



Review

Woody Encroachment as a Social-Ecological Regime Shift

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Abstract: African savannas are increasingly affected by woody encroachment, an increase in the density of woody plants. Woody encroachment often occurs unexpectedly, is difficult to reverse, and has significant economic, cultural and ecological implications. The process of woody encroachment represents a so-called regime shift that results from feedback loops that link vegetation and variables such as fire, grazing and water availability. Much of the work on woody encroachment has focused on the direct drivers of the process, such as the role of fire or grazing in inhibiting or promoting encroachment. However, little work has been done on how ecological changes may provide feedback to affect some of the underlying social processes driving woody encroachment. In this paper, we build on the ecological literature on encroachment to present a qualitative systems analysis of woody encroachment as a social-ecological regime shift. Our analysis highlights the underlying indirect role of human population growth, and we distinguish the key social-ecological processes underlying woody encroachment in arid versus mesic African savannas. The analysis we present helps synthesize the impacts of encroachment, the drivers and feedbacks that play a key role and identify potential social and ecological leverage points to prevent or reverse the woody encroachment process.

Keywords: savanna; Africa; alternate state; woody encroachment; ecosystem services; leverage points

1. Introduction

Woody encroachment has been a problem in both southern African savannas [1] and globally for over a century [2], and appears to be increasing in many regions [3,4]. Savannas are mixed tree-grass systems that are characterised by a continuous grass layer and a discontinuous tree layer [5], and support a range of livelihoods, economic activities and biodiversity [2,6]. Savannas are home to 505 million people in Africa, most of whom rely directly on these ecosystems for their livelihoods [7]. Woody encroachment is a shift from a grassy savanna to a persistently woody savanna, and typically involves indigenous woody species rather than invasive alien species [1,3]. Woody encroachment threatens the provision of ecosystem services such as food and clean water, grazing for livestock farming, and habitats for some of the world's last remaining mega herbivores [6,8,9].

There is growing consensus that managing anthropogenic impacts on ecosystems and the services they provide requires a better understanding of the interactions between ecological and social systems [10]. Much of the research on woody encroachment has focused on ecological drivers, especially the impact of disturbance (e.g., fire and grazing) and water availability on tree establishment

and persistence [11–14]. Few papers explicitly consider the role of social processes underlying these ecological changes, or how ecological changes can provide feedback to affect the underlying social processes. In this paper, we build on the ecological understanding of woody encroachment, to develop a broader social-ecological understanding of the dynamics underlying woody encroachment.

One way to conceptualise the process of woody encroachment is to view it as a regime shift [15–18]. Regime shifts are large, persistent changes in the structure and function of ecological or social-ecological systems (SES) [15,16]. SES dynamics result from feedback loops involving both ecological processes (the interaction between abiotic and biotic factors driving the system) and social processes (human behaviour and institutional processes influencing the system) [17,19,20]. SES have several competing feedback loops operating simultaneously, including both balancing and reinforcing feedback. Reinforcing feedback loops are amplifying, self-multiplying processes that can be positive or negative and hence cause growth or runaway collapse over time [21,22]. Balancing feedback loops decrease or reverse change in a system, and can be sources of stability as well as resistance to change. The set of feedback loops that dominate the system at a particular time will determine the system's present regime (Figure 1) [21]. A particular regime is characterised by a specific systemic structure and set of functions, and is created and maintained by a particular set of feedback loops.

