The Savannas: An integrated synthesis of three major competing paradigms

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Abstract

The coexistence between trees and grasses in the savannas is a contentious issue. Although necessary scientific efforts have been done, unfortunately such efforts have given rise to contrasting theories and models. This review provides a synthesis of these theories how they influenced our understanding of the savannas over time. The review found that while the equilibrium theory predicts savannas as stable ecosystems regulated by natural mechanisms such as root niche partitioning, such ideas have been disputed in favour of non-equilibrium framework. The latter suggests that savannas are unstable ecosystems largely regulated by stochastic dynamics such as inter annual rainfall variations and episodic environmental shocks such as fire and overgrazing which result in an ecosystem oscillation between grass dominated and woody dominated phases in time and space. On the other hand the disequilibrium paradigm argues that savannas are unnatural ecosystems formed as a result of anthropogenic disturbances such as fire and grazing that buffer the ecosystem from complete domination by either trees or grasses. This review demonstrates that the savannas still lack a unifying theoretical framework. The current one is characterized by conflicting, contradictory, diverging ideas. Such revelations call for a need to develop a unifying theoretical framework for the savannas.

Keywords: Savanna; paradigms; tree-grass coexistence; equilibrium.

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1 Introduction

Savannas cover approximately 20% of the earth surface, and some 40% of the African continent (Scholes & Walker, 1993). A distinctive character of the savannas is a co-dominance of discontinuous layer of trees and shrubs (hereafter referred to as “trees”) and a continuous layer of herbs and grasses (hereafter referred to as “grasses”), creating a biome with two contrasting life forms in coexistence (Accatino et al., 2010; Verweij et al., 2011). This unique coexistence is not found in any other terrestrial biome.

The uniqueness of most savannas around the world is changing through a phenomenon called bush encroachment (Van Auken, 2009; Romera Gil-Romera et al., 2010), defined loosely as an increase in cover and density of native woody species on patches previously occupied by grass species (De Klerk, 2004; Ward, 2005). Bush encroachment is a land degradation issue with significant ecological and socioeconomic consequences particularly for pastoralists in Africa (Moleele et al., 2002; Angassa), partly because of its impacts on rangeland forage productivity whereby palatable grass species decrease at the expense of increased bush thickets, making the rangeland less suitable for grazing (Figure 1). This in return result in a loss of socioeconomic livelihoods for many farmers. In Namibia for example, where approximately two-third of the country is affected by bush encroachment, it is estimated that the agricultural sector, one of the major contributors to the Gross National Product and a vital source of livelihood, losses approximately U$100 million annually due to bush encroachment (Klerk, 2004).

The coexistence between trees and grasses and the mechanism responsible for bush encroachment has attracted numerous scientific scrutiny over the years (e.g. Walter & Mueller-Dombois, 1971; Hills, 1965; Walker et al., 1981; Scholes & Walker, 1993; Accatino et al., 2010). Of great importance is the ”savannah question”, an intriguing inquiry into factors responsible for the coexistence of trees and grasses as well as the occurrence of bush encroachment in the savannas. The savannah question seeks to understand how trees and grasses, complete competitors are able to coexist, defying the competitive exclusion principle which argue that complete competitors cannot coexisting in a resource-limited environment (Gause, 1932, 1934).

Efforts to answer the ”savanna question” have given rise to diverging and conflicting ecological theories and models (Sankaran et al., 2004; Gil-Romera et al., 2010). These theories and models are still inconclusive in addressing the savanna question. Thus, our understanding of the savannas is still flawed, incoherent and lacks a consensus theoretical framework (Wiegand et al., 2006; Joubert et al., 2008; Accatino et al., 2010). Against this background, the main objective of this paper is to assess progress made in understanding the functioning and origin of the savanna ecosystem. This is undertaken through an integrated synthesis of the three major competing paradigms that have dominated the savanna debate

Figure 1: Example of a bush encroached savanna. Notice bush thickets on the right-side of the hill/fence, while the left side is clear of woody plants.

over the years and influenced the development of savanna theories and models (Sankaran et al., 2004; Gil-Romera et al., 2010). This review may help set the scene for future studies and stimulate thoughts for alternative plausible explanations.

