Interactions between Climate, Vegetation and People in East African Savannas: a Kenyan Case Study through the Post-Colonial Era

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PhD

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Environment and Geography

June 2018

for my sister and friend, Sarah Njeri Kariuki-Naya

01/02/1980 – 23/05/2017

Abstract

The interactions between biotic and abiotic factors driving savanna vegetation structure are complex that a combination of resource-based and disturbance-based theories are used to explain the coexistence between trees and grasses. Human impact further complicates these interactions and consequently, the structure of wildlife populations. As human development is linked to environmental sustainability, understanding the impact of the interactions between changing climates and land use patterns on savanna ecology requires an interdisciplinary approach that integrates social and natural factors. In this thesis, the importance of rainfall variability in driving woody vegetation biomass, production and turnover across Kenyan savannas is first assessed. It is established that woody biomass and production increases with rainfall while turnover rates decrease with rainfall. Secondly, to explore the history of land use changes, perceptions from community elders in two savanna ecosystems in southern Kenya (Amboseli and Mara) are collated using a semi-structured questionnaire. The elders from Amboseli regarded rainfall variability as key in shaping land use change decisions while those in Mara regarded socio-economic factors and conservation initiatives as important determinants of land use types. Thirdly, to explore the impact of climate and land use change, an agent based model that used grass biomass data, simulated by a dynamic global vegetation model, as input data is developed. Development of the model incorporated natural and social factors by using insights from the vegetation survey and from the community elders. The model showed that provision of conservation subsidies, up to 200 \$ yr^{-1} for 1 km^2 grazing land, is key in driving livestock and wildlife densities and further increases in conservation subsidies maintains the density of livestock and wildlife. The interdisciplinary nature of this thesis highlights the value of integrating local community perspectives and science-based interventions to address the sustainability of savannas, particularly sub-arable savannas. It also highlights the value of conservation subsidies in promoting wildlife numbers and pastoral well-being.

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Acknowledgements

Completion of this thesis would not have been successful without the valuable contribution of several people. Firstly, I would like to express my sincere gratitude to my main supervisor Prof. Rob Marchant for his support, guidance, inspiration and for constantly reminding me to look at the bigger picture. I would like to thank my other supervisor, Dr. Simon Willcock for his enthusiasm and support in my modelling work and in reading my chapter drafts. I am also grateful for his help in facilitating my access to a working area and other research facilities during my visits to the University of Southampton, UK and Bangor University, Wales. Many thanks to my supervisor, Dr. David Western for initialising my PhD journey and his support and insights on social-ecological systems in southern Kenya. Many thanks to Dr. Steve Cinderby and Prof. Robin Reid for examining this thesis and for providing an enriching discussion during the viva which has improved the quality of this thesis.

This work was funded by the European Commission through a Marie Curie Initial Training Grant to the Resilience in East African Landscapes (REAL) project. The research permit was provided by the National Commission for Science, Technology and Innovation (NACOSTI) office in Kenya. Many thanks to all the REAL project researchers. In particular, to Prof. Paul Lane, for his encouragement and support in project activities and to Dr. Lowe Börjeson for facilitating my visit to Stockholm University, Sweden.

My sincere gratitude goes to Prof. Maja Schlüter for providing me with an opportunity to join the SES-LINK research team, at Stockholm University, Sweden as a visiting researcher. I am also grateful for her patience and insights in my modelling work. Many thanks to Dr. Ingo Fetzer and all SES-LINK researchers, particularly Dr. Romina Martin and Kirill Orach for the stimulating discussions on modelling social-ecological systems. I would like to thank the staff at African Conservation Centre (ACC), Kenya for their continued friendship and good cheer during my secondment. I am particularly grateful to Lucy Waruingi and Dr. Victor Mose for their support and to John Kamanga and Samson Silantoi for introducing me to the Mara-Loita ecosystem. I would like to thank Maroula Hill and other staff at the Environment and Geography Department, University of York, UK for their support in the department. Many thanks to Dr. Andrew

Smith, from the York Advanced Research Computing Cluster, University of York for running my model code.

I wish to thank the community elders in Amboseli, Mara and Loita Plains that we talked to for their insights on the ecosystem. Many thanks to Rebecca Muriuki, Daniel Letee, John Lembakuli, Francis Sopia and Saitoti Silantoi for their assistance throughout fieldwork.

Special thanks are extended to friends in Kenya and the UK, particularly Karla, Hie Ling, Sophia, Tar and Alda for their friendship, optimism, and fun throughout the PhD journey. I extend my heartfelt gratitude to my mother, Lydia Kariuki, for her unwavering support, inspiration and for wanting the best for me. Thanks to my siblings, Shalom Muraya, Gideon Kariuki and Samuel Kariuki for their support, good cheer and the numerous ‘WhatsApp’ calls throughout my PhD journey.

Author's Declaration

I, Rebecca Wairimu Kariuki, declare that this thesis is my original work and no part of it has been, or is being submitted for another degree at this, or any other, University. All literature and data sources used in this thesis are cited in the text and the references are listed at the end of each chapter.

1 Thesis Introduction

1.1 Savannas distribution and ecosystem services provision

Savannas, are mixed tree and C_4 grass ecosystems characterised by a continuous grass cover and a discontinuous tree cover (Scholes and Archer, 1997; Bond, 2008; Lehmann et al., 2011, 2014; Ratnam et al., 2011). They are globally important ecosystems (McNaughton and Georgiadis, 1986; Scholes and Archer, 1997; Baudena et al., 2015; Hempson et al., 2015) spanning the equator, between the Tropic of Cancer and Tropic of Capricorn, where it is warm and relatively dry (Shorrocks, 2007). They occupy 20% of the terrestrial land surface (Sankaran et al., 2005; Shorrocks, 2007; Lehmann et al., 2014), account for 30% of terrestrial primary production (Mworia, 2011) and support one fifth of the human population (Lehmann et al., 2014) as well as large proportions of wild and domestic ungulates (Foxcroft et al., 2010; Mworia, 2011). In sub-Saharan Africa, savannas occupy 60-65% of the land surface (Augustine et al., 2003; Baxter and Getz, 2005) (Figure 1.1) that surrounds the tropical rainforests of the Congo Basin and is bounded by the Sahara and Kalahari deserts in the north and south respectively (Shorrocks, 2007).

Savannas are characterised by a variable climate that drives primary production (Sankaran et al., 2005; Bucini and Hanan, 2007; Bond, 2008) and the distribution of watering points (Hailegiorgis et al., 2010). Besides rainfall, other biotic and abiotic factors that drive savanna vegetation structure are soil nutrients, fire, herbivory and humans (McNaughton et al., 1988; Sankaran et al., 2005; Bond, 2008; Aleman et al., 2017; Mutiti et al., 2017). Woody cover is considered a key determinant of savanna ecosystem properties (Sankaran et al., 2005) as it follows the highly variable rainfall gradient (Bond, 2008) and reflects the spatial variation of rainfall and soil moisture (East, 1984; Bhola et al., 2012). Thus, rainfall is shown to be the most important factor driving woody plants. At mean levels < 650 mm yr^{-1}, it sets an upper limit to woody cover, and at levels > 650 mm yr^{-1}, disturbances, from fire and herbivory, are required to maintain the savanna state and prevent its succession into a forest (Bucini and Hanan, 2007; Aleman et al., 2017). Rainfall seasonality drives vegetation growth, quality and quantity by decreasing tree cover in tropics and sub-tropics (Staver et al., 2011; Bhola et al., 2012).

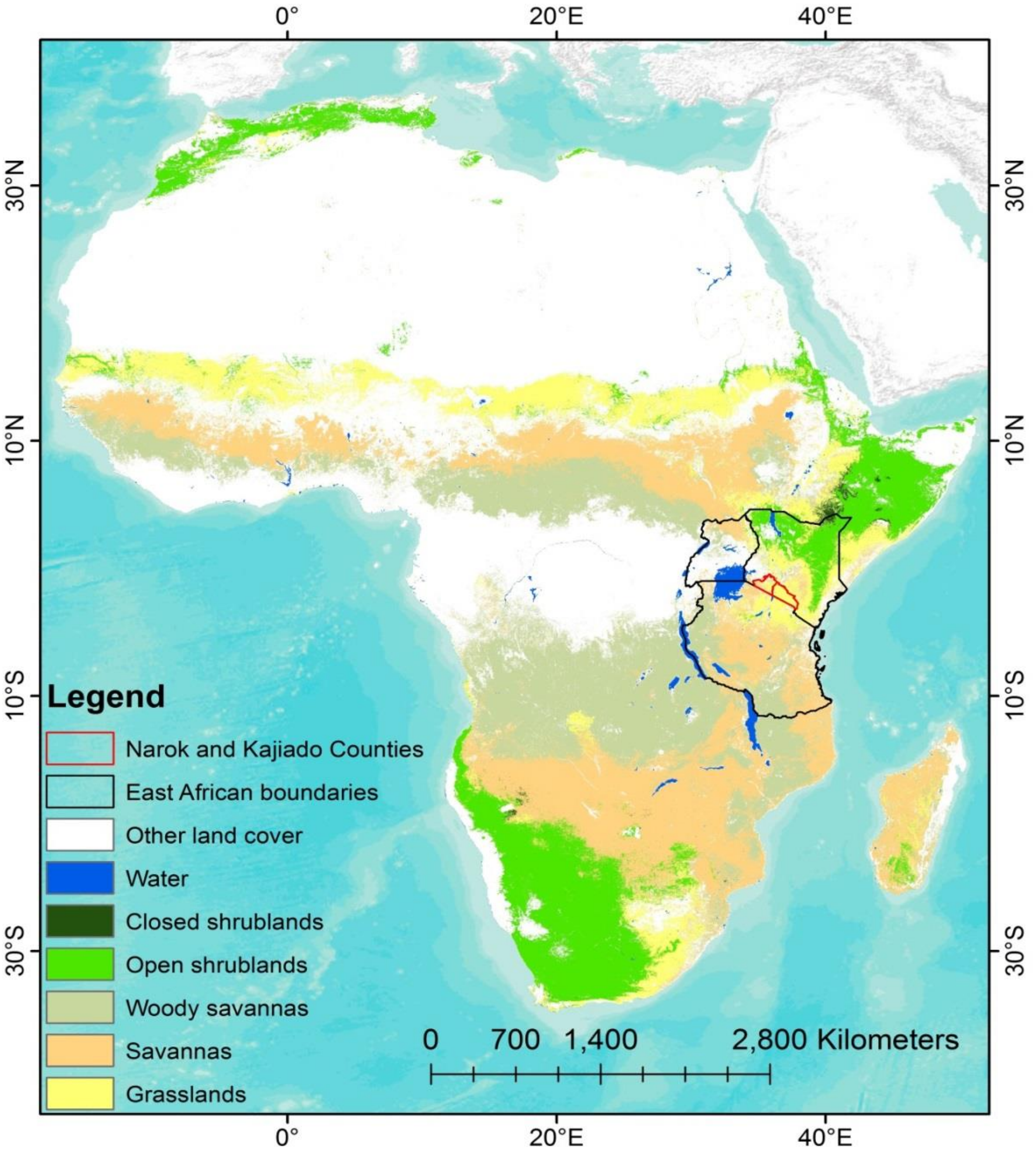
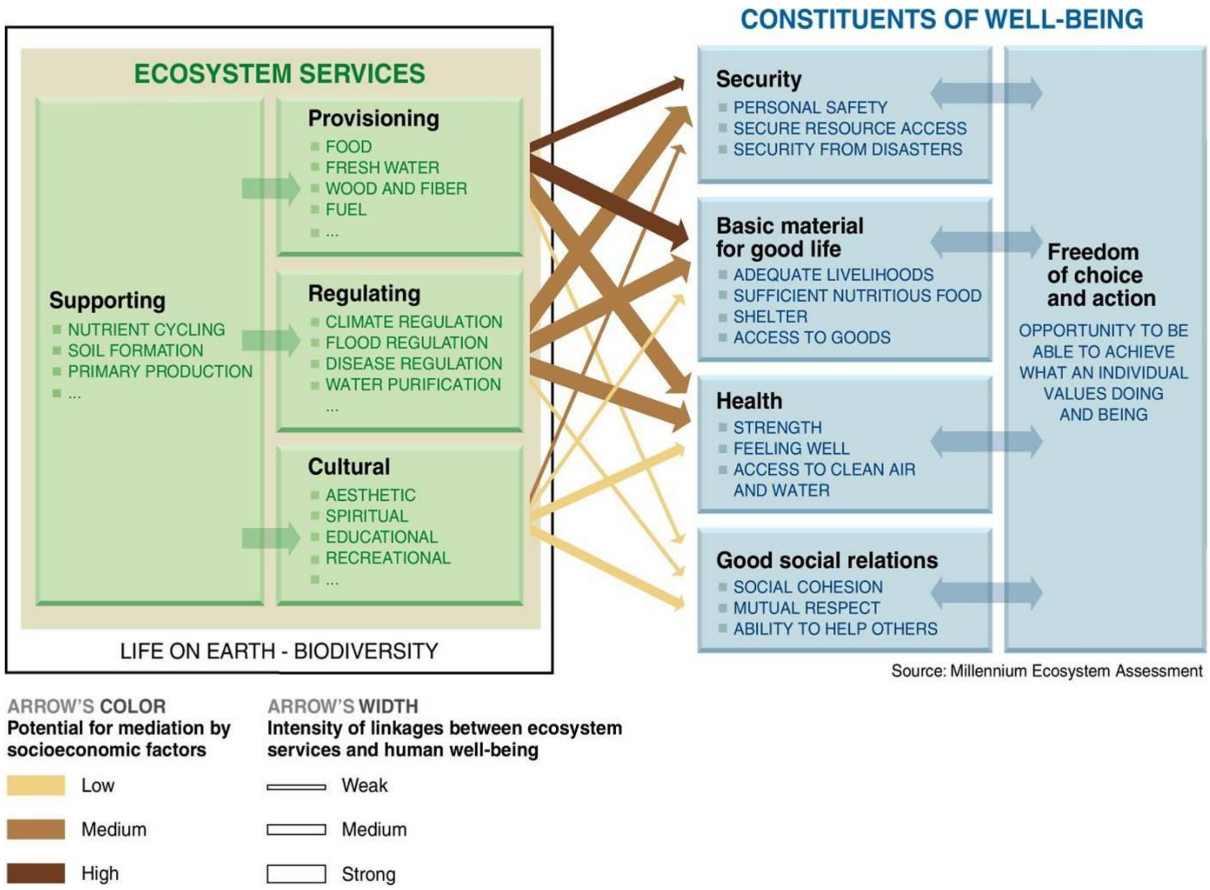


