The emergence of alternative ecosystem states in African savannas

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Summary

In Africa's diverse ecosystems, the theory of alternative ecosystem states (AES) holds particular significance, especially within its savannas. However, evidence remains unconvincing due to stringent testing criteria. Despite robust theoretical models demonstrating AES, a notable gap persists in empirical evidence. Challenges include distinguishing between environmental changes and true bi-stability, conducting long-term experiments, and replicating natural ecosystems in experimental settings. However, understanding and providing clear evidence of AES in these ecosystems is crucial for effective management and conservation strategies, especially given the challenges posed by the current impacts of climate change.

This thesis aims to contribute to the understanding and prediction of AES in African ecosystems, focusing on classic examples used to test the AES theory, such as forest-savanna mosaics and transitions within the African savanna lawn and bunch grass communities. Using a combination of a theoretical model, an experimental approach, and a paleo-ecological perspective, I explore the lawn grass-bunch grass system as an example of AES using a model system capable of describing autogenic succession driven by changes in light availability. I then demonstrate how such succession sequences can be influenced by varying grazing pressures, showing how different grazing intensities and patterns can alter plant community dynamics and lead to the emergence of AES under certain herbivore conditions, highlighting the intricate interactions between vegetation and herbivores. Using the results from the theoretical model, I designed a detailed mesocosm experiment where I manipulated grazing levels by clipping to simulate diverse African lawn grass-bunch grass communities under different grazing intensities. Here, I was able to test how a variety of African savanna lawn and bunch grass species respond to different grazing levels and to determine the specific level of grazing needed for AES to emerge.

Beyond testing the theory of AES, I introduce the role of climate in shaping vegetation change in Africa. Here, I challenge the AES theory by investigating climate as the primary driver of vegetation change across African landscapes. Climate has often been ignored when testing AES, particularly in the literature exploring the mechanisms driving forest-savanna mosaics across Africa. Using a plant-growth model system forced by climate, I explore how climate, specifically rainfall, influences forest-savanna ecosystems in Africa. Here, I use a paleo-perspective to understand the long-term patterns and trends of vegetation and climate over the Holocene epoch across Africa using pollen records and paleo-climatic data to reconstruct past ecosystems and climate fluctuations.

The overall findings of this dissertation highlight the importance of using theoretical models to understand the mechanisms driving model systems such as the lawn grass-bunch grass system. The results from the model shed light on how specific grazing conditions and light availability influence the lawn grass-bunch grass system and how initial conditions determine the natural succession of these communities. Using a theoretical approach is especially useful for guiding the

design of experiments within the AES framework, as demonstrated in this thesis. The theoretical foundation supports the design of the manipulative experiment, where I investigated the interaction between the invasion of lawn grass and different grazing levels. This experiment successfully demonstrated how this interaction can act as a mechanism to create and maintain AES within a lawn grass-bunch grass system, indicating the significance of using manipulative experiments. These results show the importance of manipulative experiments when testing the theory of AES as well as the strict requirements needed to identify AES. Indirectly this experiment sheds light on the challenges of meeting all these requirements when testing the theory of AES in natural systems as other variables such as climate need to be considered. Using a climate-forcing model within the AES theory framework, specifically using the forest-savanna mosaics as an example, highlights the challenges ecologists face when predicting true AES as climate interacts with both internal and external factors in an ecosystem. The results indicate that climate alone, specifically rainfall, plays a significant role in the formation of several forest-savanna mosaics in Africa.

The current discourse around interpreting ecosystems such as the forest-savanna mosaics and the lawn grass-bunch grass system in African savannas as examples of AES has implications for how these systems are managed. That is, misinterpretation of systems identified as true AES could lead to uninformed decisions, influencing fire regimes, controlling herbivore populations, conservation efforts and biodiversity strategies. With this being said, the compelling evidence presented in this thesis reveals the requirements that need to be met when designing and implementing experiments, as well as the importance of understanding the underlying internal and external mechanisms driving each ecosystem. This thesis reveals the role climate plays in shaping vegetation patterns and how valuable long-term climate data can be in predicting vegetation shifts, reiterating the difficulty of determining AES in African landscapes. This thesis underscores the complexity of understanding how internal and external factors interact and the importance of considering all possible drivers before interpreting ecosystems as AES.

Zusammenfassung

In den vielfältigen Ökosystemen Afrikas, insbesondere in den Savannen, ist die Theorie der alternativen Ökosystemzustände (AES) von besonderer Bedeutung. Aufgrund strenger Testkriterien sind die Beweise jedoch nach wie vor nicht überzeugend. Obwohl es robuste theoretische Modelle gibt, die AES nachweisen, besteht weiterhin eine erhebliche Lücke bei den empirischen Beweisen. Zu den Herausforderungen gehören die Unterscheidung zwischen Umweltveränderungen und echter Bi-Stabilität, die Durchführung langfristiger Experimente und die Nachbildung natürlicher Ökosysteme in experimentellen Umgebungen. Das Verständnis und die Bereitstellung klarer Beweise für AES in diesen Ökosystemen ist jedoch für wirksame Management- und Erhaltungsstrategien von entscheidender Bedeutung, insbesondere angesichts der Herausforderungen, die die aktuellen Auswirkungen des Klimawandels mit sich bringen.

Diese Arbeit soll zum Verständnis und zur Vorhersage von AES in afrikanischen Ökosystemen beitragen und konzentriert sich dabei auf klassische Beispiele, die zur Prüfung der AES-Theorie verwendet werden, wie Wald-Savannen-Mosaike und Übergänge innerhalb der afrikanischen Savannen-Rasen- und Büschelgras-Gemeinschaften. Mit einer Kombination aus einem theoretischen Modell, einem experimentellen Ansatz und einer paläoökologischen Perspektive untersuche ich das Rasengras-Büschelgras-System als Beispiel für AES und verwendet dabei ein Modellsystem, das in der Lage ist, autogene Sukzession zu beschreiben, die durch Veränderungen der Lichtverfügbarkeit bedingt ist. Anschließend zeige ich, wie solche Sukzessionssequenzen durch unterschiedliche Weidedrücke beeinflusst werden können, und zeige, wie unterschiedliche Weideintensitäten und -muster die Dynamik der Pflanzengemeinschaft verändern und unter bestimmten Bedingungen für Pflanzenfresser zur Entstehung von AES führen können, wobei ich die komplexen Wechselwirkungen zwischen Vegetation und Pflanzenfressern hervorhebe. Mithilfe der Ergebnisse des theoretischen Modells entwarf ich ein detailliertes Mesokosmos-Experiment, bei dem ich die Weidegrade durch Abschneiden manipulierte, um verschiedene afrikanische Rasengras-Büschelgras-Gemeinschaften unter unterschiedlichen Weideintensitäten zu simulieren.

Hier konnte ich testen, wie verschiedene afrikanische Savannenrasen-und Büschelgrasarten auf unterschiedliche Beweidungsintensitäten reagieren und die spezifische Beweidungsintensität bestimmen, die für die Entstehung von AES erforderlich ist. Über die Prüfung der AES-Theorie hinaus stelle ich die Rolle des Klimas bei der Gestaltung des Vegetationswandels in Afrika vor. Hier stelle ich die AES-Theorie in Frage, indem ich das Klima als primären Treiber des Vegetationswandels in afrikanischen Landschaften untersuche. Das Klima wurde bei der Prüfung von AES häufig außer Acht gelassen, insbesondere in der Literatur, die die Mechanismen untersucht, die Wald-Savannen-Mosaike in Afrika antreiben. Mithilfe eines klimabedingten Pflanzenwachstumsmodellsystems untersuche ich, wie das Klima, insbesondere der Niederschlag, die Wald-Savannen-Ökosysteme in Afrika beeinflusst.

Hier verwende ich eine Paläoperspektive, um die langfristigen Muster und Trends der Vegetation und des Klimas während des Holozäns in ganz Afrika zu verstehen, indem ich Pollenaufzeichnungen und Paläoklimadaten verwende, um vergangene Ökosysteme und Klimaschwankungen zu rekonstruieren. Die Gesamtergebnisse dieser Dissertation unterstreichen die Bedeutung der Verwendung theoretischer Modelle zum Verständnis der Mechanismen, die Modellsysteme wie das Rasengras-Büschelgras-System antreiben. Die Ergebnisse des Modells geben Aufschluss darüber, wie bestimmte Weidebedingungen und Lichtverfügbarkeit das Rasengras-Büschelgras-System beeinflussen und wie Anfangsbedingungen die natürliche Abfolge dieser Gemeinschaften bestimmen. Die Verwendung eines theoretischen Ansatzes ist besonders nützlich für die Gestaltung von Experimenten im Rahmen des AES, wie in dieser Arbeit gezeigt wird. Die theoretische Grundlage unterstützt die Gestaltung des manipulativen Experiments, bei dem ich die Wechselwirkung zwischen der Invasion von Rasengras und unterschiedlichen Weideniveaus untersucht habe. Dieses Experiment hat erfolgreich gezeigt, wie diese Wechselwirkung als Mechanismus zur Schaffung und Aufrechterhaltung von AES innerhalb eines Rasengras-Büschelgras-Systems wirken kann, was die Bedeutung der Verwendung manipulativer Experimente verdeutlicht. Diese Ergebnisse zeigen die Bedeutung manipulativer Experimente beim Testen der Theorie des AES sowie die strengen Anforderungen, die zur Identifizierung von AES erforderlich sind.

Indirekt wirft dieses Experiment Licht auf die Herausforderungen, all diese Anforderungen beim Testen der Theorie des AES in natürlichen Systemen zu erfüllen, da andere Variablen wie das Klima berücksichtigt werden müssen. Die Verwendung eines Klimabeeinflussungsmodells im Rahmen der AES-Theorie, insbesondere am Beispiel der Wald-Savannen-Mosaike, verdeutlicht die Herausforderungen, denen sich Ökologen bei der Vorhersage echter AES gegenüberstehen, da das Klima sowohl mit internen als auch mit externen Faktoren in einem Ökosystem interagiert. Die Ergebnisse zeigen, dass das Klima allein, insbesondere der Niederschlag, eine bedeutende Rolle bei der Bildung mehrerer Wald-Savannen-Mosaike in Afrika spielt.

Der aktuelle Diskurs um die Interpretation von Ökosystemen wie den Wald-Savannen-Mosaiken und dem Rasengras-Büschelgras-System in afrikanischen Savannen als Beispiele für AES hat Auswirkungen auf die Art und Weise, wie diese Systeme verwaltet werden. Das heißt, eine Fehlinterpretation von Systemen, die als echte AES identifiziert wurden, könnte zu uninformierten Entscheidungen führen, die Brandregime, die Kontrolle von Pflanzenfresserpopulationen, Naturschutzbemühungen und Biodiversitätsstrategien beeinflussen. Vor diesem Hintergrund zeigen die überzeugenden Beweise, die in dieser Arbeit präsentiert werden, die Anforderungen, die bei der Gestaltung und Durchführung von Experimenten erfüllt werden müssen, sowie die Bedeutung des Verständnisses der zugrunde liegenden internen und externen Mechanismen, die jedes Ökosystem antreiben. Diese Arbeit zeigt die Rolle, die das Klima bei der Gestaltung von Vegetationsmustern spielt, und wie wertvoll langfristige Klimadaten bei der Vorhersage von Vegetationsverschiebungen sein können, und unterstreicht erneut die

Schwierigkeit, AES in afrikanischen Landschaften zu bestimmen. Diese Arbeit unterstreicht die Komplexität des Verständnisses der Wechselwirkung interner und externer Faktoren und die Bedeutung der Berücksichtigung aller möglichen Treiber, bevor Ökosysteme als AES interpretiert werden.

Chapter 1

General Introduction

1.1 Motivation: Why do we need a mechanistic understanding of the existence of alternative ecosystem states in African savannas?

The concept of alternative ecosystem states (AES) takes on particular significance in the ecologically diverse continent of Africa. The AES theory suggests that multiple vegetation states may exist in a single ecosystem under the same climatic conditions (Lewontin, 1969). Over time, this ecosystem may transition from one state to another due to non-climatic and/or internal influences, fundamentally altering its structure and function. This phenomenon is particularly interesting in African landscapes as they feature a wide variety of vegetation types that combine to form diverse vegetation mosaics. These mosaics include savannas, grasslands, forests, shrubland, and desert ecosystems, each contributing to the continent's rich biodiversity. A large portion of the African landscape making up almost 50% of the continent are savannas (Osborne et al., 2018). Savannas are ancient ecosystems with a unique evolutionary history and a large diversity of plant and animal species that are confined to these ecosystems (Charles-Dominique et al., 2016; Simon et al., 2009).

These ecosystems are recognised for their complex interactions involving climate, soils, vegetation structure, fire, and herbivores, and they notably exhibit vulnerability to ecosystem change making them challenging to manage (Lehmann et al., 2014; Anderson et al., 2007). Given that savannas are projected to be among the ecosystems most affected to future changes in climate (Bond and Archibald, 2003a; Sala et al., 2000), it is of great importance to understand the factors shaping savanna vegetation (Sankaran et al., 2005). The continuous grass layer of African savannas is theorised to be an example of AES (Hempson et al., 2019) and understanding the mechanisms that drive a fire-driven grass state or grazing-driven lawn grass state is of utmost importance as the structure and function of these grass ecosystems depend on these mechanisms. Here, it is essential to recognise the vulnerability of these ecosystems to extreme climate change or incorrect management decisions to prevent irreversible catastrophic damage.

Beyond African savannas, forest-savanna landscapes have also been widely hypothesised and modelled as examples of AES (Beckett et al., 2022; Pausas and Bond, 2020; Allen et al., 2020; Bond, 2019; Moncrieff et al., 2014; Staver et al., 2011a; Scheiter and Higgins, 2007; Van Langevelde et al., 2003). Similar to the grass layer of African savannas, profound external perturbations can force permanent transitions between these states which could be detrimental to plant, animal and human populations (Ratajczak et al., 2018).

The effort to predict AES using mathematical models has been a recurring theme of significance since first proposed in the 1960s (Lewontin, 1969; Petraitis and Latham, 1999; Petraitis and Dudgeon, 2004). However, whether multiple states actually occur in nature has been intensely debated, in part because of the difficulty of demonstrating their existence in real-world ecosystems but also because of the lack of clear criteria regarding what needs to be considered in the field versus in experiments (Petraitis, 2013; Schröder et al., 2005). While observational data may suggest the presence of multiple states, experimental approaches are found to be most necessary to demonstrate their existence unequivocally (Petraitis and Dudgeon, 2004; Chase, 2003b; Petraitis and Latham, 1999; Scheffer et al., 1993). By manipulating ecosystem states and observing the resulting changes in the ecosystem, researchers can determine whether the system has shifted from one state to another under controlled environmental conditions. Manipulation experiments can be used to directly predict the mechanisms underlying AES, such as positive feedback loops, and determine the conditions under which they are most likely to occur (Schröder et al., 2005). Another important requirement that is often not always possible when testing for AES is having a time frame that is long enough to observe potential vegetation state shifts and investigate how and why transitions between states occur (Fukami and Nakajima, 2011).

Most modern observational studies have shown changes in vegetation states on time scales of years to decades, however, these time scales need to be extended when testing for examples of AES (Runge et al., 2021). To address this issue, over the past few decades, paleo-ecological data have been shown to be a valuable source of empirical evidence for vegetation dynamics (Runge et al., 2021). Paleo-ecological data has proven beneficial for assessing vegetation and climate trends and patterns spanning thousands of years and provide opportunities for testing the AES theory (Gosling et al., 2021; Aleman et al., 2020; Gillson, 2015).

The availability of empirical evidence supporting the theory of AES is relatively scarce as studies do not often account for the initial ecosystem state, long-term observation periods and feedback loops that are related to climate. Even though paleo-ecological time frames ensure a sufficient study period for testing AES, there are limitations which can inaccurately represent past environmental conditions, leading to uncertainties in proxy data interpretation (Tingley et al., 2012). Another recurring issue in the literature specifically seen when using ecological models, is the misinterpretation of AES due to the difficulty in distinguishing between system variables and environmental variables and the use of non-manipulative, indirect methods, where findings remain open to alternative explanations (Beisner et al., 2003; Schröder et al., 2005).

The issues highlighted in the previous paragraphs indicate the lack of consistent empirical evidence for determining AES in African savannas. To address these issues, a combination of theoretical, experimental and paleo-ecological data approaches were used in this thesis to improve our understanding of the emergence of AES in African ecosystems. The primary research questions addressed in this thesis are **(i)** What manipulative methods can be used to test the theory of AES using the grass layer of African savannas as a model system? **(ii)** How can empirical evidence be found for the theory of AES? and **(ii)** What role does climate play in the theory of AES specifically in the forest-savanna mosaics in Africa?

In this thesis, I focus on African ecosystems, including the well-studied forest-savanna mosaics and the transition within the theorised example of the savanna grass layer, where tall bunch swards can shift to grazing lawns. These ecosystems have a history of being studied as examples of AES and the impacts of understanding the mechanisms driving them are not only important from a conservation perspective but are important for human populations and ecosystem services. Overall, this thesis aims to advance our knowledge of how model and experimental systems can be used to predict the dynamics of AES in real-world systems, especially in systems where management decisions can cause profound alterations in ecosystem structure, functioning and biodiversity that are not easily reversed.

In the first part of this thesis, I use a theoretical plant-growth model to simulate the transitions from tall bunch swards to grazing lawns. This model investigates the initial conditions needed for systems to transition to alternative states as well as the level of disturbance needed to create and maintain these states. The results from the theoretical model motivated the design of a mesocosm experiment using African savanna lawn and bunch grass species. Therefore, in the second part of this thesis, I designed an experiment is designed to directly manipulate the rate of key processes and mimic the assumptions that are needed to produce dynamics predicted by the theoretical model. A mixture of lawn and bunch grasses were grown in mesocosms where I manipulated grazing by herbivores with clipping. This experiment provides evidence of how direct manipulation of grazing can be used to induce switches between AES.

The final part of this thesis uses paleo-ecological data to assess vegetation shifts across Africa. I use various climate variables as proxies to identify possible vegetation changes over the Holocene period (12000 (cal.) years BP - present (1950 CE)). Through this approach, I conduct a thorough analysis of climate-induced vegetation shifts, testing whether these changes are primarily influenced by climate variables. If these shifts are found to be unrelated to climate, it opens up the possibility of considering these state shifts as potential indicators of AES. To lay the foundation for these studies, in the following chapter, I will introduce the AES theory and the context of AES in Africa. I will then present studies testing the AES theory specifically in African ecosystems, point out knowledge gaps and introduce the aims and objectives of this thesis in more detail. I also describe African savannas and the methods and approaches used in this thesis in the chapter 'Materials and Methods'. In the chapter ‘General Results and Discussion’, I describe the findings of my studies. Specifically, the evidence of AES in the lawn grass-bunch grass model system, the ecological implications of falsely interpreting AES, the findings of how climate influences the vegetation dynamics over the Holocene epoch in the forest-savanna mosaics in Africa, and the limitations of my thesis. The ‘Conclusion’ reiterates the significance of this thesis and its contribution to the general literature on AES, emphasising the requirements needed to test and interpret AES in African savannas. The main concepts and terms used in this thesis are described in Box 1.

Box 1. Definitions of terms used in this thesis

Savannas: A mixed tree–grass system characterised by a discontinuous tree canopy in a continuous grass layer (Ratnam et al., 2011).

Alternative ecosystem states: A syndrome where the existence of multiple fixed points in a dynamical system's phase space allow for qualitatively different ecosystem states to emerge due to initial condition differences (Higgins et al., 2024).

Process-based model: Models that characterise changes in a system's state as explicit functions of the events that drive those state changes (Connolly et al., 2017).

Arrested succession: An ecosystem permanently stopped in an early successional stage (Young et al., 2001).

Autogenic process: Disturbances generated within the system which are usually biotic (Sousa, 1984).

Allogenic processes: Disturbances imposed from outside the system which are usually abiotic (Sousa, 1984).

Internal dynamics: The dynamical processes within the system itself. Internal dynamics are driven by the system's state variables and the positive and negative feedback relationships between them. In ecosystem models, internal dynamics typically include processes such as biomass growth and light competition (Higgins et al., 2024).

True AES: Observed differences in ecosystem state are caused by differences in initial conditions and not by differences in environmental drivers (Higgins et al., 2023a).

Initial conditions: Refers to the system state at time zero (Higgins et al., 2023a).

Model system: An ecosystem studied to better understand a theoretical framework and processes driving the real-world system (Evans, 2012).

Lawn grass-bunch grass system: The grass layer of African savannas (Hempson et al., 2019).

Positive feedback: A combination of mechanisms in the internal dynamics of a dynamical system where a change in a state variable of the system leads to further changes that reinforce the initial change, amplifying its effects (Higgins et al., 2024).

Bayesian state-space model: A time-series model that predicts the future state of a system from its previous states probabilistically, via a process model. The SSM describes mathematically how observations of the state of the system are generated via an observation model using a Bayesian framework (Patterson et al., 2008).

Forest-savanna mosaics: A widely studied example of alternative ecosystem states (AES) (Higgins et al., 2023a).

External forcing: Factors external to the system that impact the behaviour of the system's state variables. In ecosystem models, external forcing are typically the parameters that describe the role of environmental factors such as temperature, soil moisture, soil nutrients, solar radiation, or human factors such as fire management, deforestation, or other land use interventions (Higgins et al., 2024).

African Humid Period: The African Humid Period (AHP, 14.7–5.5 ka BP) is a key time period of the late glacial and early Holocene where most of tropical Africa experienced exceptional wetter climate conditions. This period is also known informally as the 'Green Sahara' (Phelps et al., 2020b).

Phyto-climatic regions: Geographic regions where the climate favours particular combinations of plant types (Higgins et al., 2023c; Conradi et al., 2020a).

Calibrated years BP (Before Present): radiocarbon dating, years before 1950 CE (Stuiver and Pearson, 1993).

Paleo-ecological perspective: Using paleo-data such as paleo-climatic variables and pollen records to understand vegetation patterns and trends (Runge et al., 2021).

1.2 Alternative Ecosystem States

The remarkable ability of ecosystem states to persist for long periods of time and yet be susceptible to change has resulted in the hypothesis that ecosystems can have multiple alternative states (Scheffer et al., 2001). The potential for qualitatively different ecosystems to exist under the same environmental conditions is a phenomenon seen in a wide range of ecological systems which has led to the hypothesis of Alternative Stable States (ASS). The theory of ASS suggests ecosystems can exist in multiple states under the same environmental condition. Here, ecosystems can persist in states that are considered stable for long periods of time which is maintained by internal positive feedbacks (Lewontin, 1969; Holling, 1973; May, 1977). The concept of ASS focuses on stability not because this theory necessarily characterises natural communities, but primarily due to the mathematical tractability.

Applying this theory to natural ecosystems is challenging as stable states need to be reached. However, (Fukami and Nakajima, 2011; Didham et al., 2005; Chase, 2003a) showed that theoretical predictions about alternative states being stable can be useful in understanding real communities, that is, ASS theory can be used to predict many dynamical systems. Ecologists have used this theory to test many systems, and some have adapted the terminology of the theory to fit the system that is being studied. For example, (Pausas and Bond, 2020) use the term alternative biome states to highlight the coexistence of different vegetation types within a landscape and the implications of these states for species distribution modelling and biodiversity conservation. In this thesis, I use the concept of Alternative Ecosystem States (AES) emphasising the focus on "ecosystems". Here I focus on the lawn grass-bunch grass system and forest-savanna mosaics in Africa (Box 2). These systems can be thought of as ecosystems and not necessarily as biomes. Even though the terminology can be adapted for the theory the fundamentals remain the same. (Petraitis, 2013) states that initial conditions are crucial in determining whether an ecosystem will remain in a particular state or transition to an alternative state. However, the importance of initial conditions remains largely unknown when studying AES in natural systems. Initial conditions together with feedback mechanisms such as nutrient cycling, species interactions, and disturbance regimes, induce AES (Petraitis, 2013). For example, in the savanna lawn grass-bunch grass system, the initial state of a grass community can determine the availability of resources such as light and water affecting plant growth and competition dynamics (Hempson et al., 2019).

Positive feedback mechanisms play a crucial role in driving ecosystem shifts in AES systems. Classic AES examples range from vegetation dynamics in savannas and forests (Staver et al., 2011b), coral reef systems (Norström et al., 2009), shallow lakes (Scheffer et al., 1993), and processes of desertification (Suding et al., 2004). The AES hypothesis is conceptually straightforward, however, providing empirical evidence for true AES has proven difficult as certain criteria need to be met. For example (Petraitis, 2013) established criteria for designing manipulative experiments to test for AES. According to (Petraitis, 2013): 1) the experiment must be conducted in a single environment; 2) the site must have the potential to be occupied by two or more distinct communities; 3) the communities must be self-replicating, serving as a proxy for ”stability”, and 4) experimental manipulations must be pulse perturbations (these perturbations should mimic a natural event in terms of spatial extent, temporal duration, and effects on species in the system).