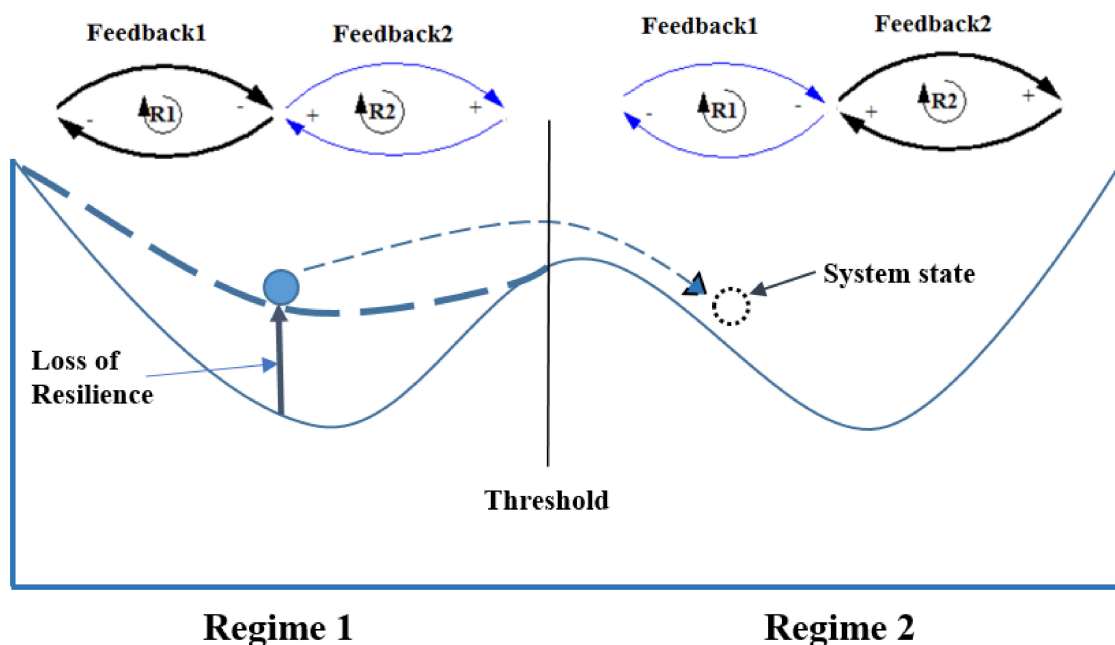


Figure 1. A simplified illustration of a regime shift. R1 represents the dominant feedback loop in the system in regime 1. Over time, as the system variables and drivers change, the strength of feedback 1 may be reduced, leading to a loss of resilience. At some point, the system may cross a critical threshold and shift into regime 2 where feedback 2 is dominant. The cup represents a particular regime and the ball represents the ecosystem state at a certain point in time. The loss of resilience is represented by a change in the shape of the cup.

A regime shift can occur when there is a change in the set of dominant feedback loops. This can occur for two reasons. Firstly, due to an external shock such a drought, and secondly, due to a gradual change in drivers that slowly weaken the dominant system feedback that maintain a particular regime [16,23]. Slow changes may gradually weaken the dominant feedback with no visible system change until an external shock hits the system, causing it to cross a critical threshold and move into an alternate regime (Figure 1). The drivers that affect system feedbacks can be internal, within a feedback loop and influenced by the feedback; or external, outside the feedback loops and not influenced by changes in the SES [21]. Most often, a regime shift results from a combination of a shock and gradual

changes in internal and external drivers. Regime shifts often have substantive impacts on the suite of ecosystem services provided by an ecosystem or SES, and consequently on human well-being [24,25].

Reversing a regime shift requires sufficient understanding of the system to know which feedback is, and was, dominant and what actions or drivers can break unwanted feedback loops or recreate lost feedback loops. The strength of the dominant feedback determines how easy it is to reverse a specific regime shift [26]. It is also important to note that the threshold levels of drivers that trigger a shift from one regime to another may differ from the threshold needed to shift the system back. This is known as hysteresis and characterizes many regime shifts [15,25].

The objective of this paper is to review woody encroachment in African savannas using a social-ecological regime shift lens. We identify the key drivers, feedback and thresholds using the Biggs (in review) regime shifts analysis framework. We specifically examine the ecological and social processes underlying encroachment and how changes in these processes weaken, strengthen or alter social and ecological feedbacks in arid versus mesic savannas. This analysis allows us to synthesize the associated ecosystem changes, and allows us to identify leverage points—or places to intervene—for preventing or reversing woody encroachment in different contexts.

2. Methods

To identify relevant literature on woody encroachment, we performed a bibliographic search using Scopus (<http://www.info.sciverse.com/>). We searched for the key terms “woody encroachment and savanna” and “bush encroachment and savanna”. The eligibility criteria included all types of documents: peer reviewed papers, books and book chapters, published between 1 January 1984 and 31 December 2015 with the defined terms in the title, keywords or abstract. The papers were imported into the online systematic review software product Covidence (Melbourne, Australia) (<https://www.covidence.org/>) for screening. We removed duplicates and papers that mentioned the search terms but were not relevant to our search, e.g., papers on alien invasive species and the invasion of trees into grasslands (as opposed to savannas). We then filtered the papers to those dealing specifically with African savannas. The selected papers were read in full, and variables and their interactions were captured in a qualitative systems model. For each paper, we recorded the proposed driver of woody encroachment and classified these into fire, grazing, browsing, moisture, tree-thinning/harvesting, temperature, tree density, CO₂, and nutrients.

We used the Regime Shift Database framework (RSDB, www.regimeshifts.org) to synthesize existing literature on woody encroachment in savannas from an SES perspective (Figure 2). We chose the RSDB framework because it draws strongly on a systems-based understanding of the dynamics underlying regime shifts. The RSDB framework systematically analyses regime shifts based on their drivers, underlying feedbacks, impacts and management options. A key aspect of the RSDB approach is the development of a causal loop diagram (CLD) which synthesizes the key drivers and internal feedbacks in a system based on the literature [21]. The CLD is accompanied by a description which includes the definition of the system and a description of the alternate regimes, the feedbacks that maintain each regime, and the drivers of the regime shift in the system. Also included are leverage points and management options for preventing, reversing or facilitating a shift. To develop the CLD, we complemented the literature from the bibliographic search with understanding from additional relevant literature on the dynamics of savanna ecosystems.

