warning indicator validation

We applied our encroachment warning to data from six shrub cover time series from a mesic grassland (tallgrass prairie) (Ratajczak et al., 2014). Each time series represented a different grazing and fire return interval (FRI) treatment combination. For the cases where abrupt encroachment occurred, this began after year 15 in the time series (Fig. 4.5a), so we excluded these years from the warning signal calculation. Instead, we used ΔSD of years 11-15 compared to years 1-5 of the experiment. ΔSD was positive for all four cases which subsequently became encroached. In the other two cases, shrub cover either remained extremely low (un-grazed, FRI 1 year) or increased slightly (grazed, FRI 1 year), albeit gradually, implying reversibility (Kéfi et al., 2013). Hence the encroachment warning signal successfully identified all cases that developed an irreversible encroachment pattern.

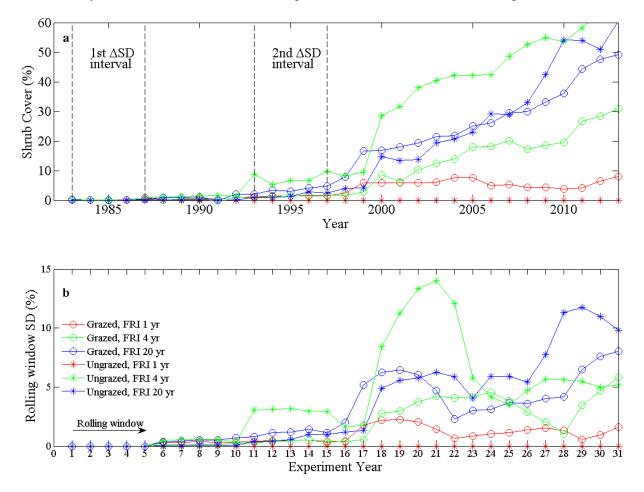


Figure 4.5 Shrub encroachment data from Ratajczak et al. (2013): (a) six time series corresponding to six treatments. Each plot in the experiment differed in the grazing (grazed, un-grazed) and fire return interval (FRI 1, 4, 20) treatments. The encroachment warning, 5-

year Δ SD, was calculated using years 1-5 and 11-15 of the time series, in order to not include years where abrupt shrub cover increases had already occurred. The resulting warning indicator values were: grazed FRI 1: Δ SD=-0.15, grazed FRI 4: Δ SD=0.27, grazed FRI 20: Δ SD=0.98, un-grazed FRI 1: Δ SD=0, un-grazed FRI 4: Δ SD=1.45, un-grazed FRI 20: Δ SD=0.84. (b) The corresponding 5-year rolling window standard deviation (SD) time series, provided as a demonstration of the SD temporal dynamics.

4.3.4 Prevention treatments

Finally, we tested encroachment prevention options on two of our simulated heavy grazing scenarios ($a_s = 0.5$, 0.8, each having undergone a 90% increase in grazing intensity over 30 years) with a high encroachment risk (~90%) (Fig. 4.6). Encroachment prevention was successful in longer treatments with strong grazing reductions. Conversely, short treatments and/or weak grazing reductions were less likely to be successful (4.7.4 Appendix D.2). The baseline grazing intensity was also important in determining the likelihood of successful prevention. For a low baseline grazing scenario (Fig. 4.6a) the prevention chances were overall better than for a high baseline grazing scenario (Fig. 4.6b). For example, all 30-year treatments with a grazing intensity reduction of 30% or more guaranteed at least a 50% prevention success probability in the low grazing baseline case. For the high baseline case, though, the same outcome required a 50-year treatment. For both cases there was a link between the treatment duration and its intensity: as the duration increased, the necessary intensity reduction dropped linearly. This relationship shifted towards stronger and longer treatments for the high baseline case and was maintained for the full treatment range. However, for the low baseline grazing case this levelled off after 30 years: beyond this point, given a constant grazing regime, increasing the treatment duration had little effect.

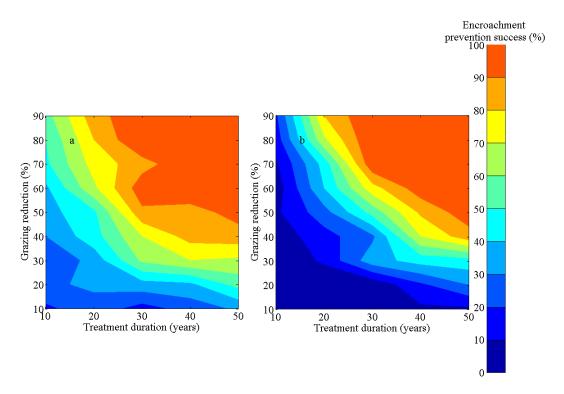


Figure 4.6 The success of encroachment prevention treatments for two different baseline grazing intensities: (a) a_G =0.5 and (b) a_G =0.8. The prevention treatments were initiated at the end of the heavy grazing period, with both cases having a high (>90%) encroachment likelihood. Here: treatment combinations of different durations (x-axis) and reductions in grazing with respect to the baseline value (y-axis). At the end of each treatment, grazing returned to its baseline value. Prevention success likelihood is the proportion of simulations out of 50 iterations that converge to the grassland state.

4.3.5 Sensitivity of model and encroachment warning

The steady state results were not sensitive to parameter perturbations (4.7.1 Appendix A), while the encroachment warning was not sensitive to initial tree cover or the duration of the heavy disturbance (4.7.2 Appendix B). When applied to data, the warning was not sensitive to the duration of the selected Δ SD window (4.7.3 Appendix C).

4.4 Discussion

Our study of grazing-induced woody encroachment in mesic African savannas demonstrated how a warning signal can identify the risk of long-term irreversible encroachment early enough for its prevention. Though temporal early warning signals have been extensively researched (Boettiger et al., 2013; Scheffer et al., 2012, 2009, 2001), very few studies have focused on applying them to avert a transition (Biggs et al., 2009; Carpenter et al., 2014). Similarly, many savanna studies have discussed the dynamics of woody encroachment (D'Odorico et al., 2012; Lohmann et al., 2014, 2012), but none have turned to early warning signals for acting against it. We focused on critical slowing down (CSD), defined as a slowing response of the system prior to transitions (Kuehn, 2011; Lenton et al., 2012) and used the standard deviation of woody cover as our key CSD indicator (Carpenter and Brock, 2006; Dakos et al., 2012).