Figure 1.1: Distribution of grasslands, savannas and shrublands in Africa, East Africa and Narok (left) and Kajiado (right) Counties in southern Kenya. Source – MODIS data (Friedl et al., 2010; Channan et al., 2014).

While climate alone is sufficient to prevent the development of a closed canopy in drier savannas, insufficient soil nutrients sometimes constrain woody density in wetter savannas (Hoffmann et al., 2012). Fire is also a strong predictor of woody cover within savannas as it maintains an open savanna canopy in areas where edaphic and climatic factors can support forests (Bond, 2008; Staver et al., 2011). Its impact is shown to be higher in plants within the 1 - 3 metres height class (Bond and Keeley, 2005; Levick et al., 2015) which makes growing trees vulnerable to fire and top-kill during fire episodes (Levick et al., 2015).

The impact of herbivory is manifested by the activities of diverse animal species, including termites, that are supported in the savannas (Du Toit and Cumming, 1999; Acanakwo et al., 2017). The high animal biomass in savannas depends on the spatial and temporal variability of vegetation production (McNaughton and Georgiadis, 1986; Du Toit and Cumming, 1999; Archibald, 2008) leading to varying distributions of animals between dry and wet seasons. Despite the accepted notion that these factors are all important in driving savanna vegetation, there is no consensus on the relative importance of each factor (Hoffmann et al., 2012). This has led to the development of different equilibrium and disequilibrium theories (Scholes and Archer, 1997; Sankaran and Ratnam, 2013; Lehsten et al., 2016; Fox et al., 2017) that integrate the role of biophysical and disturbance factors to explain the coexistence of trees and grasses as well as the occurrence of savannas in climatic regions that could support forests or grasslands (Bond, 2008; Dohn et al., 2017).

Ecosystem services (ES), the benefits that people derive from ecosystems, are often categorised into provisioning, regulating, cultural and supporting services (Millenium Ecosystem Assessment, 2005) (Figure 1.2). The ES concept emerged in the late 1970s as means of linking natural and social sciences by highlighting the dependency of humans on natural resources (Gómez-Baggethun et al., 2010; Braat and de Groot, 2012). ES contribute to human well-being and directly support more than one billion people living in extreme poverty across the globe (Egoh et al., 2009). In African countries, many people depend on provisioning ecosystem services to supplement household income (Egoh et al., 2012), thus human impact in savannas is largely through the acquisition and management of ES. Specifically, human action, through ES trade-offs and management drives their distribution and supply (Rodríguez et al., 2006; Bennett et al., 2015). Consequently, as aridity, vegetation and socio-economic conditions change across the African continent, so do the services local communities receive from their surrounding ecosystems. For example, the humid, forested areas of west and central Africa are largely used for provision of food and raw materials, while the arid and semi-arid areas of the continent are predominantly used for tourism and grazing (Egoh et al., 2012). Due to the multiple and nonlinear natural and social interactions that drive savannas, they are treated as social-ecological systems (SES) where SES are defined as systems characterised by uncertainty and nonlinearity of multiple multi-scaled interactions between components in the system and the environment (Schlüter et al., 2012). All resources used by humans are incorporated in SES (Ostrom, 2009), making humans the focus of SES (Schulze et al., 2017). Accordingly, the term ‘social-ecological’ is used to show that humans are connected with nature and separating the social and ecological components in a system is impossible (Folke et al., 2005). As the components in SES are perpetually adapting to their environment and learning from each other and their environment (Miyasaka et al., 2017), an understanding SES usually involves interdisciplinary perspectives that incorporate components of the social and natural environments (Orach and Schlüter, 2016).



Source: Millennium Ecosystem Assessment

Figure 1.2: Categorisation of ES (left side) and components of human wellbeing (right side) (Millennium Ecosystem Assessment, 2005). This framework views ecosystems through the services they offer to humans, the impact of humans activities to the provision of these services and the impact of environmental changes to human wellbeing (Yang et al., 2013; Díaz et al., 2018).

1.2 The history of land use change in East African savannas

The earliest evidence of cattle herding in East Africa is dated to 4500-4000 years ago when the increasing aridity of the Sahara forced pastoralists to move south into East African savannas (Marshall 1990; Marshall and Hildebrand 2002; Marchant et al., 2018). In Kenya, herding became widespread about 3000 years ago, after which it extended to northern Tanzania (Marshall and Hildebrand 2002). The pastoralists' livestock coexisted with wildlife (Western, 1982; Thornton et al., 2003, 2006; Lamprey and Reid, 2004; Galvin et al., 2006; Bhola et al., 2012) and their varying grazing and trampling activities created heterogeneous landscapes that account for the high animal diversity in savannas (Western and Nightingale, 2003). Pastoralism in the East African savannas was further enhanced by the low agriculture potential and the variable rainfall characteristic of savannas (Galvin et al., 2006). In dry periods, pastoral mobility was a key adaptive trait (Nelson et al., 2009) that enabled the pastoralists to escape the erratic rainfall patterns and maximize milk production and herd numbers (Western and Nightingale, 2003).

In the late twentieth century, pastoralism levels in Kenya began to drop due to land fragmentation driven by changes in land use and land tenure (Homewood et al., 2009; Boone et al., 2011; Sundstrom et al., 2012). Increasing demand for provisioning ES drove the widespread land use changes, particularly the transformation from pastoralism to sedentary agropastoralism (Du Toit and Cumming, 1999). Sedentarisation of pastoralists and intensification of livestock production in Kenyan savannas was initially promoted by national policies that aimed to control pastoralism by improving livestock production and providing social facilities for pastoralists (Reid et al., 2014). To that end, the Kenyan government created communal group ranches in the 1960s (Okello and D'Amour, 2008). However, the group ranches failed to effectively manage livestock production and to provide land security and better economic returns to pastoralists (Sundstrom et al., 2012; Osano et al., 2013) prompting the start of their subdivision from the mid-1970s to present (Homewood et al., 2009; Sundstrom et al., 2012). With subdivision of group ranches, sedentarisation of pastoralists and agriculture escalated (Lamprey and Waller, 1990; Lamprey and Reid, 2004; Reid et al., 2014) and discouraged pastoral mobility. Erratic weather patterns also contributed to increasing sedentarisation levels as multiple extreme droughts rendered pastoralists economically incapable of offsetting the expenses incurred in veterinary care, droughts and diseases (Okello and D'Amour, 2008).

Increased sedentarisation has implications on the large ungulate biomass found in the savannas. The spatial structure of wildlife communities is altered by sedentary livelihoods (Worden et al., 2003) while wildlife densities are shown to be higher in un-subdivided group ranches that have pastoral mobility (Western et al., 2009; Riginos et al., 2012). In addition, most protected areas, though key in conserving, are small and cannot protect and sustain large wildlife species (Beale et al., 2013). With over 70% of wildlife in Kenya found outside protected areas (Okello and D'Amour, 2008), land use changes outside protected areas has a large impact on the structure of wildlife communities (Thornton et al., 2003; Ogutu et al 2009; Bhola et al., 2012). This impact extends further to pastoral communities that rely on income from wildlife and tourism (Thornton et al., 2006).

1.3 Modelling social-ecological savanna systems

The difficulty in understanding SES is linked to the challenges experienced in understanding the interactions between multiple ES and the trade-offs in human impacts (Miyasaka et al., 2017). This makes modelling a probable, yet challenging, technique that can address the complex interactions in savanna SES. While, dynamic global vegetation models (e.g. the Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) (Sitch et al., 2003; Smith et al., 2014) used in this research focus on quantification of primary production, carbon cycling and storage (Moncrieff et al., 2015) and simulate detailed, individual patch based representations of vegetation structure, physiological and biogeochemical processes (Lindeskog et al., 2013; Smith et al., 2014); they do not incorporate human behaviour due to the heterogeneity and complexity of individual humans (Bitterman and Bennett, 2016). To overcome this, agent based models (ABM) are coupled to biophysical models, such as dynamic global vegetation models (Matthews et al., 2007). ABM are for studying the properties of SESs (Miller and Morisette, 2014; Schulze et al., 2017) using a bottom-up approach that simulates the individual contribution of the elements to the overall behaviour of the system (Grimm et al., 2005; Matthews et al., 2007; Filatova et al., 2013; Iwamura et al., 2014; Lawlor and McGirr, 2017). They are preferred for simulating the interactions between humans and land use change (Matthews et al., 2007; Iwamura et al., 2014) as they reflect the nonlinear relationships between socio-economic and biophysical factors of land use change at multiple scales (Bai et al., 2015; Bitterman and Bennett, 2016).