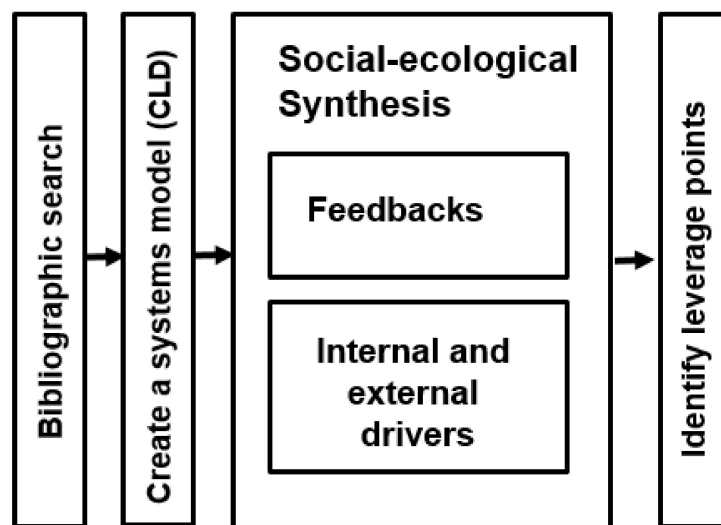


Figure 2. Summary of the steps used to synthesize the literature using a social-ecological systems lens.

To demonstrate the distribution of arid/semi-arid savannas and mesic savannas, we plotted mean annual rainfall across Africa. We used the divide of ~700 mm as a boundary to delineate the distribution of these two savanna types [27,28], with savannas receiving less than 700 mm being defined as semi-arid and arid savannas and areas receiving more than 700 mm as mesic savannas. We overlaid the distribution of savannas onto this map, using the savanna distribution defined by [29].

3. Regime Shift Synthesis

The search “bush encroachment and savanna” and “woody encroachment and savanna” returned a total of 318 papers. Of the 318 papers, 232 reported on work in African systems. 74% investigated the drivers of woody encroachment, with fire and grazing as the most commonly (45 and 40 papers, respectively) cited drivers (Figure 3).

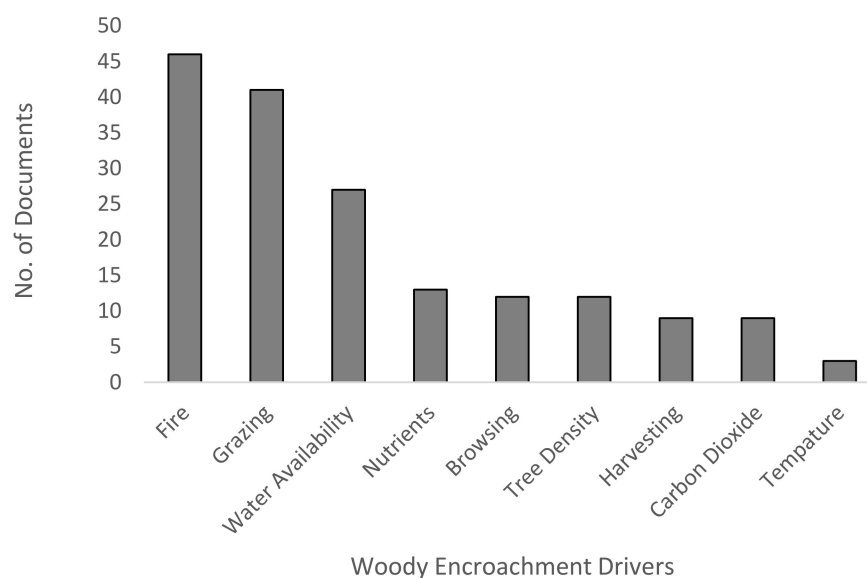


Figure 3. Number of documents reporting significant impacts of different drivers of woody encroachment.

Based on these documents, we developed a conceptual model of the main ecological and social processes underlying woody encroachment in African savanna systems (Figure 4). We used this as the

basis for developing a CLD (Figure 5), and identifying feedback loops, drivers, and leverage points of woody encroachment. Below, we first describe the two alternate regimes based on the dominant feedback loops and drivers we identified, and then discuss the key feedbacks that sustain each regime, the internal and external drivers that can lead to a regime shift, and finally conclude with a discussion of the potential leverage points.