4.4.1 Encroachment warning signal

To highlight the risk of encroachment, we first demonstrated the existence of alternative states of open and encroached savanna along a grazing gradient (Fig 1a) and how the basin of attraction of the encroached state expanded with grazing (Fig. 4.2). These alternative states of open (grassland) and woody-dominated (encroached) savanna (Hirota et al., 2011; van Langevelde et al., 2003) occur due to a positive grass-fire feedback (Higgins et al., 2000; Kéfi et al., 2015; Staver et al., 2011b): a strong fire regime maintains an open savanna while a weaker feedback allows for woody vegetation dominance (Bucini and Hanan, 2007; Calabrese et al., 2010). Grazing acts as a driver of woody encroachment (De Michele et al., 2011; Graz, 2008) by removing fire-fuelling grasses and weakening the positive grass-fire feedback (Archibald, 2008; Bond, 2008). By linking early warning signals to the transition likelihood of one state (grassland) to an alternative state (encroached) in a bistable system, we showed how a transition was preceded by increased woody cover standard deviation (Fig. 4.1b) and autocorrelation (Fig. 4.1c), which are typical CSD indicators (Kuehn, 2011; Scheffer et al., 2009; Veraart et al., 2012). Successfully preventing encroachment, though, cannot depend on indicators of steady state transitions taking place over long temporal scales (Kéfi et al., 2014). We, therefore, looked into scenarios of short-term heavy grazing followed by a return to the original grazing conditions. Our aim was to search for a distinct warning

pattern in the cases where encroachment did not subside despite the return of the conditions of their original state, thus exhibiting typical hysteresis behaviour (B. Beisner et al., 2003).

CSD indicators appeared during the short-term heavy grazing treatment: woody cover standard deviation and autocorrelation were strongly correlated to the likelihood of transition to the encroached state (Fig. 4.3b, c). Even change in woody cover (Maestre and Escudero, 2009) was a strong predictor of the transition (Fig. 4.3a). However, in the absence of any threshold in the warning signals, there was limited forecasting power in a stand-alone numerical value of an indicator. Even comparing two separate scenarios in order to get a relative estimate could not deal with our dependence on quantitative indicators lacking a clear benchmark (Dakos et al., 2015). Focusing on the temporal dynamics of woody cover variability during the heavy grazing period, though, provided us with a pattern distinguishing the cases with a high encroachment risk (>75% likelihood). In these cases, woody cover standard deviation increased with time (Fig 4).

The increase in standard deviation prior to a transition has been repeatedly observed (Boettiger et al., 2013; Dakos et al., 2012; Lenton, 2013; Scheffer and Carpenter, 2003). While in these studies, either the transitions under consideration were abrupt and discontinuous or the transition driver gradually approached its threshold over time, in our study neither was the case. The driver underwent a single increase and remained constant over the period where the warning signal appeared, while woody cover increased gradually rather than abruptly (4.7.5 Appendix E, Fig. 4.9), converging to the alternative steady state long after the heavy grazing had ceased. The observed increase in standard deviation for the cases with high encroachment likelihood occurred due to the shift toward the encroached state's basin of attraction (4.7.5 Appendix E, Fig. 4.10) rather than the convergence to the alternative state itself (Carpenter and Brock, 2006). Due to the stochasticity in the simulations, certain simulations were able to return to the grassland's basin of attraction. This was the reason that the warning signal predicted the outcome in almost all the cases (successful identification of 92% of cases with encroachment likelihood greater than 50%). However, the combined 5- and 10-year ΔSD indicators identified all high encroachment likelihood (75%) cases (Fig.4). The fact that the encroachment signal was related to the basins of attraction rather than the steady states provided a warning that the underlying dynamics had changed qualitatively, despite there being no strong evidence thereof in the vegetation composition at the time. Interestingly,

the signal worked independent of initial conditions or the treatment duration (4.7.2 Appendix B), demonstrating its independence from quantitative benchmarks.

4.4.2 Application to data

Using data from a grassland study (Ratajczak et al., 2014), which empirically demonstrated that encroachment occurred abruptly (Fig. 4.5a), we searched for the hysteresis warning prior to any discontinuous shrub cover increase. Though this abrupt transition provided a more typical example of where early warning signals have been used (Dai et al., 2012; Veraart et al., 2012), we tested the warning signal on the time series prior to any discontinuous shrub cover increase. The signal worked in all cases, highlighting the risk of encroachment in advance. Its success was most pronounced when applied to two seemingly identical time series, where it identified the one case which eventually became encroached (grazed, fire return interval 1 vs 4 years). The system from which the data was derived was a tallgrass prairie with different underlying dynamics to the African savanna on which our model was based. This further demonstrates that the application of the warning signal does not require any prior knowledge of the state of the system, its quantitative characteristics or its underlying dynamics.

4.4.3 Encroachment prevention

Predicting catastrophic transitions is only one part of averting them. It is also necessary to identify the risk in time with respect to the driver's impact on the system's dynamics and the available management actions (Biggs et al., 2009; Carpenter et al., 2014; Contamin and Ellison, 2009). In our system, the driver (grazing) was directly responsible for the transition while management actions can have an instant impact on the driver itself. As a result, the regime shift could be prevented by applying sufficiently strong grazing intensity reduction treatments for an adequate amount of time (Fig. 4.6). This highlights the importance of appropriate and timely restoration efforts and demonstrates the usefulness of the tested warning signal. The cases in which short-term heavy grazing triggered a switch to an alternative encroached state were spotted by the warning signal and only a targeted management action could prevent long-term encroachment.

4.5 Conclusions

Encroachment can be induced by increased grazing pressures (Gil-Romera et al., 2010; Lohmann et al., 2012) and management responses to prevent woody encroachment may not succeed due to hysteresis (D'Odorico et al., 2012; Ratajczak et al., 2014). Hence, once encroachment becomes evident it requires significant restoration efforts with extreme management interventions such as the cessation of grazing or the removal of woody vegetation, which can be costly and counter-productive (Scheffer et al., 2001). We identified an early warning signal of irreversible encroachment in a system undergoing a gradual and seemingly insignificant increase in woody cover. This allowed sufficient time for less extreme grazing treatments to successfully prevent encroachment, which would have been irreversible in the long term. The theory of early warning signals is too advanced to not have been proactively applied to the much-studied system of mesic savannas, which is susceptible to catastrophic transitions. Even though this warning signal would require further validation through its testing in real savanna ecosystems, it should be easily applicable via simple monitoring. We hope our study can initiate the drive for such research and a more active application of warning signals in the prevention of catastrophic encroachment in savannas.

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4.7 Appendix

4.7.1 Appendix A. Sensitivity of output variables to parameter perturbations

A sensitivity analysis was performed by perturbing a single parameter at a time, with all other parameters set to their default values (see Table 4.1 of main manuscript for default parameter set). Two different levels of perturbation were considered: -20%, +20% compared to the default parameter value. The analysis was performed with respect to the following parameters: minimum rainfall infiltration proportion over bare ground a, soil porosity (where unitary volume soil porosity $v_1 = soil\ porosity\ *unitary\ volume\ soil\ depth$), evaporation rate ε , grass transpiration rate w_G , tree transpiration rate w_T , grass colonisation rate c_T , browsing intensity rate, c_T , and the exponent of the non-linear functions c_T , for grazing, browsing and fire respectively. Grazing intensity was not part of this analysis, since our study dealt with a grazing gradient and as such the impact of grazing perturbations formed part of the main results themselves. As such grazing was set to an intermediate value throughout these simulations, c_T in the default value, c_T intensity, c_T perturbations were constrained to negative changes only. We did this because the default value, c_T cannot increase further.