1.4 Focus of the thesis

This thesis uses an interdisciplinary approach to understand the interactions between pastoralists in Kenyan savannas and their environment. The ecological component was studied using data from 46 plots located in savanna ecosystems across central, eastern and southern Kenya while the social-ecological component was studied in two ecosystems in southern Kenya; the Amboseli, in Kajiado County, and the Mara, in Narok County (Figure 1.1). Both sites have largely been used for livestock production and wildlife conservation. However, recent changes in climate and social-economic factors have altered the social-ecological interactions in each site. The Amboseli ecosystem is located in southeastern Kenya and north of Mt Kilimanjaro. It has low and unpredictable rainfall averaging 350 mm yr^{-1} (Altmann et al., 2002) and is comprised of the Amboseli National Park and the surrounding group ranches which act as wildlife migration corridors and dispersal zones. Formation of the group ranches in Amboseli occurred between 1963 and 1965 (Mwangi and Ostrom, 2009) while subdivision began in the mid-1970s (Sundstrom et al., 2012). Livestock herding within the group ranches has been the main land use type in Amboseli and has been well adapted to the variable habitat (Bulte et al., 2008). However, over the last few decades, agriculture has expanded near wetlands outside the National Park and on the slopes of Mt Kilimanjaro making these areas the centres of conflicting land uses (Campbell et al., 2000; Kioko and Seno, 2011). To discourage further loss of rangeland habitats, their connectivity, the tourism industry and livelihoods supported in the rangelands, wildlife conservancies have been formed across the rangelands. Conservancies are institutions of governing and managing wildlife which are legally recognised as a land use under Kenya's Wildlife Conservation and Management Act 2013 (Osano et al., 2013; King et al., 2015; Løvschal et al., 2017). Amboseli has 17 conservancies occupying 79,562 hectares (ha) and employing 476 rangers (KWCA, 2016).

The Mara ecosystem in southwestern Kenya consists of the Maasai Mara National Reserve and group ranches that surround it. Average annual rainfall in Mara ranges from 600-1000 mm yr^{-1} and increases along a southeast-northwest gradient (Homewood et al., 2001; Lamprey and Reid, 2004). Group ranches in Mara were formed in the 1970s and started subdividing in the same decade (Serneels et al., 2001; Homewood et al., 2009). Human population growth and institutional changes put pressure on land leading to sedentarisation of pastoralists and diversification of livelihoods through agricultural expansion and tourism (Homewood et al., 2001; Ogutu et al., 2009). Land use change in the Mara has been linked to declining woodlands, wildlife and increased competition between humans and wildlife (Ogutu et al., 2009). Like Amboseli, conservancies have been formed in Mara, where currently there are 14 conservancies occupying 147, 000 ha and supporting 6,000 land owners (Otieno 2017).

Historical data from 46, 10 x 10 km plots across Kenyan savannas were used to assess the response of vegetation to rainfall fluctuations in semi-arid savannas. These ecosystems vary in mean rainfall amount (from 200 to 1100 mm yr^{-1}) and seasonality as well as in levels of environmental disturbances from herbivores and humans. The vegetation data was collected in the late 1970s/early 1980s, using the point centred quarter technique (PCQ) (Mueller-Dombois and Ellenberg, 1974) by the Department of Remote Sensing and Resources Survey (DRSRS) in Kenya (Kuchar, 1981). The dynamics between human activities, changing climates and socio-economic factors is then studied using perspectives from community elders in the Amboseli and Mara ecosystems. These perspectives focus on the history (from 1960s to present) and drivers of land use change and land management. The insights gained from the community experts are coupled to data from other literature sources and used to design and implement an ABM for the Amboseli and Mara ecosystems. The custom-built ABM uses grass biomass data simulated by LPJ-GUESS dynamic global vegetation model as input data. The ABM simulates changing land use types, wildlife density, livestock density and pastoralist income under different climate regimes and land tenure scenarios. Simulations are done in annual time steps over the period between 1950-2005 at a spatial resolution of $1km^2$.

1.5 Research aims and objectives

The overall aim of this thesis is to understand the changing interactions between climate, vegetation and human activities in arid and semi-arid savannas in Kenya using ecological, social and modelling perspectives. The analytical chapters of this thesis explore this by 1) assessing the influence of rainfall on woody vegetation (chapters 4 and 7), 2) assessing the combined impact of climate change and social-economic factors on pastoral land use decisions (chapters 5 and 7) and 3) assessing the impact land use changes on animal densities and pastoralist income (chapters 6 and 7).

In conducting this thesis, three major aims were addressed by a series of objectives. These aims and objectives are:

1. ***To assess changes in woody vegetation structure and function along a rainfall gradient in Kenyan savannas.***
   - Establish changes in woody vegetation structure, biomass, primary production and turnover rates along a rainfall gradient in Kenyan savannas.
   - Compare woody community functions and composition in Amboseli and Mara ecosystems.
2. ***To assess changes in land use patterns across a sedentarisation gradient in southern Kenya savannas using local community perceptions.***
   - Quantify changes in land use types in Amboseli and Mara ecosystems.
   - Establish and compare the environmental and social drivers of land use changes in Amboseli and Mara ecosystems.
   - Compare land use types under private ownership in Amboseli and Mara ecosystems.
3. ***To understand the impact of land use change on animal densities and pastoral livelihoods in Amboseli and Mara ecosystems using a social-ecological model.***
   - Simulate changes in land use under different rainfall and land tenure scenarios
   - Simulate changes in land use in relation to conservation subsidies under different rainfall regimes and land tenure scenarios.

- Simulate the impact of changing land use types on wildlife density, livestock density and pastoralist incomes.

1.6 Outline of thesis chapters

This thesis is made up of seven chapters whose content is outlined below. The last four chapters (i.e. chapters 4-7) are analytical and have been written as journal articles.

Chapter 1: Introduction. This chapter discusses the background information of the thesis, its objectives and structure.

Chapter 2: Literature Review

This chapter is divided into two parts where one part discusses ‘savanna ecosystems’ and the other discuss ‘ecosystem services in African savannas’. The portion discussing savannas provides a detailed overview of the characteristics of savanna vegetation in relation to their main drivers. It also extensively discusses the recent history and impact of humans in East African savannas. The ES section discusses the definition, history, types, modelling and mapping of ES using examples from African savannas. The ES section has been published as a book chapter (Kariuki et al., 2018a) on the Routledge Handbook of African Development.

Chapter 3: Study Areas and Methodology

This chapter is divided into two sections: the study areas and methodology sections. Discussion of the study areas includes why they were selected for study, their biophysical characteristics and historical land use patterns. The methodology part provides detailed literature review of the models used in this research and their applicability to the sites studied by this research. This being an interdisciplinary thesis, some ecological and social techniques were also used in the study. However, they are not included in this chapter as they are discussed on the subsequent analytical chapters where they are used.

Chapter 4: Influence of Rainfall on Woody Vegetation Structure

This chapter is ecological and discusses changes in woody vegetation structure across a rainfall gradient in arid and semi-arid ecosystems in Kenyan savannas. It hypothesises that the importance of other variables in driving savanna vegetation structure can be understood better if the sole influence of rainfall is clearly understood. To test its hypothesis, the study uses historical data, collected in late 1970s/early 1980s, prior to the extensive sedentarisation levels that are presently common in Kenyan rangelands. In addition, the study is interested in understanding the ecology of southern Kenyan savannas under minimal human activities and linking it to the social perspectives and modelling techniques discussed in the subsequent thesis chapters. To that end, it compares the composition and function of woody vegetation in Amboseli and Mara ecosystems.

Chapter 5: Social Perspectives of Trade-offs in Land Use Change

In this chapter, land use change decisions by pastoralists are explored using insights from community elders. These insights were based on the history and drivers of land use and land tenure in post-colonial Kenya and are compared across the Amboseli and Mara ecosystems. The importance of livestock grazing in savannas, despite widespread climate variability and changing socio-economic development is discussed.

Chapter 6: ABM Insights on Climate Change, Land Use Change and Conservation

Using insights of land use change from the local communities (chapter 5) and literature sources, this chapter develops an ABM that explores changing land uses under varying climate and land tenure scenarios. The ABM uses biomass data, simulated by the LPJ-GUESS dynamic global vegetation model, as input that is linked to other socio-economic factors that drive land use change. The importance of conservation subsidies in pastoral land use change decisions under different climate and land tenure scenarios is discussed. This chapter has been published as a paper (Kariuki et al., 2018b) on Land Journal.

Chapter 7: Interdisciplinary Social-Ecological Perspectives of Climate Change, Land Use Change and Conservation

This chapter uses an interdisciplinary approach to discuss the changing interactions between climate, land use and the ecology of southern Kenyan savannas. In this chapter, changes in woody vegetation structure (chapter 4) across Amboseli and Mara ecosystems was combined with perspectives on the drivers of land use change (chapter 5) and ABM outputs on changing wildlife numbers and land use types (chapter 6). These insights were then used to discuss the influence of rainfall variability, conservation initiatives and land management strategies in driving the ecology of southern Kenyan savannas. Also discussed in this chapter are the implications of study findings to rangeland management and recommendations for future studies.

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2 Literature Review

2.1 Preface

This chapter provides literature on savanna ecosystems and the ES they provide. It begins by introducing the distribution and structure of vegetation in savanna ecosystems across Africa. This is followed by a review of literature on the main drivers of East African savannas and the theories used to explain the coexistence between trees and grasses. The independent and combined impacts of these drivers (rainfall, fire, soil nutrients, herbivores and humans) are discussed with the discussion on human impact focussed on the history of land use patterns in Kenya and the effect on land use changes on savanna ecology. The discussion on ES includes the origin of the ES concept, categories and examples of ES and methods used to map and model ES.