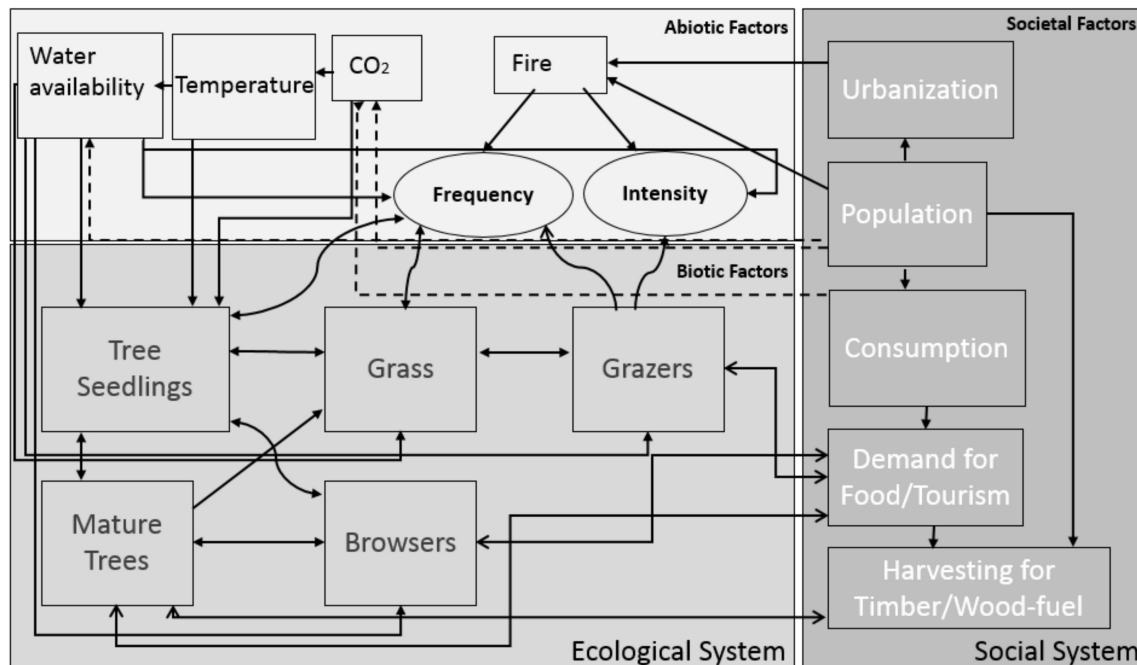


Figure 4. A simplified conceptual model illustrating the main processes and feedbacks that underlie woody encroachment regime shifts in a savanna social-ecological system.

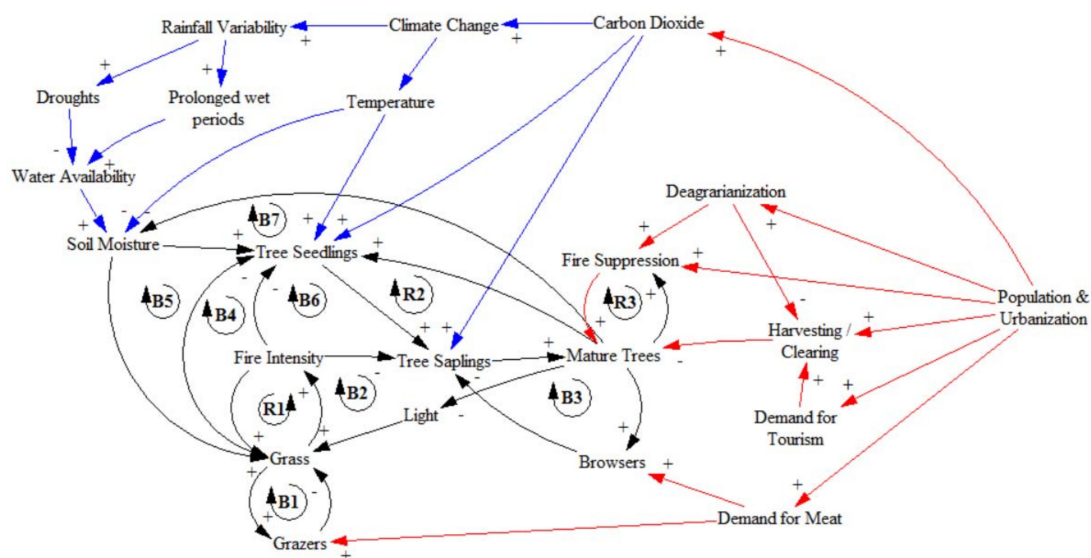


Figure 5. Causal loop diagram illustrating key feedbacks and drivers underlying woody encroachment in savanna systems. Red links denote external anthropogenic drivers, blue links denote social-ecological drivers, and black links are internal system interactions and feedback. R denotes a reinforcing feedback loop and B a balancing feedback loop. The arrow heads have polarity signs indicating whether the relationship is one that leads to either increases (+) or decreases (−) in the state variables. S refers to largely social drivers, SE to social ecological drivers and E.

3.1. Alternative Regimes: Grassy and Woody

It is well documented that savannas can exist in two alternate self-reinforcing regimes [15,30]: a grass dominated regime and a tree/shrub dominated regime. The grassy savanna regime consists of an herbaceous layer dominated by C4 grass species and a discontinuous tree layer [5]. The grassy regime is maintained by frequent fire that topkills tree saplings and prevents them from reaching heights where they are no longer affected by fire. Grassy savannas are typically used as grazing lands for livestock and free-ranging wildlife.

The woody regime is dominated by woody shrubs or trees [5]. Once established, woody vegetation persists because adult trees are seldom killed by herbivory or fire [31]. The woody regime may cover large continuous areas or be expressed as a mosaic of small patches of woody plants interspersed within open savannas. These respective patches are often highly persistent over time [32]. Woody savannas are primarily used for wood and non-wood forest products that provide fuel, food, medicines and raw materials for building, crafts, and tools.