Box 2. The rationale for using the forest-savanna mosaic and lawn grass-bunch grass systems to test and evaluate AES

Lawn grass-bunch grass savanna grass layer

In this system, the grass species are characterised by different traits and responses to external factors such as fire and grazing, leading to the coexistence of different states depending on the prevailing conditions. For example, in the lawn grass state, the lawn grass species are highly palatable to grazers, promoting their proliferation through regular grazing. On the other hand, in the bunch grass state, the bunch grass species have traits that make them highly flammable, increasing their dominance under frequent burning (Hempson et al., 2022, 2015b; Archibald, 2008). These different trait combinations create distinct ecosystem states that can persist over time due to positive feedback mechanisms with fire or grazing. The presence of these AES in the lawn grass-bunch grass system highlights the dynamic nature of grassland ecosystems and the importance of understanding the interactions between grass species, external factors, and internal dynamics shaping ecosystem structure and function.

Forest-savanna mosaics

Forest-savanna mosaics are studied as examples of alternative ecosystem states as two distinct ecosystem types coexisting with clear boundaries due to environmental factors and feedback mechanisms (Pausas and Bond, 2020). In these mosaics, the transition between forest and savanna is not gradual but rather abrupt, indicating the presence of different states maintained by internal system dynamics and positive feedback processes. The presence of forest-savanna mosaics challenges the traditional view that ecosystems are solely determined by climate, and highlights the complex interactions between vegetation types and environmental conditions in shaping landscape patterns (see discussion in (Higgins et al., 2024)).

However, studies have been conducted where (Petraitis, 2013) criteria has been misinterpreted and ecologists have invoked AES when not all criteria have been met which has implications for management (Bond, 2019). For example, the assumption that ecosystems can be shifted between states through specific interventions, such as fire exclusion or controlled burns, may not hold true if the underlying ecological dynamics do not support such transitions. In such cases, these management strategies are likely to fail. (Higgins et al., 2024) reviewed studies that have been interpreted as evidence for AES in the African savanna-forest domain, using the criteria proposed by (Petraitis, 2013) to evaluate their validity. Several studies have been misinterpreted as supporting the AES theory despite not meeting the necessary criteria. For instance, (Trapnell, 1959) found that savanna woodland persisted under fire exclusion, with no evidence of a transition to forest, thus refuting AES predictions. Similarly, (Chidumayo, 1997) showed that after 33 years of fire exclusion, the vegetation did not transition to forest, indicating insufficient changes to prevent fire invasion. (Swaine et al., 1992) found, although there was some development towards a forest state, this was attributed to high rainfall and nearby forest propagule pressure rather than fire exclusion. Collectively, these studies demonstrate that they do not adequately support AES theory.

Not only is it challenging to predict AES but to confidently show these states exist in natural systems is almost impossible because of the complex interaction between internal and external factors (Higgins and Scheiter, 2012; Bonan and Doney, 2018; Warman and Moles, 2009; Staver et al., 2011a). Predicting AES remains challenging and most of the supportive evidence for the AES hypothesis comes from theoretical models. Theoretical evidence for AES models commonly use the ball-in-cup analogy (Beisner et al., 2003; Higgins et al., 2024), with the state of the ecosystem being represented by the position of the ball and each cup representing multiple basins of attraction. That is, each basin is an ecosystem state existing under the same set of conditions (Fig.1.1). Figure 1.1, depicts a savanna grass layer which consists of tall bunch grass and short lawn grass mosaics, as an example ecosystem to illustrate AES. The diagram shows two ways in which a state can move from one state to another. That is states can move due to disturbances and history or states can move to another state due to shifting parameters. In the lawn-grass-bunch grass state, a previous large disturbance such as a fire could initiate a state shift (Fig.1.1 (c and d)). Alternatively, when there is a change in the parameters that determine the direction of the state variable AES can emerge. For example, a change in herbivore population could influence a shift from a lawn grass state to a bunch grass state (Fig.1.1 (e and f)).

1.3 Alternative Ecosystem States in Africa

African ecosystems are anticipated to be drastically altered as a result of the current climate change crisis, as well as an increase in human-induced disturbances leading to further landscape transformations (Midgley and Bond, 2015). The complex mosaic of biomes found within Africa represents a unique challenge

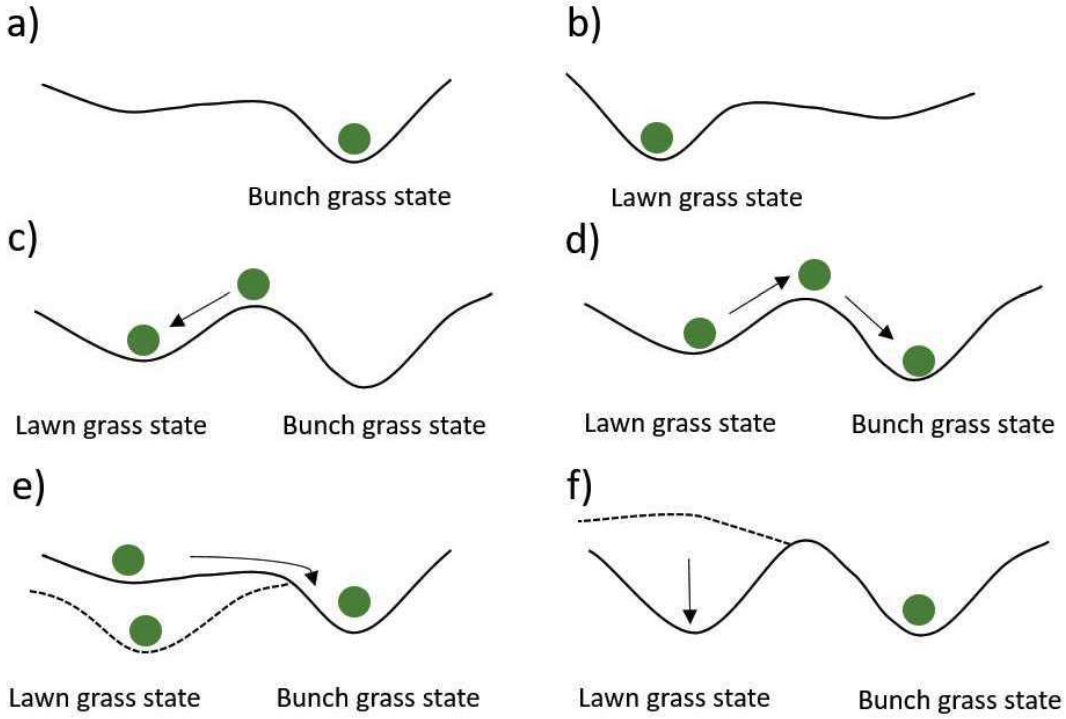

Figure 1.1: Ball-in-cup diagram representing models of alternative ecosystem states based on (Higgins et al., 2024; Beisner et al., 2003) interpretations. The position of the ball is located in a basin which represents an ecosystem. a) is always a bunch grass state, b) is always a lawn grass state, c) and d) represent AES due to history and previous disturbances and e) and f) show AES due to shifts in parameters.

to ecologists attempting to understand the factors controlling plant distributions (Moncrieff et al., 2015). These biome boundaries are often controlled by multiple factors such as soil properties, atmospheric CO_2 concentrations and climate or disturbance regimes which may create feedback loops or interact in non-linear ways (Bond and Midgley, 2012; Hoffmann et al., 2012). For example, African savannas in particular contain the last near-intact communities of large mammal species and their existence as herbivores influences the structure and functioning of these landscapes thus effective conservation management of African savannas is of primary importance for global conservation efforts (Cromsigt et al., 2017). The effect of large herbivores in altering the function and structure of landscapes is enormous and a well-documented example is the creation of grazing lawns (McNaughton, 1984).

Grazing lawns have been identified in many ecosystems with a large portion of the literature focusing on African landscapes (McNaughton, 1984; Archibald, 2008; Hempson et al., 2015b). The concept that grazing lawns can arise due to continuous herbivore activity and different initial conditions, implies that the lawn-bunch grass system can be a model system for testing the AES theory (Belsky, 1986).

While extensive research has been conducted on the structure and function of the savanna grass layer, the transition of fire grass states to grazing lawn states and their interactions are difficult to identify because fire and grazing influence each other. In recent years there has been an interest to understand these grass communities through the lens of the AES framework. (Hempson et al., 2019) championed this idea theoretically and highlighted the importance of positive feedback mechanisms in maintaining these grassy systems by fire and herbivory.

While the lawn-bunch grass example has been a more recent AES interest and is primarily seen in savanna biomes, a more well-documented example of AES occurs between the two most widespread biomes in tropical African landscapes. The forest-savanna mosaics have captured the attention of ecologists for decades and have often been modelled as alternative biome states with fire identified as the main driver shaping these landscapes (Bond et al., 2005a; Staver et al., 2011b,a). However, the balance of forest and savannas is not only determined by fire but rather by the complex interactions between edaphic, climatic and non-climatic drivers (Oliveras and Malhi, 2016). Since many factors can be responsible for the formation of forest-savanna mosaics, not all of these mosaics can be identified as AES because climate variables have a large influence on plant growth (Higgins et al., 2023a).

Rainfall stands out as one of the most influential climatic factors frequently featured in forest-savanna mosaic studies in the tropics (Hirota et al., 2011; Favier et al., 2012; Aleman et al., 2020; Archibald, 2008). Several of these studies carried out in Africa found that rainfall plays a crucial role in shaping forest-savanna dynamics. That is, in regions with intermediate levels of rainfall, both forests and savannas can co-exist, leading to a bi-modal distribution of tree cover with the potential for abrupt shifts between these states triggered by changes in rainfall patterns (Staal et al., 2016). Such transitions are often mediated by feedback mechanisms; for example, in a savanna state, low tree cover can lead to higher grass biomass, promoting more frequent fires that inhibit tree growth, thereby reinforcing the savanna state. In a forest state, higher tree cover can suppress grasses, reduce fire frequency, and maintain the forest state. This suggests that rainfall is a primary control on biomass burning in African savannas, and understanding the initial hydro-climate conditions is essential for predicting fire responses to long-term shifts in rainfall over time (Karp et al., 2023; Sala et al., 2012).

While external factors such as fire and herbivory are crucial drivers in shaping forest-savanna landscapes, the changing climate has often been excluded as an influential driver of forest-savanna-grassland ecosystems as most studies view these ecosystems through the lens of the AES theory. This lack of consideration can cause misinterpretation of studies identifying ecosystems as examples of AES when in fact they are climate-driven. Higgins and colleagues 2023 highlight the importance of distinguishing between true AES (AES caused by system variables) and apparent AES (caused by environmental drivers). They use a correlative model approach which statistically shows how climate can account for vegetation states which suggests that the role of feedbacks causing AES in African landscapes is less prevalent than previously suggested. This is not to say that fire and herbivory can not be responsible for vegetation dynamics, rather, they are themselves influenced by climate, which makes it very difficult to disentangle the role of system variables and climate variables in these ecosystems. Ecological models have however been useful for understanding the multitude of climatic and non-climatic variables and their impact on the distribution of vegetation (Conradi et al., 2020b; Whittaker, 1975; Walter, 1973; Schimper, 1902). This approach is invaluable for gaining a deeper understanding of the complex systems of potential AES in Africa.

1.4 Testing Alternative Ecosystem States

Ecological research poses a challenge when bridging theory and practical application and this is certainly the case for the study of alternative ecosystem states. Mathematical models have made advances in showing how different communities could arise in the same environment and have been the most influential theoretical evidence that can be applied to a variety of ecosystems (May, 1977; Tilman, 1982; Harrison, 1979; Dublin et al., 1990; Noy-Meir, 1975). Simple mathematical models can easily explain dynamic ecosystems, however, when applying the AES theory to natural systems it becomes extremely challenging. Observational data such as time series studies offer the potential for detecting the existence of alternative attractors in natural systems (Bowman et al., 2010; Buitenwerf et al., 2012; Stevens et al., 2016; Ploton et al., 2022; Ives et al., 2003; Scheffer, 2009).

In the last few decades, the use of paleo-ecological data have been used to observe long-term vegetation patterns and natural disturbance regimes which in turn have been used to infer potential multiple states (Fletcher et al., 2014; Reyer et al., 2015; Colombaroli et al., 2014; Cramer et al., 2019; Gillson and Ekblom, 2020). However, observational data alone are not conclusive since there is always a possibility that discontinuities in time series or spatial patterns are due to discontinuities in environmental factors (Higgins et al., 2023a).

Moving from theory to practice is not straightforward and translating the terminology of mathematical model—parameters, state variables, and stability—into functional concepts can be tricky when testing the AES theory. Therefore, experimental ecology has been used to bridge the gap between theoretical models and observational studies of AES. Manipulative experiments are seen as the strongest empirical evidence for identifying true AES (Petraitis, 2013). That is, when designed with the AES criteria, these experiments can unequivocally demonstrate AES. This is being done as researchers can establish controlled plots where it is possible to manipulate variables such as fire frequency, grazing pressure, or nutrient availability (Donaldson, 2019; de L. Dantas et al., 2013). Many manipulative experiments are conducted over extended periods, allowing researchers to observe changes in vegetation composition, species diversity, and ecosystem functions over time. However, designing and conducting direct experiments in natural systems poses many difficulties when testing AES successfully as there are requirements that need to be met in the system that is being tested (Beisner et al., 2003). Systems described as examples of AES are required to show evidence of hysteresis or bi-stability (Scheffer and Carpenter, 2003).

Convincing evidence for the presence of bi-stability and hysteresis in natural systems is lacking as systems represent bi-stability or not respond to environmental drivers, and in some cases, the response patterns may appear similar, particularly if the driver values are not explored across a wide range (Sarania et al., 2022). To show two community states that are consistently being assessed at different spatial or temporal locations, and proving that the environment stays the same in space and time is a challenging task, especially when trying to distinguish between community shifts due to environmental changes or instances where there is true bi-stability or hysteresis (Petraitis and Latham, 1999; Connell and Sousa, 1983). Not only is this challenging to detect in real-time, but running these long-term experiments in natural systems is often expensive and time-consuming.

An alternative is to use mesocosms as experimental platforms to manipulate and observe ecological processes under controlled conditions. This approach offers the statistical power of replicated experiments while maintaining many of the key dimensions of the structure and functioning of natural systems. Mesocosm experimental designs have been used to test various ecological principles, especially on a community and ecosystem level, allowing for testing theories such as AES (Stewart et al., 2013). Several studies have used this approach to support the theory of AES in a wide range of ecosystems testing the mechanisms driving each mesocosm community. For example, (Chase, 2003b) designed and conducted one of the first mesocom analysis providing evidence for AES in a food web structure resulting from the local environment, initial conditions and the interaction between these variables. (Morris et al., 2003) showed that mesocosm experiments testing the mechanisms driving the loss of aquatic plants showed that under different shading conditions the mesocosm system was able to transition.

However, designing mesocosm experiments can be challenging due to the intricacies of replicating highly complex and dynamic natural ecosystems. To address these challenges, ecologists often use mathematical models to guide and motivate the experimental design process (Petraitis, 2013). Here, mathematical models provide a framework for predicting how ecological systems may behave under various conditions. By simulating different scenarios, ecologists can predict the potential outcomes of experiments and formalise the assumptions and mechanisms driving alternative states, making the theory more precise and testable.

1.5 Aims and objectives

The general aim of this thesis is to understand vegetation patterns across African landscapes, using the AES theory as a theoretical framework. This thesis specifically focuses on the dynamics within the lawn grass-bunch grass system of the African savannas and forest-savanna mosaics. These ecosystems have been studied as examples of AES dynamics in Africa due to their unique characteristics and the complex interplay of biotic and abiotic factors influencing them. Presenting compelling evidence for the presence or absence of AES in these systems is crucial, as there are significant implications for how these ecosystems should be managed as these systems are important for human livelihoods, conservation biology and are vulnerable to changing climates.

The specific objectives of this thesis are to 1) use empirical methods to test for the existence of AES in African savanna ecosystems, 2) show the challenges ecologists face when predicting true AES, and 3) emphasise the role of climate in shaping forest-savanna mosaics within the context of AES.

1.6 Thesis outline

This thesis is centred around testing and evaluating evidence for the theory of AES in savannas and forest-savanna mosaics in Africa. **Chapter 3** focuses on a model system that is capable of describing autogenic succession driven by changes in light availability. I show how such succession sequences can be influenced by consumption processes, such as grazing. The plant community considered consist of shade-intolerant and shade-tolerant plants where light is a limiting factor. Simulations illustrate successional replacement of shade-intolerant plants by shade-tolerant plants. The results and analysis from **Chapter 3** motivated the design of the mesocosm experiment in **Chapter 4**. In this chapter, I manipulated the grazing levels needed to produce different grass states that the theoretical model from Chapter 3 predicted. **Chapters 3 and 4** employ typical methods used to test for AES in the grass layer of African savannas. These chapters explicitly focus on finding evidence for the existence of AES using disturbance regimes. However, what has been lacking in the AES literature is the impact climate has on vegetation change. Therefore, while **Chapters 3 and 4** present evidence supporting the existence of AES in the grass layer of African savannas, **Chapter 5** delves into the impact of climate on vegetation change throughout the Holocene epoch across Africa, specifically focusing on forest-savanna mosaics which is a well-studied example of AES. This chapter does not aim to test the existence of AES; rather, it focuses on demonstrating how climate alone can drive vegetation change. It takes a paleo-perspective, seeking to understand shifts in factors such as precipitation and grass pollen over time across Africa.

This thesis uses a unique combination of theoretical models, direct experimental approaches and the paleo-record to understand the emergence of AES. The general thesis sheds light on the challenges ecologists face when predicting and testing for AES by designing models or manipulative experiments that meet the requirements for AES. This thesis emphasises the importance of considering the influence of climate when determining AES, particularly in well-studied systems like forest-savanna mosaics where large areas are posited to support AES but may be driven by climate instead. This thesis also supports the current literature revealing the difficulty of providing evidence of AES in savannas and forest-savanna mosaics in Africa and highlights the need for ecologists to consider multiple alternative hypotheses when interpreting observational data.

Chapter 2

Materials and Methods

2.1 Study Area - African savannas

African savannas are ancient ecosystems defined as ”tropical grasslands with scattered trees” (Bourliere and Hadley, 1983). Due to the diverse types of savannas found in Africa, the mechanisms that facilitate the tree–grass co-existence differ. The different types of savannas found in Africa relate to their distribution and mean annual precipitation (MAP). These savanna types include arid fertile savannas, moist-infertile savannas and mopane savannas (Fig. 2.1, (White, 1983). Savannas are often found adjacent to grasslands and forest ecosystems (Fig. 2.1, (Solbrig, 1996). The most widespread savannas in Africa are found in subtropical and tropical regions of Africa. Tropical and subtropical savannas can be more explicitly characterised as a discontinuous layer of trees within a continuous layer of mostly C4 grasses (Solbrig, 1996). African tropical regions are home to the vast and striking transition zones between forests and savannas (Oliveras and Malhi, 2016; Smith et al., 1997) (Fig. 2.1).

The evolution of tropical savannas is more recent than other types of savannas, dating back to the late Miocene, (8–10 Mya) (Sankaran and Ratnam, 2013). This evolution is linked to the expansion and assembly of mega-herbivores such as the elephant, antelope and rhino which are still present in tropical African ecosystems today (Beerling and Osborne, 2006; Cromsigt et al., 2017). The conservation of African savannas is of primary importance as the last near-intact communities of large mammal species exist in these ecosystems. However, managing savannas for nature conservation is a challenge because of how dynamic these ecosystems are especially when trying to understand the mechanisms that drive tropical savanna systems (Anderson et al., 2007; Lehmann et al., 2014). Traditionally the main non-climatic external drivers supporting the tree-grass coexistence in tropical savannas are fire and herbivory (Bond et al., 2005b). In the next paragraph, I will expand on these drivers and how they shape the structure and function of tropical savannas in Africa.

2.1.1 Non-climatic drivers

Fires are well acknowledged as a major driver of savanna structure (Higgins et al., 2000; Bond et al., 2003; Bond and Keeley, 2005; Bond, 2008). The grass layer of savannas supports high densities of large grazers and provides fuel for frequent fires (Murphy and Bowman, 2012). Savanna fires are fuelled by tall bunch grasses, and often do not spread to tree canopies or kill adult trees (Higgins et al., 2000; Bond, 2008). The role of fire in savanna ecology has been studied for decades (Trollope, 1984; Higgins et al., 2000; Van Wilgen, 2000; Bond and Van Wilgen, 2012; Andersen et al., 2003). Studies have shown how fire can be used as a mechanism for shaping ecosystems within tropical savannas and how fire can be a valuable tool for managing landscapes (Van Wilgen, 2000; Bond and Archibald, 2003b; Govender et al., 2006; Archibald, 2016). Ecological models provide a framework to explore the mechanisms that influence and drive external factors such as fire (Langan et al., 2017; Scheffer, 2009; Archibald et al., 2005; Scheiter and Higgins, 2009). For example, (Staver et al., 2011b) showed that fire regimes in African savannas depend on the MAP and grass abundance. This is a clear indication that there is an interaction between external and internal drivers, and as much as fire is important in savanna landscapes, other factors such as climate should not be ignored when trying to make sense of the vegetation dynamics in African savannas.

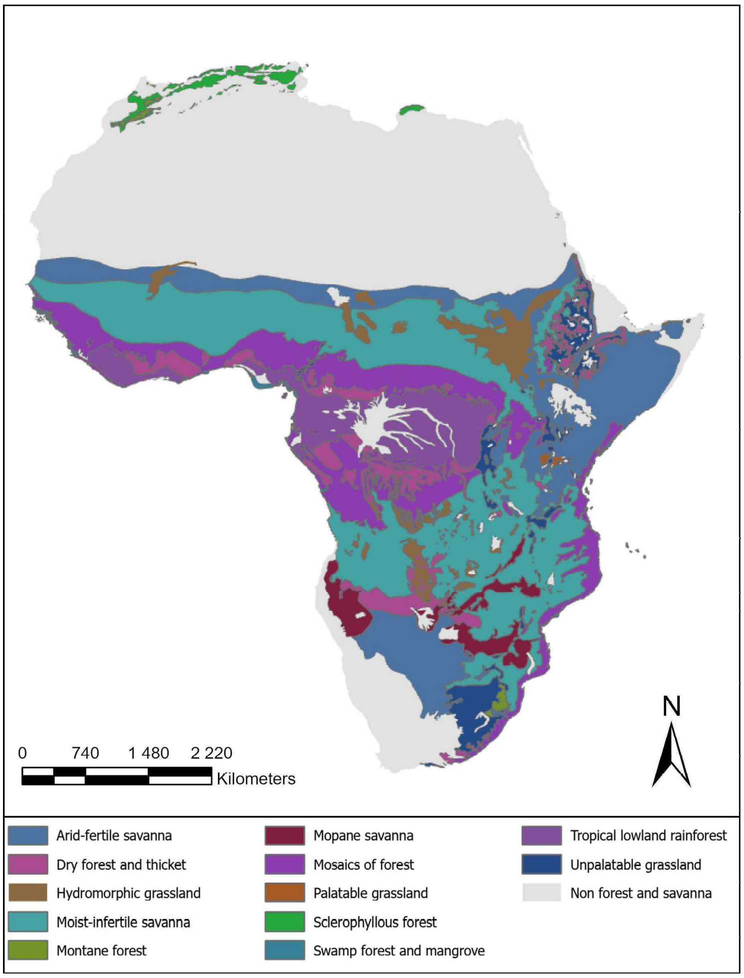

Figure 2.1: Vegetation types according to White (1983)

The long evolutionary history between large herbivores and African savannas has shaped the structure and function of these ecosystems, specifically the distribution of the grass layer. Herbivores can create and maintain lawn grass communities and keep fire-driven bunch grass out of the system (Hempson et al., 2019). In this way, herbivores directly influence the fuel needed for fire (Archibald and Hempson, 2016), indicating the interaction of these two external factors. Herbivores influence grass communities as they can either be general feeders or have specific preferences. These feeding behaviours impact plant communities essentially contributing to species heterogeneity (du Toit, 2003). For example, (Owen-Smith, 2004) show herbivores such as the rhino or hippopotamus are specific feeders and contribute to the creation of grazing lawns. Herbivores themselves are influenced by climate, specifically rainfall (Augustine, 2010). Many studies found that rainfall is a central climatic factor governing herbivore populations because of the reduction in food supply (Archibald et al., 2005; Ogutu et al., 2011; Gandiwa et al., 2016). However, to explain the dynamics of African savannas, the interactions between herbivores as well as the interaction with other influential factors such as rainfall need to be considered. Plant-herbivore models have been used to test various herbivore interactions giving insight into the internal dynamics in savanna ecosystems (Noy-Meir, 1975; De Knegt et al., 2008; Staver et al., 2021). An influential study by van Koppel and colleagues 1998 found that different herbivore interactions, through mechanisms of facilitation and competition, significantly influence the transitions between grassland and woodland ecosystems suggesting the importance of investigating the internal dynamics. Herbivores have always been an important driver of savannas and understanding the dynamics within herbivore populations together with the external factors influencing them is important for conservation management decisions in African savannas. That is, different management decisions could potentially cause irreversible change if not understood correctly.