2.2 Introduction to savanna vegetation

Vegetation types in savannas are characterised by C_3 woody plants and C_4 grasses (Lehmann et al., 2014) and their distribution is influenced by climatic, edaphic, hydrology, herbivory and fire patterns (Bond, 2008; Lehmann et al., 2011). The grass cover is relatively continuous and the woody vegetation cover discontinuous (Sankaran et al., 2008; Bond and Parr, 2010; Foxcroft et al., 2010; Marchant, 2010; February et al., 2013) resulting in a vegetation structure that lacks consensus on a uniform way of categorizing it. While classification of some savannas is based on plant height, canopy cover and woody vegetation attributes (Scholes and Archer, 1997), for others is based on the ecological characteristics and climatic patterns (Bucini and Hanan, 2007). For example, Shorrocks and Bates (2015) adopted a simplified version of White (1983) and categorised vegetation patterns in African savannas into four groups: 1) Grass and shrub savannas, 2) trees and shrub savannas, 3) woodland savannas and 4) forest-savanna mosaic. The extent of coverage of these four savanna types as well as the dominant woody and grass species are included in (Table 2.1). Using an ecological and climatic approach, savannas have been classed either as arid/eutrophic or moist/dystrophic. The arid/eutrophic savannas are characterised by mean rainfall of 400-800 mm yr^{-1}, high soil nutrients, low biomass of high quality vegetation and high biomass of herbivores while the moist/dystrophic savannas are largely made up of pre-

Cambrian rock which weathers into highly leached soils and are characterised by high rainfall (> 600 mm yr^{-1}), low soil nutrients, high vegetation biomass of poor quality and

Table 2.1: Dominant vegetation species and their distribution in African savannas. Source - (Shorrocks and Bates, 2015)

Savanna type	**Coverage**	**Dominant woody species**	**Dominant grass species**
Grass and shrub savanna	From northern Senegal and Mauritania to Sudan	*Acacia tortilis*. *A. laeta* *Balanites aegyptica* *Boscia senegalensis* *Commiphora africana*	*Aristida stipoides* *Cenchrus biflorus,* *Shoenefeldia graciis*
Tree and shrub savannas	North and south of the rainforest and miombo woodland savannas in central Africa	*Acacia seyal* *Anogeissus leiocarpus* *Balanites aegyptica* *Boswellia payrifera* *Commiphora africana* *Kigelia aethioptica* *Lannea schimperi* *Prosopis africana* *Stereospermum kunthianum*	*Cymbopogon* *Echinochloa* *Hyparrhenia* *Pennisetum* *Sorghum*
Woodland savannas	Miombo in central and south Africa	*Brachystegia* trees *Combretum* *Copaifera* *Faurea* *Julbernardia* *Marquesia* *Monotes* *Uapaca*	
	Doka in the north	*Afzelia,* *Anogneissus* *Borassus* *Burkea* *Isoberlinia doka* *Terminalia*	
forest-savanna mosaic	Guinean forest-savanna mosaic of West Africa, the Congolian forest-savanna mosaic and the Zambezian forest - savanna mosaic	*Berlinia* *Cola* *Cynometra* *Diospyros* *Parinari* *Pterocarpus*	*Andropogon* *Hyparrhenia* *Loudetia*

low biomass of herbivores (East, 1984; Du Toit and Cumming, 1999). The arid/eutrophic savannas are dominated by Acacia plants and occur in the Sahel, Karoo and Kalahari regions in Africa while the moist/dystrophic are the miombo woodlands that occur in southern and central Africa (Figure 1.1) and are dominated by Brachystegia/Julbernadia woodland interspersed with grassland along drainage lines (Du Toit and Cumming, 1999).

2.3 Drivers of savanna vegetation

'Bottom-up' and 'top-down' approaches have been used by ecologists to characterise abiotic and biotic controls on savanna vegetation. The former is resource based and proposes that vegetation growth is affected by availability of water and soil nutrients while the latter is disturbance based and proposes that disturbances, such as fire and herbivory, regulate vegetation patterns of savannas. Of the major controls (rainfall, soil nutrients, fire, herbivory and humans) of savanna vegetation patterns, rainfall amount and seasonality are considered the most important control (Sankaran and Ratnam, 2013). However, the combined effects and intensities of different controls lead to varying proportions of grasses and trees in different ecosystems.

2.3.1 Rainfall in savannas

The Intertropical Convergence Zone (ITCZ) is the main driver of East African rainfall (Plisnier et al., 2000) causing a bimodal rainfall pattern in near equatorial (5^{o}S-5^{o}N) areas, such as Kenya and northern and eastern Tanzania, and a unimodal rainfall pattern in areas further away from the equator, such as southern and central Tanzania (Omeny et al, in review). Although East Africa has an equatorial position, it is rainfall deficient (Plisnier et al., 2000; Shorrocks and Bates, 2015) making its savannas water limited in certain months of the year (Scholes and Archer, 1997). The influence of rainfall on savanna ecology is also modified by topography, soils and drainage (Shorrocks, 2007). Topographical variations associated with the Great Rift Valley and large inland water bodies, together with the Congo air mass and the Indian Ocean, influence the spatial distribution of rainfall by causing highlands west of the Rift valley to be wetter during the long rain season and highlands east of the Rift Valley to be wetter during the short rain season (Omeny et al, in review). In addition, montane areas cause large rainfall variation to savannas near them. For example, the Laikipia plateau and Amboseli ecosystem, in Kenya, receive low rainfall as they are located on the leeward side of Mt Kenya and Mt. Kilimanjaro respectively (Shorrocks, 2007).

Based on the rainfall received, savannas have been classified as arid, semi-arid or moist. The boundaries for the rainfall amount vary amongst savanna ecologists and are not clear cut. Shorrocks and Bates, (2015) classified the mean annual rainfall range in savannas to be between 200 and 1250 mm yr^{-1}. Bucini and Hanan (2007) identified, defined and selected savanna regions in Africa as those that received < 2200 mm yr^{-1} mean annual rainfall. They categorized arid savannas as those receiving < 400 mm yr^{-1} mean rainfall and have low tree cover that is insensitive to increasing rainfall, semi-arid savannas as those that receive 400-1600 mm yr^{-1} mean rainfall with average tree cover that increase with rainfall and moist savannas as those with > 1600 mm yr^{-1} mean rainfall and have high tree cover that is insensitive to increasing rainfall but sensitive to other disturbances.

Rainfall is considered the most important climate factor governing primary production in East African savannas as it sets an upper and lower limit to tree cover (Sankaran and Ratnam, 2013) and plays a primary role in regulating herbaceous vegetation biomass (Shorrocks and Bates, 2015). Tree cover has been documented to increase linearly with rainfall in areas receiving < 650 mm yr^{-1} while areas receiving > 650 mm yr^{-1} of rainfall require vegetation disturbances such as fire and herbivory to maintain the ecosystem as a savanna. In dry savannas, tree growth is limited and grasses have competitive advantage over woody vegetation because grasses can access water better than tree seedlings at the same surface layer. On the other hand, in less arid savannas, adult trees can out compete grasses as they can grow long roots and access deeper water layers that grasses cannot (Baudena et al., 2015). In addition to the amount of rainfall falling in an area, the seasonal distribution of rainfall determines the length and the severity of the dry season and consequently, vegetation structure (Shorrocks, 2007). Rainfall seasonality in savannas is highly variable and dry seasons occur between wet seasons and range from two to nine months of the year (Figure 2.1). Regions receiving frequent and less intense rainfall have higher tree cover compared to those receiving less frequent but intense rainfall (Sankaran and Ratnam, 2013). An area with two short rains seasons and two short dry seasons may produce a woodland while an area with the same amount of rainfall but spread in one short wet season and has a long dry season may produce a shrub land (Shorrocks and Bates, 2015). This is because most rainfall is lost as surface run-off in areas receiving a lot of rainfall in few rainfall events. Water use efficiency also varies between trees and grasses and is dependent on the architect of the plant. Zizka et al. (2014) show that tall single stemmed trees in seasonally arid environments are conservative in their water use as they are likely to be deciduous due to the risk of transpiration. In some southern African systems, like the Kalahari sand woodlands, frost also plays a key role in shaping vegetation by killing and damaging above ground plant biomass (Holdo, 2007).

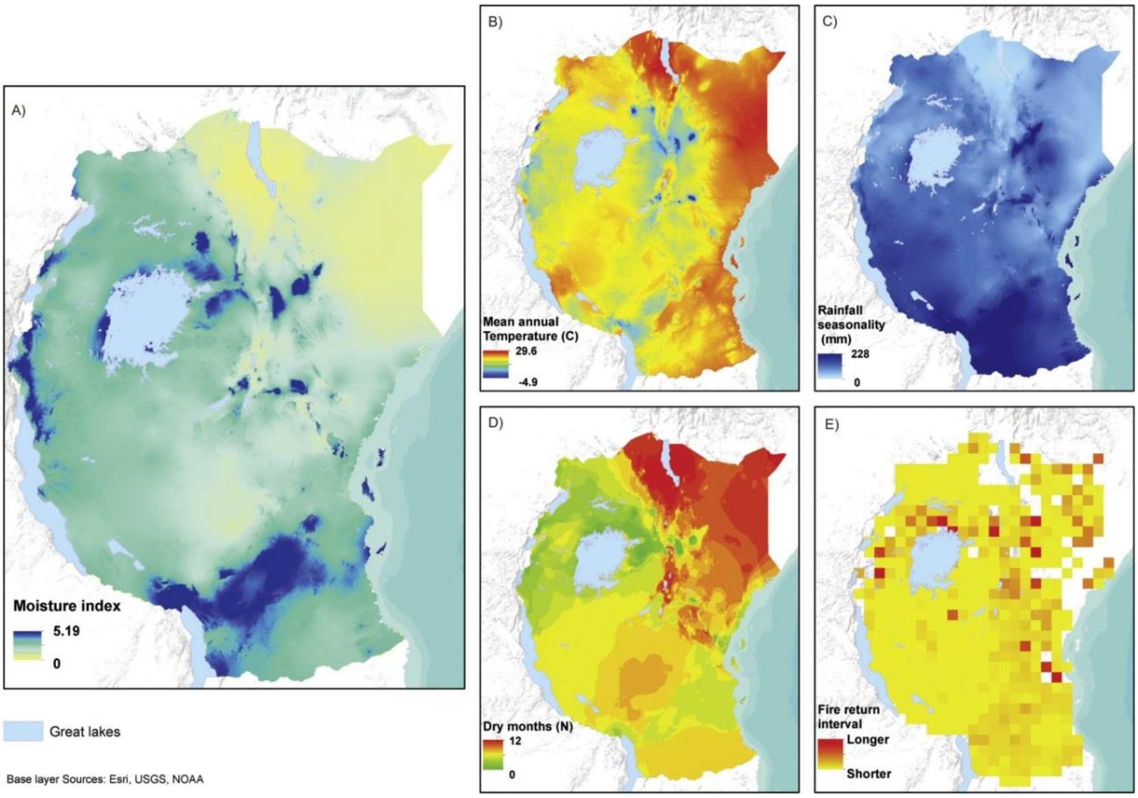

Figure 2.1: Variations in moisture index (A), monthly mean annual temperature (B), rainfall seasonality (C), length of longest dry season (D) and fire return intervals (E) in East Africa (Marchant et al., 2018).

Although tree cover in tropical savannas increases with rainfall; disturbance and climatic variability account for significant variation in tree cover (Bucini and Hanan, 2007). 'Climatically determined savannas' are savanna types where tree-grass coexistence is driven by rainfall and disturbances such as fire and herbivory are not required for their coexistence while 'disturbance driven savannas' are savanna types receiving moderately high rainfall that requires disturbance for the coexistence of tree and grasses (Shorrocks and Bates, 2015). 'Climatically determined savannas' can become 'disturbance driven savannas' and vice-versa as biotic and abiotic conditions change. Also, most savannas are in a disequilibrium state due to climate variability and disturbances but tend to relax in periods of near average climate and less disturbance (Bucini and Hanan, 2007).