3.2. Feedback Mechanisms

Each of the regimes are dominated by particular feedbacks that determines the vegetation structure (Figure 5). The dominant processes differ between arid and mesic savannas (Figure 6). Arid savannas receive less than ~700 mm of rain and maximum tree cover is constrained by water availability [27]. Mesic savannas receive over 700 mm of rain, so there is sufficient water availability for canopy closure, but this is prevented by the action of fire and herbivory [27].

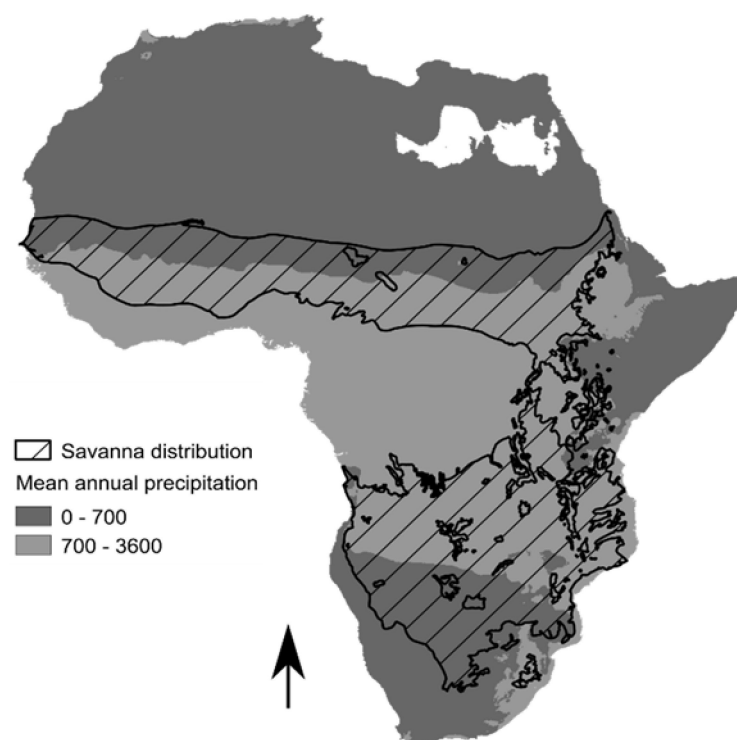


Figure 6. The distribution of arid/semi-arid and mesic savannas across Africa.

3.2.1. Grassy Regime

This regime is dominated by the fire feedback (R1) [27]. Fire rarely kills mature trees but has a negative impact on the seedling and sapling regeneration of woody plants [12,31,33,34]. Frequent fire prevents saplings from escaping the fire trap where they remain reproductively immature [31]. Tree saplings can spend decades in this immature state where they are not able to resprout quickly

enough to escape frequent fires. Fire therefore reduces the number of seedlings and tree density in the system, and prevents canopy closure, which ensures there is sufficient light for C4 grasses. Fire is particularly important in mesic savannas as a reinforcing feedback as there is sufficient rainfall for canopy closure to occur [27,35]. Arid savannas have a lower fire frequency due to lower grass productivity [36], as water and nutrients are a limiting factor that prevents canopy closure [27]. Although fire is an ecological element, the extent, frequency and intensity of fire is largely determined by anthropogenic factors. Human population size and land use have a substantial impact on the fire regime by influencing fire frequency, season, and location, which influences fire intensity [37]. A high grass biomass (which is affected by the soil moisture and nutrients, light and grazers feedbacks), causes more frequent and intense the fires [27,36]. The number of grazers (especially cattle) are in turn affected by demand for food, consumption preferences, access to land and different institutional arrangements based on land use and value systems [38–40].

3.2.2. Woody Regime

This regime is dominated by two reinforcing feedbacks, the micro-climates/recruitment feedback (R2) that dominates in arid savannas, and the fire suppression feedback (R3), which is most likely to occur in mesic savannas. The fire suppression feedback is directly affected by fire policies, which are related to regional population growth and urbanization.

In arid savannas, tree recruitment occurs when seed availability and high rainfall events occur over the same spatial area [41,42], and facilitation can outweigh competition for resources [32,43]. Facilitation occurs when existing mature trees trap and retain nutrients and water by lowering evaporation and increasing infiltration through shading and root penetration, creating a microclimate that fosters tree recruitment [32,43]. Additionally, established trees have a positive effect on each other by accumulating local water deeper in the soil profile and nutrients from the surroundings and creating “islands of fertility” [32,44]. However, inter tree competition for resources can also reduce tree growth in arid savannas [43].

In mesic savannas where canopy closure is possible, fire suppression (through fire legislation and land management strategies) allows saplings to escape the demographic bottleneck and establish as mature trees where they can no longer be killed by fire or herbivory [31]. Once woody cover surpasses ~40%, light attenuation occurs [43,45]. A reduction of light reduces C4 grass biomass as they are adapted to greater light intensity [46]. This creates a powerful reinforcing loop as a decline in grass biomass leads to reduced fire intensity and frequency [36], which further favours woody plant establishment.