Steady states were attained within t=1,000 simulation years. The steady state was taken to be the mean variable value over the last 100 simulation years. The mean of the steady states of 20 iterations was used for the results. The analysis was produced for low (T_0 =5%) and high (T_0 =50%) initial tree cover to account for the alternative state outcomes.

We define the relative sensitivity (RS) as the output variable's value given the parameter perturbation (V_p) minus the output variable's value given the default parameter (V_d) , normalized by V_d , $RS = \frac{V_p - V_d}{V_d}$ (Reineking et al., 2006). A negative sensitivity corresponds to a decreased variable value compared to the default scenario, RS < 0, and a positive

sensitivity refers to the cases where RS > 0. A variable is sensitive to a parameter if the absolute value of RS exceeds the magnitude of the perturbation. In the subsequent figures we demonstrate relative and absolute change of the output variables in response to parameter perturbations.

4.7.1.1 Appendix A.1 Soil moisture content, M

Soil moisture content was not sensitive to changes in any of the parameters (Fig. 4.7a, b).

4.7.1.2 Appendix A.2 Grass cover, G

Grass cover was also robust to parameter perturbations (Fig. 4.7c, d). In the scenario with T_0 =5% (grassland state), grass cover was only sensitive to a reduction in fire intensity (Fig. 4.7c, a_s). The weakening of the positive grass-fire feedback allowed trees to survive and a mixed tree-grass savanna replaced the grassland. This role of fire as a key driver of mesic savannas dynamics has been well documented (Bond, 2008; Higgins et al., 2000) and as such this result underlines the importance of fire in maintaining an open landscape. In the case where T_0 =50% (savanna woodland state) grasses were positively sensitive (RS>0) to a drop in tree colonisation (c_T) and an increase in tree mortality (d_T) (Fig. 4.7d). A reduction in these parameters led to a steep loss in tree competitiveness, allowing grasses to dominate. Given the strong fire disturbance, such an outcome is to be expected (Bucini and Hanan, 2007).

4.7.1.3 Appendix A.3 Tree cover, T

Tree cover was sensitive in the same parameter as grass cover, but in the opposite direction (Fig. 4.7e, f). In the low initial tree cover case (T_0 =5%), trees were positively sensitive to a decrease in fire intensity, leading to a savanna biome instead of grassland (Fig. 4.7e). For high initial tree cover (T_0 =50%), trees were negatively sensitive to a reduction in tree colonisation and an increase in tree mortality (Fig. 4.7f).

4.7.1.4 Appendix A.4 Summary

The analysis of the sensitivity of the output variables to parameter perturbations essentially confirmed the assumptions implicit in the model: mesic savannas are controlled by a combination of tree-grass competition for resources and the fire disturbance (Sankaran et al., 2004). A weakening of the grass-fire feedback allowed for the establishment of significant

tree cover, while a loss of tree competitiveness increased the effectiveness of the grass-fire feedback and led to the establishment of an open grassland. All other parameter perturbations did not impact the simulation outputs, demonstrating that our results did not depend on a specific parameter configuration.

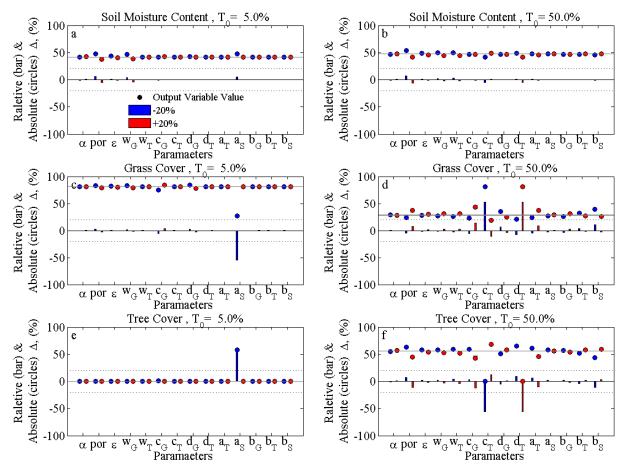


Figure 4.7 Sensitivity analysis of moisture content (a, b), grass cover (c, d) and tree cover (e, f). Parameters along the x-axis in order of appearance: minimum rainfall infiltration proportion over bare ground, unitary volume soil porosity, evaporation rate ε , grass transpiration rate w_G , tree transpiration rate w_T , grass colonisation rate c_G , tree colonisation rate c_T , grass natural mortality rate d_G , tree natural mortality rate d_T , browsing intensity rate a_T , fire intensity a_S , grazing function exponent b_G , browsing function exponent b_T , fire function exponent, b_S . Bars represent relative sensitivity, while circles show the actual variable value for each perturbation scenario. Grey horizontal line: the steady state variable value for the default parameter set. Initial tree cover differs between the left and right plots: T_0 =5% and T_0 =50%. All outcomes correspond to the steady state solutions after t=1,000 time steps and are the mean value over 20 simulation iterations.

4.7.2 Appendix B: Sensitivity of warning signal to simulation conditions.

We tested the success of the ΔSD indicator in predicting high risk encroachment cases for three different durations of heavy grazing treatments (15, 30 and 45 years) given three different initial tree cover values (90%, 95% and equal to the minimum T_c value). The simulations were run in the same way as in the main study: total simulation time was t=2,000 time steps and each grazing scenario (baseline intensity and intensity increase) repeated 50 times. The 5- and 10-year ΔSD indicators were calculated in the same way as well: we subtracted the SD of the first 5 or 10 years, depending on the indicator, from the SD of the last 5 or 10 years respectively and used the mean over the 50 iterations.

Even though the actual risk of encroachment was linked to the proximity to the bistability threshold and the duration of the heavy grazing treatment (longer treatments and higher T_0 led to more cases of high encroachment risk, red dots), the encroachment warning indicator remained independent of the simulation setup (Fig. 4.8). The combined 5- and 10-year Δ SD indicators had almost 100% success rate in predicting the high encroachment likelihood cases (>75%). Only when the starting conditions were on the cusp of the basin of attraction (T_0 = T_{c_min} , Fig. 4.8c, f, i) did the indicators miss certain cases: for the 15-year treatment 1 out of 3 (66% success rate), for the 30-year treatment 2 out of 29 (93% success rate) and for the 45-year treatment 1 out of 36 (97% success rate). In all other configurations it had 100% success in predicting high encroachment risk.