2.1.2 Climate change in Africa savannas

Climate change is adding an additional level of complexity to ecosystem dynamics and conservation management in African savannas. African savannas, specifically tropical savannas are predicted to be highly vulnerable to climate change (Loarie et al., 2009). Here, the predicted rainfall changes and elevated CO_2 will have significant impacts on savanna vegetation, in particular, increasing woody encroachment, which is already a challenge in these ecosystems today (Scheiter et al., 2018). Changes to these ecosystems will have detrimental impacts on the structure and function of the different ecosystems found in African savannas, however, these impacts are not only affecting these systems ecologically but are also affecting the human populations that rely on these ecosystems (Dixon et al., 2003). The importance of African savannas to the human population is enormous as these ecosystems support the livelihoods of tens of millions of people (Osborne et al., 2018). The foundational premise of ecology is that climate determines ecosystems (Higgins et al., 2024; Schimper, 1903). However, the studies investigating ecosystem dynamics in tropical savannas have had a clear focus on non-climatic external drivers such as fire and herbivory being the main drivers of vegetation dynamics without recognising the dominant influence of climate. Climate models are valuable for predicting potential ecosystem scenarios resulting from climate change (Conradi et al., 2020a; Higgins et al., 2023a). These predictions play a crucial role in identifying vulnerable ecosystems that are likely to change due to climate change, serving as a useful tool for conservation management.

2.2 Methodologies

In this section, I describe the methods and approaches I employed to test and evaluate the theory of AES. These methods include; a theoretical and ecological modeling approach, a direct experimental approach and a paleo-ecological perspective. All three methods have previously been used in the AES context in a wide range of ecosystems.

2.2.1 Theoretical approach and ecological modeling

To understand ecosystem dynamics, theoretical frameworks are useful for testing complex ecological hypotheses. Theoretical frameworks help to simplify these complex systems which is best achieved through mathematical models (Soetaert and Herman, 2009). In ecological sciences, the Lotka-Volterra model was one of the first models based on mathematical principles and since then the importance of mathematical models as tools to test ecological theories has become necessary (Lotka, 1925; Volterra, 1928). One of the earliest mathematical models used to test the theory of AES in ecology was developed by (Noy-Meir, 1975) for grazing animals on pasture land. In the model, vegetation grows based on resource availability, but the density of herbivores is controlled by human managers who decide how many grazers to allow on a patch of land. Other influential models that followed the Noy-meirs approach include (May, 1977; Tilman, 1982; Harrison, 1979; Chase, 2003a; Dublin et al., 1990; Holt and Polis, 1997; Diehl and Feißel, 2000; Wilson et al., 1999).

The value of mathematical models for testing the theory of AES is that it allows for the mechanisms and processes that create and maintain these systems to be investigated by illustrating different outcomes essentially indicating what to expect when testing this theory experimentally. In this thesis, I use a process-based model to understand the mechanisms and processes driving the lawn grass-bunch grass system. This model system allows for different degrees of herbivory pressure and light availability to interact and predict different grass communities as well as indicate if, under any of these scenarios, AES can emerge.

2.2.2 Manipulative experimental approach

Since introduced by (Hurlbert, 1984), manipulative experiments have greatly expanded our capability to study ecological systems. The defining features of manipulative experiments are that different experimental units receive different treatments and that the assignment to these experimental units is or can be random with the control of external parameters (Hurlbert, 1984). What is most crucial when conducting manipulative experiments is the experimental design (Hurlbert, 1984; Petraitis, 2013). Manipulation experiments offer direct empirical evidence for the presence or absence of AES in a system, however are often ambiguous in their design. (Schröder et al., 2005), investigates studies that have presented arguments for AES using experiments. However, (Schröder et al., 2005) found that many of these experiments were not designed to be manipulative meaning that results are open for other explanations for state shifts and often there is difficulty in distinguishing between system variables and environmental parameters.

If designed correctly, manipulative experiments can determine if there are causal links between a manipulated variable and some measured response (Tilman, 1980). In the context of AES (Petraitis, 2013) suggests that manipulative experiments provide the most significant empirical evidence for AES. Given this context, theoretical models are useful for designing manipulative experiments as there is a prior understanding of the mechanism and process that drive the system (Soetaert and Herman, 2009). To use an appropriate experimental design to test the theory of AES, I designed a manipulative experiment based on the outcomes from the lawn grass-bunch grass model system. Here I could test the assumptions predicted by the theoretical model under a variety of manipulative treatments.

2.2.3 Paleo-ecological perspective

Paleo-ecological investigations of vegetation dynamics offer the possibility of obtaining reconstructions of conditions in the past. That is, it provides a window of temporal and spatial resolution into past environmental conditions, plant communities and human activities. This information is valuable to those who are interested in tracing ecological dynamics of the past and/or trying to make sense of ecological phenomena that need thousands of years to be observed (Runge et al., 2021).Theories such as the AES need long time periods to identify evidence, test the timescales of their stability, and discover the causes of vegetation changes (Gosling et al., 2021). Paleo-records have been used for evaluating the AES theory by using a time series approach reconstructed from historical data (Taranu et al., 2018). A body of literature exists for using a paleo-ecological perspective to test for AES in a variety of ecosystems (Taranu et al., 2018; Dakos et al., 2008; Lenton et al., 2012; Spanbauer et al., 2014; Beck et al., 2018; Gillson, 2015). For example, an influential study by (Desjardins et al., 1996) using ^{13}C isotopes to investigate the boundary in the Brazilian Amazonia provides critical insights into the history of the forest-savanna boundary(Desjardins et al., 1996). The isotopic data from deeper soil layers reveals significant past changes in vegetation types, highlighting the dynamics of this boundary. Factors such as fire frequency and environmental conditions have always been influencing these dynamics, revealing a complex history of vegetation shifts between forest and savanna ecosystems over the Holocene.

Tracing the temporal trends and patterns of vegetation and climate is useful to infer change over time, however, paleo-ecological results alone cannot determine the existence of AES and should be interpreted carefully taking into account the nature of the paleo-data being used. To cover a long time span, I use paleo-ecological data—specifically paleo-climatic variables, the pollen record, and evidence of domestic farming across Africa. This data provide insights into the timing of vegetation responses to past climate changes and the interactions among climate, human activities, and vegetation over long timescales. With the recent literature emphasising the risk of only using paleo-ecological data to test AES (Higgins et al., 2023a, 2024). I do not use this data to test for the existence of AES but rather to evaluate how climate influenced the vegetation dynamics across Africa throughout the Holocene epoch.

Chapter 3

Arresting succession to create alternative ecosystem states

3.1 Abstract

Ecosystems with qualitatively different structures and dynamics can exist under the same climate and edaphic domains. The processes that allow alternative ecosystem states (AES) to emerge are however poorly understood. We argue that progress could be made by explicitly analysing the development of AES in the context of succession theory. We hypothesise that AES emerge when succession is arrested. We use a model system that is capable of describing autogenic succession driven by changes in light availability. We go on to show how such succession sequences can be influenced by consumption processes, such as grazing. This model infers that processes that influence trade-offs between the growth and mortality rates of species and the extent to which these rates are influenced by ecosystem-level processes that species engineer themselves determines the extent to which alternative ecosystem states can develop. Our analysis shows how the interaction of plant traits and community-level processes determine whether alternative ecosystem states can emerge.

keywords: alternative ecosystem states, arrested succession, succession theory, lawn and bunch grass, herbivory

3.2 Introduction

Ecosystems with qualitatively different dynamics can exist in the same climate and edaphic domains. In many cases, this existence represents alternative ecosystem states (AES). Currently, we understand that for alternative ecosystem states to emerge, the shift between these states can be driven by both internal and external factors (Scheffer et al., 2001). Internal drivers encompass processes and dynamics that originate within the ecosystem itself. These include biological interactions such as predation, competition, and symbiosis, as well as physiological responses of individual organisms and internal feedback mechanisms that regulate population dynamics and resource distribution (Connell and Slatyer, 1977; Persson et al., 2007; De Roos and Persson, 2002). External factors include disturbances and climate forcing. Many AES studies have used herbivory as an external factor to test the AES theory (Petraitis and Dudgeon, 2004; Augustine et al., 1998; van Andel et al., 1993; Scheffer, 1990). The interest and recognition of this theory has become an influential concept in ecology, and although well-documented in theoretical frameworks, empirical evidence for the existence of AES has been inconclusive, primarily due to the difficulty of designing experiments meeting the requirements for testing AES (Petraitis, 2013; Charles-Dominique et al., 2016; Schröder et al., 2005). Despite the lack of evidence, the theory of AES continues to support the idea that ecosystems can contain multiple stable or temporary states. However, there is an inherent difficulty in empirically demonstrating the stability of a system (Connell and Sousa, 1983). It is more accurate to think of a system as being in a transient state that can move into another state depending on initial conditions and internal and external drivers (Fukami and Nakajima, 2011). These drivers interact to create feedback loops which create and maintain AES. However, these feedback loops can prevent a system from moving towards its climate potential (Clements, 1916). That is, feedback mechanisms prevent a linear successional pathway from developing towards its climax ecosystem state. This halt in succession can be defined as arrested succession (an ecosystem permanently stopped in early succession) (Young et al., 2001). In AES literature, the idea that AES reflects instances of arrested succession has not been a major focal point. However, it is well appreciated that both autogenic (internal) and allogenic (external) factors contribute to vegetation development in both theories (Tansley, 1935).

Succession theory views allogenic factors as resetting the successional process, while AES theory recognises allogenic factors as potential triggers for transitions between states (Connell and Slatyer, 1977; Walker and del Moral, 2009). For example, herbivory is an allogenic factor influencing ecosystem dynamics and affecting plant communities (Walker, 2012). Velben and colleagues 2010 found that intense herbivory can prevent the establishment of late-successional species and maintain the dominance of early-successional species. This is a non-linear pathway of succession where herbivory interacts with autogenic processes, an example of this is grazing lawns (McNaughton, 1984). In African savannas, grazing lawns are considered examples of AES as frequent grazing maintains the lawn dominant state and does not allow tall bunch grass to invade, essentially arresting succession (Hempson et al., 2015b). The link between the two theories suggests that arrested succession can be used as a framework to support the theory of AES. This is because herbivores adjust the natural progression of succession by influencing light and nutrient availability (Walker and Chapin, 1987; Davidson, 1993). However, this is only possible under certain conditions (Noy-Meir, 1975). Here, high or low biomass systems can occur under specific grazing levels depending on the initial conditions showing true AES. Theoretical studies, such as those by (Noy-Meir, 1975), are crucial for testing theories like AES and succession. These studies are important for understanding the mechanisms driving ecosystem states as it is possible to simulate multiple outcomes under different conditions and the testing of these theories in a variety of model systems (Young et al., 2001; Tilman, 1985, 1990; Noy-Meir, 1975; Walker and Noy-Meir, 1982; May, 1977; Noy-Meir, 1978).

I hypothesise that succession processes and ecosystem drivers, specifically herbivory, contribute to the shifts observed in ecosystems demonstrating AES. In these ecosystems, arrested succession may result in the persistence of a non-climax state due to the interaction of internal dynamics and herbivory. To investigate this hypothesis, a lawn grass-bunch grass system is used as a model. This system represents the co-existence of two different functional and structural grass types competing for the same resources, here light availability is fundamental to the dynamics within the system and the presence of herbivory interacts with autogenic processes influencing the natural succession of the grass community. Multiple outcomes are possible under different levels of herbivory. This can be seen as a powerful model system as it can predict the dynamics of lawn grass-bunch grass systems in real-world systems, for example, the transition from tall bunch swards to a grazing lawn in African grazing ecosystems. The lawn grass-bunch grass system is well-studied by field ecologists and rangeland scientists (van der Plas et al., 2013; Archibald, 2008; Archibald et al., 2005; Cromsigt et al., 2017; Valls Fox et al., 2015; Hempson et al., 2015b; Veldhuis, 2016; Stock et al., 2010; Anderson et al., 2013), but is not well-studied as an example of AES. We use this system to propose a series of general autogenic processes that determine state changes in AES systems. We aim to illustrate that ideas from succession theory and AES theory can be combined to create a single framework for understanding alternative ecosystem states.

3.3 Methods - A model for arresting succession

We first propose a model capable of describing an arrested succession sequence driven by changes in light availability and how such a succession sequence could be influenced by a consumption (e.g. grazing) process.

The model considers the biomass (B) of each of N species which are each regulated by a growth (G) process and consumption (C) process,

$$\frac{dB}{dt} = G - C. \tag{3.1}$$

Growth is influenced by photosynthesis a and mortality m,

$$G = g\ a\ B - m\ B, \tag{3.2}$$

where m is loss of biomass due to respiration and senescence. The parameter g is a growth efficiency parameter that serves to convert photosynthetic rates measured in μmol.g^{-1}.s^{-1} into g.g^{-1}.day^{-1}. The photosynthetic rate a is assumed to be determined by a light response curve,

$$a = a_{max}\left(1 - \exp\left(-\frac{1}{\kappa}(Q - Q_{lcp})\right)\right), \tag{3.3}$$

where a_{max} is the maximum rate of photosynthesis, Q is light, Q_{lcp} is the light compensation point of photosynthesis, and κ is a constant which defines the initial slope of the light response curve.

To expand this to a multi-species succession model we assume that a trade-off between Q_{lcp} and a_{max} exists, such that bunch grasses (low Q_{lcp} species) have low a_{max} and lawn grasses (high Q_{lcp} species) have high a_{max}. Specifically, we assume that a linear equation governs this trade-off, $Q_{lcp} = \alpha_{lcp} + \beta_{lcp}\ a_{max}$. We further assume that Q decreases exponentially with increasing vegetation biomass in the community as is commonly assumed in vegetation models,

$$Q = Q_{max}\exp(-\lambda\sum_{i=1}^{N} B_i) \tag{3.4}$$

here λ describes how rapidly light availability decays from Q_{max} as the sum of the biomass of over the N species in the community increases.

Consumption of biomass by herbivores C is assumed to follow a saturation curve,

$$C = h\, c \left(1 - \exp\left(-\frac{1}{\eta}(B - r)\right)\right). \tag{3.5}$$

Here h defines the herbivore population size and c is the maximum consumption rate per herbivore. The parameter η controls the slope of the saturation function and thereby describes the grazing efficiency of the herbivore. That is, more efficient herbivores will consume a greater proportion of the available biomass per time interval. We further allow the η parameter to be influenced by the species' palatability. Specifically, we assume that fast-growing species, lawn grasses (high a_{max}, high Q_{lcp}) are more palatable and that this palatability ensures that they are consumed more efficiently, that is that they have lower η. Specifically we assume that $\eta = \alpha_\eta - \beta_\eta\ a_{max}$. The parameter r is a grazing reserve, this ensures that when B drops to r that consumption by herbivores is zero.

To explore the importance of apparent palatability we also allow for η to be defined as $\eta = \omega\bar{\eta} + (1-\omega)\eta_i$. Here $\bar{\eta}$ is the biomass-weighted community average of η, η_i is the species-specific η and ω is a proportion that mixes the influence of η_i and $\bar{\eta}$ on the η experienced by each species.

3.3.1 Simulation experiment design

In plant communities consisting of lawn and bunch grasses where light availability is the limiting factor, a systematic successional replacement of lawn plants by bunch plants can be observed. When the parameter C in equation 3.1 is set to zero, the system models a succession dynamic as depicted in (Fig. 3.1). In this model, the species that ultimately dominates the community is the one with the lowest Q^*.

The Q^* value in our model is derived from (Tilman, 1985) R^* theory. According to this theory, the dominance of species in an environment with a single limiting resource can be predicted based on their R^* values, which represent the minimum equilibrium resource level required for their survival. The species with the lowest R^* (or Q^* in our model) can out-compete all other species, as it can sustain itself at lower resource levels, thus becoming the dominant species over time. Q^* is defined as,

$$Q^* = \kappa\ \log\left(\frac{g\ a_{max}}{g\ a_{max} - m}\right) + Q_{lcp}. \tag{3.6}$$

This model design indicates that plant-herbivory systems can support AES, which are dependent on the relationships between plant growth, herbivory consumption and herbivore density. This finding is consistent with (Noy-Meir, 1975), which suggests that simple plant-herbivore interactions can result in complex dynamics. Our graphical analysis, as shown in (Fig. 3.2), supports (Noy-Meir,

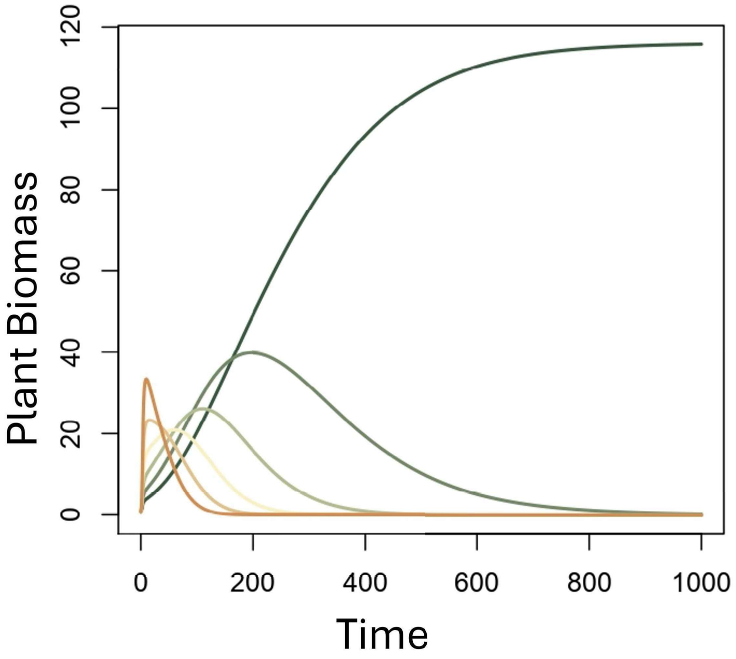

Figure 3.1: Simulated successional replacement sequence of six species following a trade-off between maximal photosynthetic rate a_{max} and shade tolerance Q_{lcp}. The orange end of the colour ramp indicates a species at the high Q_{lcp} end of the gradient and the dark green end indicates species with low Q_{lcp}.

1975) conclusion that continuously grazed ecosystems may exhibit discontinuous stability.

In our model, the concept of the grazing reserve r is introduced, which refers to the portion of vegetation that is left ungrazed to allow for recovery and continued growth in a lawn system. This ensures that the system maintains a minimum biomass level. At low consumption levels without a grazing reserve, the system supports one stable equilibrium state, as depicted in (Fig. 3.2 (A)). When consumption levels are high, the model predicts no point of intersection, indicating that consumption exceeds growth (Fig. 3.2 (B)). At intermediate consumption levels without a grazing reserve, the model allows for the existence of two equilibria (Fig. 3.2 (C)). (Fig. 3.2 (D)) represents a system with a grazing reserve greater than zero. The growth and consumption curves intersect once, producing a steady state. This is similar to (Fig. 3.2 (A)) however equilibrium is reached at a lower biomass. In these scenarios, the open point intersection represents an unstable equilibrium, while the solid point intersection denotes a stable equilibrium. These findings highlight the nuanced dynamics of plant-herbivory interactions and the critical role of consumption rates and grazing reserves in determining vegetation states.

By plotting $G(B)$ and $C(B)$ we have graphically explored the different equi-

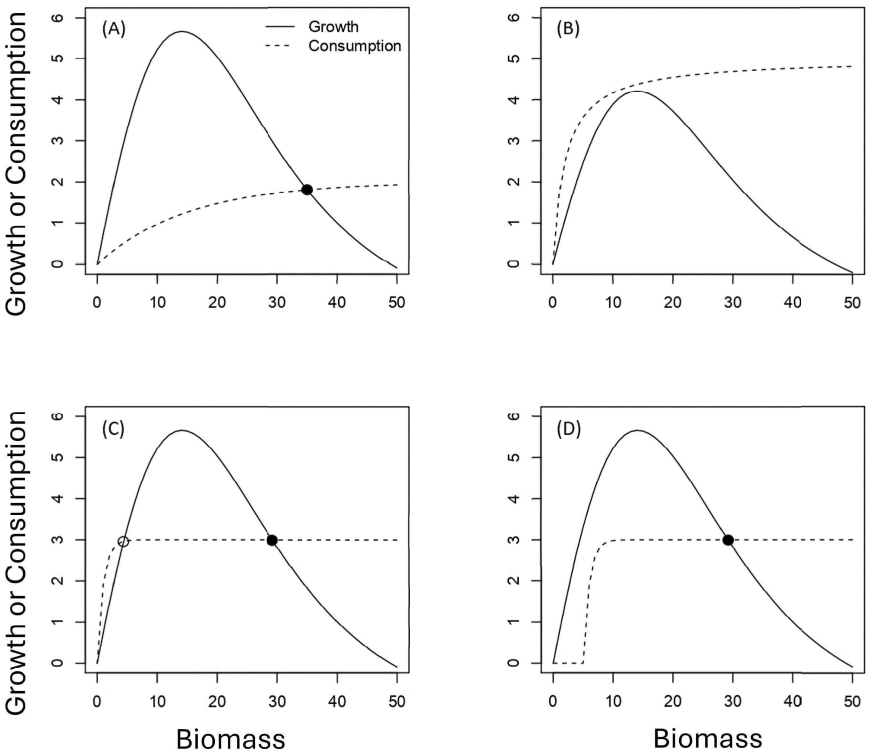

Figure 3.2: Graphical analysis of three different outcomes of growth (solid lines) and consumption (broken lines) functions described in equations 3.1 to 3.5. Solid points indicate stable equilibrium points, open points indicate unstable equilibrium points. The last panel shows a consumption curve with a grazing reserve $r > 0$.

libria that are possible when a single species is growing in monoculture and is exposed to grazing. We ask how these equilibria might change when considering the growth function with different traits (Fig. 3.1). To add to the single species model illustrated in (Fig. 3.2) we then used the linear trade-off between a_{max} and shade tolerance Q_{lcp} representing six species with different a_{max} and Q_{lcp} and It is apparent that the equilibrium points shift (Fig. 3.3).

For bunch grass species only stable points occur and for lawn grass species both unstable and stable points are present. This graph illustrates the equilibrium biomass expected for lawn and bunch species growing in monoculture when exposed to different grazing levels (h) and efficiencies (parameter η).

3.4 Results

We explore simulated multi-species communities, following the trade-off between maximal photosynthetic rate a_{max} and light compensation point Q_{lcp} for six species in (Fig. 3.2). To understand how initial conditions influence community states, we examine scenarios with either a lawn-dominant or bunch-dominant initial start. (Fig. 3.4 and 3.5) visualize species dominance under conditions of either high or

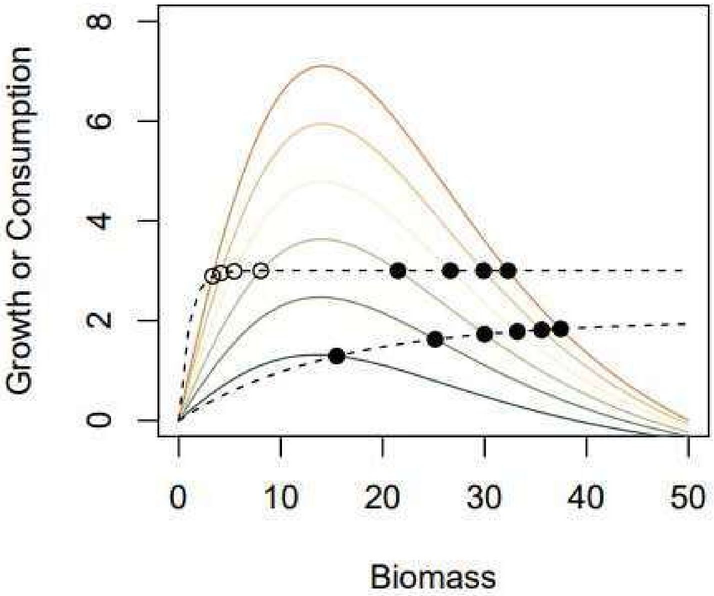

Figure 3.3: Growth functions of species conforming to a trade-off between maximal photosynthetic rate a_{max} and shade tolerance Q_{lcp} and two different consumption functions suggest different equilibrium biomass. Some of these equilibrium points are stable (solid points) others are unstable (open points).

low grazing efficiency, with the assumption that all species have equal palatability. In contrast, (Fig. 3.6 and 3.7) depict scenarios where palatability is linked to the a_{max}-Q_{lcp} trade-off and in these simulations, palatability varies among species, with lawn species attracting higher grazing rates compared to bunch grass species.