3.3. Drivers of Woody Encroachment

Woody encroachment has been attributed to a variety of processes that can be encompassed in two models: demographic bottleneck models and competition-based models. Demographic-bottleneck models emphasise the impact of disturbance and water availability on tree establishment and persistence [1,31,44,47]. Competition-based models, as the name suggests, emphasise competitive interaction in determining tree-grass co-existence, with co-existence resulting from spatial or temporal niche separation [1,47–49].

The drivers of woody encroachment can be categorized into internal system changes, external drivers and shocks. A recent overview of 23 studies by [1] concludes that the occurrence of woody encroachment depends on the interplay of these shocks, internal and external drivers; recognition of this is essential for containing encroachment. These drivers play different roles in enabling, initiating and sustaining woody encroachment depending on the processes they influence in the broader social-ecological system.

3.3.1. Internal System Changes

There are a set of well-established internal system drivers that can push a savanna towards either a grassy or woody regime. These include changes in tree density, grazers, browsers and soil moisture. All of these affect fire frequency and intensity.

Tree Density

Tree density changes slowly but affects and responds to the micro-climate/recruitment feedback (R2) and the fire suppression feedback (R3) that are dominant in the woody regime. Changing tree density also influences fire behaviour [50], which is affected by grass biomass, rainfall variability and seasonality, tree cover, topography, grazing [36,50,51].

Grazers and Browsers

Grazing and browsing are a natural component of savanna systems, but the number of grazers (especially cattle) and browsers are affected by demand for food, consumption preferences, access to land and different institutional arrangements based on land use and value systems [38–40]. Sustained heavy grazing by livestock ranching promotes woody seedling regeneration through reduced grass competition, provided that seedling mortality is not increased through consumption and trampling, and there has been above average rainfall in more arid savannas [1,12,52]. Heavy grazing in mesic savannas reduces fuel load through consumption and trampling, thereby reducing fire frequency and more significantly fire intensity [1,31,36,44,53]. Overgrazing has also been reported to reduce the effect of grass competition on tree seedlings and saplings, as a dense grass layer can negatively affect tree growth and survival [54–56]. Long-term grazing trials in both mesic and arid systems have consistently reported increases in the density of woody plants over 5–40 year periods of observation [52].

The loss of browsers due to anthropogenic landscape changes and hunting, especially the loss of mega-herbivores such as elephants, is thought to be one of the major drivers of woody encroachment [1,57]. Bark-stripping and uprooting of trees by elephants can result in mortality of adult trees and seedlings, and maintain plants within flame height [1,58]. Browsing of seedlings, on its own, appears capable of containing woody encroachment under some circumstances [1,13,59], by minimizing the dominance of the micro-climates/recruitment feedback [60]. Recent research has empirically shown the impact of the loss of mega-herbivores [61–63]. The release of trees from browsing pressure in a study in Mozambique resulted in tree cover increases ranging from 57% to 134% over a 35 year time period—with no directional trend changes in fire and rainfall [62].

Soil Moisture

Water availability influences all of the components of the system and is the critical limiting factor to plant growth in savannas [27]. Any measure of plant productivity from phenology to growth rate relies on the amount of precipitation in the region [27,64]. In arid savannas, increased soil moisture (high rainfall frequency) promotes seedling regeneration and establishment, and tends to favour the establishment of woody species [1,41,43,44,65]. Ref. [42] documents that three consecutive years of above average rainfall are necessary for the recruitment of woody species. This has also been reported in Australian semi-arid savannas and in bin experiments [41]. In mesic savannas, increased soil moisture contributes to increased grass biomass, therefore higher levels of grass competition, fuel loads and higher fire intensities [13,27,34,66], which maintain the grassy regime.

3.3.2. External Drivers

External drivers include either social or socially driven ecological drivers (e.g., fire suppression or land use). These include quantifiable physical drivers such as population growth and tree harvesting, as well as complex emergent features that are difficult to quantify such as governance and worldviews or mental models. The latter tend to impact both the social drivers and the socially driven ecological

drivers through legislation and value systems that have an impact on land use and institutional arrangements/management systems.

Population Growth and Urbanization

Human population growth can affect internal system variables and processes in ways that can either increase or decrease woody cover and the potential for encroachment. As human population grows, food demand increases incentives to increase cattle numbers, given current consumption preferences [38]. Furthermore, in most African cultures, large cattle numbers represent power and wealth because they provide milk and meat, their droppings can be used as fuel for fires, and for plastering walls and floors in houses, and they are used as a form of money to pay fines and lobola [67]. At high densities, cattle reduce the grassy layer and fire frequency, which facilitates tree establishment and hence encroachment [31,36].

A demand for wildlife tourism has led reserve managers to increase the number of certain game species that appeal to tourists [68,69]. The reestablishment of elephants in many reserves in South Africa has led to reductions in woody plant cover [58,70]. Demand for tourism also influences tree cover as visibility of animals is a contributing factor for returning to a game reserve [9]. Reserve managers therefore invest in tree clearing or increasing fire frequency to manage tree cover.