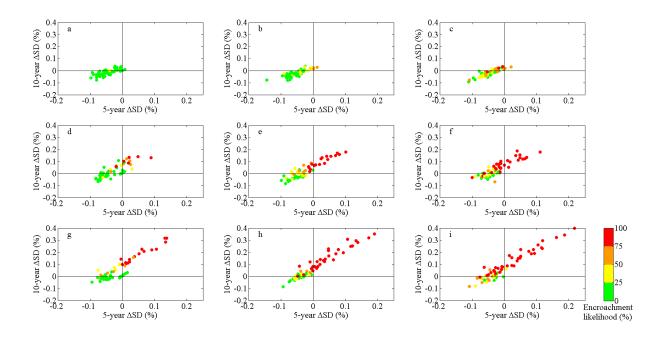


Figure 4.8 The combined 5- and 10-year ΔSD indicators for a range of initial tree cover values and heavy grazing treatment durations. Initial tree cover was either 90% (left column), 95% (middle column) or identical (right column) to the minimum value of the bistability threshold (see Table 4.7.2). The heavy grazing treatment increased from 15 (top panel) to 30 (middle panel) to 45 (bottom panel) years. The scenario shown in the main manuscript is the one in plot e. Each point in the plots corresponds to a different baseline grazing and heavy grazing treatment combination (60 in total). The colours represent different ranges of the likelihood of a simulation converging to the encroached state. This likelihood was calculated as the proportion of simulation iterations (50 in total) which converged to the encroached state.

4.7.3 Appendix C: Sensitivity of warning signal to time interval selection applied to data.

Since the shrub cover data used to validate the warning signal were short (only 15 years were used in the warning signal calculation), we applied different ΔSD intervals to demonstrate the robustness of the warning signal (3-, 5- and 7-year ΔSD). Moreover, we generated three different rolling window standard deviation time series (3-, 5- and 7-year rolling window SD) in order to create another version of the indicator and further demonstrate its validity. We then applied the same intervals as with the original ΔSD indicators to create an equivalent one: we subtracted the mean of the first interval (e.g. from the first 3 years) from the mean of the second interval (e.g. the final 3 years preceding year 15), as with the original ΔSD indicator. We, thus, created a secondary group of indicators: 3-, 5- and 7-year rolling ΔSD .

In all plots where abrupt encroachment was subsequently observed (Fig. 4.5a), all indicators were positive (Table 4.3), correctly predicting this development. In the one case where encroachment was gradual and reversible, certain indicators produced a false positive encroachment likelihood (Table 4.3, grey boxes). Given the limited number of years available within these time series, we are encouraged by the fact that different configurations of the encroachment indicator continued to successfully predict impending shrub encroachment.

Table 4.3 The Δ SD warning signal values when applied to the Ratajczak et al. (2014), calculated using different intervals (3, 5, 7-year intervals). Additional Δ SD of the same intervals of the rolling window SD are given as a further measure of accuracy.

			Plot treatment						
			3-year ΔSD	5-year ΔSD	7-year ΔSD	3-year rolling ΔSD	5-year rolling ΔSD	7-year rolling ΔSD	
Grazed, Fire return interval	erval	Yes, 1 year	-0.1090	-0.1485	0.1823	-0.0991	0.0981	0.0191	
	return int	Yes, 4 years	0.0511	0.2659	0.4044	0.2028	0.2573	0.0588	
	Fire	Yes, 20 years	0.9157	0.9796	1.1849	0.6012	0.6344	0.1566	

No, 1 year	0	0	0	0	0	0
No, 4 years	1.685	1.4503	2.6834	1.8291	2.5555	0.3959
No, 20 years	0.7324	0.8434	1.0260	0.7411	0.6219	0.1406

4.7.4 Appendix D: Tables of results.

4.7.4.1 Appendix D.1 Bistability threshold range.

Table 4.4 The proportion of simulations converging to the encroached state is provided in the main body of the table. The initial tree cover (T0) of the simulations is given in the left column. The top row shows the baseline grazing intensity. A value of 0 means that no simulations converged to the encroached state, while a value of 100 means that all simulations converged. The cases where the outcome was uncertain (neither 0 nor 100) determines the bistability threshold range. The results are based on 50 simulation iterations per scenario, each requiring t=2,000 time steps to reach the steady state.

Baseline grazing intensity, a_{G}							
		0.3	0.4	0.5	0.6	0.7	0.8
	1	0	0	0	0	0	0
	2	0	0	0	0	0	0
	3	0	0	0	0	0	0
	4	0	0	0	0	0	0
	5	0	0	0	0	0	0
	6	0	0	0	0	0	0
	7	0	0	0	0	0	0
	8	0	0	0	0	0	0
	9	0	0	0	0	0	4
	10	0	0	0	0	0	36
	11	0	0	0	0	0	72
	12	0	0	0	0	0	96
	13	0	0	0	0	0	100
	14	0	0	0	0	2	100
	15	0	0	0	0	18	100
	16	0	0	0	0	42	100
	17	0	0	0	0	76	100
	18	0	0	0	0	96	100
	19	0	0	0	0	100	100
	20	0	0	0	8	100	100
	21	0	0	0	26	100	100
	22	0	0	0	44	100	100
	23	0	0	0	84	100	100
	24	0	0	0	100	100	100
(%	25	0	0	2	100	100	100
06)01	26	0	0	14	100	100	100
	27	0	0	50	100	100	100
	28	0	0	62	100	100	100
	29	0	0	80	100	100	100
	30	0	0	98	100	100	100
	31	0	4	98	100	100	100
	32	0	28	100	100	100	100
	33	0	38	100	100	100	100
	34	0	70	100	100	100	100
	35	0	84	100	100	100	100
	36	0	100	100	100	100	100
	37	6	98	100	100	100	100
	38	14	100	100	100	100	100
	39	14	98	100	100	100	100
	40	32	100	100	100	100	100
	41	100	100	100	100	100	100
	42	100	100	100	100	100	100
	43	100	100	100	100	100	100
	44	100	100	100	100	100	100
	45	100	100	100	100	100	100
	46	100	100	100	100	100	100
	47	100	100	100	100	100	100
	48	100	100	100	100	100	100
	49	100	100	100	100	100	100
	50	100	100	100	100	100	100

4.7.4.2 Appendix D.2. Encroachment prevention success for four baseline grazing intensities

Table 4.5 Encroachment prevention success for treatments of different durations and reductions with respect to the basis grazing, $a_G = 0.5$. The restoration success is the relative frequency of simulations (out of a total of 50) converging to the grassland state after original overgrazing would have led to long-term encroachment. The results in this table are shown in Fig. 4.6a.

Treatment duration (year

		10	20	30	40	50
	90	56	86	98	100	100
©	80	50	80	100	100	100
) uc	70	48	74	86	98	100
uctic	60	38	68	96	98	100
Grazing reduction (%)	50	36	48	88	86	94
ızing	40	30	46	70	84	86
Gr	30	20	34	62	70	68
	20	28	32	36	38	54
	10	18	26	16	24	32
		1				

Table 4.6 Encroachment prevention success for treatments of different durations and reductions with respect to the basis grazing, $a_G = 0.6$. The restoration success is the relative frequency of simulations (out of a total of 50) converging to the grassland state after original overgrazing would have led to long-term encroachment.