3.4.1 Low grazing efficiency

In an initial high and low biomass lawn grass state (Fig. 3.4 (A) and (B)), bunch grass is excluded from the system as herbivory levels increase. Lawn and intermediate grasses persist and dominate until the end. Under lower herbivore pressure, both bunch and intermediate grasses prevail (Fig. 3.4 (A) and (B)), suggesting that increased herbivory favours lawn grass and for an initial low lawn grass state the system is able to return to a lawn grass state. In scenarios with an initial high biomass bunch grass state, bunch grass continues to dominate despite increasing herbivory (Fig. 3.4 (C)). Conversely, in an initial low biomass bunch grass state, bunch grass is replaced by lawn grass, which dominates by the end of succession (Fig. 3.4 (C) and (D)). These findings indicate that lawn grass cannot establish in environments with initial high biomass bunch grass, implying that light availability is the most influential limiting factor. Lawn grass, with higher light

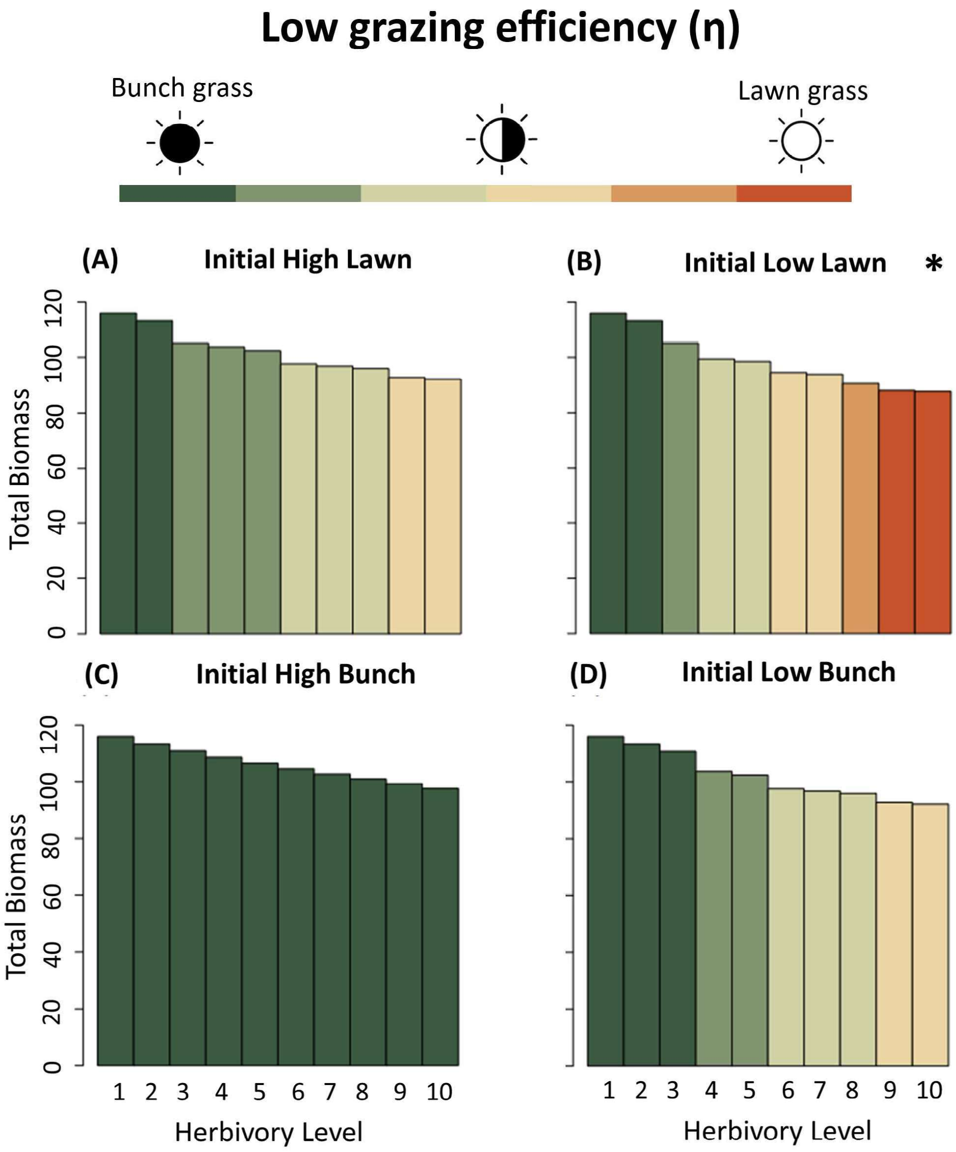

Figure 3.4: Scenarios predicted for six species following a trade-off between Q_{lcp} and a_{max} under low grazing efficiency. Each predicted scenario had a unique initial condition. A = Initial high lawn biomass, B = Initial low lawn biomass, C = Initial high bunch biomass, D = Initial low bunch biomass. The orange end of the colour ramp indicates a lawn grass species with a high Q_{lcp} and the dark green end indicates bunch grass species with low Q_{lcp}. The y-axis represents the total biomass predicted at each herbivory level at the end of the simulation * indicates scenarios where there is a clear shift in the species dominance.

compensation points (Q_{lcp}), requires more light, and thus a community dominated by high bunch grass biomass prevents lawn establishment.

3.4.2 High grazing efficiency

(Fig. 3.5 (A) and (B)) display two scenarios: one where the initial lawn biomass is high (A) and another where it's low. In both cases, lawn grass dominates as herbivory levels rise. In (Fig. 3.5 (C) and (D)), I explore scenarios based on the initial bunch grass biomass: high (C) and low (D). (Fig. 3.5 (C)) reveals that intermediate and lawn grasses fail to establish, indicating they fell below the tipping point and were consequently excluded from the system. This paves the way for bunch grass dominance, even under high herbivory levels. Initiation with low bunch grass biomass (D) triggers a shift from a bunch grass dominant system to one dominated by lawn grass. This suggests that low bunch grass biomass cannot withstand increasing herbivory, allowing lawn grasses to invade successfully. However, as herbivory levels intensify, the initial biomass isn't sufficient for recovery causing a biomass collapse, resulting in net biomass changes upon reaching a tipping point (unstable equilibrium). These simulations underscore the crucial role of initial biomass levels in systems featuring two equilibrium points.

3.4.3 Selective grazing

(Fig. 3.6) illustrates simulated scenarios of multi-species grass communities under selective herbivory. In these simulations, herbivores exhibit strong feeding preferences, targeting certain species more heavily based on their palatability. Specifically, lawn grasses, which have higher palatability values, are more frequently consumed, while bunch grasses, with lower palatability, are less targeted. This selective feeding demonstrates species-specific preferences, leading to differential impacts on the grass community structure and composition. (Fig. 3.6 (A)) illustrates a scenario where the system starts with a high initial biomass of lawn grasses. Despite this, under all levels of herbivory, lawn grass does not dominate due to the strong feeding preferences of herbivores, who target lawn grasses first because of their higher palatability. These preferences, coupled with the initial conditions, significantly influence the community structure, effectively shifting the system from a lawn grass-dominated state to a bunch grass-dominated state. This highlights the role of initial conditions and selective herbivory in driving community composition changes. In contrast, (Fig. 3.6 (B)) shows that when the system starts with low lawn biomass, the dynamics shift differently under selective grazing. As herbivory levels increase, the system transitions from being dominated by bunch grasses to being dominated by lawn grasses. This demonstrates how varying initial conditions and herbivory pressures can lead to different community outcomes, emphasising the complex interplay between initial biomass, herbivore preferences, and community dynamics. (Fig. 3.6 (C) and (D)) further explores these dynamics. When the system starts with either high or low initial biomass of bunch grasses, lawn grasses are unable to invade the system under selective grazing

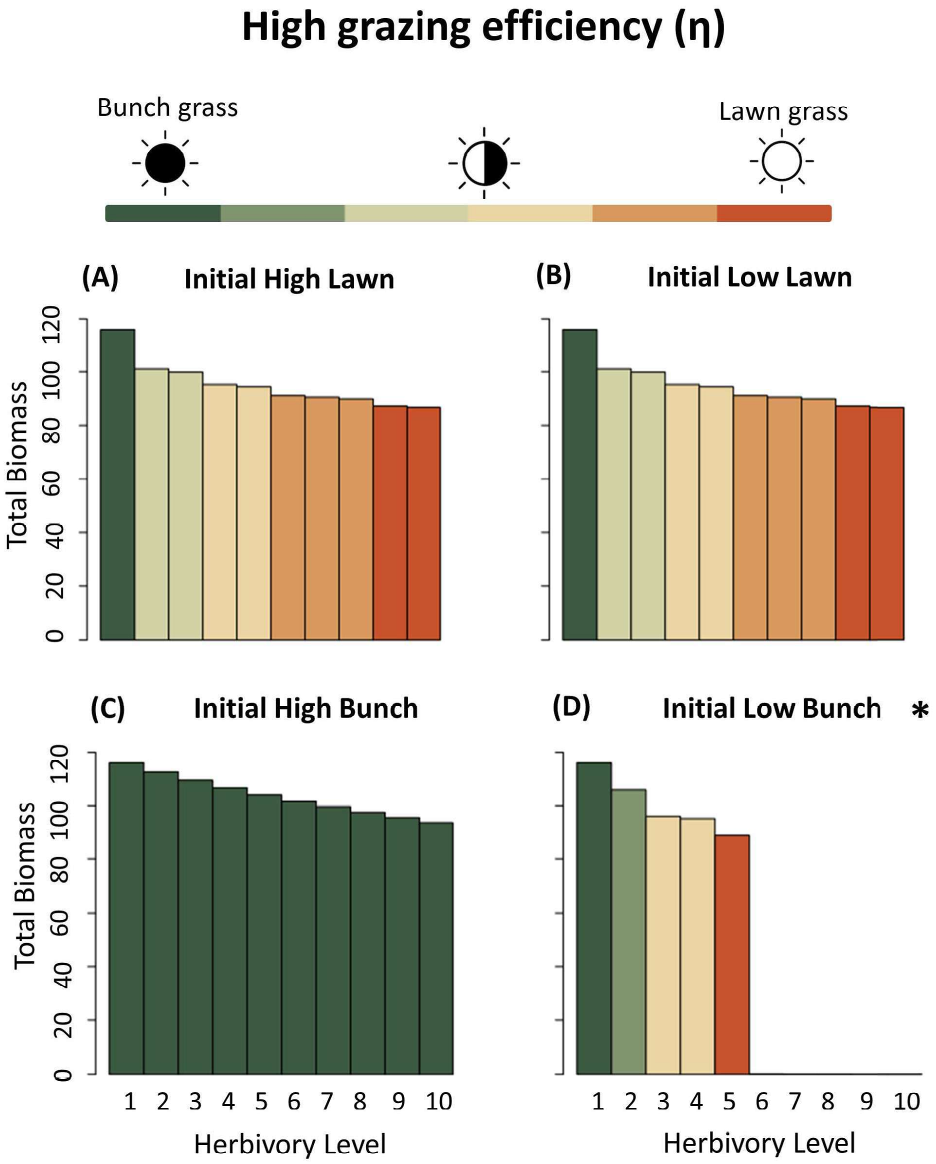

Figure 3.5: Scenarios predicted for six species following a trade-off between Q_{lcp} and a_{max} under high grazing efficiency. Each predicted scenario had a unique initial condition. A = Initial high lawn biomass, B = Initial low lawn biomass, C = Initial high bunch biomass, D = Initial low bunch biomass. The orange end of the colour ramp indicates a lawn grass species with a high Q_{lcp} and the dark green end indicates bunch grass species with low Q_{lcp}. The y-axis represents the total biomass predicted at each herbivory level at the end of the simulation * indicates scenarios where there is a clear shift in the species dominance.

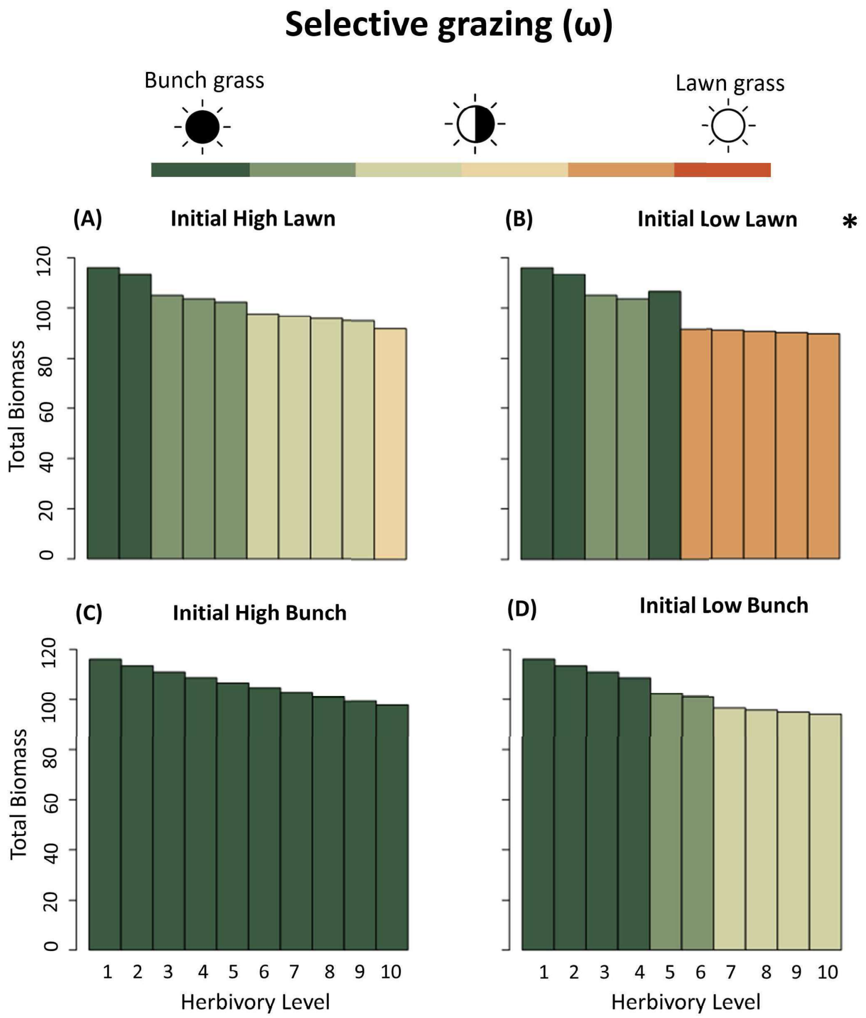

Figure 3.6: Scenarios predicted for six species following a trade-off between Q_{lcp} and a_{max} under selective herbivory. Each predicted scenario had a unique initial condition. A = Initial high lawn biomass, B = Initial low lawn biomass, C = Initial high bunch biomass, D = Initial low bunch biomass. The orange end of the colour ramp indicates a lawn grass species with a high Q_{lcp} and the dark green end indicates bunch grass species with a low Q_{lcp}. The y-axis represents the total biomass predicted at each herbivory level at the end of the simulation * indicates scenarios where there is a clear shift in the species dominance.

and increased herbivory levels. This indicates that regardless of the initial bunch grass biomass, the strong feeding preferences of herbivores and higher herbivory pressure prevent lawn grasses from establishing dominance.

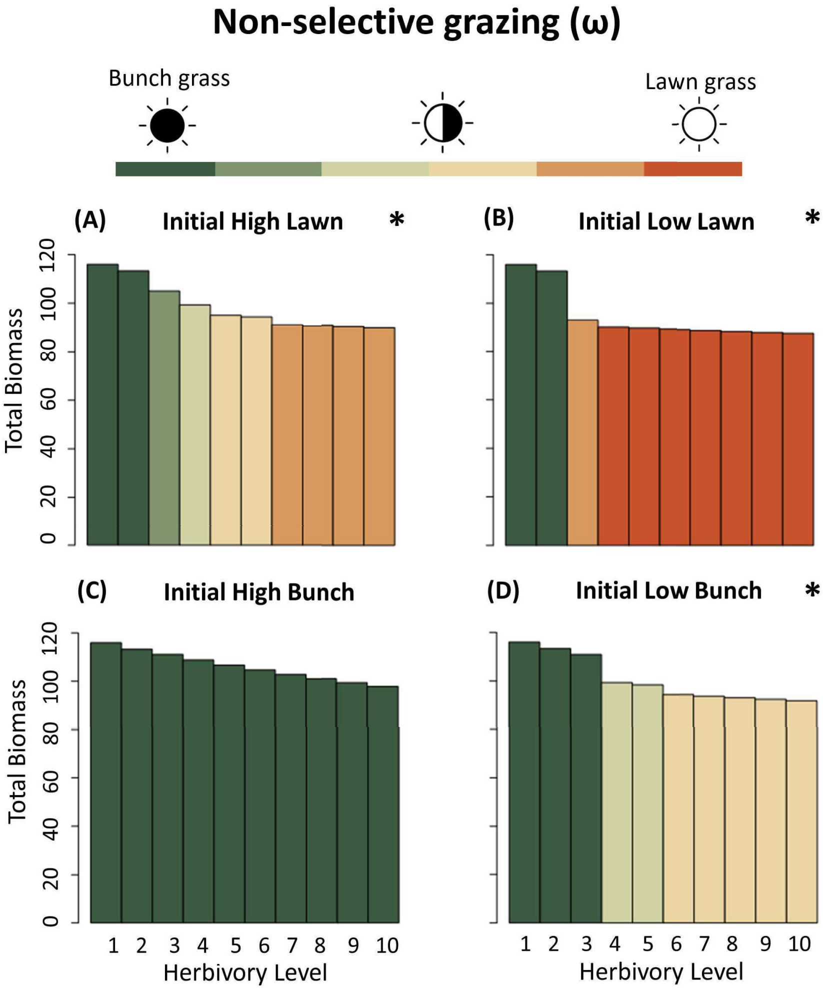

Figure 3.7: Scenarios predicted for six species following a trade-off between Q_{lcp} and a_{max} under non-selective herbivory. Each predicted scenario had a unique initial condition. A = Initial high lawn biomass, B = Initial low lawn biomass, C = Initial high bunch biomass, D = Initial low bunch biomass. The orange end of the colour ramp indicates a lawn grass species with a high Q_{lcp} and the dark green end indicates bunch grass species with a low Q_{lcp}. The y-axis represents the total biomass predicted at each herbivory level at the end of the simulation * indicates scenarios where there is a clear shift in the species dominance.

3.4.4 Non-selective grazing

(Fig. 3.7) represents scenarios with non-selective grazing, showing different outcomes compared to selective grazing. In (Fig. 3.7 (A)), there is a transition from high bunch grass to more lawn type species indicating a shift to a more open system when herbivory levels increase. In contrast, when the system starts with low lawn biomass, as shown in (Fig. 3.7 (B)), there is a drastic shift from a dominant bunch grass system to a lawn grass system. This shift occurs even at low herbivory levels, indicating that non-selective grazing can facilitate a rapid change in community structure when initial lawn grass biomass is low. When the system starts with a high initial biomass of bunch grasses, as shown in (Fig. 3.7 (C)), the results do not differ between scenarios of selective and non-selective grazing. This suggests that light availability drives this system, as lawn grasses are unable to compete with the tall-growing bunch grasses. (Fig. 3.7 (D)) results are similar to those where grazing is selective; however, there is an earlier shift to intermediate grass species, indicating a quicker transition in community composition under non-selective grazing.

3.5 Discussion

Simulations like the ones presented in this paper show that an intricate mix of autogenic and allogenic processes can trigger changes in ecosystem shifts. Here, interactions can create positive feedbacks where a change in one process amplifies another. For example, herbivory levels (allogenic) reduce bunch grass biomass which then influences light availability (autogenic) further reducing grass biomass leading to a more lawn dominated grass state. Mathematical models, such as (Tilman, 1985), show that community interactions, especially competition between species, play a major role in ecological succession. How species compete depends on the environmental challenges they face and the trade-offs they use to overcome these challenges. In our model, the assumed trade-off between Q_{lcp} and a_{max} allows species to co-exist due to their varying resource requirements. This assumed trade-off represents the mechanism that determines state changes in the model. Models incorporating trade-offs can predict ecological interactions among numerous species and improve our understanding of how species will adapt to new conditions (Tilman, 1990). As light is crucial for the development of grass communities, the trade-off between Q_{lcp} and a_{max} affects how each species will respond to herbivory levels simulating realistic scenarios. The inverse relationship between traits such as a_{max} and the Q_{lcp} is particularly important when light becomes limiting during succession (Bazzaz and Pickett, 1980). Changes in light availability can lead to the favoring of one plant type over another through autogenic processes, which are directly influenced by the plants themselves.

When herbivory is incorporated into the model, the interaction between internal processes such as light competition and herbivory activities creates positive feedback loops. These feedback loops can lead to a sudden and significant change, diverting succession towards an AES. However, this is only possible under certain herbivory activities (Hempson et al., 2019). Under low grazing efficiency and low herbivory levels, bunch grass is dominant (Fig. 3.4). This supports the literature (McNaughton, 1984; Hempson et al., 2015b) stating frequent grazing levels are needed to maintain a lawn grass system. High grazing efficiency (Fig. 3.5) allows both systems starting with low or high lawn grass biomass to return to a lawn grass state under higher herbivory levels. That is, herbivory interrupts the natural succession by returning the system to an earlier successional state not allowing for late succession species to invade (Davidson, 1993). Non-selective grazing affects the competitive interactions among the lawn and bunch grasses by altering the successional trajectories and arresting it completely when there is an initial lawn grass state (Fig. 3.7 (A) and (B)). Generalist herbivores reduce the grazing pressure whereas selective herbivores depend on a focal species essentially eliminating this species from the system over time (Huntly, 1991). (Waldram et al., 2008) show that in the savanna grass layer, rhinos impact landscape-level fire behaviour and the removal of these selective feeders have impacts on landscape fire dynamics. The model results support this statement as selective herbivory does not arrest succession allowing for late succession species (bunch grass) to dominate over time when there is an initial condition of high lawn grass. This suggests that selective grazing (lawn grasses most preferred) will allow the system to transition into a dominant bunch grass system removing lawn grasses from the system as herbivory levels increase changing the structure and function of the grass community to a fire-driven system.

This study shows that under different levels of herbivory and initial conditions, herbivory specifically influences the resource availability in the system and because of our assumed trade-off between Q_{lcp} and a_{max}, the grass community was able to switch to either a lawn (fast growing) or bunch (slow growing) dominated system or the system was able to remain in its initial state. The level of herbivory showed to have a strong impact on which species would dominate the system. Under lower herbivory levels bunch grass species are always dominating the system indicating that a more intense perturbation is needed to shift the system from a bunch grass state to a lawn grass state. Usually, this would require fire or external drivers as low herbivory levels indicate this system is not controlled by herbivory. Under increased herbivory levels the grass system represents an example of an AES.

Parallels can be drawn between this model and grazing lawn systems. In these systems, transitions into AES can occur if grazing intensity is too frequent or too infrequent. Light competition underpins the dynamics of lawn and bunch grass states, and if grazing lawns are used too infrequently, they are vulnerable to being shaded out by tall bunch grasses (Hempson et al., 2019). This can be seen in the model where bunch grasses become dominant in the system when herbivory levels are low, however, as herbivory increases, we see that lawn grasses become dominant, and these lawn communities are maintained in this state because of high herbivory levels (Fig. 3.7). Initial conditions shape how states can shift (Scheffer et al., 2001) and depending on these initial conditions, the model can predict scenarios where succession is arrested. That is, different initial conditions can lead to different final states (Scheffer et al., 2001).

(Fig. 3.7 (B)) illustrates the natural sequence of succession being arrested due to frequent herbivory, creating lawn dominant systems. This model can distinguish between mechanisms and causes of the grass community succession. Allogenic processes can be seen as causes and autogenic succession processes represent the mechanisms (van Andel et al., 1993). What is important to note and what can be seen in the model results is that both autogenic and allogenic processes are present in succession however under continuous grazing, herbivory exemplifies how external biotic factors (herbivory levels) and internal ecosystem processes (light competition) are intertwined, making it challenging to distinguish between allogenic causes and autogenic mechanisms in the context of vegetation succession. Using a theoretical approach allows us to grasp the complex dynamics of succession and simulate the interactions between external and internal factors under different conditions. This model design can predict the dynamics of a lawn grass - bunch grass community in real-world systems contributing to the mechanisms and causes that drive these systems to represent examples of alternative ecosystem states.

3.5.1 Can these results be interpreted as examples of AES?

Some of the scenarios presented in this paper can be seen as examples of AES (figures with *). These figures indicate a clear shift in species dominance under different herbivory levels. True AES occurs when observed differences in ecosystem states are caused by differences in initial conditions and are maintained by positive feedback processes. Here certain herbivory levels act as the positive feedback mechanism and light availability is the internal dynamics of the system. The critical feature determining the system's predictions is how herbivores consume and in this case, at certain herbivore levels, efficiency and selectivity influence the scenario results. However, herbivory alone does not change the system state but rather interacts with the internal dynamics to create and maintain AES. These results indicate that herbivory and internal processes can prevent the establishment of a bunch dominant grass state, creating a state dominated by lawn grasses. This state represents an example of arrested succession because, without the grazing pressure, the ecosystem might progress towards its climax community. Thus, scenarios that are examples of AES are a result of arrested succession.