On the other hand, in many rural areas, food demand may also lead to an increase in browsers such as goats. Goats are the only livestock herbivore known to effectively reduce woody cover, and hence counteract encroachment [1]. Increased human populations also increase tree harvesting, which reduces the amount of adult tree biomass in savanna system [71,72]. This has a direct impact on the microclimate/ recruitment feedback that reinforces woody growth.

As countries develop, they tend to restructure their economies away from agriculture into manufacturing and services [73]. With the world rapidly urbanizing, 50% of the population in developing countries is estimated to be living in cities by 2020 [74]. Deagrarianisation in large parts of South African communal areas has resulted in a significant increase in woody encroachment in abandoned cultivated fields [75,76], and this is likely to happen elsewhere as well as rural areas depopulate.

Land-Use, Institutional Arrangements and Worldviews

Management practices and institutional arrangements are based on specific mental models or worldviews that draw on scientific understanding and local ecological knowledge. Mental models reflect our understanding of how a system works: the interactions between factors or components, the critical issues, and the causal links [77].

In early colonial days, fire suppression laws were passed in southern Africa, which were based on European attitudes/worldview towards fire. These views were amplified by the Drought Investigation Commission report in 1926, which promoted the view that fire was undesirable in savannas [1,78]. Fire suppression refers to the reduction in the frequency and intensity of fire in a system compared with the natural or historic fire regime. As fire has a strong negative impact on tree growth and recruitment, fire suppression promotes an increase in woody vegetation, reduces the dominance of the fire feedback and increases the dominance of the microclimates/recruitment feedback. As the recognition of the importance of fire in African savannas became more apparent, a number of fire trials were set up across Africa in the 20th century. An analysis of 28 fire trial experiments, found that fire exclusion has an unequivocal influence on the increase of trees in savannas within a rainfall range of 386–1900 mm per annum [1]. Tree density increased by 5.8% more under fire exclusion compared with other burning regimes.

South Africa's changing social and political regimes and structures provide a great example of how interlinked social and ecological systems are. The Apartheid government forced the majority of black people into smaller portions of land, which led to degradation in communally managed areas compared to privately owned white farmlands [76]. A democratic government brought with it the

freedom to live in any area, which contributed to a rise in rural-urban migration as people move to cities in pursuit of better opportunities, and land reform structures which contributed to a significant portion of cultivated land being transferred to inexperienced and poorly supported farmers [75,76]. These changes have indirectly contributed to an increase in woody encroachment [76].

Carbon Dioxide

Currently, the anthropogenically-driven warming climate and increased atmospheric carbon dioxide are thought to be the leading drivers of woody encroachment as they accelerate root growth and enhance sapling resprouting after fire. In addition, these drivers enhance tree water use efficiency, and can potentially extend the summer growing period, which increases the survival rate of woody plants [79–81]. The underlying mechanism is still debated, but several possibilities have been proposed. The first hypothesis is that higher carbon dioxide (CO₂) concentration levels favour C3 (woody plant) photosynthesis relative to C4 (tropical grass) photosynthesis, which accelerates woody plant growth and can promote a faster escape of saplings from the fire trap [79,81]. This has been supported by evidence from multiple Free-Air Carbon Dioxide Enrichment (FACE) experiments that expose vegetation to elevated CO₂ [82]. A comparison of different ecosystem responses to elevated CO₂ showed significant differences among arid savannas, grasslands and forests. On average, increases in above ground production were significantly greater in arid savannas than in forests and grasslands, with forests having greater net primary production than grasslands [83]. The second hypothesis is that higher CO₂ levels may reduce transpiration of plants through reduced stomatal conductance, causing greater water filtration and increased soil water [79,84]; this is especially important in arid savannas, as woody plants can produce more biomass for the same amount of rainfall [79,80,82].

3.3.3. Shocks

Drought plays an important role in woody encroachment by decreasing the likelihood of fires. As the grass dies and is grazed out, there is seldom any fire [1]. An extreme drought reduces grass biomass and, when rain does arrive, grass recovery is slow. During this time, tree establishment can occur rapidly in the absence of grass competition [1,41]. In contrast, high rainfall frequencies in arid savannas give woody seedlings a competitive edge over grass. Seedling recruitment (R2) in arid savannas usually occurs during consecutive higher rainfall years [41]. The frequency and intensity of drought and high rainfall events are being influenced by rising CO₂ and a warming climate.

3.4. Management Options and Leverage Points

Effective management needs to find points in the system to intervene, where a change in the system will produce the most gain. These are called leverage points. This requires a good knowledge of the system, including knowledge of variables, flows, delays in flows or response of variables, and different feedback loops [21]. Effective management centres on manipulating the flows and feedback in the system, taking account of possible delays. The key leverage points in savanna systems include manipulation of fire, browsing and manual clearing.