Treatment duration (years)

		10	20	30	40	50	
	90	38	84	96	100	100	
(%)	80	28	68	88	100	100	
tion	70	10	52	88	96	100	
aduc	60	8	50	68	94	100	
Grazing reduction (%)	50	8	22	62	90	98	
ìrazi	40	6	22	34	62	70	
0	30	8	20	18	46	60	
	20	2	2	16	20	26	
	10	6	4	6	10	12	
		I					

Table 4.7 Encroachment prevention success for treatments of different durations and reductions with respect to the basis grazing, $a_G = 0.7$. The restoration success is the relative frequency of simulations (out of a total of 50) converging to the grassland state after original overgrazing would have led to long-term encroachment.

		T	reatme	ent durat	tion (yea	ars)
		10	20	30	40	50
	90	32	86	100	100	100
(0)	80	28	82	100	100	100
%) uc	70	16	64	94	100	100
Grazing reduction (%)	60	16	50	84	98	100
	50	10	36	62	92	100
	40	8	24	52	72	90
	30	4	16	34	46	70
	20	2	12	16	26	32
	10	2	2	4	6	16
		I				

Table 4.8 Encroachment prevention success for treatments of different durations and reductions with respect to the basis grazing, $a_G = 0.8$. The restoration success is the relative frequency of simulations (out of a total of 50) converging to the grassland state after original overgrazing would have led to long-term encroachment. The results of this table are shown in Fig. 4.6b.

	T	reatmer	nt durat	tion (ye	ars)
	10	20	30	40	50
90	18	80	100	100	100
80	14	68	100	100	100
70	8	44	98	100	100
60	4	40	76	96	100
50	8	26	54	82	96
40	4	16	28	70	86
30	0	12	36	44	46
20	0	0	2	18	30
10	2	2	2	8	8
	80 70 60 50 40 30 20	10 90 18 80 14 70 8 60 4 50 8 40 4 30 0 20 0	10 20 90 18 80 80 14 68 70 8 44 60 4 40 50 8 26 40 4 16 30 0 12 20 0 0	10 20 30 90 18 80 100 80 14 68 100 70 8 44 98 60 4 40 76 50 8 26 54 40 4 16 28 30 0 12 36 20 0 0 2	90 18 80 100 100 80 14 68 100 100 70 8 44 98 100 60 4 40 76 96 50 8 26 54 82 40 4 16 28 70 30 0 12 36 44 20 0 0 2 18

4.7.5 Appendix E: Temporal dynamics of tree cover.

Here we demonstrate that the increase in tree cover occurs gradually rather than abruptly (Figure 4.9). We also show the tree cover at the end of the heavy grazing period with respect to the grassland and encroached states' basins of attraction (Figure 4.10).

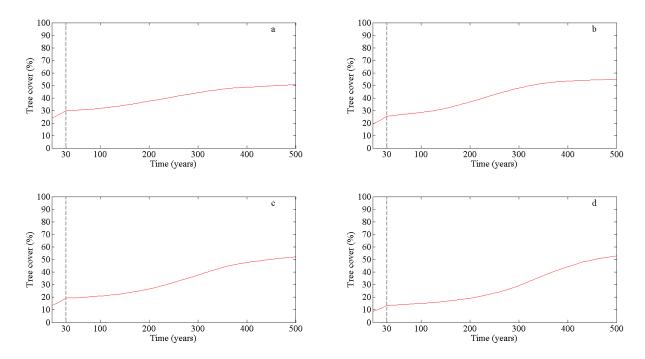


Figure 4.9 Tree cover (%)time series for the four grazing scenarios with a high likelihood of encroachment, Appendix D.2: (a) a_G =0.5, (b) a_G =0.6, (c) a_G =0.7, (d) a_G =0.8. All scenarios undergo a heavy grazing increase of 90% for the first 30 years (dotted line), before grazing returns to the respective baseline value. Tree cover here is the mean over the 50 iterations for each point in time. No simulation has converged to the steady state after 30 years, demonstrating that the warning signal picked up a change in the underlying dynamics, which are demonstrated in Fig. 4.10.

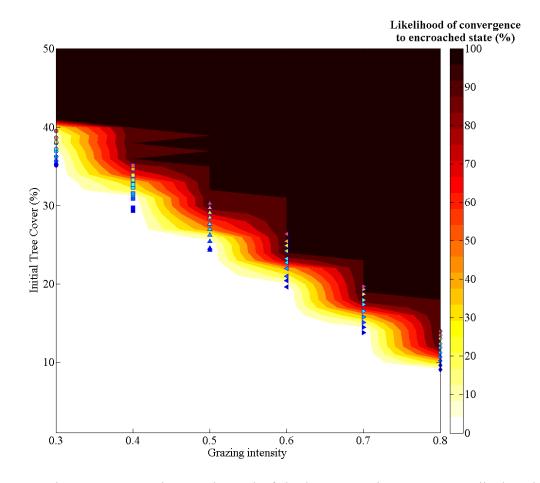


Figure 4.10 The tree cover values at the end of the heavy grazing treatments displayed with respect to the basins of attraction of the two states. Different colours of the points correspond to grazing treatments (as in Fig. 4.3). At the end of the heavy grazing treatments, simulations had not converged to a steady state, but had in certain cases shifted into the bistability threshold range or even the encorached state's basin of attraction.

4.7.6 Appendix F. References

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5 General Discussion

The complex interactions which ultimately make tree-grass coexistence in savannas possible have been - and continue to be - the subject of much research and debate (Higgins et al., 2010; Lehmann et al., 2014; Ward et al., 2013). In this dissertation, I studied these interactions with a theoretical ecohydrological model which bore both theoretical and practical advancements. I argued for the role of facilitation as a coexistence mechanism under extreme aridity (Chapter 2), demonstrated how increasingly variable rainfall patterns interact with competition and disturbance affecting coexistence and savanna resilience (Chapter 3) and developed an indicator for the early identification, and thus prevention, of irreversible woody encroachment (Chapter 4).

In the following chapter I first present the theoretical platform upon which this dissertation was built and then discuss these outcomes on their own merit. Then I shift my focus on the advancements they can yield within the context of savanna research, thus fulfilling the main objective set out at the beginning, namely 'to relate important and well-studied aspects of ecological theory, which have been developed in their own right, to savanna dynamics and thus extend the scope of savanna research'. I will conclude with some questions that stem from this work with the aim to build upon the insights gained within it.

5.1 Underlying dynamics: theory and applications

Savannas are spread globally across the tropics and beyond (Bond et al., 2005). As such, the term itself encompasses a variety of different ecosystems, with the related research questions to be answered never seeming to run out. However, on a more abstract level, all savannas share a common feature: woody and herbaceous plants compete for the same resources and despite this they coexist in the long term (Scholes and Archer, 1997). Starting with splitting the vegetation into two plant types may be a simplification not all ecologists are comfortable with, however, modelling requires a certain level of abstraction, and mathematical modelling even more so. The trade-off is that through the simplified representation of the study system, insights into its functioning can be achieved (Tietjen and Jeltsch, 2007). This is the perspective from which I approached the study of savannas: representing these biomes as an array of direct and indirect interactions between soil moisture, grasses and trees, I wanted to know how specific climatic conditions and environmental settings impact coexistence by altering the strength and importance of these interactions.