2 A synthesis of competing paradigms

Over the years, our understanding of the savannas has been dominated by three major paradigms with contrasting views, theoretical assumptions and believe systems that influence our management of such ecosystems. The term paradigm, largely accredited to the work of Kuhn (1962) is defined as the outline of the general theoretical assumptions, laws, and techniques which members of a particular scientific community adopt. A paradigm can also be viewed as a comprehensive belief system, world view, or framework that guides research and practice in a particular field (Willis et al., 2007). Paradigms strongly influence our views on how natural systems such as the savannas work, and the approaches we advocate to manage or manipulate them (Ellis & Swift, 1988). The three emergent paradigms pertaining to the savanna are thus synthesized below to shed light on how they evolved to influence our current understanding of this biome, as well as to highlight enduring gaps.

2.1 Savannas as equilibrium ecosystems

The equilibrium theory emerged in vegetation studies in the early 1930s following the work of Clements (1936) and Dyksterhuis (1949), among others. This theory depicts terrestrial ecosystems as stable ecosystems at an end growth maturity level called climax. Climax was defined as a stage at which plants growth is in equilibrium with prevailing environmental conditions such as soil and climate. Equilibrium was considered a critical factor, because without it, such ecosystem would otherwise not exist. To reach climax, vegetation community's development would typically progress steadily and predictably along well-defined deterministic succession trajectory, moving from pioneers' species to climax species (Meeker & Merkel, 1984). According to this paradigm, the climax stage would represent a more permanent stage of vegetation succession. Under this paradigm, savannas are perceived as stable ecosystems whereby tree-grass growth and coexistence is in equilibrium with the prevailing climate and soils for which the ratio between trees and grasses is regulated by natural mechanism such as niche partitioning. This perspective would later manifest itself in a popular savanna model referred to as Walter's two-layer hypothesis (Walter and Mueller-Dombois, 1971; Walker et al., 1981; Walker & Noy-Meir, 1982). This model argues that tree-grass coexistence in water limited environments such as the savannas is made possible through a natural mechanism of root niche partitioning. It perceives grasses as superior competitors for water in the upper soil layer by developing shallow root systems, grow fast and intercept soil moisture within the upper soil layer. On the other hand, trees would have exclusive access to water at lower soil depth by developing deeper tap roots which extract water from the subsoil, unreachable by the grassy species (Figure 2). Thus, the two life forms coexist in equilibrium. This model further hypothesize that bush encroachment is a result of overgrazing which reduce grass layer, making trees more superior competitors for water through an increased percolation of water in the subsoil (Walker et al., 1981). Increased subsoil water would enhance recruitment for woody species as compared to grasses. Accordingly, it is that process that we call bush encroachment. Evidence has been claimed in support of Walter two layer hypotheses, as reviewed in Ward et al. (2013). This hypothesis has since been integrated into models of species coexistence, arid ecohydrology and climate change (Foley et al., 1996).

Decades of research in arid and semi-arid regions has gathered evidence strongly disputing the equilibrium paradigm and its subsidiary model, the Walters-two-layer hypothesis. The following weaknesses have been observed. Firstly, the equilibrium paradigm downplayed the role of disturbances such as grazing, fire and drought in shaping the savannas. The assumption that anthropogenic disturbances such as overgrazing or fire play a negligible role in the structure and functioning of ecological systems was ill conceived. In terms of grazing systems for example, this paradigm argue that in order to maintain the integrity of ecological systems, it was imperative that an equilibrium balance between grazing pressure and vegetation succession tendency is sustained (Dyksterhuis, 1949). This is because