According to (Sankaran and Ratnam, 2013), after water availability, fire is the second most important factor for determining vegetation structure within African savannas, followed by the effect of soil nutrients and herbivory. Without fire, African savannas have the potential to succeed to closed woodlands (Bond and Keeley, 2005). This observation is supported by fire exclusion experiments which show that excluding fires from grassy ecosystems leads to the development of a forested ecosystem; a process that may take one to five decades and is slower in nutrient poor and water logged soils (Bond, 2008). Grass provides most of the fire fuel in savanna (Staver et al., 2011) while in other biomes, such as boreal forests, woody vegetation provides the bulk of the fuel load for fires (Bonan and Shugart, 1989; Baudena et al., 2015). The average return period for savanna fires range from two to six years (Staver et al., 2011) with an intensity that can completely destroy above ground biomass (Zizka et al., 2014). Additionally, fire intensity and frequency is related to moisture availability, temperature and grass biomass (Lehmann et al., 2014) and is higher in humid areas (one to three years) and lower in semi-arid and arid areas (greater than three years) (Tomlinson et al., 2012).

Fire has differential effects on woody and herbaceous vegetation. Its effect depends on the season, frequency and intensity. Fire damages tree saplings preventing their establishment to adult trees and from reaching their potential maximum as defined by climate (Staver et al., 2009). Fire frequency determines the probability of tree seedlings escaping fire effects and developing to adult trees (Bucini and Hanan, 2007; Bond, 2008; Charles-Dominique et al., 2017) and to survive frequent fire episodes, plants must complete their life cycle faster than the period between two successive fire episodes (Charles-Dominique et al., 2017). C_4 grasses are highly flammable and promote the spread of fire in open ecosystems. They also benefit from fire as they recover faster than trees whose seedling recruitment and growth is hindered by fire (Baudena et al., 2015). Grasses can also influence fire regimes in tropics and subtopics by maintaining a grassland or a savannas in areas that could climatically support forests (Bond, 2008; Charles-Dominique et al., 2017). Depending on the plant size and species, some plants can survive fire effects. For instance, larger saplings are less affected by fire compared to smaller saplings while species with thick barks and high moisture content are able to survive frequent fires. In addition, savanna tree saplings store starches in their roots from which they can re-sprout new shoots after a fire event (Staver et al., 2009; Tomlinson et al., 2012; Levick et al., 2015). Other coping mechanisms by woody species from the effects of fire involve avoiding fire where woody plants reproduce before the fire season, tolerating fire where woody species re-sprout after a fire event and escaping fire where woody plants reproduce after fire resistant size classes have been reached (Zizka et al., 2014).

In East Africa, human induced fires are used for several reasons. Pastoralists have used fire to promote sprouting of new growth for grazers, to create new areas for planting, to eliminate dangerous animals such as snakes and to kill pests and diseases (Riginos et al., 2012; Kamau and Medley, 2014). In some wildlife conservation areas, prescribed burning is practiced as a management tool and measures are put in place on the role of fire in shaping vegetation patterns (Van Wilgen et al., 2004; Thiollay, 2006). Prescribed burning is shown to create heterogeneity in vegetation and to improve the quantity and quality of grass that is key to maintaining small-bodied and wild ruminant herbivores (Riginos et al., 2012). Though fire promotes the coexistence of trees and grasses by suppressing woody cover (Bucini and Hanan, 2007) and causing ecosystem heterogeneity in vegetation structure (Scholes and Archer, 1997; Bucini and Hanan, 2007); fire does not act alone and the disturbance effect is also caused by herbivores.

2.3.2 Soil properties in savannas

Soil properties are important determinants of vegetation structure and composition in low rainfall savannas. They include organic carbon concentration, soil pH and minerals such as nitrogen (N), calcium (Ca) and phosphorus (P) (Figure 2.2). McNaughton et al. (1988) discuss that savanna soils were derived from the weathering of pre-Cambrian rock which had low levels of plant nutrients thus are generally deficient of nutrients. Other soil properties such as infiltration rates and penetration depth are driven by vegetation characteristics whereby dense woodlands, due to higher organic content, have higher rain water infiltration rates cover (Mwangi et al., 2016). While loss of forest cover and agricultural expansion in the Mara catchment has been linked to reduced soil water infiltration rates and increased surface run-off, high infiltration rates in the Nyangores sub-catchment of the Mara River Basin has been attributed to high woodland cover (Mati et al., 2008). The impact of soil texture on savanna vegetation structure leads to higher water holding capacities in fine structured soils which then reduces soil water infiltration rates favouring grasses with shallow roots over trees with deeper roots cover (Sankaran et al., 2008).

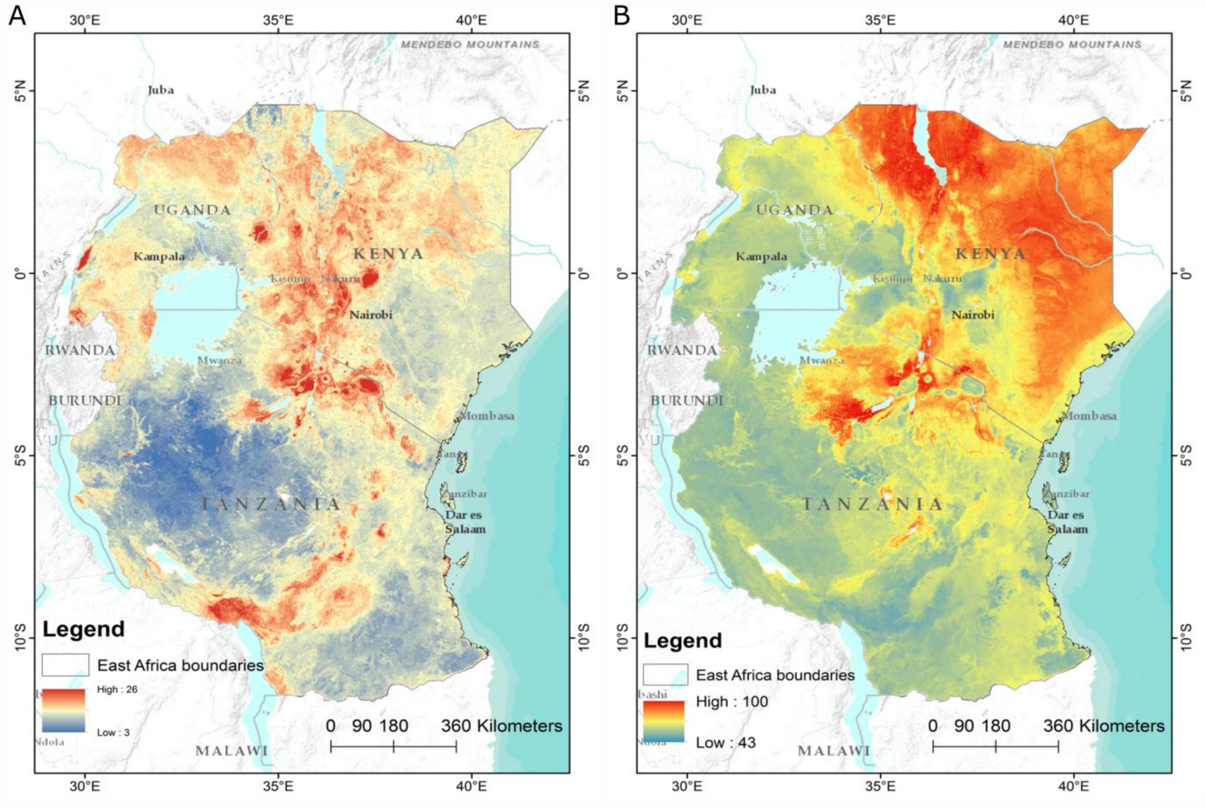

Figure 2.2: Available soil water capacity at 45 cm (A) and soil pH at 22.5 cm (B) for East African soils. Source – Africa Soil Information Service (AFSIS)

Soil N and P can limit vegetation production in areas receiving < 200 mm yr^{-1} of rainfall (Augustine et al., 2003). Additionally, the amount of soil nutrients and moisture in a particular ecosystem affect the response of vegetation to disturbances such as herbivory and fire. Tree cover in African savannas is negatively correlated to soil N availability with tree seedling survival and growth decreasing with increases in soil N availability (Sankaran and Ratnam, 2013). Further, the effect of increasing soil N suppressing tree seedling survival and growth tends to promote herbaceous growth through high depletion rates of soil water. This effect varies across rainfall gradients and is more pronounced in arid compared to mesic ecosystems. The effect of soil P on tree cover is complex and non-linear with P deficient soils limiting the growth of grass seedling (Sankaran and Ratnam, 2013). C_4 grasses have higher carbon to nitrogen ratios with lower decomposition rates; thus are more efficient in nitrogen use leading to their high productivity in nutrient poor soils (Bond, 2008). As a whole, nutrient poor soils have been cited as the reason why grasslands persist in climates that can support forests though this has also been associated with low succession rates due to reduced growth and productivity (Bond, 2008).

2.3.3 Effect of herbivores in savannas

Savannas support high densities of diverse herbivore species (Figure 2.3) than other terrestrial ecosystems (Augustine et al., 2003; Bond et al., 2005; Galvin et al., 2006; Kimuyu et al., 2017). Through their movements, herbivores follow the variable quality and quantity of vegetation biomass that is shaped by the availability of resources and disturbances (Reid et al., 2008; Sensenig et al., 2010). Their impact on savanna vegetation depend on the intensity of feeding, trampling and seed dispersal habits (Staver et al., 2009) which in turn depends on the characteristics of the herbivores such as species types, density, feeding habits and body size. Grazers can promote bush encroachment while browsers maintain open ecosystems by preventing the recruitment of seedlings and saplings to trees (McNaughton et al., 1988) and keeping the woody vegetation susceptible to fire. African elephants, wildebeest and zebras are considered keystone species in savannas as they play crucial roles in nutrient cycling, seed dispersal and opening up closed woodlands for other smaller animals (McNaughton et al., 1988; Baxter and Getz, 2005; Holdo, 2007). Elephants create different patch dynamics in savannas by changing the structural composition of woodlands. They convert big trees into smaller height classes by breaking their branches and not killing them (Claudius et al., 1999). However, their effect on woodland species composition is not significant probably because they are bulk feeders and not quality feeders (Hempson et al., 2015). The combined impacts of both meso and mega herbivores also shapes savanna vegetation structure and composition. For example, through browsing both meso and mega herbivores could suppress the growth of tree saplings thus limiting their recruitment (Staver et al., 2009). Browsing by small antelopes, such as the impala, suppress shrub growth while big animals, such as the elephant, change the height class distribution of shrubs (Bond, 2008). The effect of different herbivore guilds on vegetation varies across different sites. For instance, browsers and mixed feeders have been recorded as having negative effects on some ecosystems while having positive effects on others (Sankaran et al., 2008). Termites, sometimes considered as disturbance agents in savannas, play important roles in plant decomposition and nutrient cycling (Muvengwi et al., 2017). As termite mounds have more water and nutrients compared to soils surrounding them (Acanakwo et al., 2017), they induce resource heterogeneity in floristic composition of African savannas by supporting unique plant species (Sileshi et al., 2010; Davies et al., 2016; Acanakwo et al., 2017; Muvengwi et al., 2017). At a site in Tsavo National Park, Kenya, with mean annual rainfall of 352 mm yr^{-1}, dead wood took 11 years to decompose with termites mediating 90% of the decomposition (Sileshi et al., 2010).