What is noticeable in all simulated scenarios is that lawn grass cannot invade a system when the initial state is high bunch grass biomass dominance. Here, the effect of herbivory patterns cannot drive the system to a new equilibrium as light is not available for lawn grasses. That is, lawn grasses are being shaded out by bunch grass. For example, (Hempson et al., 2015b) explains that lawn systems that are used too infrequently are vulnerable to being shaded out by bunch grass. The result of this study suggests that under these circumstances AES are not possible. However, since this system is also driven by fire, it can be assumed that fire or external factors could be the main driver to push the system into a new equilibrium, changing the structure and function.

3.6 Conclusion

In conclusion, the results predicted in this simulation study demonstrate the interplay between autogenic and allogenic processes in a lawn grass-bunch grass system. The model reveals that herbivory, an allogenic factor, interacts with internal ecosystem dynamics, such as light competition, causing arrested succession leading to the emergence of AES. Here, a simple model illustrates the interaction between life traits, species engineering and consumers in a lawn-bunch grass system. Inverse correlations among life history traits and species competition for light are shown to produce successional replacement and coexistence. By showing how varying levels of herbivory can either maintain or disrupt these dynamics, our findings emphasise the complexity of ecological succession and the importance of both internal and external factors when developing models used to investigate AES. This model can be used to understand the mechanisms and processes that determine lawn-bunch grass systems, specifically in African savannas offering valuable insight into ecosystem management.

Chapter 4

Effects of clipping and invasion on African savanna lawn and bunch grass communities

4.1 Abstract

The grass layer of African savannas can be described as a heterogeneous mosaic of lawn and bunch grass communities. Lawn grasses are adapted to frequent grazing and can invade bunch grass communities under frequent grazing. Circumstantial evidence suggests that lawn and bunch grass communities can exist as alternative ecosystem states, however direct empirical evidence is lacking. In this study, we focus on how the invasion of lawn grasses into bunch-dominant grass communities may be influenced by grazing frequency. We used an experimental approach to create artificial ecosystems in mesocosms to test if clipping coupled with invasion by lawn grasses can shift bunch grass communities to lawn grass communities. Our experiment investigated under which clipping frequencies lawn grasses are able to invade bunch grass systems. The initial species composition was 80% bunch grass with 20% lawn grass. Clipping treatments ranged from every week to every six weeks. To interpret the results we used a plant growth model in a state-space modelling framework. We found lawn grasses have higher growth rates and are able to invade bunch-dominated systems under frequent clipping. Lawn grasses are unable to invade bunch grasses under infrequent clipping. Results suggest frequent clipping can maintain grass communities in a lawn-dominant state while infrequent clipping results in the disappearance of lawn grasses from the system. Our analysis provides evidence for the theory that lawn grasses persist under frequent grazing and two alternative grass states can exist under different clipping frequencies.

keywords: alternative ecosystem states, lawn and bunch grasses, invasion ecology

4.2 Introduction

Tropical and sub-tropical African savanna grasslands are diverse landscapes, consisting of mosaics of lawn and bunch grass communities (Veldhuis et al., 2016). Lawn communities are dominated by species that are typically short, clonal and high in nutrients while bunch grasses grow vertically, are nutrient-poor and less attractive to herbivores (McNaughton, 1984; Bonnet et al., 2010; Hempson et al., 2015b). Grazing significantly influences the structure and function of grassland ecosystems in African savannas. Depending on the frequency of grazing either lawn grass or bunch grass communities can develop and establish. However, if an initial bunch grass community has already been invaded by lawn grass species, lawn persistence is primarily dependent on non-selective frequent grazing assuming that after an initial disturbance lawn grasses have the opportunity to invade a previous bunch grass community (McNaughton, 1985; Scott et al., 1997).

Since McNaughton formalised the concept of grazing lawns, there has been a significant amount of research on the formation and maintenance of these systems in African savannas (Hempson et al., 2019; Donaldson et al., 2018; Hempson et al., 2015b; Archibald, 2008; Cromsigt and Olff, 2008). A common theme in these studies suggest that frequent grazing can initiate positive feedbacks to maintain grazing lawn systems (Donaldson et al., 2018; Archibald, 2008; McNaughton, 1984). For example, (Hempson et al., 2019) proposed a theoretical model showing how lawn and bunch grass states in African savannas are stabilized by positive feedbacks created by fire or grazing and can be considered an example of alternative ecosystem states (AES). This theoretical model illustrates that an initial disturbance as well as prior presence of lawn grass species in a bunch grass community are required for these systems to be considered an example of an AES.

Frequent grazing is suggested to be the main agent responsible for the transformation of grazing intolerant bunch communities to grazing tolerant lawn communities potentially shifting these grass systems to AES (Hempson et al., 2019; Howison et al., 2017; Bond and Archibald, 2003a). The existence of AES is well represented in African savannas, with research having a strong focus on savanna-forest mosaics (Pausas and Bond, 2020; Favier et al., 2012; Staver et al., 2011b,a). However, the grass layer of African savannas provides a comparable example as similar positive feedbacks create and maintain lawn and bunch grass states. Until now, empirical evidence has so far been lacking to recognise lawn-bunch grass systems as an example of AES.

In this study, I used a mesocosm experimental approach, to demonstrate the theory of AES in lawn-bunch grass communities. I hypothesise that lawn invasion coupled with frequent grazing could allow lawn grasses to persist and dominate a bunch dominate grass communities. I focused on how the invasion success of lawn species in bunch dominant grass communities may change under different grazing intensities. Here I explore grazing as a feedback mechanism and simulate grazing by clipping. We manipulated different clipping frequencies ranging from grass communities clipped every week to clipped every six weeks. To quantify dominance in each grass community, above-ground biomass was measured after each clipping event. To interpret the results we fit the biomass data to a Bayesian state-space model which estimated growth rates of lawn and bunch grass species under different clipping treatments. The initial species composition of each grass community was 80 % bunch grass with an invasion of 20% lawn grass. Using a combination of greenhouse experiments and Bayesian state-space models can be useful for developing models of plant community dynamics which can provide empirical evidence for theories that are challenging to test in the field.

4.3 Methods

4.3.1 Experimental design

A mixture of one lawn and three bunch grass species were grown together in a mesocosm experimental platform in the greenhouse at the University of Bayreuth, Germany. Lawn and bunch grass species chosen for this experiment were common perennial species found in savanna ecosystems in Africa. The lawn grass species chosen for this experiment is an example of a common lawn species, *Cynodon dactylon* (Hempson et al., 2015b). For the bunch grasses the following species were chosen: *Eragrostis gummiflua*, *Heteropogon contortus* and *Melinis nerviglumis*. The mentioned lawn grass grow laterally, allowing for persistence under heavy grazing, whereas the bunch grasses grow vertically. All grass species in this experiment use the C4 photosynthetic pathway.

Grass species were grown from seeds purchased from Silverhill Seeds (Cape Town, South Africa), Swarzenberger (Völs, Austria), The Original Garden Shop (Valladolid, Spain), and Jelitto,(Germany). All seeds were sown in December 2020 on trays that were filled with oven-dried sand, and placed in a greenhouse that had a temperature range of 21-25 degrees Celsius. All species began to germinate after two weeks. After one month, individual plants were transplanted into micro-pots and then subsequently grown for two months (February-March 2020). In April 2020, plants were then transplanted into experiment boxes (Fig. 4.1) and after two weeks of growth 90% of all biomass was clipped to simulate an initial disturbance.

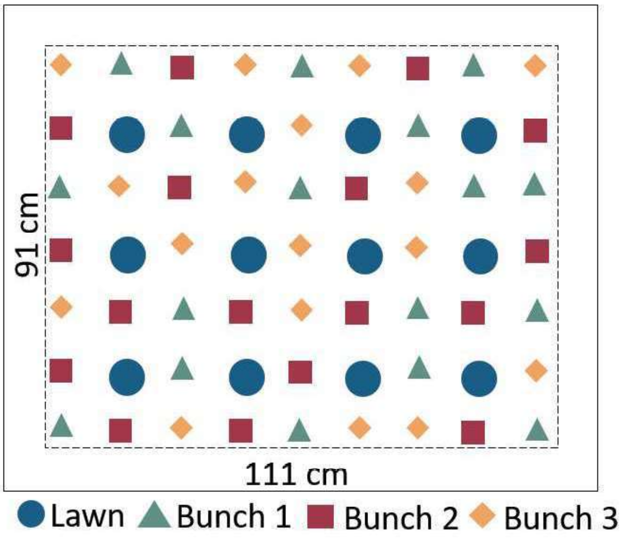

Figure 4.1: Experimental design.

In total, we had five experiment boxes, each with 63 plants. The 63 plants in each box were divided into 12 lawn plants and 51 bunch plants (three species). Each experiment box had a volume of 900 litres and was filled with perlite substrate purchased from Knauf-aquapanel, Germany. In each box, plants were planted at the intersections of a 9 x 7 grid with a distance of 12 - 13 cm between the nearest neighbours in the 111 x 91 cm surface area of the mesocosm (Fig. 4.1) Plants were planted 12 cm away from the edge of the box to avoid edge effects. Bunch grasses were planted randomly while lawn grasses were planted systematically (Fig. 4.1).

4.3.2 Clipping regime

In order to test biomass response of lawn and bunch grasses under different clipping treatments, an experimental period of 16 weeks (May- September 2021) was selected. This allowed for five clipping treatments, ranging from frequent to infrequent clipping. Boxes were clipped either every 1, 2, 3, 4 & 6 weeks and each clipping treatment was randomly assigned to each box. After four weeks of growth, the plants were sufficiently large enough for clipping to commence. To quantify lawn and bunch grass dominance, we removed all above-ground plant material just above ground level on each clipping occasion. Clippings of all species were collected separately for each box, and dried for 48 hours at 75 before being weighed. All boxes were watered once a week until saturated and given the same amount of fertiliser.

4.3.3 State-space model

We implemented a Bayesian state-space model (SSM) to predict grass biomass and estimate growth rates for each species under different clipping treatments. We used a Bayesian SSM as these models are useful for modelling time series data, which is relevant for this study as we are predicting the growth of grass biomass over time. SSM are especially useful for predicting biomass because they incorporate both the observed data and the underlying processes that generate predictions. This functionality of the model can capture the dynamic nature of the system and make predictions about how it will respond to different clipping scenarios. SSM can also be used to estimate unobserved variables, which can provide valuable insights into the structure and function of the grass layer. In theory, the SSM has two components, an observation model and a process model. Theoretically, the analysis is structured in the following manner,

$$B[t] = f(B[t-1], gr[t-1], cr[t-1]) + pr \tag{4.1}$$

$$y[t] = B[t] + e[t] \tag{4.2}$$

The process model is given by (equation (4.1)) where $B[t]$ is the predicted biomass at time t and pr is the process error associated with B. The function $f(B[t-1], gr[t-1], cr[t-1])$ summarizes that the development of B is influenced by the gr and cr parameters. gr is the proportion of biomass increased at each time step and is defined as $gr = a.gr + i.gr$. $a.gr$ is the average growth rate parameter estimated over the entire time series for each species. $i.gr$ is the growth rate estimated at each time step for each species. The clipping rate, $cr[t-1]$, represents the proportion of above-ground biomass that is removed at each clip event. In this model, it is fixed at 0.90, meaning that 90% of the above-ground biomass is removed at each clip event.

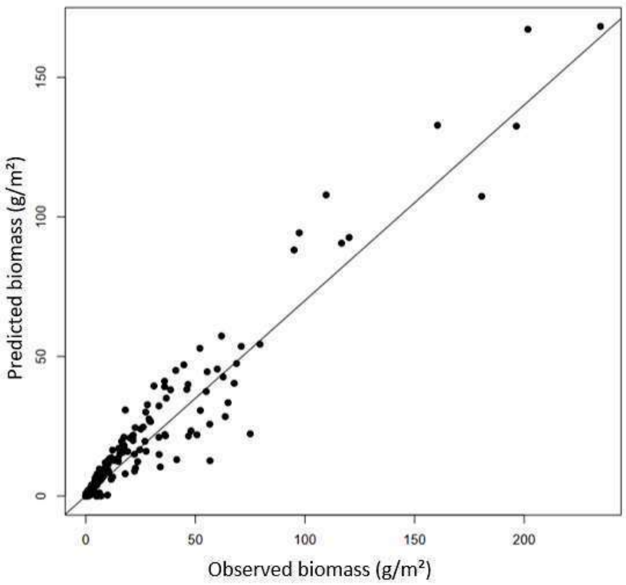

Figure 4.2: Modeled vs. observed above ground biomass for lawn and bunch grass species.

The observation equation (equation (4.2)) describes the relationship between the observed biomass, denoted by $y[t]$, and the predicted biomass, denoted by $B[t]$, at time t. The equation states that the observed biomass is equal to the predicted biomass plus a random error term, denoted by $e[t]$. The observation model is based on the experimental setting and how the biomass data was collected. In the process model we consider a time step to be one week matching the time series of the experiment. Bayesian statistics provide a framework for modelling and quantifying uncertainty by incorporating prior knowledge of the underlying process. Here credible intervals are used to quantify the uncertainty, this provides a reliable comprehensive method to assess the precision of the parameter estimates (Supplementary material: Fig. 4.5). The model was developed using the R-package LaplacesDemon (Statisticat and LLC., 2021). We used the biomass data measured from the experiment to estimate the posterior distributions of the estimated parameters.

The parameter gr was given vague half-t distribution priors. The parameter $a.gr$ was given a vague half-normal distribution prior (truncated to be > 0). The process error term pr was modelled using a half-t distribution and the observation error e was modelled using a half-normal distribution. The model also requires the parameterisation of $B[1]$, the initial vegetation biomass. To standardise the initial vegetation biomass for all species, we made sure that each species had a biomass value within the same range as that measured during the first week of the experiment, here $B[1]$ is given a vague half-t distribution prior. We used the Delayed Rejection Adaptive Metropolos algorithm (DRAM) MCMC algorithm as implemented in LaplacesDemon and its default control parameters to estimate the posterior distributions of the model parameters.

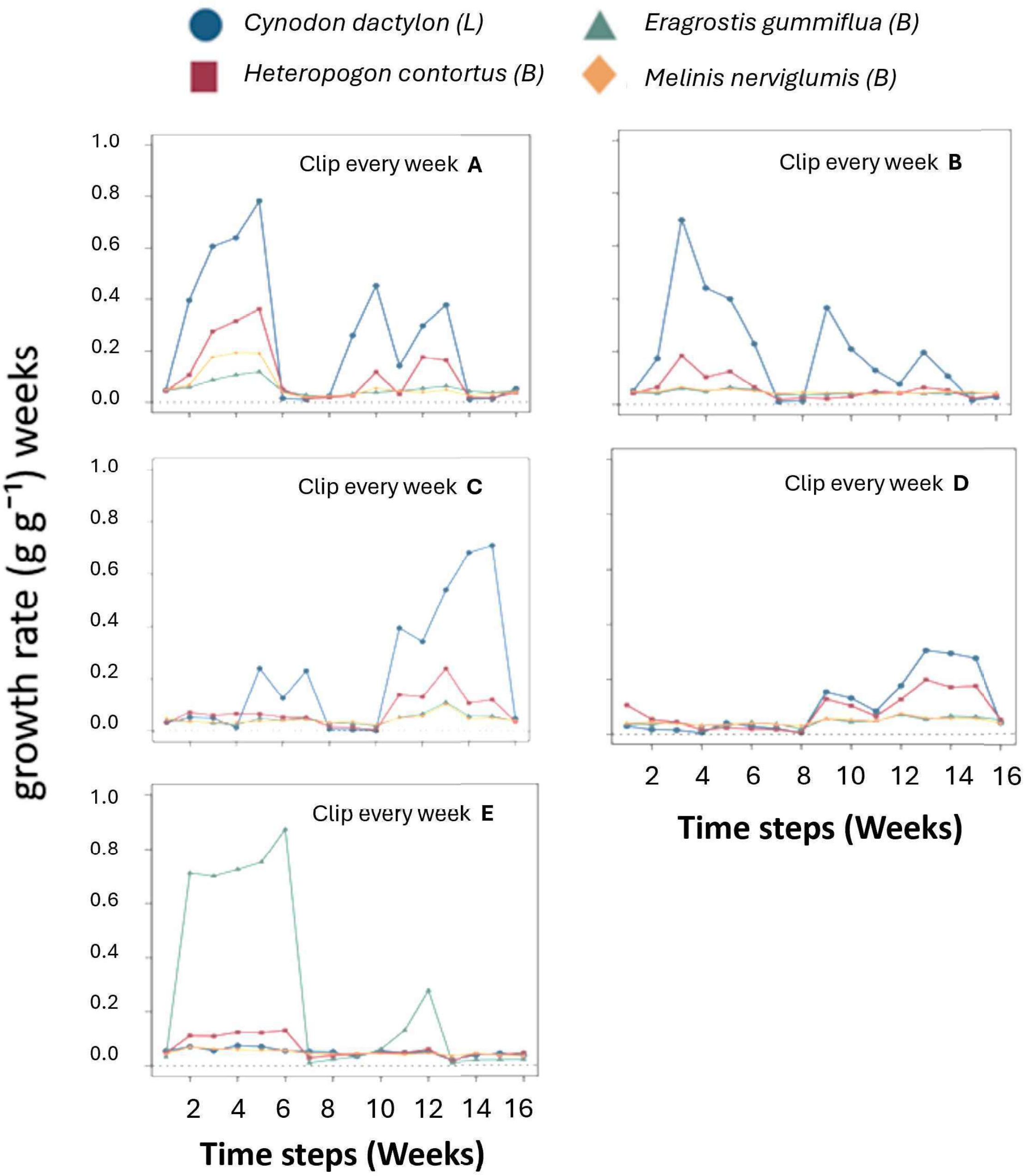

Figure 4.3: The posterior average for estimated weekly growth rate for all clipping treatments from most frequent (A) to most infrequent (E).

In each case, we ran each Markov chain for 20 000 iterations with a 10 000 burn-in period and thinning by 100 iterations. Visual examinations of diagnostic plots (trace plot and auto-correlation function plot) were used to confirm that the chains had converged. Model fit was assessed by visual inspection of the predicted and observed biomass and through a linear regression to determine the 1:1 ratio. All analyses were performed using R version 3.6.

4.4 Results

4.4.1 Estimated growth rate

Overall, the flexibility of the model allows it to effectively simulate the grass biomass estimated empirically for most of the samples across all the clipping treatments. The model fits the data well which indicates that the model describes observed patterns from the experiment (Fig. 4.2). The caterpillar plots of the parameter estimates show all parameters estimated (Supplementary material: Fig. 4.5).

The estimated average posteriors of the growth parameter indicate that the growth rate of *Cynodon dactylon* is significantly affected by the frequency of clipping (Fig. 4.3). When the frequency of clipping is most frequent (i.e., weekly), *Cynodon dactylon* exhibited the highest growth rate (Fig. 4.3 (A)). The maximum growth rate during the first few weeks of the experiment is observed to be 0.80 ($g.g^{-1}$) (credible interval = 0.75 - 0.86 ($g.g^{-1}$)), which decreases over time. The average growth rate over the time series for *Cynodon dactylon* was 0.66 ($g.g^{-1}$) (credible interval = 0.63 - 0.68 ($g.g^{-1}$)) (Supplementary material: Fig. 4.5). Interestingly, when the frequency of clipping is every three and four weeks, the growth rate of *Cynodon dactylon* increases towards the end of the experiment period. During the initial few weeks, the growth rate is relatively low with a maximum growth rate at week five when clipping is every three weeks, however over time, the growth rate increased to reach a maximum growth rate of 0.71 (credible interval = 0.64 - 0.78 ($g.g^{-1}$)) towards the end of the experiment. When the frequency of clipping is most infrequent (i.e., once every six weeks), the growth rate of *Cynodon dactylon* is consistently low throughout the experiment period, with an average growth rate of 0.27 (credible interval = 0.24 - 0.36 ($g.g^{-1}$)) (Supplementary material: Fig. 4.5). This indicates that frequent clipping is necessary to promote the growth of *Cynodon dactylon*.

The growth rates of the bunch grass species are consistently low across all clipping treatments (Fig. 4.3). However, there are some notable differences observed in the growth rates of *Eragrostis gummiflua* in response to different clipping treatments. When clipping is most infrequent (i.e., once every six weeks), *Eragrostis gummiflua* exhibits the highest growth rate among the bunch grass species. The maximum growth rate during the first few weeks after clipping is observed to be 0.82 (credible interval =0.76 - 1.03 ($g.g^{-1}$)) at week six and then declines over time. This decline in growth rate after clipping suggests that *Eragrostis gummiflua*

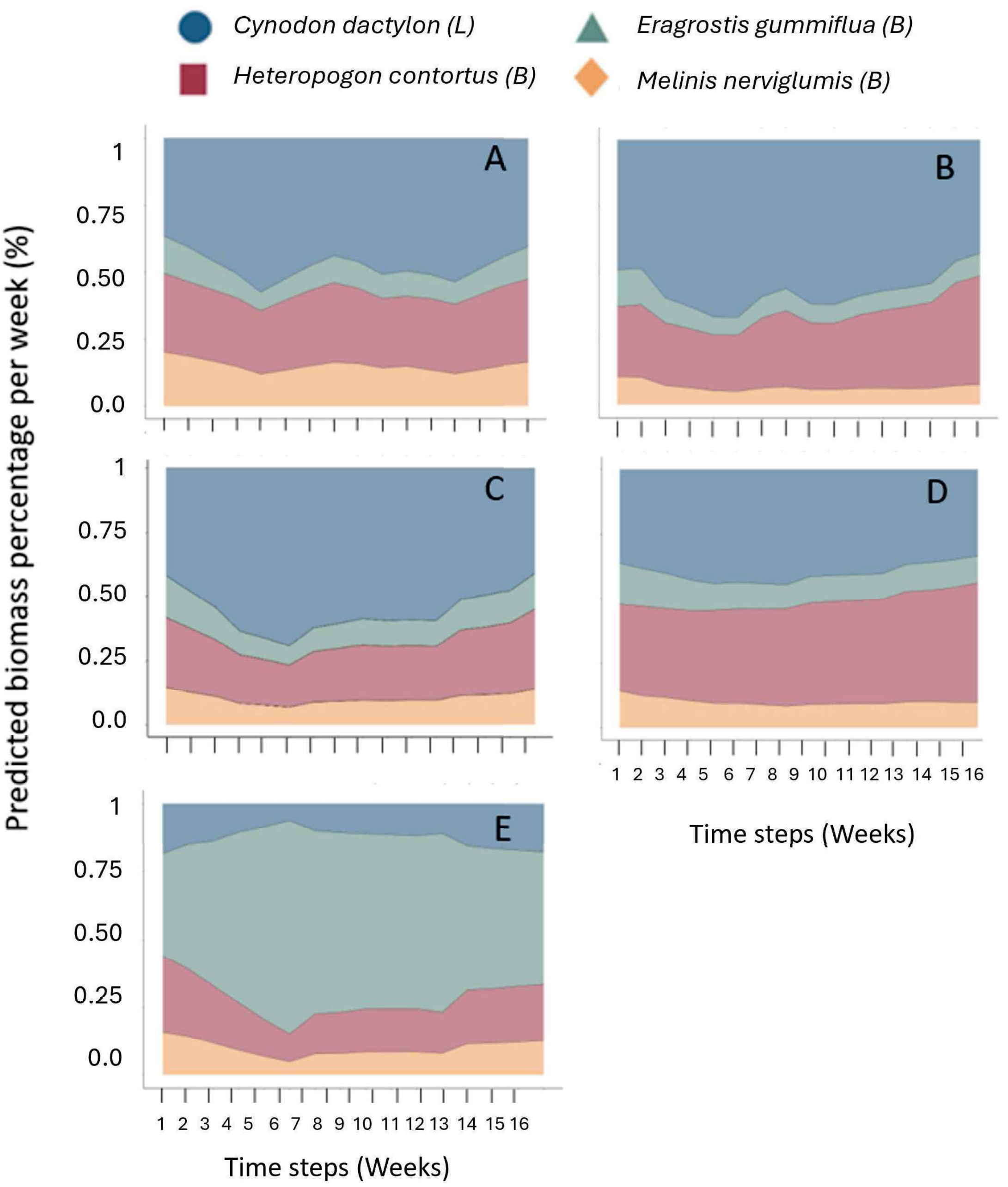

Figure 4.4: Total predicted biomass in percentage for all clipping treatments from most frequent (A) to most infrequent (E). Here (A) shows a strong feedback and (E) shows a weak feedback.

is highly sensitive to clipping frequency and may require a longer recovery period between clipping events. The average growth rates for all species under each clipping frequency is shown in the supplementary material 4.7.