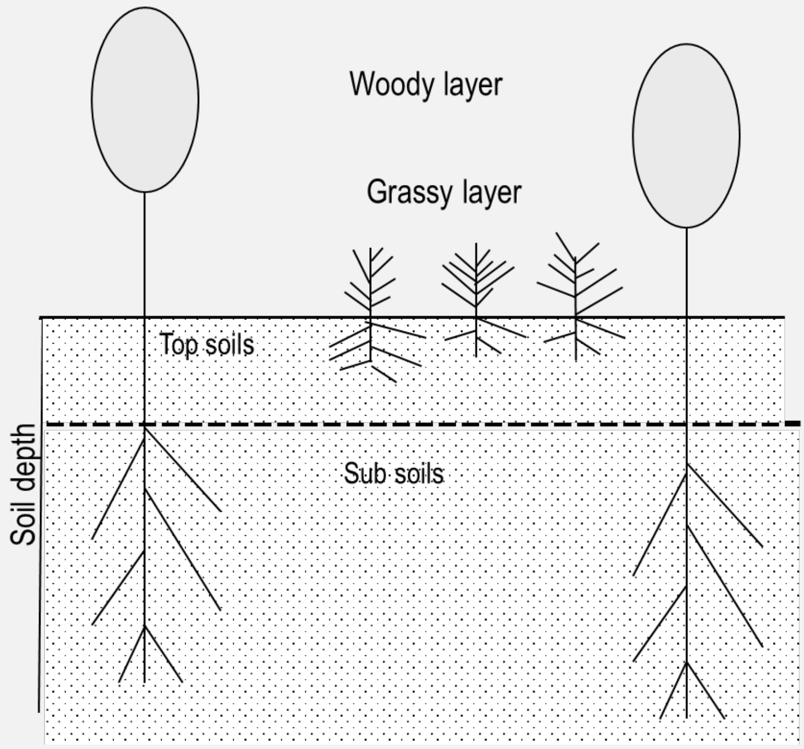

Figure 2: Walter's two-layer hypothesis illustrating root niche partitioning between trees and grasses (adapted from Walker et al., 1981; Walker and Noy-Meir, 1982).

vegetation succession toward climax was considered as a steady and predictable process, while grazing on the other hand was considered as a progressive process directly opposite vegetation succession tendency (Dyksterhuis, 1949). Studies on ecosystem disturbance more especially in arid and semi-arid regions have demonstrated that vegetation response to disturbances such as overgrazing is often not consistent, not continuous, and not reversible nor is it predictable (Westoby et al., 1989). Arguably, this is because such disturbances are often characterised by various factors such as frequency, intensity, extent and duration, and those significantly influence how vegetation respond to such disturbances (Voller & Harrison, 2011). Secondly, the equilibrium paradigm overlooked the significant impact of climate variability on terrestrial ecosystems. For example, it was perceived that above average rainfall increase vegetation succession toward climax, while drought merely affect vegetation the same way as grazing does (Clements, 1936). Thus the impact of drought can equally be managed by reducing grazing pressure to avoid degrading the ecosystems. However, studies on vegetation response to climate variability has lately demonstrated that terrestrial ecosystems dynamics are consistently varying to a greater or lesser extent due to climatic factors, and those variations are usually irregular in period, amplitude and space (Sprugel, 1991; Hutyra et al., 2005; Marshall and Smajgl, 2013). As a result organism would adapt to such climatic variations and thereby changing their equilibrium point. In addition, ecosystems such as the savannas are characterized by strong spatial heterogeneity brought about by spatio-temporal variation in soils, rainfall and disturbance frequency, duration and intensity which affect how such ecosystems behave in response to environmental stressors.