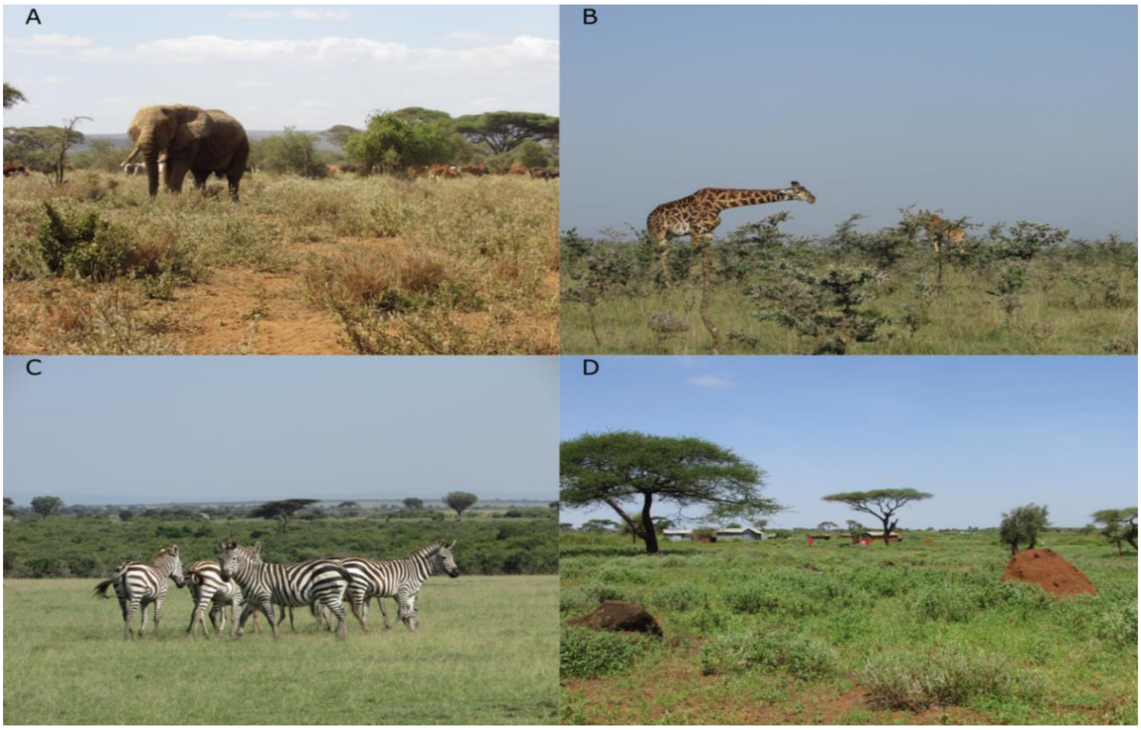

Figure 2.3: Herbivory in savannas. A) Elephants and cows grazing in Amboseli, B) giraffes browsing in Amboseli, C) plains zebras in Mara and D) a termite mound and surrounding vegetation in Amboseli. Photos source: The author

Savanna grass species respond differently to grazing pressure and their response can be used to determine the grazing capacity of an area. Based on the response of grass species to grazing, three categories of grasses have been identified: Increaser I, Increaser II and Decreaser species (Kioko et al., 2012). Increaser I grass species (e.g. *Pennisetum mezianum* and *Pennisetum stramenium*) increase when under grazed, Increaser II grass species (e.g. *Cynodon dactylon*) increase when overgrazed while decreaser grass species (e.g. *Cenchrus ciliaris, Panicum maximum* and *Themeda* *triandra*) decrease when under grazed or overgrazed, but dominate rangelands in good condition (Kioko et al., 2012; Trollope et al., 2014).

The combination of browsing and fire tends to reduce younger saplings particularly those within the reach of herbivores. Grazers, on the other hand, can promote shrub encroachment in grasslands by suppressing the growth of grasses as well as reducing fuel for fires and in the process promoting fire sensitive trees (Bond, 2008). Also, grazing intensity varies across sites and depends on the stocking rate and time taken by grazers on a particular area. High intensity grazing generally suppresses grass growth by reducing its biomass and fuel for fires while low intensity grazing enhances grass growth and productivity.

2.3.4 Effect of humans on savannas

Long term historical records show that East African savanna have strongly been shaped by human activity (Curtin and Western, 2008; Marchant et al., 2010; Greiner et al., 2013). The introduction and expansion of pastoralism in East Africa about 4000 years ago marked the beginning of large scale human impact on East African savannas (Marshall and Hildebrand 2002; Muchiru et al., 2009; Marchant et al., 2018). Other activities like ivory trade, fire and settlement patterns also account for the changing ecology of East African savannas. Over the last two millennia, elephants from eastern and south-eastern Africa have been the main sources of ivory to western Europe, China, India, the Persian Gulf and the Mediterranean region (Coutu et al., 2016). In East Africa, ivory trade intensified in the 19th century due to higher demand for East African ivory, driven by its affordability and desirability in colour, texture and carving properties, compared to that from south-east Asia (Beachey, 1967; Lane, 2010; Coutu et al., 2016). By the mid-19th century, the high demand for ivory in Europe and North America escalated further and East Africa became the primary source of ivory in the world (Lane, 2010; Coutu et al., 2016). However, by 1890, ivory exports from East Africa, and elephant populations, particularly along the coasts, declined greatly leaving significant consequences on the ecological and socio-economic dynamics across East Africa savannas (Lane, 2010; Coutu et al., 2016).

East African savannas are characterised by erratic climate and poor agricultural production making pastoralism the dominant and most efficient land use type (Galvin et al., 2006). Two major challenges facing most pastoral systems in sub-Saharan Africa are 1) fragmentation of grazing lands caused by land use and land tenure changes and 2) environmental changes brought by erratic climate (Hailegiorgis et al., 2010). Land use patterns in pastoral areas in East Africa are a result of pre-colonial and post-colonial land policies and activities. The Maasai community, a Nilotic pastoral community, moved into Kenyan rangelands in the 17th century (Lamprey and Reid, 2004). Despite utilising the rangelands for centuries, pastoralism was perceived as an inefficient and uneconomical land use by the colonial government, and later the independent government of Kenya (Seno and Shaw, 2002; Evans and Adams, 2016). The colonial government aimed to separate people from animals by forming game reserves and national parks in key resource areas such as dry season grazing lands and where there were salt-licks (Majule et al., 2009; Evans and Adams, 2016). In Kenya, formation of protected areas began in 1930, and though protected areas were formed to conserve wildlife and their habitats, they took land away from pastoralists (Western, 1982). Besides forming protected areas, the colonial government in Kenya evicted pastoralists from their territory in the northern and wetter rangelands, resettled them in the south, and appropriated large swaths of their land to European settlers who used them for farming and commercial ranching (Mwangi and Ostrom, 2009; Evans and Adams, 2016). To the colonial government, pastoralists’ activities led to environmental degradation and were a threat to wildlife populations but to the pastoralists, constrained grazing, following a reduction of grazing land that was allocated for European settlement, was the cause of environmental degradation (Mwangi and Ostrom, 2009). Demarcation of land for formation of protected areas and land appropriation by European settlers brought pressure on land availability (Campbell et al., 2000).

Kenya’s independent government, which came into power in 1963, also viewed pastoralism as inefficient and wanted to halt it by enacting policies that promoted subdivision and privatisation of pastoral land (Seno and Shaw, 2002). The perception of policy makers then was that private land ownership was more productive than communal land ownership in that it allows the intensification and commercialisation of livestock production (Homewood et al., 2009). Two stages of land privatisation then ensued in Kenyan rangelands from the 1960s to present (Figure 2.4). Firstly, group ranches were formed from the 1960s (Kioko and Seno, 2011) from previously managed communal trust lands and secondly, the group ranches were later subdivided among registered group ranch members where each received an individual title deed (Thompson and Homewood, 2002; Thornton et al., 2006). The 'Land Group Representatives and Land Adjudication Act' of 1968 (Figure 2.4) was enacted and allowed the formation of group ranches, through issuance of title deeds, on land previously held in trust by the government (Lamprey and Reid, 2004; Homewood et al., 2009). Group ranches are livestock production systems set up in Kenyan rangelands where a group of individuals, with kinship ties, are jointly granted ownership of land titles (Kioko and Seno, 2011). Though the group ranches are owned jointly, livestock ownership is individual based. Through group membership in the ranches, pastoralists elect group committees and form constitutions that manage the activities of the group ranch (Lamprey and Reid, 2004). To policy makers, formation of the group ranches was a step towards formal privatisation of land and intensification of livestock production and to pastoralists it was a way of protecting their land from invasion by foreign communities (Seno and Shaw, 2002; Galvin et al., 2008; Mwangi and Ostrom, 2009; Evans and Adams, 2016). The government also felt that if pastoralists were settled on their land, in the group ranches, it would be easier to provide basic services such as health care and education (Lamprey and Reid, 2004). It was also assumed that formal registration of land titles by pastoral households would give them access to credit and other opportunities that would lead to development of their land (Homewood et al., 2009).

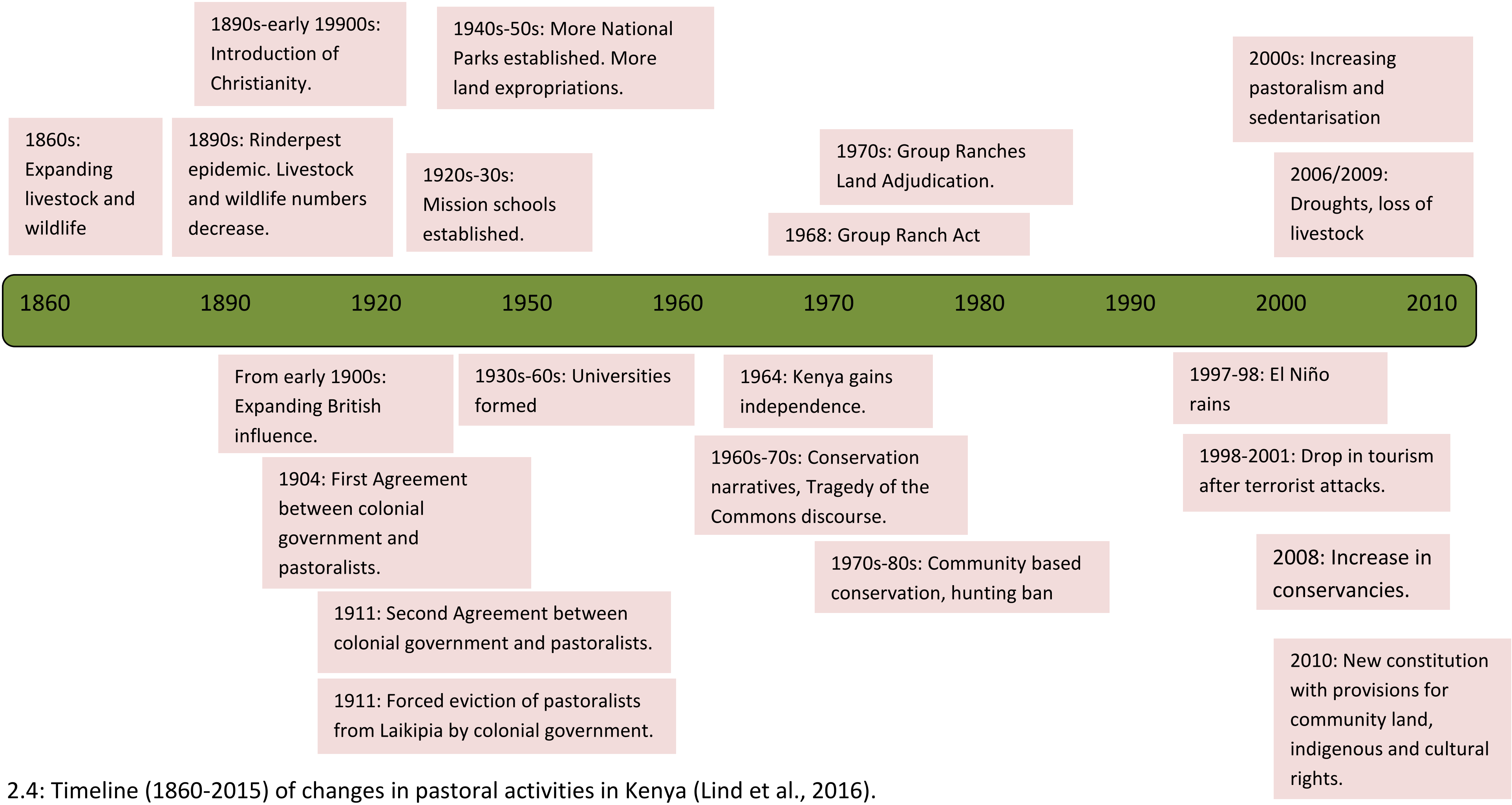

Figure 2.4: Timeline (1860-2015) of changes in pastoral activities in Kenya (Lind et al., 2016).