When clipping is more frequent (i.e., once every 3 or 4 weeks), the growth rates of *Eragrostis gummiflua* remain low over time. This suggests that more frequent clipping may be detrimental to the growth of *Eragrostis gummiflua*. The growth rate for *Heteropogon contortus* and *Melinis nerviglumis* were always low regardless of the the clipping frequency indicating a low grazing tolerance within the grass community.

4.4.2 Predicted biomass

Analysis of the proportions of the predicted biomass revealed that lawn dominance is possible under frequent clipping treatments (Fig. 4.4). *Cynodon dactylon* was found to be the dominant species when the frequency of clipping was every week, every two weeks, and every three weeks. The observed dominance of *Cynodon dactylon* under frequent clipping treatments suggests that it may be better adapted to the rapid growth and recovery demanded by such regimes. However, the dominance shifted towards bunch grass species when the frequency of clipping was less frequent, specifically when the frequency was every 4 and 6 weeks. *Heteropogon contortus* was found to dominate the predicted biomass when the frequency of clipping was every 4 weeks, while *Eragrostis gummiflua* dominated when the frequency was every 6 weeks. Furthermore, *Melinis nerviglumis* was consistently the weakest bunch grass species across all clipping treatments.

4.5 Discussion

The transition from bunch grass communities to lawn grass communities in African savannas is largely driven by grazing by herbivores (Hempson et al., 2015b). However, the processes and grass community conditions required for herbivores to have a significant impact on ecosystem state shifts have been poorly understood. (Schröder et al., 2005) highlights the importance of direct experimental evidence for AES, as opposed to relying solely on theoretical models or indirect observations. Therefore, in this study, we utilised a direct experimental approach that combined the clipping of biomass as a method of manipulation and used a Bayesian state-space model as a framework to interpret the data. The aim was to investigate the potential of lawn invasion to cause a shift from a bunch-dominated system to a lawn-dominated system under different clipping treatments. By doing so, we were able to quantify the degree to which lawn species can successfully invade bunch grass communities. By estimating growth rates and predicting biomass using an SSM, we can gain valuable insights into how different grass species perform under various clipping treatments.

Our results show that lawn grass species, such as *Cynodon dactylon*, exhibited the highest growth rates under the most frequent clipping treatment (every week and every 2 weeks) but showed a decrease in growth rate over time (Fig. 4.3). Although grazing-tolerant lawn grass species such as *Cynodon dactylon* can withstand the stress of frequent clipping and defoliation better than other grass species such as all three bunch grasses, their growth rates can still decrease over time due to the cumulative effects of grazing (Leriche et al., 2003).

When clipping is relatively frequent (every 3 and every 4 weeks) (Fig. 4.3), we see that the growth rate of *Cynodon dactylon* increases toward the end of the time series. *Cynodon dactylon* is an opportunistic lawn grass species which colonises disturbed areas and recovers from grazing relatively quickly, making it a preferred forage species for many herbivores in African savannas (Anderson et al., 2014). The literature suggests that in a bunch-dominant community, grazing pressure can create disturbances that result in opening up gaps between the bunch grasses. Here, *Cynodon dactylon* is able to invade these gaps and colonise the areas, ultimately leading to a shift towards a lawn grass-dominant community. Conversely, the growth rates of bunch grass species were significantly lower under frequent clipping, suggesting a lower tolerance to defoliation. Under infrequent clipping *Heteropogon contortus* and *Melinis nerviglumis* had consistently lower growth rates, but with variations in the response of each species. *Eragrostis gummiflua* show high growth rates when clipping is most infrequent (every 6 weeks) and shows the lowest growth rates when clipping is most frequent (every week). This decline in growth rate can be attributed to the level of repeated clipping and the severe clip rate. While a decrease in growth rate does not necessarily indicate lower biomass production, differences in tolerance and strategies of bunch and lawn grasses under constant defoliation can affect their growth rates. While multiple factors such as soil nutrients, water availability and light availability influence the growth rates of African savanna grass species, the frequency and intensity of grazing is the mechanistic driver (Veldhuis et al., 2014; van der Plas et al., 2013; Archibald, 2008; Cromsigt and Olff, 2008; O'connor et al., 2001; Augustine and McNaughton, 1998).

The persistence of lawn species is primarily dependent on frequent grazing that prevents invasion by tall light competitors, as light competition underpins the formation of either grazing lawn or bunch grass community states (Hempson et al., 2015b). In our experiment, tall bunch grasses shaded out lawn grasses when clipping became less frequent, resulting in bunch grasses dominating the grass community (Fig. 4.4). These findings suggest that frequent and intensive clipping is necessary to create a positive feedback mechanism that allows lawn grasses to persist, while infrequent clipping results in a weaker feedback mechanism that is not conducive to the persistence of lawn grasses. It is important to note that changes in grass community dominance will only occur when a specific level and intensity of grazing is reached. The dynamic reversion of lawn and bunch communities is a common phenomenon in savanna landscapes where the grass layer is consumed by either herbivores or fire (Bond and Keeley, 2005). Our experiment demonstrates that successful lawn invasion coupled with frequent grazing can shift a bunch-dominant system to a lawn-dominant system relatively quickly. However, when clipping is infrequent, the grass community remains in a bunch dominant state. Our study supports the theoretical model proposed by (Hempson et al., 2019) showing that the grass layer of African savannas can exist as an example of AES by providing empirical evidence of shifts in dominance and testing the intensity and frequency of clipping required for bunch-dominant systems to shift to lawn-dominant systems.

4.6 Conclusion

In conclusion, this study has shed light on the frequency and intensity of clipping needed to trigger a shift in the dominance of lawn and bunch grass communities. Specifically, we found that lawn persistence was successful when clipping was frequent and intensive and when clipping was infrequent, lawn grasses could not compete in the bunch-dominant community. These findings support the important role that herbivory plays in shaping the structure and function of the grass layer in African savannas and how herbivore feeding behaviour can lead to the emergence of AES. The grass layer of African savannas is a complex and dynamic system, and understanding the underlying processes that drive ecosystem dynamics is crucial for predicting future shifts in savanna landscapes. By testing different clipping scenarios, we identified the conditions under which AES are likely to occur. Understanding the conditions for AES to emerge in lawn-bunch grass communities using direct manipulation is essential for developing effective management strategies aimed at maintaining the desired ecosystem state and avoiding undesirable transitions. Therefore, we propose that a combination of greenhouse experiments and Bayesian state-space models can provide valuable insights into the complex dynamics of plant communities, especially for testing challenging theories in the field.

4.7 Supplementary material

The figures in the supplementary material show the posterior means for each estimated parameter for each clipping frequency and each grass species, along with the upper and lower intervals. The means are represented by the solid dots, and the intervals are represented by the vertical bars. The upper and lower intervals were computed using the 95% credible interval, which is the range of parameter values that contains 95% of the posterior distribution. Specifically, the upper interval was computed as the 97.5th percentile of the posterior distribution, and the lower interval was computed as the 2.5th percentile of the posterior distribution.

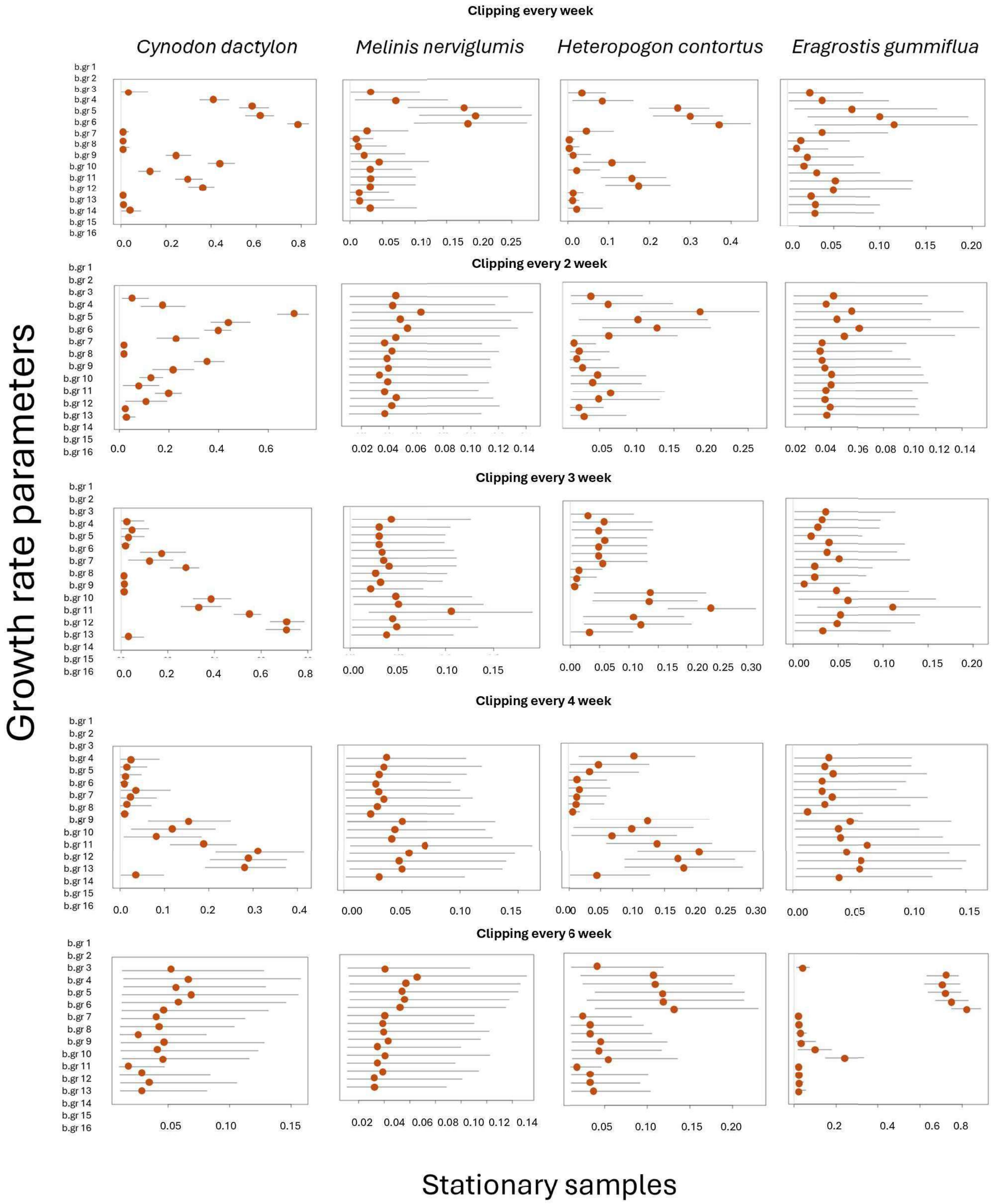

Figure 4.5: Posterior means for each estimated parameter under clipping frequencies. Each parameter represents the estimated growth rate for 16 weeks (b.gr1–b.gr16).

Chapter 5

Exploring vegetation changes within forest-savanna mosaic landscapes in Africa throughout the Holocene epoch

5.1 Abstract

Tropical forests and savannas are commonly recognised as examples of alternative ecosystem states (AES) across a wide range of environmental conditions. The existence of AES can be demonstrated by two lines of evidence: 1) by showing that an ecosystem can remain in its original state even though the local climate has shifted to a state that supports a qualitatively different ecosystem elsewhere or 2) by showing that persistent shifts in ecosystem state can occur in the absence of climatic changes. However, both are difficult to prove due to the long time spans required to demonstrate stability. Here we analyse Holocene pollen data from across Africa to detect times of climatic stability as well as ecosystem shifts between forest and savanna. We then link the observed vegetation dynamics to paleo-climate data to assess if and where persistent ecosystem shifts occurred despite climatic stability and where ecosystems persisted despite changes in climate.

keywords: paleo-ecology, alternative ecosystem states, climate change, Africa, forest-savanna

5.2 Introduction

Forests and savannas are widespread in the tropics, each exhibiting unique vegetation characteristics and ecological processes. While these two ecosystem types have clear differences in structure and function, they can be found in areas of similar climate and soils (Bond et al., 2005a). The distribution of forest-savanna mosaics is spread throughout the tropics with large areas found in Africa (Oliveras and Malhi, 2016). Forest-savanna mosaics are inherently dynamic and any changes in environmental conditions or disturbances can lead to vegetation shifts. The causes of these shifts are varied, resulting from complex interactions of environmental factors and ecological processes making it almost impossible to identify one influence. Despite this challenge, a significant body of research suggests that in large areas of forest-savanna mosaics, ecological processes are the primary drivers of shifts with much of the focus being on fire (de L. Dantas et al., 2013; Bond et al., 2005a; Bond, 2008, 2005; Bowman, 2000; Charles-Dominique et al., 2018; Staver et al., 2011b,a; Pausas and Bond, 2020). Many of these findings have used the forest-savanna transitions as an example to explain the theory of alternative ecosystem states (AES) in the tropics.

The existence of AES can be demonstrated if 1) an ecosystem can remain in its original state even though the local climate has shifted to a state that supports a qualitatively different ecosystem elsewhere or 2) by showing that persistent shifts in ecosystem state can occur in the absence of climatic changes and proving this is difficult due to the long time spans needed to determine stability (Schröder et al., 2005; Beisner et al., 2003). However, studies have not provided sufficient evidence supporting the existence of AES in these systems and environmental factors are often overlooked. For example (Beckett et al., 2022) conducted a study showing an initial state (forest) was reset by a perturbation, specifically a fire. Beckett and colleagues considered air temperature, relative humidity, wind speeds, and rainfall patterns to assess the impact of extreme fire events on vegetation structure and composition essentially showing that fire together with climate is the key factor shaping the studied forest-savanna mosaics. Other studies such as (Lebamba et al., 2016) and (Pellegrini et al., 2021) do show signs of AES however these studies were not designed using AES criteria (Petraitis, 2013).

Even though these studies have long time frames to identify bi-stable areas, it is still unclear if these areas are driven by disturbances such as fire and herbivory or climate.

Long-term studies (>100 years) can be used to trace climate and vegetation trends in forest-savanna transitions (Runge et al., 2021; Ametsitsi et al., 2020). Paleo-ecological data can provide clues to identify possible AES by analysing pollen records, charcoal deposits and climate proxies (Fletcher et al., 2014; Gillson et al., 2021; Gillson, 2015; Aleman et al., 2020) and can therefore be a valuable tool for examining how ecosystems responded to fire events, rainfall change, or human activities. However, drivers of vegetation change are numerous and difficult to disentangle. The complexity of AES makes the spatial and temporal dynamic patterns of forest-savanna vegetation mosaics challenging to prove empirically. To address these issues, isolating climate as the key driver for vegetation shifts can provide insight into determining whether specific forest-savanna ecosystems can be regarded as examples of AES or not.

Methods for exploring past climate patterns have come from multiple proxy data and climate models. Proxies such as pollen grains, isotope analysis, archaeological evidence and charcoal data have been used to reconstruct past climates alongside vegetation patterns over long timescales (Chevalier et al., 2020; Bartlein et al., 2011; Rachmayani et al., 2015; Phelps et al., 2020b; Cruz-Silva et al., 2023; Schleser et al., 1999). Climate proxies are also used to validate climate models by comparing model simulations with observed past climate conditions (Braconnot et al., 2012; Vincens et al., 2000; Breman et al., 2012; Lynch et al., 2007). In recent years the use of ecological models has increased to predict forest-savanna ecosystems in the tropics (Favier et al., 2004; Higgins and Scheiter, 2012; Murphy and Bowman, 2012; Higgins et al., 2000; Hirota et al., 2011; Zeng et al., 2014; Aleman and Staver, 2018; Aleman et al., 2020; Wuyts et al., 2017; Langan et al., 2017). In addition, significant efforts have been made to improve the quality and accessibility of present and future climate variables and in more recent years the access to paleo-climate datasets (Karger et al., 2021; He, 2011). These datasets are not as abundant as present climate data as there are challenges in simulating past climate conditions from proxy records (Gaillard et al., 2008). However, these datasets are valuable for understanding long-term climate trends, variability, and drivers of climate change over geological timescales.

Here, I analyse pollen data from forest and savanna sites across Africa to detect patterns and shifts between savanna and forest ecosystems. This study aims to provide insights into the long-term trends of paleo-climate and vegetation across

Africa throughout the Holocene epoch. Specifically, I test whether climate variables such as rainfall, can be used to explain the most well-studied example of AES, forest-savanna landscapes. Here, I challenge the theory that the majority of forest-savanna landscapes in Africa is driven by disturbances but rather driven by climate. To test whether climate is responsible for vegetation dynamics, I use a plant growth model to assess persistent ecosystem shifts that occurred despite climatic stability, and where ecosystems persisted despite climate changes. Structurally, the main vegetative difference between forests and savannas is the presence or absence of grass. For this study, I considered only the grass pollen counts as it can be used as an indicator for savanna or forest ecosystems (Bond, 2019). I expect changes in climate variables, specifically rainfall, to coincide with changes in the presence of C4 grass during the African Humid Period (AHP). After the end of the AHP, moving to more recent times, I assume that human activities play a role in shifts towards savanna landscapes. This study focuses on climate change, emphasising the importance of understanding past vegetation shifts and how climate could influence these ecosystems. This knowledge is crucial for understanding how climate affects these landscapes, especially in an era where climate change is occurring at an undeniable rate.

5.3 Methods

5.3.1 Pollen data acquisition

The pollen data used in this study was sourced from the (Phelps et al., 2020b) dataset. This pollen dataset is compiled for Africa from pollen records extracted from the African Pollen Database, the European Pollen Database, the ACER pollen and charcoal database and additional recent publications. (Phelps et al., 2020b) created a harmonised pollen taxa list with calibrated radiocarbon dates for a total of 349 sites across Africa. Time is represented as calibrated (cal.) years BP.

Each pollen dataset underwent screening to eliminate aquatic and semi-aquatic taxa, adhering to standard paleo-ecological methodology. The harmonised pollen taxa list however was not equivalent to species, as identifications vary from family and genus to occasional species or pollen types. To ensure a more accurate comparison, we classified the pollen taxa into growth forms using the method outlined by (Conradi et al., 2020b). To enable comparability between all pollen taxa, we calculated relative percentages for each sample using only the taxa belonging to the growth forms from (Conradi et al., 2020b). Pollen presences lower than 0.5 % were excluded to improve the reliability and accuracy of the data analysis. From the initial 349 sites, our refinement process involved the exclusion of duplicates and sites exhibiting minimal or negligible pollen counts. Consequently, 24 sites were eligible for further data analysis (summary of each site found in Supplementary material: 5.7.1).

Table 5.1: TRACE21K-II Climate variables

TRACE21k-II Climate Variables	**Units**
Maximum surface temperature (TSMX)	Degrees Celsius
Minimum surface temperature (TMIN)	Degrees Celsius
Precipitation rate (PRECT)	kg/m^2
Net radiative flux at surface (FSDS)	W/m^2
Downwelling solar flux at surface (SRFRAD)	W/m^2

Forest-savanna mosaics sites

This study concentrated on sites found in tropical and sub-tropical Africa regions with sites predominately representing forests and savannas. We assume that if a high percentage of grass pollen is in a specific site, the ecosystem would represent a savanna ecosystem state. We focus on the last 14000 (cal.) years BP, coinciding with the African Humid Period (AHP, ca 14800 – 5500 (cal.) year BP) which was an interval of wetter conditions over much of tropical and subtropical Africa (Demenocal et al., 2000). The end of the AHP exhibited a spatial and temporal complexity, ending earlier in northern, western, and central Africa, and ending later in eastern and southern Africa. (Shanahan et al., 2015). Many studies investigating historical climate and vegetation changes in Africa have identified the AHP as a pivotal event that influenced vegetation across Africa, specifically in the Sahel (Pausata et al., 2020; Hély et al., 2009; Vincens et al., 2010; Phelps et al., 2020b; Salzmann and Hoelzmann, 2005). That is, the AHP serves as a valuable starting point for assessing whether changes in vegetation can be attributed to this climatic event across Africa (Supplementary material:5.7.1).

5.3.2 Paleo-climate data and climate suitability

To examine the potential influence of climate changes on the presence or absence of grass in sub-tropical and tropical Africa from 14000 (cal.) years BP to 1950 CE. We adopted the method used by (Higgins et al., 2023a) where a plant growth model, species distribution data, and long-term transient climate data variables were used to estimate the physiological niches for 4542 African plant species.

Climate variables were sourced from the TraCE-21k simulation monthly dataset (at 3.25° horizontal resolution) (He, 2011). Covering the period extending back to 14,000 years BP, this dataset provides valuable insights into climate dynamics over this period. The selected climate variables were specifically chosen to capture signals indicative of changes during the AHP (Table. 5.1). We then estimated the climatic suitability of geo-locations for C4 grasses by averaging the niche projections for all species belonging to this growth form. To understand if the suitability of C4 grasses changed over time we focused on climate suitability projections of C4 grasses from 14000 (cal.) years BP to 1990 CE with 1000 year increments. The climate suitability scores for C4 grasses were then used to explain the patterns of the grass pollen percentages for each pollen site along a matching time series.

5.3.3 Human settlements and domestic animal farming

Understanding the timing of human settlements and the initiation of domestic animal farming is important for gaining insights into the historical climate conditions of a region. It is especially useful for this study where the presence or absence of grass percentages are being investigated. I considered the recorded dates of the start of domestic animal farming in different locations across Africa (Jousse, 2017; Phelps et al., 2020a). We considered samples that were found to be cattle, sheep and goat, camel, pig, donkey, horse and chicken indicating the presence of domestic farming.

5.3.4 Data analysis

Pattern detection of time series data

To ensure a continuous and smooth representation of each pollen dataset we applied a spline interpolation method to fill in the missing data points. To identify rainfall changes during the study period, we used precipitation rate as a proxy and applied a moving average smoothing technique to the data. We then conducted statistical trend analysis on our time series dataset to identify abrupt changes in grass percentage and precipitation rate. Here we applied a break-point regression analysis to the total grass percentage and the total precipitation rate over time. The estimated break-point was extracted for both variables. Both the moving average technique and break-point analysis are commonly used for analysing paleo-ecological data as the nature of the data often exhibits distinct shifts or changes over time and these methods contribute to a clearer understanding of long-term patterns (Supplementary material: Fig. 5.5)

Grass suitability maps

Grass suitability scores were calculated for each time period derived from the method used by (Higgins et al., 2023a; Conradi et al., 2020b). This method used a plant-growth model where a phytoclimatic transformation was used to estimate the ability of climate to support different types of plants based on their physiological requirements and the environmental conditions. Here, from the species range projections, climate suitability scores for C4 grass at every period were predicted. This modelling process allowed for the prediction of where species could grow under current and past climatic conditions. The model output provided information on the suitability of each grid cell for C4 grass based on the modelled potential ranges for each species. The suitability score for C4 grass in a grid cell was calculated as the proportion of species with a C4 growth form that could grow in the cell according to the model predictions. A higher proportion indicates that a higher amount of C4 grass species can grow in that grid cell. We assume that a suitability score of 0.5 or lower indicates grid cells where at least half the number of C4 grass species would not be able to grow. We also assume that suitability scores of 0.5 and above represent grid cells where the majority of C4 grass species can grow making these areas the most suitable. Suitability scores were visualised for each period using QGIS.

5.4 Results

Our results represent a comprehensive understanding of vegetation change, climate variation, and human settlement across Africa. For many sites, the estimated break-point of precipitation rate closely fits the estimated break-point where observed patterns in grass percentage changed (Fig. 5.1 (A)). For other sites, the change in precipitation rate is not associated with the major shifts in grass percentage change (Fig. 5.1 (B)). (Fig. 5.1 (C)) illustrates sites where an association exists between precipitation change and human settlement. Additionally, there are sites where the predefined time of human settlement aligns with the estimated time of the change in grass dominance (denoted by sites marked with *). The orange line shows where the major changes in precipitation over time occurred. The vertical blue lines indicate the recorded date of domestic animal arrival. These findings may be indicative of the distinct local characteristics inherent to each site. A detailed explanation describing the results of each site can be seen in (Supplementary material: Table 5.2) The high variation in grass percentage between sites indicates that even though sites may be in the same region, sites were independent of each other through time (Fig. 5.2).

The suitability of C4 grasses across different temporal and spatial contexts in Africa, predicted by the plant growth model, offers insights into the potential distribution of C4 grasses across Africa (Fig. 5.2). High suitability scores for C4 grasses are concentrated primarily in central/western Africa throughout each time slice. There are noticeable shifts in suitability scores in specific areas (changing from green to brown over time) (Fig. 5.2). It is crucial to identify regions that show these shifts between high and low grass suitability as these areas are vulnerable to change when a climatic tipping point is reached (Fig. 5.3). The majority of the areas experiencing these changes are situated in central and eastern Africa, with smaller regions in west and southern Africa (Fig. 5.3).