In a similar fashion, despite its prominence in savanna ecology, Walter's-two-layer hypothesis is accompanied by several shortcomings. Firstly, field evidence has demonstrated root system overlap between some grass species and savanna woody shrubs (Seghieri, 1995; Hipondoka et al., 2003; Hipondoka & Versfeld, 2006; Kambatuku et al., 2013). Secondly, studies using stable isotope has revealed that trees and grasses might have the same water source (February & Higgins, 2010; Kulmatiski et al., 2010). Moreover, evidence of bush encroachment has also been reported on ecosystems that are historically known to have received very little grazing pressure (Andresson 1856 as cited in Wiegand et al., 2006). Meanwhile, recruitment of some bush encroaching species such as *Prosopis glandulosa* (Brown and Archer, 1989; Simmons et al., 2008), and *Acacia mellifera* (Kraaij & Ward, 2006) has been found to be not necessarily influenced by grass cover as most seedlings also depend on shallow soil water during germination. Similarly, Wiegand et al. (2005) found evidence suggesting that tree-grass coexistence is possible on shallow soils, too shallow to allow root niche separation, ruling out the possibility that root niche partitioning is the main factor responsible for tree grass coexistence.

The views provided above demonstrate how the savannas have been perceived over the years. This does not only demonstrate how flawed our understanding of such ecosystems is , but also its management. For example, until lately, the perception among many policy makers is that bush encroachment which is an integral part of the savannas and widespread in Namibian commercial farms in particular, is a result of poor utilization of land by farmers through overstocking. However, there is still no conclusive explanation as to what mechanism really regulate the coexistence between trees and grasses as well as competition between the two life forms, which potentially trigger bush encroachment. It is interesting to note that farms that are supposedly well managed through rotational grazing such as around Otjiwarongo and Otavi, are the most affected by bush encroachment.

2.2 Savannas as non-equilibrium ecosystems

The work of Ellis and Swift (1988) and Westoby et al. (1989) are credited for stimulating the debate that brought about paradigm shift in the way we perceive terrestrial ecosystems, eventually shifting our world view into a non-equilibrium paradigm. The non-equilibrium paradigm argues that terrestrial ecosystems such as the savannas are open and unstable ecosystems controlled by abiotic factors such as inter-annual rainfall variation (DeAngelis and Waterhouse, 1987).

Contrary to the equilibrium theory that predict one steady state at the end of the succession pathway, the non-equilibrium theory predicts a web of non-linear, dynamics and complex behaviors, multiple steady states and thresholds that such ecosystems shift into in a spatio-temporal manner (DeAngelis & Waterhouse, 1987; Hobbs & Suding, 2008). The State and Transition model (S&T model) first developed by Westoby et al. (1989) is the first and most popular non-equilibrium model to date which has been applied to vegetation dynamics to demonstrate this non-equilibrium behaviours (figure 3). This model postulates arid environment vegetation such as the savannas represented by a catalogue of discrete states and numerous transitions taking place between those states. States are defined as recognizable, resistant and resilient complex of soils, climate and vegetation structure connected through an integrated ecological processes that interact to produce a sustained stable vegetation community, while transitions refer to those ecosystems trajectory of change that are precipitated by stressors such as drought, fire, grazing (Westoby et al., 1989).

In order to understand the vegetation dynamic using the state and transition model, there is a need to characterize a catalogue of possible alternative states as well as a catalogue of possible alternative transitions and factors that drive the ecosystem from one state to the other. In advancing the State and Transition model Stringham et al. (2003) suggested that vegetation transition from one state to the other follows either a reversible or irreversible pathways/transitions. The main difference between the reversible and irreversible transitions is embedded in the ecosystem's ability to self-repair. This self-repair is determined by the resistance and resilience of such ecosystems to prevailing stressors (Stringham et al., 2003). In this context, resistance refers to the ability of the ecosystem to withstand impacts of the prevailing stressors and be able to perform the necessary ecological process and provide ecosystems services. On the other hand, resilience refers to the ecosystems ability to return to its pre-disturbance state when the stressors cease to exist either naturally or as a result of management interventions. Resistance and resilience are considered as inherent properties found in ecosystems based on their physical components and the functional capacity of the associated ecological processes (Stringham et al., 2003). Transition from one state to another does not necessarily mean moving across thresholds into a completely new type of community, but merely an oscillation of species composition within a community also termed as phase shift. But when that transition happens, an ecosystem has moved into a completely new irreversible state which means that the ecosystems has passed a critical point threshold where one or more of the primary ecological processes responsible for maintaining the stability of a certain state has been degraded beyond the point of self-repair (Westoby et al., 1989; Stringham et al., 2003). Joubert et al. (2008) used the state and transition framework to model the dynamics of senegalia mellifera, one of the bush encroaching native woody plants in the highlands of Namibia (Figure 4).