Manipulating the fire frequency strongly affects the tree/grass ratio, especially in mesic savannas. Increasing fire frequency in a system promotes grass regeneration, which has a negative impact on tree seedling establishment through competition, and suppresses tree saplings to control tree dominance. Long-term research suggests that normal fire regimes will not be able to curb the effects of CO₂ [14], suggesting that higher fire intensities are required to prevent the spread of woody plants. Ref. [85] demonstrates that a fire regime that includes regular storm-burning (high intensity burning) can be effective for maintaining grassy savannas by preventing encroachment by trees [85]. Smit et al. found that repeated high-intensity late season fires greatly reduce tree cover over low to moderate intensity fires [86]. However, these high-intensity fires came at the expense of losing tall (5–10 m) trees, which is not desired. Strategic use of high-intensity fires is therefore necessary to maintain a heterogeneous landscape.

Browsers (ranging from goats to elephants) can suppress woody growth, limit the establishment of woody seedlings, and reduce canopy cover [61,62,87]. The widespread elimination of megafauna e.g., elephants, and the overall reduction in the numbers of browsers, is considered a wide scale driver of tree cover increases in Africa [60,62]. Reintroducing browsers back into savanna systems can have a negative impact on both mature trees and tree seedlings, and shift feedbacks in favour of the grassy regime.

Grass production declines more rapidly for initial increments in tree basal area than it does for subsequent increments [49]. With this knowledge, Ref. [30] proposes that 40–50% tree cover in savanna systems is the threshold at which the system shifts from the grassy to the woody regime. This is due to the influence of fire on the spread, frequency and intensity of fire above a threshold of 45% to 50% tree cover [28]. Clearing trees and maintaining tree cover below 40% may be critical for preventing a shift from a grassy to a woody system. Tree clearing is an expensive endeavour and unrealistic in some systems [86], but if done strategically in patches to increase grass cover and keep trees below 50% cover [88], over time this could weaken the micro-climate/recruitment (R2) and fire suppression (R3) feedback loops that help sustain the woody regime. Though clearing efforts are widely attempted, the costs of clearing are not generally reported in the literature [89]. Namibia estimates that the total cost for the control of woody encroachment through clearing is US\$2.1 billion. A study on different clearing strategies of 29 woody species in Ethiopia concluded that the most effective rehabilitation strategy was clearing and fire combined with grazing [89].

All the above leverage points involve manipulating internal system variables. Recent research documenting fence studies indicate that global change (particularly increased CO₂) may be overriding local management [14,90,91]. Land use can be manipulated to yield different tree cover percentages. Currently, without excessive human intervention through mechanical clearing, fire storms or introducing elephants into the system, global drivers such as increased carbon dioxide concentration, which are driven by anthropogenic changes, are probably overriding the system.

4. Discussion and Conclusions

This review expands current ecological understanding of woody encroachment in savannas, to a broader social-ecological perspective. Considering woody encroachment as a social-ecological regime shift takes the focus away from single drivers and considers the broader system with an emphasis on the interconnections amongst underlying feedback processes, particularly the interplay between social and ecological processes.

Our analysis highlights that humans have both local and global influence on savannas, and that the increasing shift from grassy to woody savannas may ultimately be largely linked to growing human populations. Given current consumption preferences and technologies, growing human populations are linked to increased demand for livestock production as a source of food, and to increasing carbon dioxide emissions through various human activities. There is also a direct link between growing human populations and fire suppression. All of these factors mostly affect savanna systems in ways that increase the likelihood of woody encroachment.

Identifying key leverage points in the form of feedback loops and drivers is imperative for effectively managing savanna systems. Our analysis highlights that, in mesic savannas, fire and fire-competition feedbacks maintain the grassy regime, while water is the limiting factor that prevents tree establishment in the arid savannas. A frequent fire regime that includes fire storms and strategic clearing is therefore key leverage in maintaining a grassy regime. On a broader scale, influencing consumption preferences or technologies in ways that reduce grazing pressure and carbon dioxide emissions could also play a key role in maintaining open savanna systems. The possibility of identifying both direct local and indirect global leverage points in an integrated way in a single analysis is a key strength of the RSDB framework.

The review focuses on woody encroachment in savannas, but similar processes can lead to shifts between biomes. In certain areas, grasslands, savannas and forests occur as alternate regimes under

the same climatic conditions [28], and shifts between them may occur when factors such as rainfall and fire frequency are altered [57,92]. We suggest that the loss of C4 grass in mesic savannas is coupled with the loss of resilience associated with anthropogenic climate change and increased carbon dioxide concentrations. Similarly, increased rainfall events (frequency) are shocks that can overwhelm the arid system, pushing it towards a woody regime.

Changes in the concentration of carbon dioxide provide new research opportunities as savanna dynamics seem to be changing as carbon dioxide concentrations are overriding the historical dynamics of these systems [81]. This reveals a need for new research to investigate the effect of temperature, carbon dioxide concentration on savanna and forest trees, and how this affects tree-grass competition, and hence management policies and strategies.

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