Table 5.2: Site results expanded

Site Name	**Results**
Lake Tilla	It is clear that when rainfall changes around 7000 BP there is a dramatic decrease of C4 grasses. However, around the same time rainfall changes, C4 grasses start to increase allowing for savanna systems.
Lake Albert	There is a very close match for rainfall and C4 grass change around 5000 BP. Here C4 grass percentage increases significantly.
Lake Tilo	Both human and rainfall changes coincide with C4 grass change around 3000 BP. Here there is a decrease in C4 grasses essentially moving the system from a savanna to forest.
Yevi	Both human and rainfall changes coincide with C4 grass change around 2000 BP. There is an increase in C4 grasses moving the system from forest to savanna.
Lake Kitina	Around 2500 BP there is a shift from a forest to savanna system as there is a significant increase in C4 grass percentage.
Blydefontein stream	Both human and rainfall changes coincide with C4 grass change around 4000 (cal.) years BP. There is an increase in C4 grasses moving the system from savanna to forest.
Craigrossie	There is a close match around 7000 cal. years BP with rainfall change and C4 grass changes. There was a drastic decrease in C4 grass before the climate changed.
Lake Masoko	There is a close match around 3000 BP with rainfall change and C4 grass changes. There is a slight increase in C4 grass percentage.
Lake Tanganyike	Both human and rainfall coincide with C4 grass percentage change. C4 grass percentage increases around 2000 BP.
Nyamuswaga Valley	Around 7500 BP there is an increase in C4 grass. However, the grass percentage is low throughout the Holocene.
Lake Bogoria	Human and rainfall changes occur around 2500 BP. Here C4 grass percentage decreases.
Lake Laboot Swamp	Around 12000 BP rainfall coincides with C4 grass percentage change. Here there is a drastic decrease in C4 grass around 7000 BP. Here, the system shifts from savanna to forest.
Bal Lake	C4 grass percentage changes around 9000 BP and rainfall changes around 8000 cal. years BP.

Lake Guier	C4 grass changes around 8000 cal. years BP, here there is a steady increase in C4 grasses. Around 6000 cal. years BP rainfall changes. C4 grass changes around 8000 cal. years BP while rainfall changes around 6000 cal. years BP. Around 3000 cal. years BP there is a sharp decrease in C4 grass percentage.
Lake Rukwa	Here rainfall changes around 8000 BP while C4 grass percentage changes with human activities around 2000 BP.
Tjeri	Rainfall changes around 12000 (cal.) years BP while C4 grass percentage changes around 6000 (cal.) years BP.
Pilikington Bay	C4 grass percentage changes around 7000 (cal.) years BP while rainfall changes later around 2000 (cal.) years BP.
Tamsaa Swamp	Around 2000 (cal.) years BP human activities and rainfall changes occur.
Mare d'Oursi	Around 2000 (cal.) years BP human activities and rainfall changes occur.
Eastern Niger Delta	Around 2000 (cal.) years BP human activities and rainfall changes occur.
Lake Sinnda	Around 2000 (cal.) years BP C4 grass percentage change, human activities and rainfall changes coincide. Here, there is a drastic increase of C4 grasses, suggesting a shift from forest to savanna.
Lake Andolonomby	C4 grass changes around 3000 (cal.) years BP, while human activities and rainfall change occur around 2000 (cal.) years BP.
Lake Tritrivakely I	Around 2000 (cal.) years BP human activities and rainfall changes occur.
Lake Victoria II	There is a significant increase in C4 grass percentage around 7000 (cal.) years BP with a later change in rainfall and human activities around 2000 (cal.) years BP.

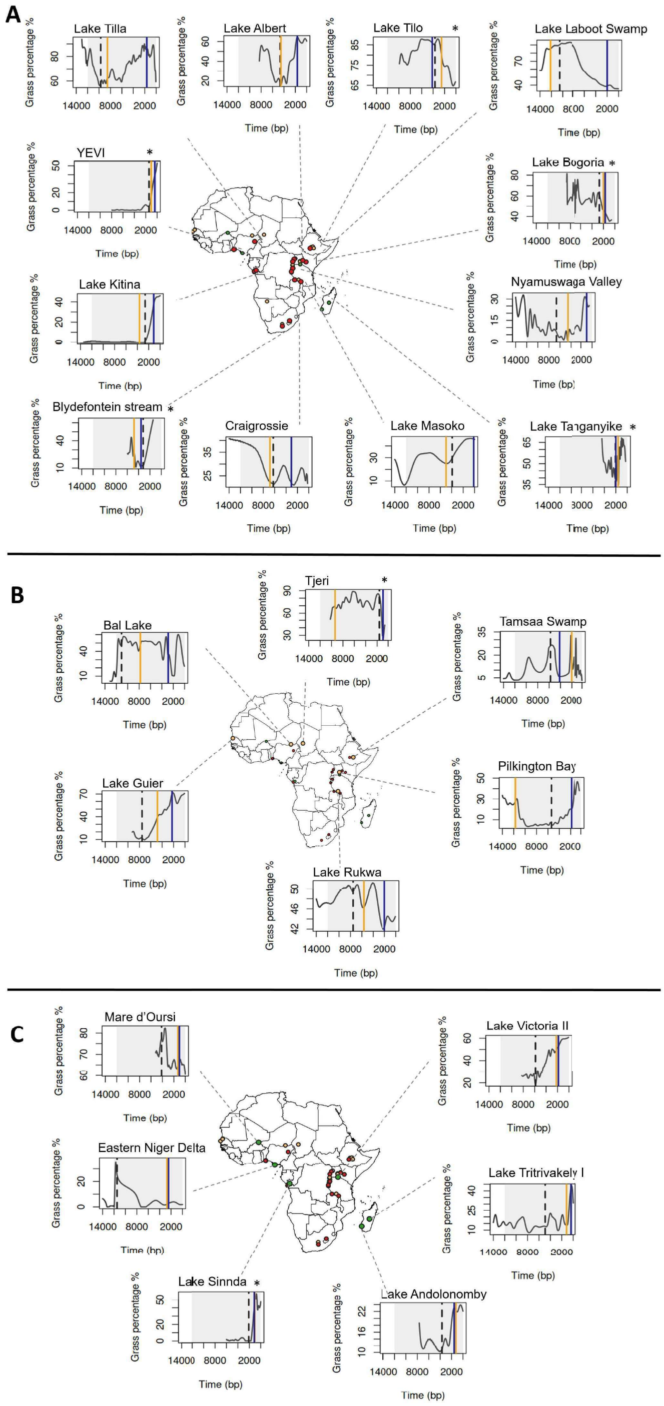

Figure 5.1: **Total grass percentage across pollen sites in subtropical and tropical Africa.** (A) Pollen sites marked with red dots exhibit closely linked breakpoints in precipitation and grass pollen percentages. (B) Pollen sites indicated by yellow dots show instances where there are no closely linked breakpoints in precipitation and grass pollen percentages. (C) Pollen sites marked with green dots exhibit closely linked breakpoints in precipitation and the recorded domestic animal records. Shaded areas (grey) represent the Holocene epoch era. The black dashed line represents the estimated break-point detected for statistical changes in the total pollen grass percentage over time. The orange line shows where the major changes in precipitation over time occurred. The vertical blue lines indicate the recorded date of domestic animal arrival.

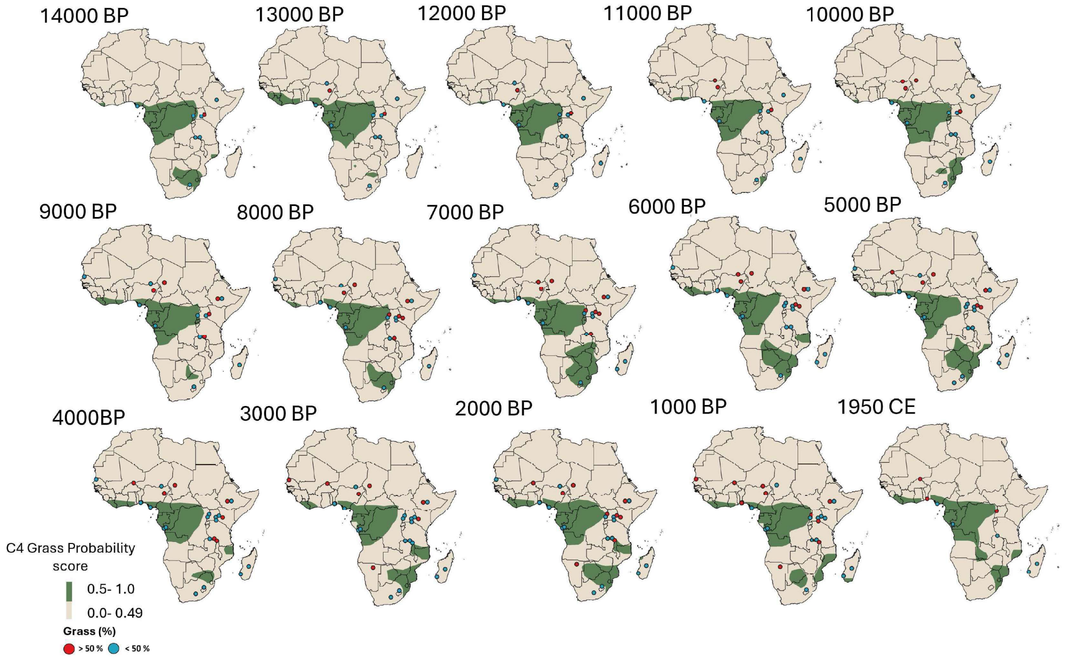

Figure 5.2: **Climatic suitability surfaces for C4 grasses for each time slice.** Dark green represents pixels with a suitability score above from 0.5 to 1 and beige represents pixels with a suitability score from 0.4 to 0. Pollen sites are displayed by red or blue points. Blue points represent grass pollen percentage lower than 50 % and red points are sites with grass pollen percentage higher greater than 50 %.

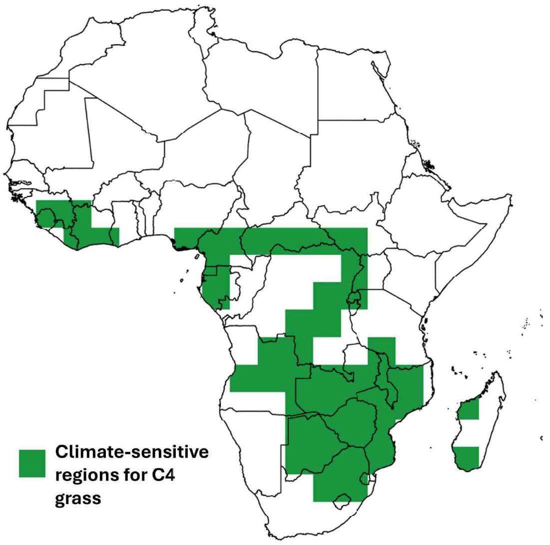

Figure 5.3: **Climate sensitive regions for C4 grasses according to climate suitability scores.** Green areas represent pixels that had both a high and low suitability score within 14000 (cal.) years BP - 1950 CE.

5.5 Discussion

These findings contribute to the ongoing research aimed at demystifying the causes of past vegetation changes in tropical and sub-tropical Africa. While existing research may support fire being the primary cause of forest-savanna mosaics in the tropics and sub-tropics, this paleo perspective provides a more robust view of how climate can be a possible driver of vegetation change thus fire regimes should not be assumed to be the only driver supporting forest-savanna mosaics. Here, exploring paleo-climatic patterns, particularly precipitation rates revealed apparent trends in rainfall variability across Africa during the Holocene epoch (Fig. 5.1). Changes in precipitation rate in 12 out of 24 sites (Fig. 5.1 (A)) have shown similar directional change with grass percentage over time. But there are regions where climate changes are not attributed to shifts in vegetation (Fig. 5.1 (B)).

In Africa, savanna and forest ecosystems can exist under the same edaphic and climatic conditions and many studies have explored this phenomenon in central Africa as forest and savanna constitute the two main ecosystems in this region (Cardoso et al., 2021; White, 2001; Cuni-Sanchez et al., 2016). The savannas in central Africa are characterised by a mix of grasses and scattered trees, with C4 grasses being a dominant component of the grass layer (Aleman et al., 2017). The forests in Central Africa have experienced both expansion and contraction over time due to a combination of climate events and human activities (Maley et al., 2002). Projections generated by the plant growth model indicate inconsistent patterns, revealing central and southern Africa with both high and low suitability scores for C4 grass growth throughout the Holocene (Fig. 5.2). Despite favourable climate conditions which may have supported the growth of C4 grasses in the region, other environmental factors likely played a significant role in determining their distribution and abundance. While the suitability for C4 grasses was high, the percentage of C4 grass pollen remained below 50% (Blue dots). This suggests that additional factors such as soil conditions, fire regimes, ecological interactions, and human activities may have influenced the presence and dominance of C4 grasses in central and southern Africa over time.

Non-climatic factors, such as human activities through the introduction of domestic animal farming, have also played a significant role in vegetation dynamics across Africa. A large amount of research demonstrates how human activities have left legacies on vegetation across Africa (Bond, 2019; Oslisly et al., 2013; Oksanen and Oksanen, 2000). However, the emergence of domestic animal expansion in Africa was dependent on the climatic conditions (Kuper and Kropelin, 2006; Marshall and Hildebrand, 2002; Smith, 1992). This influenced the patterns and time of domestic animal spread and distribution across sub-tropical and tropical Africa. It is likely that when there was a change in rainfall, human activities were affected (Fig. 5.2). At these sites, we see that domestic animals were active at the same time as when there were changes in precipitation rate and the dominance of grass. This complex process shows how different factors work together, making it difficult to separate their effects from the influence of climate.

Some regions are more vulnerable to the impacts of climate change due to various factors such as topography, environmental characteristics, disturbance regimes and human activities (Hirota et al., 2010). During the AHP, there was a significant increase in rainfall and humidity across various regions of Africa (Shanahan et al., 2015). However, despite favourable conditions, some areas remain vulnerable to changes in environmental conditions, including temperature, precipitation, soil moisture, and atmospheric concentration. (Fig. 5.3) illustrates projected areas that have exhibited both high and low suitability for C4 grasses over time. These regions represent climate-sensitive areas, where changes in environmental conditions can substantially impact vegetation dynamics. Fluctuating suitability scores suggests the potential for ecosystem shifts or transitions in these areas. In the literature, most of these transitions, especially in Africa, have been viewed through the lens of the AES theory. Here, different studies have presented various interpretations of the size and distribution of AES zones, leading to contrasting perspectives (Higgins et al., 2023a; Aleman et al., 2020; Williamson et al., 2023; Staver et al., 2011b). Various data sources, such as climate proxies, field observations, and model predictions, can lead to different interpretations of ecosystem dynamics and the potential existence of AES. Currently, there is an ongoing discussion about how widespread AES forests and savannas are across Africa. (Aleman et al., 2020) predicted that 7.5 million km^2 represents bi-stable regions in Africa and these regions span from 700 to 1,900 mm of mean annual precipitation (MAP). This is a large area essentially described as AES. Several AES studies acknowledge rainfall gradients and rainfall changes influencing ecosystem mechanisms such as fire and herbivory however many of these studies still claim that these are examples of AES (Karp et al., 2023; Lehmann et al., 2011; Archibald et al., 2009; Warman and Moles, 2009). In contrast, the study does not find evidence for this, rather we find that +-7.3 million km^2 of Africa (not including Madagascar) is a climate-sensitive region for C4 grass from 14000 (cal.) years BP-1950 CE (Fig. 5.3). This is indeed a large area however our interpretation does not indicate that climate alone is responsible for the presence or absence of C4 grass but rather that within these areas climate changes should be considered when exploring the emergence of AES in Africa. The varied interpretations of AES indicate the complexity of ecosystem dynamics and the importance of considering multiple datasets and modelling approaches to gain an understanding of potential alternative states in the savanna-forest domain. In this study there are sites where the changes in C4 grasses do not coincide with climate or human changes suggesting possible forest-savanna AES at these sites.

5.6 Conclusion

Our findings provide insights into the long-term trends of paleo-climate and vegetation across Africa throughout the Holocene epoch. Our findings suggest that localised changes in precipitation show similar trends to the presence of grass pollen in certain areas. However, many of these sites not only showed similar trends in changes in precipitation but also evidence that these changes coincide with the timing of human activities, with the timing of human activities, which highlights the complexity of teasing apart the cause of vegetation shifts. Some sites did not show any overlap between precipitation and vegetation changes indicating the possible influence of non-climatic drivers such as fire and herbivory. Identifying sites where vegetation shifts can occur regardless of changes in precipitation or human activities suggests the possibility of the existence of forest-savanna AES.

While paleo-ecological data alone is insufficient to definitively determine the existence of forest-savanna AES, understanding the environmental conditions conducive to growth forms and in our case, C4 grasses, serves useful when trying to locate forest-savanna AES. Our findings reveal a significant region in central Africa demonstrating variable climate suitability for C4 grasses during the AHP, which is characterised by fluctuating scores indicating both high and low suitability. By analysing the climate suitability scores, researchers can assess the likelihood of AES, such as shifts in vegetation composition or biome shifts. For example, higher suitability scores for C4 grasses in forested areas may suggest a potential transition from forest to a more savanna-like state.

The conflicting discourse supporting AES is a reminder of how challenging it is for this theory to be proved. This study adds to the ongoing discussion of AES in Africa. However, it shows how climate affects ecosystem dynamics as well as highlights the difficulties posed by considering climate change within the AES framework. The varying scientific opinions on the existence of AES should encourage researchers to integrate data resources such as field observations, climate proxies, floristic data and model predictions to develop a more robust understanding of the AES theory. This study does not ignore the role of non-climatic drivers shaping tropical and subtropical ecosystems but rather focuses on how there is much complexity when trying to demystify the causes without considering climate influence.

5.7 Supplementary material

5.7.1 Summarised interpretation of main paleo-environmental stages recorded in pollen sites

East Africa The general pattern in climate change shaping the vegetation and ecological conditions in East Africa over the Holocene period is consistent with our results (Fig. 5.1(A)). For Lake Tilo grasses dominated the landscape throughout the Holocene, indicating a savanna environment. Around 4500 years (cal.) years BP, conditions became drier, and an increase in grazing-resistant grasses such as *Podocarpus*, *Juniperus*, and *Hagenia* suggests human settlement and pastoralism (Lamb, 2001). Literature on Lake Bogoria suggests that climate became more humid ca 4500 years (cal.) years BP, leading to a decrease in grass pollen and an increase in *Podocarpus*, indicating a shift towards a more forested region (Vincens et al., 1986). This is consistent with our results as precipitation changed with grass percentage change. At Lake Laboot the climate changed from cold dry conditions to warmer humid conditions ca 13000 years (cal.) years BP (Bakker and Coetzee, 1988). As the climate changed so did the vegetation, our site information shows a rapid decrease in grass percentage ca 9000 years ago indicating a forested system. As each site is independent of one another, some sites did not show alignment with precipitation change and grass percentage change. These sites include Tamsaa Swamp, Pilkington Bay, Lake Rukwa and Lake Victoria II.

Central Africa Central Africa has exhibited forest expansion and extraction throughout the Holocene epoch. During the late Holocene, central Africa underwent a warming period and ca 4000 (cal.) years BP the contraction of forest occurred supporting savanna expansion at its northern and southern boundaries (Maley et al., 2018). Around 2500 (cal.) years BP further contraction of the forest block occurred. Lake Albert shows a rapid and abrupt shift to drier conditions ca 11400 to 9900 (cal.) years BP (Beuning et al., 1997). This dry period is seen in the site information where a decrease and rapid increase in grass percentage aligns with precipitation change suggesting a more open area. Nyamuswaga Valley remained generally humid with forest throughout the Holocene (Fer, 2018). Grass dominance was consistently low ($< 30\%$) and changes in grass percentage corresponded to precipitation changes, indicating a consistently forest ecosystem. At Lake Tanganyika and Lake Masoko the climate became more conducive to human activities such as domestic farming, correlating with increased grass pollen (Makoba and Muzuka, 2019; Vincens et al., 2003). At Lake Kitina, the period between ca 5400 and 2500 (cal.) years BP densely forested areas were recorded, this can be seen from the significantly low grass pollen percentage from our site information (Elenga et al., 1996). This suggests this was a forested region with more humid climate conditions. Around 2000 (cal.) years BP there was an abrupt shift in grass presence and climate conditions became drier. These drier times correspond to the expansion of domestic animals suggesting climate and human impact (Elenga et al., 1996). Lake Sinnda is located in the driest region of Congo, here a major climatic change ca 3000-2500 (cal.) years BP. is indicated by an abrupt decrease in forest pollen and by a corresponding increase in grassland pollen (Vincens et al., 1998). This can be seen in site information where there is an abrupt shift from significantly low grass pollen percentage indicating a forest ecosystem to grass being dominant indicating a more savanna landscape. The drying up of the lake shows that climate, in particular aridity, was the major cause of this change (Elanga et al. 1998). This can be seen in our site information as there is a strong alignment with the precipitation change and grass percentage change. The island of Madagascar experienced climate and human activities during the late Holocene. The literature focuses on climate and anthropogenic drivers as the main drivers of vegetation change on the island (Razanatsoa et al., 2022). This can be seen in both sites Lake Andolonomby and Lake Tritrivakely. Here, precipitation change and domestic animal evidence align around 1500 (cal.) years BP. This coincides with the literature on human presence and climate change. From our site information, it is clear that the sites shifted from a forest to a savanna as a result of climate and human activity.

West Africa The literature on vegetation changes in West Africa is non-linear where fire, herbivory, humans and climate are investigated. At Lake Tilla the period from ca 10000 BP to 6800 (cal.) years BP the climate was conducive for the formation of savannas. This is consistent with our site information, here grass pollen percentage increased with precipitation change. The pollen diagram of Lake Tilla reflects a history of savanna which appears to have been controlled by climatic changes (Salzmann, 2000). Site YEV1 in Benin had an increase in precipitation in the early-mid period of the AHP (Tossou et al., 2008). Our site information shows significantly low grass percentage until ca 2000 (cal.) year BP with a strong alignment to precipitation change and domestic animal evidence. This is consistent with the literature as climate conditions got drier and human activities accelerated grass dominance in the region. The sites described correspond to precipitation changes however Bal Lake, Lake Guier, Eastern Niger Delta, Tjeri and Mare d'Oursi do not align with precipitation changes which means that non-climatic drivers could be responsible. For example, (Gosling et al., 2021) used paleo-ecological data to parameterise vegetation openness and fire (charcoal) to provide 'snap shots' of vegetation states in tropical western Africa during the Middle and Late Pleistocene. They used this data to identify periods of time when consumers (both animals and fires) did, and did not, exert a dominant control over the vegetation openness.

Southern Africa In Southern Africa, wetter conditions were seen during the early to mid-Holocene (7500 to 6500 (cal.) years BP). From ca 5000 (cal.) years BP climate started to get drier and the driest part of the Holocene in southern Africa seems to have been during the early Holocene and most of the vegetation changes can be attributed to the oscillating climate. Human impact on vegetation is recorded from about 2000 (cal.) years BP which can be seen in Blydefontein stream and Craigrossie (Zhao et al., 2016). Rainfall decreased ca 4500 (cal.) years BP in northern regions, followed by more apparent drying from ca 3800 (cal.) years BP. The Blydefontein stream went from a more drier time to a more humid period ca 6000 (cal.) years BP. From our site information, the grass percentage decreased drastically around the same time there was a significant change in precipitation. The general drying trend across southern Africa in the late Holocene (after 5000 (cal.) years BP) is represented by the increase in grass parentage and domestic animal activities. This suggests that as climate conditions became more conducive to human pastoralism, the influence of human activities could have accelerated grass increase.