Under this framework, savannas are seen as unstable ecosystems comprising of different heterogeneous states. Such states are not static, but continuously shift from one state to the other in a spatiotemporal manner. For example, transitions from a grass dominated

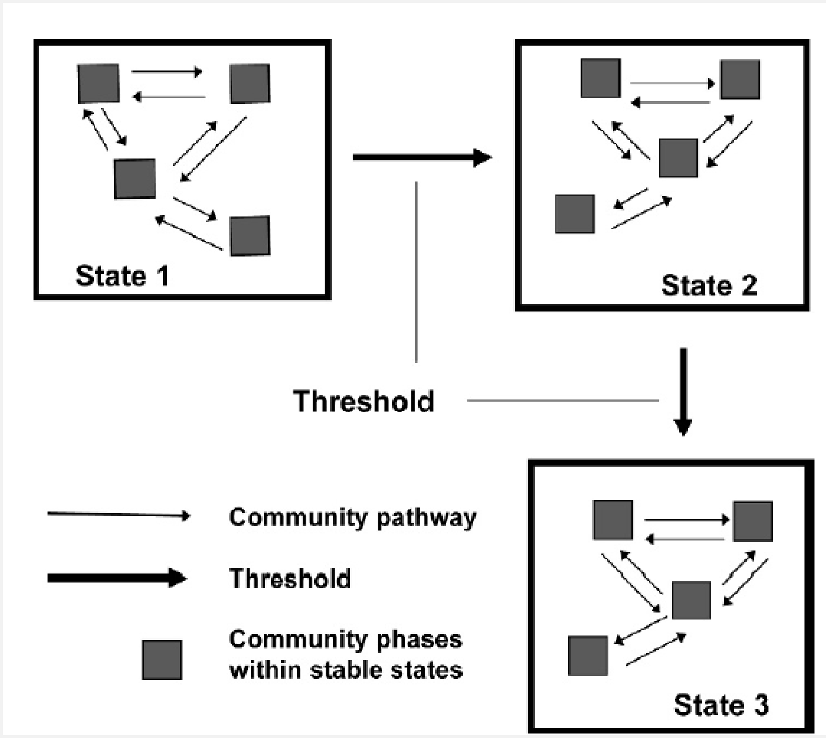

Figure 3: State and Transition model illustrating how non-equilibrium vegetation communities oscillate between states. (adapted from Stringham et al., 2003).

savanna to a bush encroached woodland would be a nonlinear and unpredictable process. Bush encroachment is seen as one of the states where vegetation has passed an irreversible threshold which can only be reversed through management such as debushing. Such dynamical changes are mainly triggered by stochastic factors such as inter annual rainfall variation as well as anthropogenic practices such as grazing, fire, deforestation and other human land uses (Vetter, 2005). Rainfall fluctuation over the years would cause temporal variation in species recruitment rate, whereby during drought times, the ecosystem would favor grass recruitment and growth at the expenses of trees, while tree growth and dominance would be common during the rainy periods (Vazquez et al., 2010). It is those dynamical behaviors that cause a long term coexistence between trees and grasses, commonly known as the savannas under this paradigm. Despite its popularity more especially in arid and semi-arid region, the non-equilibrium paradigm has not adequately satisfied ecologist's quest for knowledge on the savanna question.