The savanna debate has spanned the best part of the past half century starting with the big question relating to the long-term coexistence of the two competing plant types (Sarmiento, 1984). Though access to sun light and soil nutrients are important, the key controlling resource in savannas is water (Sankaran et al., 2005). Walter's two-layer hypothesis stated that grasses and trees developed different spatial niches, accessing water from different soil depths and hence did not directly compete (Walter, 1972). The corollary was that coexistence was actually a state of competitive equilibrium and hence stable (Walker et al., 1981; Walker and Noymeir, 1982).

It was only later that coexistence began to appear the result of more complex processes (Jeltsch et al., 1996). A strong hint for the incompleteness of the competition model was the variation in tree cover among wetter savanna sites. New hypotheses described coexistence as an inherently unstable outcome, preserved by temporal variability in environmental factors such as herbivory and fire which either produced a 'storage effect' (Higgins et al., 2000) or buffered against a transition to an alternative biome (Jeltsch et al., 2000). In this way environmental factors became an integral part of the narrative (Sankaran et al., 2008) and consequently coexistence is currently described in terms of both competition and disturbances (Lehmann et al., 2014).

5.1.1 A different coexistence mechanism: facilitation

In 'Facilitation in drylands: modelling a neglected driver of savanna dynamics' (Chapter 2) I presented an alternative mechanism responsible for coexistence: facilitation. Focusing on dry conditions, I showed that tree cover was higher with grasses in the system than it was when grasses were not present. This was the result of the indirect impact of grasses on trees via the shading of the ground and rainfall infiltration, both of which helped maintain more moisture in the soil. Critically, the strength of this positive interaction outweighed resource competition under arid conditions. Thus, trees survived in drier conditions than they would have done if there was only competition from grasses. Hence, I postulated that the presence of grasses expanded the rainfall range where savannas could establish into drier conditions and as such facilitation represented an alternative coexistence mechanism.

This feature of plant-plant interactions under stressful conditions was not a new discovery. The Stress Gradient Hypothesis, which was first formulated over twenty years ago, stated that as environmental stress increased, so did the strength of facilitative plant-plant interactions (Bertness and Callaway, 1994). Of course this is neither a simple nor a universally applicable relationship (Maestre et al., 2005); however, there exists plenty of evidence to suggest an increase in the importance of facilitative interactions with environmental stress (Brooker et al., 2008). In the study presented in Chapter 2, grasses would have eliminated trees under extreme conditions were it not for the positive grass cover – soil moisture feedbacks. The resulting higher soil moisture availability facilitated trees by increasing their establishment and survival chances.

Facilitation of grasses towards trees at the local scale had already been described in some empirical studies. Anthelme and Michalet (2009) showed that tree seedlings performed better in the proximity of grasses. In this case facilitation took place through the increase in soil productivity and the physical protection of seedlings from herbivores. The latter, referred to as associational resistance (Smit et al., 2009), was not explicitly included in the model I used. Arguably, factoring this into the model would have produced an even stronger facilitative effect of grasses toward trees, particularly for increased grazing intensities. Iacona et al. (2012) found that grasses improved microsite conditions, providing more humidity and milder temperatures for trees to grow, even though shading itself was harmful for young seedlings. In my model design shading did not limit light access, but rather reduced the loss of soil

moisture through evaporation. Hence the facilitation pathway leading to my results was directly comparable to the effect of improved microsite conditions observed by Iacona et al. (2012). Finally, Maestre et al. (2003) had demonstrated that shrubs in a semi-arid Mediterranean grassland benefited from grasses via increased soil moisture availability and improved microclimatic conditions, resembling both the processes described in my model and the results of my study.

Though the manifestation of facilitation differed among the aforementioned studies, the common feature was the amelioration of biotic (herbivory) or abiotic (aridity) stress. Despite my model utilising a simplified representation of only the latter process, facilitation dominated plant interactions under extreme conditions. Moreover, facilitation was strong enough to extend the coexistence range into more arid conditions. Critically, this was the first savanna study to argue for facilitation as a mechanism which leads to coexistence at the biome level rather than the local scale.

5.1.2 Insights into savanna responses to rainfall variability

In 'Inter-annual rainfall variability impacts plant interactions and fire to produce contrasting responses of savannas along a rainfall gradient' (Chapter 3) I simulated conditions of increasing rainfall variability in semi-arid and mesic savannas. The inclusion of stochasticity in the occurrence of fires created alternative states of tree-less grassland and tree-dominated savanna. Within this bistable system, increasing inter-annual rainfall variability favoured grasslands in the dry and savannas in the moist conditions. In the former case, savanna tree cover dropped gradually with increasing variability, until at high variability the savanna state was eliminated and grassland became the only possible outcome. In the mesic case, however, savanna resilience increased along the variability gradient.

Currently, only a handful of studies explicitly focusing on savanna responses to inter-annual rainfall variability exist and they found this had a positive effect on trees. However, a closer look at the studies themselves and the mechanisms they invoke showed that the results presented in Chapter 3 do not contradict existing literature. Holmgren et al. (2013) used satellite data from the tropics to record tree cover changes due to rainfall variability. Even though there was a net positive effect in South America and Australia, African sites did not show any particular response. According to the authors, the mechanism of rapid tree growth

during wet extremes did not function as well in Africa, probably due to fire and herbivory. In agreement with this, I demonstrated that tree growth was limited by competition and fire during wet extremes. Strong competition from grasses limiting tree growth during years of high resource availability has already been observed in savannas (February et al., 2013; Riginos, 2009) as has the increased potency of fires during wet years (Bond, 2008; Higgins et al., 2000). In a field study of manipulated rainfall treatments Gherardi and Sala (2015) found that variability benefited trees; their key argument resting on the ability of trees to withstand droughts. However, this may be cancelled out when droughts are extreme (Fensham et al., 2009) and post-drought tree cover growth slow (Fensham et al., 2015), both of which occurred in my model simulations. Moreover, Gherardi and Sala (2015) did not consider fire in their experimental design, a critical factor in suppressing tree growth in my model and a process whose role in shaping African savanna dynamics is more or less undisputed (Lehmann et al., 2014; Sankaran et al., 2008; Staver et al., 2011). Finally, the loss of tree cover in my study took place so gradually that over short time scales - relative to the time to extinction - a clear response pattern to variability would probably not show up, as in Holmgren et al. (2013).

In the mesic case, the mechanisms involved were the same but the outcome was different due to the ability of trees to achieve cover growth in years of high rainfall. Here, not only were dry extremes less harmful compared to the semi-arid case due to the overall higher moisture availability, but wet extremes provided trees with rapid growth opportunities, as proposed by Holmgren et al. (2013). In these years, the balance between fire limiting tree cover expansion and extremely high soil moisture availability facilitating tree colonisation shifted in favour of the latter. As Harrington (1991) argued, this is key for trees to increase their survival chances. The increase in inter-annual rainfall variability produced more frequent extremes as in the semi-arid case, but this time with a net positive effect due to these 'windows of opportunity' (Holmgren and Scheffer, 2001) where rapid tree cover expansion was made possible. Another aspect of high variability was that it increased stochasticity in the occurrence of fires, also facilitating tree survival (Higgins et al., 2000). Thus, increased interannual rainfall variability in mesic conditions favoured tree survival, which ultimately increased savanna resilience.