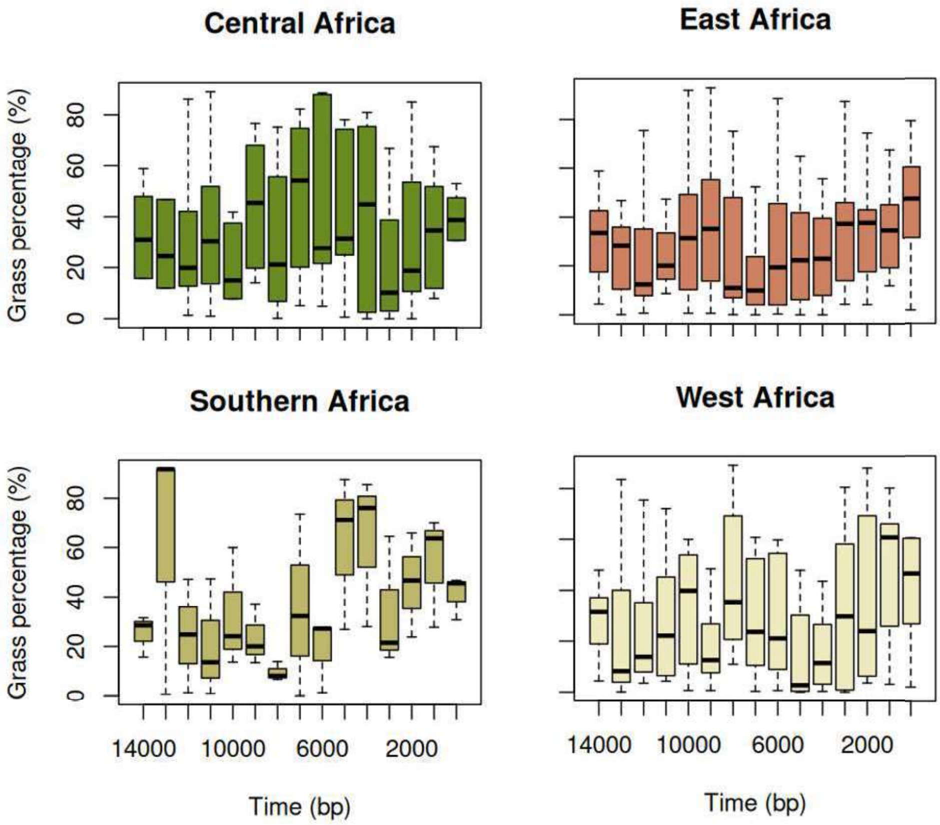

Figure 5.4: **Descriptive statistics illustrating the sum, mean, and variance of grass percentage at sites found in each region in Africa for each time slice from 14000 (cal.) years BP - 1950 CE.**

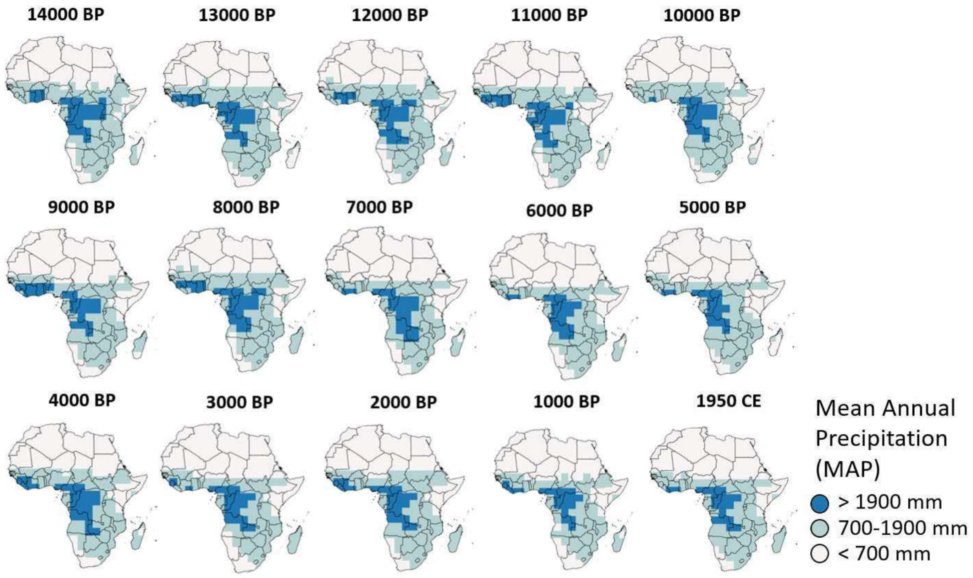

Figure 5.5: **Mean Annual Precipitation (MAP) in mm** Maps represent precipitation for each time slice from 14000 (cal.) years BP - 1950 CE.

Chapter 6
General Results and Discussion

6.1 Summary

This thesis investigates vegetation patterns across African savannas and forest-savanna landscapes through the lens of the AES theory and aims to provide a predictive and experimental example of AES as well as emphasise the importance of considering climate influence when determining AES.

The existing evidence regarding AES challenges the simplistic assumptions of the AES theory applied to the study of African ecosystems indicating the need for a more nuanced understanding of the factors influencing ecosystem dynamics and transitions (Petraitis, 2013). Therefore, more comprehensive studies are needed to explore the interactions between ecological, climatic, and anthropogenic factors to better predict and manage ecosystem changes. Additionally, integrating long-term monitoring data and advanced modeling techniques could provide deeper insights into the resilience and adaptability of ecosystems facing environmental variability.

By adopting a theoretical, experimental and paleo-ecological approach, this thesis aimed to gain a holistic understanding of AES using the grass layer of savannas and forest-savanna mosaics as examples to test the AES theory. Here, the specific working objectives were (1) to present evidence that can be used to test for the existence of AES, (2) to show the challenges ecologists face when predicting true AES and (3) to emphasise the role climate plays in the context of AES. Additionally, this combined approach provides new insights into how different types of evidence complement each other when investigating the existence of AES, providing valuable insights into the complex interactions shaping ecosystem dynamics and transitions between alternative states. In the paragraphs that follow, I discuss the main findings of each of the component studies.

Theoretical model: This process-based model provides a framework for investigating the lawn-bunch grass system of African savannas as an example of AES. Here, herbivory is simulated and is shown to be the underlying mechanism for creating and maintaining either a bunch (fire-driven) or lawn (grazing-driven) system. That is, by simulating scenarios with different initial conditions, the model was able to predict a lawn state, a bunch state and transitions between the two states where either a bunch dominant or lawn dominant state is sustained by a positive feedback process which in this case is herbivory. Light availability was the internal dynamic influencing the initial grass state in this model as there is an assumption that certain grass species are more light-tolerant and others are less tolerant. Here, lawn grass species are assumed to be more light-tolerant and the high Q_{lcp} and a_{max} suggest their dominance in early succession. Bunch grass species are assumed to be less light-tolerant due to their low Q_{lcp} and maximum assimilation rate a_{max}. This trade-off indicates their dominance in late succession. It is empirically established that there is a trade-off between the Q_{lcp} and a_{max}; that is, an ability to attain a positive carbon gain in low light leads to lower light-saturated rates of photosynthesis (Lambers et al., 2008). Identifying the Q_{lcp}-a_{max}

trade-off provides an explanation for the co-existence of these grass species and indicates the differential use of light.

These findings align with previous studies (Cumming, 1982; Asner et al., 2009; du Toit, 2003; Archibald et al., 2005; Hempson et al., 2015a; Staver et al., 2021) that have highlighted the role of herbivory in shaping the savanna grass layer. This study successfully showed that for the same set of parameters, the model can predict multiple AES for the lawn-bunch grass system, with the state predicted depending on the differences in the initial state of the system. These results contribute to the existing body of theoretical evidence for the existence of AES in complex ecological systems (Scheiter and Higgins, 2007; Van Langevelde et al., 2003; Staver et al., 2011b; May, 1977; Moncrieff et al., 2014; Noy-Meir, 1978). However, previous studies rarely used this theoretical framework to empirically test the AES theory (Schröder et al., 2005). To bridge the gap and empirically test the assumptions predicted by the model, I designed and conducted a manipulative experiment to understand the response of the lawn-bunch system to different grazing intensities in a controlled mesocosm experiment.

Manipulative experiment: A manipulative experimental design was used to test for the existence of AES in lawn grass-bunch grass communities ensuring a detailed investigation into how different clipping frequencies can change grass community states. This approach allowed for the identification of critical clipping frequencies required for grass communities to change states, the prediction of how grass communities responded to clipping as a disturbance and provided empirical evidence to support the theoretical framework in Chapter 3.

The experimental design met the required criteria (Petraitis, 2013) for demonstrating AES in a bunch grass system invaded by lawn grasses. That is, there were no environmental differences between each mesocoms grass community, and each mesocoms was subjected to a disturbance that mimics a natural disturbance event which in this case was grazing frequency. This experiment was able to demonstrate that the invasion of lawn grass in a dominant bunch grass system is possible when there is a positive feedback mechanism. The higher the frequency of clipping, the more successfully lawn grass was able to invade the bunch grass system. This result was also noted in east-African savannas where high grazing disturbances of large migratory herds prevents bunch grass from out shading the lawn grass and essentially facilitating lawn grass invasion (Huisman and Olff, 1998). Studies by (Cromsigt and Olff, 2008; Owen-Smith, 2004) found that a disturbance of bunch grass combined with increased nutrients can favour the invasion of lawn species. The experiment in this thesis provides experimental evidence for AES in a lawn grass-bunch grass system. This evidence supports the theory posed by (Hempson et al., 2019) that the grass layer of African savannas serves as an example of AES.

Paleo-ecological perspective: The primary limitations of observational research testing for AES in forest-savanna mosaics are the inadequate time periods of observation and the failure to consider climate variables in the AES framework (Higgins et al., 2023a). This study was not designed to test the AES theory but rather to explore the effects of not considering climate as a driver of change when investigating vegetation patterns across Africa. To isolate the influence of climate on vegetation patterns, a climate-forcing model approach was used on paleo-ecological time-series data. The aim was to understand the long-term vegetation and climate dynamics across different sites in Africa during the Holocene epoch. The patterns and trends shown at the site level indicate that local changes in precipitation exhibit similar trends to the site level presence of grass pollen, suggesting the dominant influence of climate. However, where precipitation change and grass patterns do not correlate over time, non-climatic drivers are to be investigated for shifts in these forest-savanna mosaics, which could potentially represent examples of AES or point to the influence of human activities on the landscape.

There is a substantial debate regarding the impact of human activities on vegetation changes during the African Humid Period. For instance, studies have discussed the human role in the decline of West-Central African forests around 2500 cal BP (Clist et al., 2018; Garcin et al., 2018). Additionally, there is controversy over whether the expansion of pastoralism accelerated (Phelps et al., 2020a; Wright, 2017) or delayed the end of the AHP (Brierley et al., 2018). In this study domestic farming and grass pollen dominance correlate in certain regions in the same time period. This is also true for domestic farming and changing precipitation which supports the theory of climate influencing pastoralism (Foerster et al., 2015; Garcin et al., 2012; Lesur et al., 2014). This result is crucial not only for reconstructing past climates but also for understanding the current climate context. It highlights the climate trajectory we are facing today and underscores how human activities are likely to adapt and change as a result. Overall, the study emphasises the fundamental importance of considering climate as an external driving force influencing the formation of forest-savanna mosaics. This perspective challenges the current research suggesting that most forest-savanna mosaics in Africa represent AES.

The combined approach of this study reveals a more in-depth evaluation of the internal and external influences on the African savanna ecosystem of the lawn grass-bunch grass layer and forest-savanna mosaics in tropical and subtropical Africa. Knowledge of how these ecosystems shift or these influences contributes to a mechanistic understanding of the emergence of AES, with implications for conservation practice and climate change. Most of the current knowledge on dynamics in the savanna grass layer and forest-savanna mosaics derives from literature that investigates internal ecosystem mechanisms, however, these studies often overlook the significant role of external drivers (Mills et al., 2006). The findings from this thesis provide sound evidence of AES in a theoretical and experimental context but also challenge the conventional AES theory by emphasising the need to explore external factors such as climate and human activities when predicting vegetation patterns. Rainfall is a critical climate factor shaping ecosystems in the tropics and subtropics of Africa. (Thornton et al., 2014). The assumption is that high levels of rainfall support forests with high biodiversity, while more savanna systems thrive in areas with lower and more seasonal rainfall (Fynn and O'connor, 2000; Murphy and Bowman, 2012; Lehmann et al., 2011; Staver et al., 2011a; Bond, 2008). A study by Karp et al. 2023 conducted a paleo-climate analysis that examined the long-term effects of rainfall changes on savanna fire activity during the AHP and observed how increased rainfall influences fire activity in savannas which could potentially lead to a savanna-forest transition. This study considers both climatic and non-climate factors. This study's findings are not only applicable to savanna-forest systems but also relevant to the lawn grass and bunch grass layers. However, the majority of literature on both of these systems has been overly focused on consumers such as fire or herbivory as the overriding drivers (Archibald et al., 2005; Van Langevelde et al., 2003; Staver and Bond, 2014; Pueyo et al., 2010; Pausas and Bond, 2020; Bond et al., 2005a; van der Plas et al., 2013), even though these consumers are also influenced by climate and vegetation, making it difficult to isolate their role from climatic drivers (Higgins et al., 2023a; Mills et al., 2006). I have shown that understanding how climate factors interact with internal drivers is crucial for predicting AES. This new perspective challenges the traditional notion that the majority of forest-savanna mosaics and lawn-bunch grass layers serve as definitive examples of AES. I show that they reflect the influence of a combination of climate and internal drivers.

Finally, this thesis demonstrates that when ecosystem dynamics are being tested through the lens of the AES theory it is important to meet all the AES criteria in theoretical and experimental approaches. Challenging the AES theory by reviewing paleo-ecological records of vegetation and climate shows that the AES theory is not the only explanation for ecosystem dynamics and that climate and human activities play a significant role when exploring vegetation dynamics, especially in African savannas.

6.2 Limitations: The Alternative Ecosystem States theory in an African context

This thesis demonstrates how the grass layer of savannas serves as an intriguing model system for testing the AES theory. It represents a lawn-bunch grass system influenced by both internal and external factors, creating positive feedback loops. In natural lawn-bunch grass systems, herbivores and fire play crucial roles in determining grass states (Hempson et al., 2019, 2015b; Stock et al., 2010; Veldhuis et al., 2014; Cromsigt et al., 2017; Archibald, 2008; McNaughton, 1984). Evaluating forest-savanna systems in Africa using paleo-data poses several challenges. In the following paragraphs, I will highlight the limitations of each study and suggest ways to address these limitations in future research.

Limitations in Chapter 3 - Theoretical model: The theoretical model developed in this thesis primarily addressed herbivory dynamics. The theoretical model from this thesis predicts that the system will be drawn towards an equilibrium point and whether or not it reaches that point and how long it remains there will depend on the size of the herbivore population. Because of this, the model system could be designed to ignore the role of fire when predicting grass states and only test the role of herbivory. However, the flexibility of this model design allows for the inclusion of additional disturbances, such as fire as another dynamic variable. That is, to gain a deeper understanding of the lawn grass-bunch grass system, it would be valuable to use this model design to explore the interactions between fire and herbivory. However, since the research objectives of this thesis focused on herbivory dynamics, fire would be considered a secondary factor. Nevertheless, theoretical models, such as the one presented here, can predict scenarios that are consistent with the AES theory making it a valuable model design for testing AES as well as enhancing our mechanistic understanding of the savanna grass layer.

Limitations in Chapter 4 - Experimental approach: This experiment was able to validate the theoretical model. That is, under a controlled environment where light was the only limiting resource, the highest frequency of grazing allowed for lawn grasses to persist and dominate bunch grass communities. Because light was the only limiting resource in the experiment, light availability decreased exponentially with an increasing community biomass, however, this was not quantified in the experiment for several reasons. Firstly, there were no replicas in the experiment, here each mesocosm was subjected to different levels of clipping, which could have affected the robustness of the results. Secondly, to understand the light requirements needed for each grass species, it would be necessary to expose these species to varying light levels. This would require a more detailed experimental setup, which was beyond the scope of this study.

Therefore, this experiment should be expanded in the future to examine the unique traits of the African lawn and bunch grass species used in this study. Knowing the light requirements for each species is a useful way to understand the competitive dynamics within the lawn-bunch grass communities (Tilman, 1980). This will further reinforces the theoretical model, which assumes lawn grasses are less tolerant to shade compared to bunch grasses, aligning with existing literature on grazing lawn formation (Hempson et al., 2015b). This experiment was challenging for several reasons. First, there was uncertainty about the time needed for communities to assemble and stabilise as well as for new equilibria to be reached for each mesocosm before applying a disturbance. The grasses selected were species of African lawn and bunch grasses, however, knowing if they occur in the same grass communities in African savannas is uncertain. Nevertheless, even with these challenges, the experiment presented in this thesis demonstrates an experimental design that fulfils the requirements needed to test AES.

Time series studies offer greater potential to reveal the dynamics and the processes of an ecosystem (Xu et al., 2016). Using fast-growing species allows for an experiment time frame that is within a reasonable scope logically and financially. To keep the integrity of the time series data, a plant growth model in a Bayesian state-space framework was used to interpret the results. These models are an incredibly powerful tool for capturing unobserved processes given the observed data (Higgins et al., 2023b; Hobbs and Hooten, 2015). Using a combination of greenhouse experiments and Bayesian state-space models can be useful for developing models of plant community dynamics which provide empirical evidence for theories that are challenging to test in the field (Auger-Méthé et al., 2021). This experiment contributes to the few existing studies that can be used as evidence for determining true AES (Ng'habi et al., 2018).

Limitations in Chapter 5 - Paleo-perspective: Paleo-ecological studies are significant in revealing vegetation patterns and trends over long periods of time. However, one must take care when interpreting results based on paleo proxies. The reliability of vegetation and precipitation proxies can vary. Different proxies may respond to a range of environmental factors, not solely to climate, potentially complicating the interpretation of the results. This study primarily focused on climate as an external factor influencing ecosystem states. Other external factors, such as fire and herbivory by large mammals were not integrated into the analysis which would enhance the results providing a more robust understanding of the dynamics of forest-savanna mosaics in Africa. Another common limitation is the temporal gaps in the paleo-ecological records which can affect the continuity and completeness of the data.

This study indicates variability in the results across different forest-savanna sites. This site-specific variability suggests that local factors, such as soil type, topography, and specific disturbance histories, also play significant roles in determining ecosystem states. That is, future studies addressing forest-savanna mosaic distribution should incorporate both internal and external factors offering a more holistic interpretation of forest-savanna mosaics. Climate-forcing vegetation models reveal the influences of climate change on vegetation dynamics in both time and space by dynamic modelling. However, the accuracy of climate reconstructions over the Holocene epoch is limited by the precision of climate models and the availability of reliable paleo-climate data. The TRACE21k and TRACE21k-II datasets are the only paleo datasets extending back 22,000 years BP, limiting the variety of paleo-climatic data available for use in climate-driven models (He, 2011; Karger et al., 2023). To address these limitations, more comprehensive datasets such as charcoal and stable isotopic data will improve proxy accuracy and give insight into how other external non-climatic factors influenced vegetation dynamics in forest-savanna across Africa.

6.3 Ecological implications

6.3.1 Understanding the Emergence of AES

This thesis recognises the existence of AES in African savanna ecosystems and emphasises the importance of testing the theory of AES empirically. In real-world ecosystems, AES has important implications for ecosystem management and conservation. Profound external perturbations can force permanent transitions between these states (Ratajczak et al., 2018). Such perturbations can be extreme natural disturbances such as severe droughts, fire, storms or high population densities of ecosystem engineers such as elephants (Beuchner and Dawkins, 1961), but can also result from management decisions that influence fire regimes and animal populations. With this being said, ecologists aim to understand and predict the behaviour of ecosystems, and the possibility of AES means ecosystems can shift between different states under the same environmental conditions, leading to unexpected changes. For example, the shift from a fire-driven system to a grazing-driven system, which has contrasting functioning and structure can exist in savannas under the same environmental conditions. Not only can these shifts be irreversible, but different states can provide different ecosystem services to human populations such as carbon sequestration, and habitat provision and changes in states can affect the availability and quality of these services. Understanding the mechanisms that drive change, especially if an ecosystem represents an AES in African savannas, is crucial information that should be included in ecological frameworks, particularly for predicting sudden changes.

As climates change, the trajectory and behaviour of AES will change. For example, some states may become more attractive and others less attractive (Higgins and Scheiter, 2012). This complexity however means that such shifts are challenging to test however using modelling applications can predict such scenarios. Here, the studies in this thesis are structured to demystify the complexities of savanna ecosystems when explored through the lens of the AES theory by highlighting how dynamic these systems when both non-climatic and climatic factors are considered.

6.3.2 Misinterpreting ecosystems as examples of AES

Misinterpretation of contrasting states as AES has high-risk implications for conservation management. That is, if ecosystems are mistakenly categorised as having alternative states when they do not, management strategies may be misdirected. Here the mechanisms causing these shifts will be investigated often overlooking external factors such as climate. For example, in African savannas fire regimes could be adapted or herbivore populations can be altered based on the assumption of alternative states which could be ineffective, unnecessary or detrimental to the ecosystem. An existing example reiterated by (Higgins et al., 2023a) is the widespread tree planting and afforestation of savannas, this is a major threat to the biome, with limited carbon sequestration potential and major biodiversity costs (Zhou et al., 2022; Abreu et al., 2017). However, studies have predicted that large parts of forest-savanna mosaics in Africa are AES regions indirectly implying that tree planting is suitable in these areas (Aleman et al., 2020). Higgins and colleagues (2023) point out that studies have overestimated how large the regions of AES are in Africa and that models used to predict ecosystem distribution will have ecosystem uncertainty. However, this ecosystem uncertainty should not be interpreted as regions that can be considered examples of AES. The interpretation of the widespread regions of AES in Africa assumes that climate is not influencing state changes. In a world where climate is changing at a concerning rate, it is essential to consider climate and how climate interacts with the mechanisms driving AES.

Conclusion

This thesis demonstrates the complexity and the challenges that are inherent when interpreting ecological phenomena, particularly the theory of AES in an African context. In this thesis, I have used a variety of methods to test the existence of AES as well as evaluate the role of climate in the AES framework. The results emphasise the importance of designing and conducting theoretical and empirical experiments that fully meet the criteria to confirm true AES. The lawn-bunch grass system proved to be an excellent system for testing the emergence of AES both in theory and through a manipulative experiment. The scenarios produced by the the process-based model showed how initial conditions and the interaction between internal dynamics such as light availability and a variety of different grazing conditions determine the final grass state. The manipulative experiment found that with non-limiting resources, the frequent removal of biomass by clipping was sufficient for lawn grasses to invade a bunch-dominated grass community, shifting the grass state. Here the model results and the experimental results support each other illustrating the importance of theoretical and experimental exploration when testing AES.

This thesis also challenges the traditional understanding of AES by highlighting the significant role climate plays in shaping forest-savanna mosaics across Africa, suggesting that vegetation patterns may not always be attributed to external disturbances such as fire or grazing but could be simply influenced by climate. The phyto-climatic approach used in the species distribution model was able to use climate variables to estimate the ability of climate either supporting or not supporting the growth of C4 grasses in specific geographical locations over time. The paleo-climatic records proved to be useful in providing valuable data for exploring vegetation and climate patterns and trends over time by comparing the percentage of C4 grass and total precipitation over the same time axis across Africa. Using these data to visualise ecological patterns and trends is a valuable resource when investigating vegetation dynamics over long time spans.

The study specifically explored precipitation proxies across Africa, recognizing precipitation as one of the most critical environmental factors influencing forest-savanna mosaics. By examining how precipitation changes correlated with vegetation shifts in various regions across Africa over the Holocene period, the research provided valuable insights into past climate conditions and their effects on ecosystem transitions, particularly in areas where forest and savanna ecosystems coexist. The current synthesis of fire being the major driver in shaping forest-savanna landscapes in Africa needs to be revisited, and future research should give more attention to the undeniable role precipitation or other climate variables have on vegetation patterns as well as how internal factors such as fire are, in fact, dependent on external factors such as climate. Using a climate approach does not disregard the theory of AES but rather emphasises the importance of considering the role of climate in creating and maintaining forest-savanna mosaics in African landscapes.

This thesis reiterates the difficulty of determining AES in African landscapes and emphasises that the complexity of distinguishing between internal and external influences should not be ignored when applying the AES framework to ecosystem analysis. This complexity underscores the importance of conducting controlled manipulative experiments to isolate and analyse the impacts of internal mechanisms influencing ecosystem dynamics. If the aim is to predict vegetation patterns in African landscapes during a time when the climate is changing at an alarming rate, it is essential to not ignore the role of climate in shaping these ecosystems in the first place.

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Contributions statement

Chapter 3: Arresting succession to create alternative ecosystem states
Own contribution: concept and study design 50%, model development 100% Prof.Dr Steven Higgins, data analyses and figures 100%, discussion of results 100%, manuscript writing 100%. The study was designed by Amy Schroeder and Prof.Dr Steven Higgins. Amy Schroeder performed simulations. Amy Schroeder and Prof.Dr Steven Higgins interpreted and discussed the results. Figures and tables were created by Amy Schroeder and Prof.Dr Steven Higgins.

Chapter 4: Effects of clipping and invasion on African savanna lawn and bunch grass communities
Own contribution: concept and study design 70%, data acquisition 100%, data analyses and figures 100%, Bayesian state-space model design Prof.Dr Steven Higgins, discussion of results 90%, manuscript writing 90%, Amy Schroeder performed the greenhouse experiment with the support of Plant Ecology lab members (see acknowledgements). Amy Schroeder interpreted and discussed the results. Figures and tables were created by Amy Schroeder.

Chapter 5: Exploring vegetation changes within forest-savanna mosaic landscapes in Africa throughout the Holocene epoch
Own contribution: concept and study design 60%, data acquisition 70%, data analyses and figures 100%, discussion of results 100%, manuscript writing 100%. The study was designed by Amy Schroeder, Dr Timo Conradi and Prof.Dr Steven Higgins. Paleo-climate data was analysed by Amy Schroeder and Prof.Dr Steven Higgins. Pollen data was analysed by Amy Schroeder, Dr Timo Conradi and Prof.Dr Steven Higgins. Model designed by Prof.Dr Steven Higgins, and Amy Schroeder interpreted and discussed the results. Figures and tables were created by Amy Schroeder.

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