We believe that the State and transition model best under the non-equilibrium model offer a more plausible explanation for the coexistence of trees and grasses. It acknowledge both the effect of climatic variation and anthropogenic disturbances in shaping the savanna

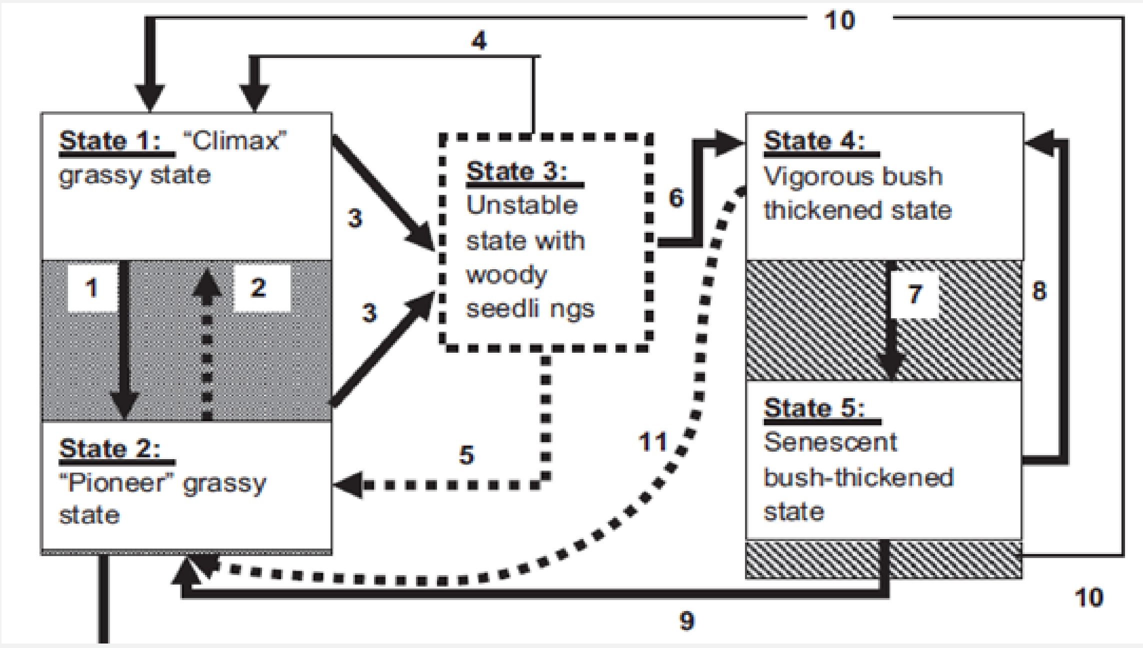

Figure 4: Schematic State and Transition model for vegetation in the highland savanna of Namibia. (adapted Joubert et al., 2008).

ecosystem structure. It also acknowledge the dynamical behaviors of such ecosystems in response to both climatic and non-climatic stressors, unlike the equilibrium paradigm that predict stable coexistence over time. Anthropogenic disturbances are integral parts of human dominated ecological systems and should be incorporated in ecological models. However, the non-equilibrium theory nor the State and Transition model was able to put to rest the savanna controversy.

2.3 The Disequilibrium paradigm and the savannas

The search for plausible answers to the savanna questions have gone as far as generating ideas that are classified within the disequilibrium paradigm. According to Luo & Weng (2011) a disequilibrium system occur when opposing internal and external forces prevent the system from achieving an equilibrium point, resulting in an unstable system. Although this paradigm has received relatively little scientific attention over the years as compared to the previously presented paradigms, its rise has stimulated new thoughts on how the savannas function. Popular in support of the disequilibrium theory is the demographic bottleneck hypothesis (Sankaran et al., 2004). The basic premise underlying demographic-bottleneck models is that trees and grasses persist in the savannas because of climatic variability and disturbances such as fire and herbivory which affect the life-history stages of savanna plants (Sankaran et al., 2004) and acting as bottleneck for either trees or grasses to grow. The disequilibrium theory thus argues that under natural circumstances, long term coexistence between trees and grasses to form savanna ecosystems is not possible because of interspecific competition between the two life forms. Competition between trees and grasses will segregate the two contrasting life forms, leading to two distinct and extreme vegetation communities in equilibrium, a grassland and forest woodland where each one of the two life forms is a superior competitor (Sankaran et al., 2004; Figure 5). However this process is never completed due to a persistent occurrence of ecological disturbances in the ecosystem, shifting the segregation process off its natural course by serving as bottleneck blockage (Sankaran et al., 2004). According to Van Auken (2009) for example, trees could invade grassland if the grass cover is reduced by herbivores leading to bush encroachment which will turn the ecosystem into either shrubland or woodland or inversely, an increasing tree cover could be reduced by fire, allowing grass to grow in the open areas, turning the ecosystem into a grassland. It is those bottleneck effects that sustain tree grass coexistence by buffering the system and preventing it from transiting into one of the extreme vegetation communities, keeping it in a disequilibrium state (Jeltsch et al., 2000). In the absence of such disturbances thereof, the ecosystem would be dominated by one superior competitor, turning the ecosystem into either a grassland or forest.