Though pastoralists were expected to sedentarise and commercialise livestock production in the group ranches, they did not. Most of them continued to use their land in common where they grazed their livestock across the ranches (Seno and Shaw, 2002). Group ranches also faced governance issues (Evans and Adams, 2016). To begin with, the allocation of land titles was marred by problems where individuals, from pastoralists and non-pastoralist communities, that were educated or had influence over the land titling procedures were privately registered and allocated land titles for large parcels of land that were cut from the group ranches (Homewood et al., 2009). Other climatic and socio-economic factors such as climate variability, declining authority by traditional institutions in the management of grazing resources, habitat fragmentation due to land tenure changes and high population growth further threatened the sustainability of pastoralism (Thornton et al., 2006; Sundstrom et al., 2012; Kibet et al., 2016). Group ranches started subdividing and in 1983, a national policy on group ranch subdivision into individual land parcels was formed (Galvin et al., 2008).

With subdivision of the group ranches, changes in property rights became, and still are, important drivers of pastoral land fragmentation and sedentarisation (Reid et al., 2004, 2008). Fragmentation of pastoral grazing lands often began in wetter areas or key resource areas, such as water points (Reid et al., 2004) leading to clustered sedentarisation patterns near water points and social amenities (Western et al., 2009; Vuorio et al., 2014). As a result of land fragmentation in the savannas, pastoralism has declined, agriculture has expanded and per capita livestock herds among pastoral communities have declined (Reid et al., 2008; Greiner et al., 2013). Pastoralists and wildlife have gradually been pushed to drier areas where currently, about 35-50% of wetter areas that formed grazing lands, are used for irrigated and rain-fed agriculture while 2-4% are used for towns and cities (Reid et al., 2008). Similar trends of pastoral land subdivision and sedentarisation of pastoral livelihoods have been documented in various parts in East Africa. For instance, in the first half of the twentieth century, the pastoral Pokot of northern Kenya resisted colonial efforts for settling them and remained highly pastoral with large herds of cattle. However, in the latter half of the century, they increasingly became sedentary (Figure 2.4) and expanded their agricultural activities and marketing of livestock and other products such as honey

(Greiner et al., 2013; Bollig, 2016; Greiner and Mwaka, 2016). Many Samburu pastoralists in northern Kenya have adopted agriculture as their main livelihood source (Bollig, 2016) while in Ngorongoro District in Tanzania, agriculture is documented as having expanded from the 1970s (McCabe et al., 2010; Greiner and Mwaka, 2016).

As sedentarisation levels increased over the late twentieth century, different land use patterns that were driven by socio-economic and ecological factors emerged (Figure 2.5). Initially, when the inadequacies of protected areas became obvious, the concept of community based conservation initiatives emerged. Protected areas fell short of conserving wildlife and their habitats due to their limited size, limited monitoring and poor administrative management and enforcement of resources (Bulte et al., 2008). Local communities saw wildlife on community land as problematic leading to human-wildlife conflicts and their decline. It was taken that the success of protected areas and wildlife conservation depended on support of communities living near protected areas and community based conservation initiatives were developed to mitigate human-wildlife conflict and to promote the compatibility of biodiversity and development (Galvin et al., 2006). The main assumption of these initiatives was that if communities got economic benefits from wildlife, they would have a positive attitude towards it (Galvin et al., 2006).

These initiatives were practiced where communities had communal land tenure and legal rights to provisioning services and were willing to collaborate with conservation organizations to improve their socio-economic status and conserve natural resources in their area through sustainable land management (Bulte et al., 2008; Egoh et al., 2012). Despite the good intentions for forming community based initiatives, human-wildlife conflict increased when wildlife numbers soared (Galvin et al., 2006) and the animals no longer feared people (Western and Nightingale, 2003). Elsewhere, the approach was challenged by studies that raised concerns on the ability of development projects to combine biodiversity conservation goals with poverty alleviation (Bulte et al., 2008). This was largely driven by unequal distribution of tourism income, along age, gender and education lines making only few pastoralists earn their main livelihood from tourism (Galvin et al., 2006; Bedelian and Ogutu, 2017).

Figure 2.5: Livestock grazing and agriculture land use types in the Amboseli ecosystem. A) cattle going to the watering point while grazing and trampling on vegetation, B) cattle dung left by calves in their overnight enclosure, C) a section of land that is live fenced and prepared for planting onions and tomatoes, D) a water canal constructed to divert water courses by directing water to farmlands. Photos source: The author.

With the unsuccessful implementation of community based initiatives and changing socio-economic and climatic factors, other concepts of sustainable land use came up. In some subdivided and privately owned land, neighbouring private landowners now agree to jointly use their land for livestock grazing with an objective of enhancing livestock mobility and avoiding land degradation through overgrazing (Kibet et al., 2016). This largely occurs in very arid areas that are far from permanent water sources. In community areas closer to protected areas, which form wildlife dispersal and migratory corridors, wildlife conservancies have been formed (Figure 2.6). Conservancies refers to institutions of governing and managing wildlife as well as lands set aside by individual owners, group of owners or corporate bodies for wildlife conservation purposes in accordance with the ‘Wildlife Act’ (Osano et al., 2013; KWCA 2016; Løvschal et al., 2017). They occupy 11% of Kenya’s land surface (KWCA, 2016) and though their main focus is to conserve habitats for wildlife and tourism initiatives, they also aim to improve the incomes of pastoralists (Bhola et al., 2012; Bedelian and

Ogutu, 2017). There are several different governance models of conservancies. For example, in Mara, running the conservancies involves partnership between tourism operators and land owners where the tourism operators manage the conservancy and pay the landowners a fixed monthly land lease payment to vacate their land, practice controlled livestock grazing and avoid putting up settlements (Bhola et al., 2012; Osano et al., 2013). As at 2006, there were 2 conservancies in areas surrounding the Maasai Mara National Reserve and by 2015, they had grown to 17 conservancies located across the wider Mara ecosystem (Bedelian and Ogutu, 2017). Management of the conservancies is autonomous and as at 2015, there were 178 conservancies in Kenya (reid et al., unpublished; Bedelian and Ogutu, 2017).

Besides farm-income (i.e. from pastoralism, conservancies and agriculture), other off-farm income sources are from waged labour, business income, wildlife and conservation related activities and remittances from educated family members working in other towns (Homewood et al., 2009).

Figure 2.6: Conservancies are autonomous in their objectives and management. Figure A shows the entry to Mt Suswa Conservancy in the Kenyan Rift Valley. It is 30km^2 and it aims to improve pastoralists' income and conserve geological features, such as caves and craters that characterise the area (Photo source: Christine Adongo). Figure B is a vehicle for the Meibae Community Conservancy in Samburu County in north Kenya. The conservancy was formed in 2006 and its core conservation area is 1159 km^2. Photo source: (Schrijver and Lenkaina, 2017).

The impact of human activities on savanna ecology depends on the type of activity. Fires form an important part of pastoral livelihoods and are used to clear bushes, stimulate growth of soft and palatable pasture for their animals, kill pest and diseases and harvest honey (Butz, 2009; Kamau and Medley, 2014). Land used for pasture, agriculture and fuel changes the structure of woody vegetation and eliminates wildlife (Bucini and Hanan, 2007). Overgrazing by livestock promotes bush encroachment and degradation of the herbaceous layer (Scholes and Archer, 1997) while conversion of grazing lands to farmlands causes habitat loss for key resource areas for wildlife (Reid et al., 2008). With livestock biomass in East African savannas exceeding that of wild ungulates (Muchiru et al., 2008), livestock impact on savanna vegetation structure is significant. Livestock plays a key role in redistribution of organic matter and soil nutrients (Augustine et al., 2003). They redistribute soil nutrients from pastures that they graze on during the day to their overnight enclosures, where they spend their nights (Reid 2012). They do this by leaving a huge reservoir of dung when they abandon their overnight enclosures (Augustine et al., 2003; Muchiru et al., 2008; Vuorio et al., 2014), which leads to the growth of high quality vegetation, rich in nitrogen, calcium, sodium, phosphorous and crude proteins, which remain in the soil for 40-100 years shaping vegetation and wildlife communities in the area (Vuorio et al., 2014). For example, in Kenyan rangelands, the distribution and abundance of *Acacia tortilis* is influenced by past distribution of cattle corrals used by pastoralists (Reid and Ellis 1995; Scholes and Archer, 1997; Muchiru et al., 2008) while in South Africa, distinct communities of *A. tortilis* in the *Burkea africana* savannas are found on Iron Age settlement sites (Scholes and Archer, 1997).

Sedentarisation among pastoralists in arid and semi-arid lands poses a serious threat to wildlife and rangeland health (Western et al., 2009). Wildlife in Kenya has reduced by 35-50% over the last 30 years due to agricultural encroachment into wetter areas of pastoral lands (Western et al., 2009). Sixty five percent of Kenya's wildlife is found outside protected areas (Kinnaird and O'brien, 2012), making the impact of land use change on wildlife significant (Ogutu et al., 2009). In Kajiado, wildlife decline on subdivided and settled lands relative to adjacent communal group ranch, has been attributed to the distribution of permanent settlements rather than densities of livestock, people and settlements (Western et al., 2009; Groom and Western, 2013).

Fragmentation of pastoral lands near protected areas changes the behaviour of small and medium sized mammals making them forage near pastoral settlements while larger mammals, like elephants and lions, change their behaviour by avoiding human settlements (Reid et al., 2004). Birds, especially large ones, are also sensitive to human activities. In a savanna in Burkina Faso, in West Africa, avifauna in exotic trees was significantly poorer relative to that of natural woodlands while two scavengers, the Black Kite and Hooded Vulture, were associated with human settlements and rubbish rather than resources found in natural savannas (Thiollay, 2006).