Despite the plethora of studies on tree-grass interactions in savannas, or perhaps because of them and the multitude of different findings, the impacts of rainfall variability on savannas both at the local and the biome scale have yet to be fully understood. My holistic and mechanistic approach produced somewhat unexpected outcomes. These findings, though, were resulted from well-established aspects of tree-grass interactions and as such warrant some attention. Besides the actual outcomes of plant interactions though, my work highlighted another emerging and important aspect of rainfall variability: its influence on the competitive balance of plants through its temporal aspect, what I referred to as the temporal niche.

5.1.3 Applying early warning signals to protect savannas

'Forecasting and preventing irreversible encroachment in savannas' (Chapter 4) dealt with the problem of encroachment from a conservation perspective. It is well documented that grazing drives encroachment (Graz, 2008), which can be irreversible by a return to the pre-transition grazing conditions (D'Odorico et al., 2012), a typical hysteresis case (Beisner et al., 2003). Early warning signals were developed to predict exactly this type of transitions (Scheffer et al., 2001), but somehow were never applied to grazing-induced encroachment in savannas. In this study, I developed an indicator which quantified the risk of encroachment early enough for the process to be stopped.

My simulations produced alternative states of grassland and woody-dominated (encroached) savanna along a grazing gradient, as anticipated both by theoretical studies (De Michele et al., 2011) and the data (Hirota et al., 2011). Furthermore, grazing expanded the encroached state's basin of attraction, which like a bathroom sink pulls populations into this state (Nolting and Abbott, 2016). The challenge in preventing encroachment stems from a time lag between a switch in the basins of attraction occurring in the underlying dynamics and its manifestation in the vegetation composition. Simulating multiple short term heavy grazing treatments demonstrated exactly that: despite only small increases in tree cover, certain cases had switched into the encroached state's basin of attraction. This resulted in hysteresis, since reducing grazing to its original value was not enough to prevent these cases from converging to the encroached state in the long term.

However, a system on the cusp of two alternative basins of attraction will become less resilient, which may be reflected in its slower response to perturbations, known as critical slowing down (CSD) (Scheffer et al., 2009). CSD can reveal itself via increased variability or

autocorrelation (i.e. correlation between consecutive years) of a leading system variable (Dakos et al., 2012). Using the temporal dynamics of woody cover exclusively during the heavy grazing treatment, variability and autocorrelation were correlated to the likelihood of irreversible encroachment, indicating that this system exhibited signals of CSD (Boettiger et al., 2013). Even though these indicators could not be used as forecasting tools in the absence of a clear threshold or benchmark (Dakos et al., 2015), they led me to the identification of one that could. Increasing woody cover variability over time provided a strong forecasting tool, accurately identifying all cases with a high likelihood (>75%) of irreversible encroachment and almost all cases which had a likelihood of irreversible encroachment greater than 50%. Even more encouragingly, when applied to encroachment data from a prairie in the US (Ratajczak et al., 2014), an ecosystem quite different to the African savanna, the encroachment warning was successful in distinguishing between the cases which eventually became encroached and those which did not.

This was the first time early warning signals were applied to encroachment in savannas as a forecasting tool. Forecasting and preventing, however, present different challenges: forecasting needs to occur early enough for prevention measures to be successful. The key lies in recognising the driver of the transition and the availability of appropriate management actions (Contamin and Ellison, 2009). Since the former was known, I showed that either aggressive short term or more conservative long term reductions in grazing succeeded in preventing encroachment. Applying an early warning signal as a prevention tool has only been achieved in a handful of experiments or modelling studies to date (Biggs et al., 2009; Carpenter et al., 2014; Contamin and Ellison, 2009). This demonstrates the difficulty of finding appropriate signals, but simultaneously highlights the potential of my study, as the indicator I presented could prove extremely significant. Given our knowledge of the savanna dynamics, our understanding of the impacts of grazing and the level of control we have upon grazing from a management perspective, I consider this result as breakthrough in the conservation of savannas.

5.2 Expanding the frontiers through 'bridging'

Savanna theory and vegetation dynamics were the focal point throughout this dissertation. With this as a starting point I delved further into the theory of tree-grass coexistence, investigated the impact of temporal stochasticity on plant interactions and tested a practical tool for the timely identification and prevention of woody encroachment. Taken in isolation, the savanna dynamics I investigated have all been extensively covered in savanna literature. Tree-grass coexistence itself has been debated for decades (Jeltsch et al., 1996; Ward et al., 2013). This has yielded insights with respect to savanna responses to rainfall conditions (February et al., 2013; Higgins et al., 2000) and provided a strong foundation for understanding the phenomenon of woody encroachment (D'Odorico et al., 2012). However, I went a step further and merged each of these aspects with a different area of ecological theory or research.

Facilitation theory is a big part of ecology in its own right (Bruno et al., 2003), but had not played a significant role in the savanna debate. Hence, the Stress Gradient Hypothesis (Bertness and Callaway, 1994) with its applicability to highly stressful environments had not been extensively tested in savannas apart from certain empirical studies investigating local plant interactions (Moustakas et al., 2013). What these studies were missing, though, was a scaling up of their findings so as to present a facilitation-based coexistence hypothesis in arid savannas. 'Facilitation in drylands: modelling a neglected driver of savanna dynamics' (Chapter 2) was the first study to demonstrate how facilitation expanded tree-grass coexistence range at the biome level. Bringing together savanna and facilitation theory, I showed that indirect facilitation of grasses toward trees allowed savanna persistence in drier environments. Even though this was a theoretical study, evidence of the dynamics described in it exist in empirical studies (Anthelme and Michalet, 2009; Iacona et al., 2012), meaning that there is real potential in probing this topic further.

Following this, I demonstrated how increased rainfall variability interacted with the underlying savanna dynamics (Chapter 3). This is another area where sufficient research is lacking (Seddon et al., 2016). Apart from demonstrating how plant interactions and processes responded to increased variability, a fundamental corollary of this study was the emergence of the temporal niche as a critical component of the dynamics. If, as expected (Fischer et al., 2013), climatic conditions do become more variable over time and individual events more

extreme, it may be that water use strategies relating to the responsiveness to external conditions will be vital for plants to gain a competitive advantage (Hoover et al., 2014; Xu et al., 2015).