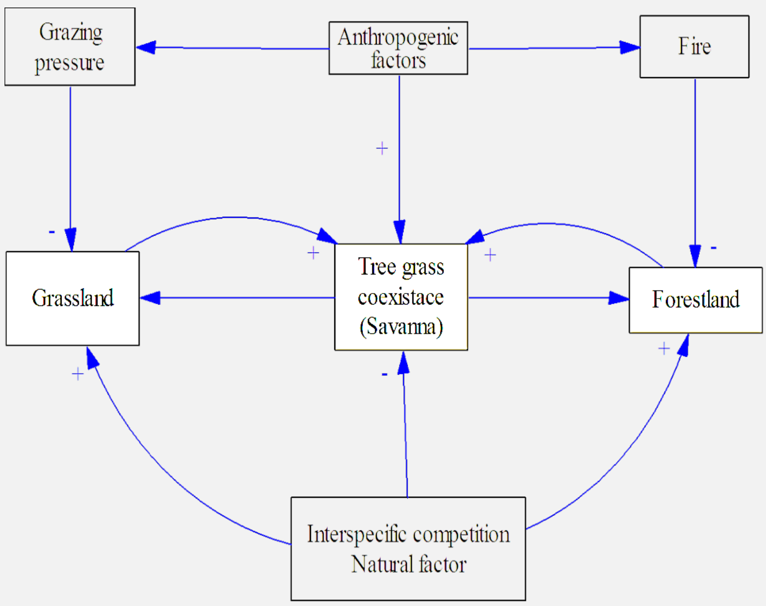

Figure 5: Conceptual model illustrating how fire and grazing may promote tree-grass coexistence. (adapted from Sankaran et al. (2004) and Van Auken (2009).

Based on that premise, it is further urged that there are no primary determinants of the savannas, because savannas are considered as un-natural ecosystems. Disturbances from fire and herbivores does not only modify tree-grass coexistence, but also maintain that long term coexistence. This theory has thus created a strong link between the persistence of savannas and human settlements. This paradigm provide a perspective which is contrary to the latter, such that it view savannas as ecosystem of mainly anthropogenic origin. This is improbable because savannas can also be found around areas that received very little human footprint. The bottleneck hypothesis is manly based on the importance of competitive exclusion, overlooking the ability of organisms to adapt to such competition.

3 Conclusion

The savannas has attracted diverse theoretical explanations over the years and continue to attract contentious debates to date. All the three paradigms reviewed in this paper are still inconclusive in addressing the savanna question. Conflicting and contradictory ideas have been proposed. Those ideas have not only broaden our knowledge on how the savannas possibly function, but has also significantly increased our uncertainties on the ecology of the savannas. There is a need to develop a unifying theoretical framework which is inclusive of the different perspectives presented in the three main paradigms presented here. It is probable that the coexistence between trees and grasses as well as the occurrence of bush encroachment is a result of multiple interacting biotic and abiotic factors operating at various spatial and temporal scales, while current scientific endeavours are geared to pin pointing one single explaining factor for the savannas.

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