Early warning signals have been, and continue to be, thoroughly researched from a theoretical perspective (Dakos et al., 2015; Scheffer et al., 2012). However, their application as a management tool to prevent an impending catastrophe has been lacking (Contamin and Ellison, 2009) nor have they been applied to the much investigated phenomenon of irreversible woody encroachment. Given, on the one hand our knowledge of encroachment dynamics (D'Odorico et al., 2012) and how well they fit with systems which produce early warnings (Boettiger et al., 2013), and on the other hand our need for preventing encroachment (Lohmann et al., 2012), it was baffling that such a research gap persisted. In Chapter 5, I was not only able to bridge this gap, but I implemented the theory of early warning signals in a way which provided a management-oriented indicator for the actual prevention of encroachment, thus providing a benchmark for the application of an early warning for woody encroachment in savannas.

5.3 Outlook

In the general introduction (Chapter 1) I referred to questions which never cease to appear in research. If the work within this dissertation provided new insights, it raised some interesting questions of its own, too. Chapter 2 focused on facilitation as a possible coexistence mechanism. However, the model did not include certain plant-plant interactions which could have affected the importance (Brooker et al., 2005) of facilitation. Associational resistance, through which tree seedlings can grow within grass tussocks shielded from grazers, could be key for tree establishment in heavily grazed savannas (Smit et al., 2009). At the same time, however, these seedlings would be susceptible to strong resource competition (Riginos, 2009) and fires (Higgins et al., 2000). Another important aspect of plant interactions is spatial scale. The redistribution of resources in arid environments, for example, plays a contrasting role at different spatial scales (Gilad et al., 2007), where 'local facilitation and long-range competition' lead to vegetation patches (Rietkerk et al., 2002). Facilitation in sayannas may also function in the opposite direction, with grasses benefitting from the presence of trees (Dohn et al., 2013), with spatial scale being an important factor here as well (Riginos et al., 2009). It is clear that the formulation of the hypothesis that facilitation can act as a biomelevel coexistence mechanism will require refinement with respect to all of the above and more (de Dios et al., 2014). Nevertheless, the work presented here can act as the first step in this direction.

Chapter 3 was one of the very few studies to explicitly focus on how the plant interactions in the African savanna may respond to increased rainfall variability. Another aspect of varying rainfall patterns is increasing intensity of individual rainfall events. The impacts thereof on mixed tree-grass systems are not yet well understood leading to conflicting findings (Gherardi and Sala, 2015; Xu et al., 2015). Climate change, however, has many other aspects too which will collectively play a massive role in the future of savannas (Higgins and Scheiter, 2012; Konecky et al., 2014; Midgley and Bond, 2015). Answering questions on the impact of increasing atmospheric CO₂ concentrations on the balance between C4 grasses and trees will be key (Bond and Midgley, 2012; Buitenwerf et al., 2012; Stevens et al., 2016). Increasing temperatures are also likely to affect savanna plant interactions (Fernández-de-Uña et al., 2016) and traits (Sage and Kubien, 2007). Climate change itself is a complex issue, which adds to the difficulty of understanding how savannas will respond to it. Nevertheless, the

mechanistic approach in Chapter 3 and other theoretical studies (Xu et al., 2015) can provide a platform for searching for the answers in the right places.

Early warning signals were applied in Chapter 4 as a forecasting tool for the prevention of woody encroachment in savannas for the first time. Unlike the previous two chapters, the results did not concern the understanding of underlying dynamics and processes, but rather the creation of a management tool for the conservation of savannas. Hence, the next step would be its thorough validation. Luckily there are methods for the monitoring of vegetation cover and some time series already exist (Holmgren et al., 2013). However, these will need to be correlated to grazing intensity records. Testing the indicator against more data could lead to its improvement too. Early warnings can manifest themselves in many ways other than increasing variability (Dakos et al., 2012), so it may be that a more refined indicator can be developed. Finally, my approach focused on temporal dynamics. The use of spatial warning signals may have stalled (Maestre and Escudero, 2010), but there is much potential in it (Kéfi et al., 2014). Combining temporal indicators with spatial ones could conceivably provide a robust encroachment warning. Notwithstanding, the catastrophic consequences of encroachment (Burg et al., 2014) and the magnitude of the problem (D'Odorico et al., 2013) call for the immediate development and application of appropriate warning mechanisms.

5.4 Conclusions

This dissertation approached savannas from a theoretical perspective, studying plant interactions under stress and variable conditions as well as using plant response patterns to quantify the 'health' of the system. All three studies herein (Chapters 2-4) combined our existing understanding on tree-grass processes and interactions with a different area of ecological interest each time. The product of merging two distinct, well-studied areas of research yielded insights with respect to the outlook of savannas under dry, moist and variable conditions.

Facilitation between plants has long been accepted as an important aspect of vegetation dynamics (Brooker et al., 2008). However, it was not given particular consideration with respect to its role in savanna vegetation interactions, particularly at the biome level. Using simple and well-established assumptions about indirect facilitative interactions (Gilad et al., 2007), I demonstrated the potential of facilitation in preserving arid savannas. Even though sparse evidence for this existed in certain empirical studies (Anthelme and Michalet, 2009; Iacona et al., 2012; Moustakas et al., 2013), incorporating facilitation into the larger savanna debate was simply a matter of taking a slightly different perspective. I anticipate that there is still much scope for enhancing our knowledge in these two areas of ecological theory by bringing them together.

A similar case presented itself with increasing inter-annual rainfall variability and savanna dynamics. The role of resources on tree-grass interactions has been extensively debated (Holdo, 2013; Kulmatiski and Beard, 2012; Ward et al., 2013). To a certain extent, so has the role of varying these resources (D'Odorico and Bhattachan, 2012; Gherardi and Sala, 2015). However, a holistic approach focused on the processes, feedbacks and interactions dominating African savannas was missing. My results underline the importance of competition and fire in variable conditions. They also support the notion of the temporal niche (Xu et al., 2015), where the speed of response to resource variations may define the winners and losers (Hoover et al., 2014), showing how the outcomes may not necessarily be the expected ones.

The application of early warning signals to encroachment in savannas was another case of merging two separate, but well studied areas of research. The dynamics of encroachment due

to heavy grazing are well documented (Graz, 2008), while the process has been shown to be irreversible (D'Odorico et al., 2012) and thus represents a typical type of transition where early warning signals could be applied to (Scheffer et al., 2009). The only question that persisted was why early encroachment warnings did not already exist. For this reason, I produced a warning signal which can conceivably be used as an encroachment forecasting tool subject to further validation. If it can be shown to work, we could use simple temporal data of woody cover to quantify the risk of encroachment in the future which would be hugely helpful in conserving endangered grazed ecosystems.

My dissertation qualifies as a theoretical study of savanna dynamics. However, it also stands for something more: a case for how shifting the research perspective can yield new insights on our way to understanding the bigger picture. I used a simple modelling approach, including existing theoretical assumptions and applied this to questions which had not yet been asked in relation to savannas: can facilitation dominate savanna plant interactions with an impact on the biome as a whole; how does rainfall variability affect plant interactions in different environments; can we find early indicators of woody encroachment in order to prevent it? This dissertation answered the questions I set out at the beginning, but I hope future studies will discuss, enhance and refine the findings presented here with the aim of protecting our environment in an uncertain future.

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