2.4 Interaction between savanna vegetation controls

At the African continental level, rainfall is a significant driver of tree cover, however, it cannot provide sufficient explanation on the variability of tree cover in savannas without considering the effect of other drivers (Bucini and Hanan, 2007). Tree cover in savannas is directly proportional to rainfall and disturbances, such as fire, herbivores, and frost maintain the system as a savanna. The impact of disturbances on woody vegetation are higher in semi-arid and mesic savannas (400-1600 mm yr^{-1}) relative to arid savannas (mean rainfall < 400 mm yr^{-1}) (Bucini and Hanan, 2007; Bond, 2008). Bond (2008) show that high rainfall periods in mesic savannas promote high grass biomass which in turn leads to frequent fires which limit tree establishment and growth. By contrast, low rainfall periods in mesic savannas limit grass growth and fire thus promoting the establishment of saplings and tree cover. The absence of fire and herbivory leads to an accumulation of unpalatable, nutrient poor vegetation biomass that can cause serious fires (Butz, 2009) due to its high standing biomass. Govender et al. (2006), in studying fires in South African savanna vegetation, found that grass biomass, which provides fuel for fires, is proportional to rainfall for four to five years, after which it declines due to grazing, decomposition and the loss of grass vigour. Soil substrate acts as a temporary store for rainfall that seeps through it and a control for outflows such as evapotranspiration and deep infiltration (Bucini and Hanan, 2007). At mean annual rainfall > 400 mm yr^{-1}, fine textured soils are able to support higher net primary production than coarse soils which can support higher net primary production at low rainfall (Bucini and Hanan, 2007).

Rainfall controls the population dynamics of African ungulates through its influence on vegetation growth and availability of surface water (Ogutu et al., 2009). For example, in Serengeti, Tanzania, the seasonal migration of 1.4 million wildebeests, zebras and Thomson's gazelles is driven by a strong seasonal rainfall gradient characterised by plains and short grass in the south and woodlands and tall grass in the north, centre and west of the ecosystem (Holdo et al., 2009). While seasonal fluctuations of water and pasture influence the migration of animals inside and outside protected areas across savannas, human activities, such as agriculture and land fragmentation, modify these patterns. In Amboseli, seasonal migration of elephants outside Amboseli National Park diminished after 1977, due to heavy poaching in early 1970s, agriculture expansion outside the national park and removal of pastoralists and their livestock from national park in 1977 (Western and Lindsay, 1984).

Abandoned pastoral bomas (settlements) are nutrient hotspots that improve the quantity and quality of plants in most savannas, consequently attracting high numbers of diverse species of herbivores, birds and invertebrates to nutritious vegetation (Porensky and Veblen, 2012). The effect of abandoned bomas on plants disappear faster in wet savannas, such as the Mara in Kenya, because dung decomposes faster in areas where soils remain wet for a longer time whereas in regions receiving < 500 mm yr^{-1} their impact on soils, animals and plants can remain for a long time (Vuorio et al., 2014). In Amboseli, where mean rainfall is 350-400 mm yr^{-1} (Western and Van Praet, 1973), abandoned bomas had higher soil nutrients that enhanced herbaceous biomass production and species richness for up to six decades (Muchiru et al., 2009). In central Laikipia, where rainfall is about 500 mm yr^{-1}, abandoned bomas increased soil minerals (nitrogen, potassium, carbon, calcium and sodium), vegetation species diversity and recorded livestock and wildlife dung density was ten times more than areas adjacent to the bomas (Young et al., 1995; Vuorio et al., 2014). In central Kenya, abandoned pastoral bomas persist for many decades as treeless sites that are surrounded by woodlands in areas adjacent to them (Porensky and Veblen, 2012). During active use of cattle bomas, intense livestock activity and human presence may promote tree establishment by reducing grass cover, preventing browsers, increasing nutrient levels and reducing fire intensity (Porensky and Veblen, 2012).

The impact of herbivory may drive transitions between woodlands and grasslands (Rucina et al., 2010). In Amboseli Basin, the loss of *Acacia xanthophloea* woodlands and expansion of grasslands over the last five decades is attributed to elephant activities (Western and Maitumo, 2004; Okello et al., 2016). In a Kalahari woodland savanna in western Zimbabwe, elephants are the main drivers of woodland change and their impacts are aggravated by fire and frost, which cannot suppress the woodlands on their own (Holdo, 2007). In Serengeti, the distinct rainfall gradient influences woody vegetation structure in the absence of fire; however, with fire, patterns of woody cover are shaped by the grazing habits of wildebeest, which are shaped by rainfall (Holdo et al., 2009). In the Serengeti-Mara ecosystem, woodlands changed rapidly in the 1960s due to elephants and fire leading to the transitioning of the woodland into a grassland in the 1980s (Dublin et al., 1990). The effect of invertebrate grazers in the savannas is to facilitate the impact of other savanna controls. Dung beetles, aid in dung disintegration, and their abundance and impact is higher in wetter savannas and in the wet season because during the dry season, dung dries up fast thus attracting fewer dung beetles (Vuorio et al., 2014). In savannas where fire frequency is high, interaction between termites and fire modifies vegetation heterogeneity as termites consume and use large quantities of grass for nest building, thus creating spatial patchiness in fuel load (Sileshi et al., 2010). Interactions between other herbivores, particularly, livestock and wildlife are shaped by dietary overlap between members of the same feeding guild; for example, resource competition between cattle and zebras which are grazers (Kimuyu et al., 2017).

Trees and grass interactions in savanna may lead to facilitation or suppression of one state. Trees canopies tend to enhance grass production in arid and semi-arid areas by improving the microclimate under tree canopies and altering the soil substrate characteristics (Weltzin and Coughenour, 1990; Scholes and Archer, 1997). For example, trees in a Kenyan savanna, facilitated grass growing beneath their canopies through lower soil temperature, lower water stress and greater soil organic matter, mineralizable nitrogen and microbial biomass (Belsky et al., 1989; Scholes and Archer, 1997). Reduction of the density of large trees may enhance the growth of tree seedlings which do not grow under tree canopies (Claudius et al., 1999).

2.4.1 Theories of tree-grass interactions

Coexistence between trees and grasses in savannas is explained by the equilibrium and dis-equilibrium theories (Scholes and Archer, 1997; Govender et al., 2006). Equilibrium theories, also known as ‘bottom-up’ forces, are resource based mechanisms that are based on the ability of trees and grasses to acquire and partition limiting resources, mainly water and soil nutrients. They include the root niche separation theory, phenological niche separation and balanced competition (February et al., 2013; Shorrocks and Bates, 2015). Disequilibrium theories, also referred to as 'top-down' forces, are disturbance based mechanisms that involve fire, herbivory and human beings (Shorrocks and Bates, 2015). Equilibrium theories propose the stable coexistence between trees and grasses (Scholes and Archer, 1997) while disequilibrium theories propose that there is no stable equilibrium between trees and grasses and frequent disturbances lead to competition between trees and grasses by promoting conditions which favour one state of the other (Govender et al., 2006). Disequilibrium theories argue that the challenges facing trees are demographic in nature with different age groups experiencing varying levels of disturbance from fire, droughts and competition from grasses (February et al., 2013).

The root niche separation hypothesis shows that coexistence between trees and grasses occurs because the roots of trees and grasses occupy different niches allowing differential soil water utilization hence minimizing direct water competition (Scholes and Archer, 1997). This theory advances that tree growth and production is promoted in high rainfall areas where rain percolates into deeper soil layers and the roots of trees have sole access to deeper soil waters while grasses only have access to surface soil water leading to an increase in tree cover from arid to mesic savannas favouring trees over grasses (Scholes and Archer, 1997; Bond et al., 2005). This theory has been supported by experimental studies by Tomlinson et al. (2012) which show that grasses invest in fine root biomass, nine times more than trees, and are able to access soil moisture effectively as they can access it even when the soils are dry while trees cannot. This theory, however, has been challenged because tree seedlings directly compete with grasses (Bond, 2008).

The phenological niche separation theory shows that trees, unlike grasses, can be able to access and store water and nutrients early and late in the growing season thus exhibiting a niche difference in time. The ability of trees to access and store nutrients better than grasses allows them to achieve peak leaf expansion before or shortly after the rainy season while grasses achieve maximum leaf expansion later in the growing season (Shorrocks and Bates, 2015). Additionally, trees can retain their leaves for longer periods after the senescence of grass leaves (Sankaran and Ratnam, 2013) allowing them to persist longer than the grasses. The balanced competition theory shows that coexistence of trees and grasses is possible because trees are superior competitors compared to grasses and are limited by intraspecific competition thus allowing grasses to grow and establish themselves (Shorrocks and Bates, 2015). The resource based hypotheses view savannas as stable ecosystems that require disturbances such as fire and herbivory for modifying the tree-grass balance but not for maintaining the savanna ecosystem.

The disturbance ’top-down’ mechanism is based on the role of disturbances which impose or eliminate demographic bottlenecks to germination, seedling establishment and recruitment of trees (Shorrocks and Bates, 2015). For example, grazing reduces grass biomass and promotes tree biomass while fires and browsing impose bottleneck to recruitment of trees to adulthood in mesic savannas (Sankaran and Ratnam, 2013). Disturbance based theory considers savannas to be unstable ecosystems that are prevented from transitioning into either forests or grasslands by disturbances such as fire and grazing.

Though savanna vegetation structure has been shown to be driven by equilibrium and disequilibrium theories, it is recognised that these processes interact and both approaches are used to enhance the understanding of savanna ecology (Sankaran et al., 2008; Staver et al., 2017).

Almost all ecological processes in dry areas are shaped by temporal variability in water availability and vegetation production and the welfare of humans and animals in these areas depend on their ability to cope with these variabilities (Reid et al., 2014). Additionally, besides grazing, rangelands provide a wide range ecosystem services (Galvin et al., 2008; Reid et al., 2014) and the high demand for these ecosystem services is perhaps the greatest force changing rangelands (Reid et al., 2014). Temporal variability of water creates variable vegetation quality, quantity and composition that may affect habitat use by herbivores (Kimuyu et al., 2017) and humans. The effects of herbivores and human activities, such as increased settlements, burning and poaching, may have contributed to changes in savanna woody cover over time (Claudius et al., 1999, Holdo, 2007); thus, to understand the coexistence between tree and grasses, both resource-based and disturbance-based theories can be integrated.

2.5 Ecosystem services in Africa

Ecosystem services (ES) are the benefits that societies derive from the ecosystems comprising of the flow of materials, energy and information from the natural environment to societies (Costanza et al., 1997; Wangai et al., 2016; Vaz et al., 2017). The definitions of ES, however, vary amongst authors who apply varying emphasis on the ecological or economic importance of ES, though all definitions acknowledge a link between ecosystem processes and human utility and well-being (Braat and de Groot, 2012; Müller and Burkhard, 2012).

The concept of ES began in the late 1970s (Gómez-Baggethun et al., 2010; Braat and de Groot, 2012) as a bridging concept between natural and social science views of environmental pollution, resource scarcity and the subsequent views of managing economic development in a sustainable way (Braat and de Groot, 2012). ES have emerged as a means of showing the dependency of societies on the biosphere (Gómez-Baggethun et al., 2010; Daw et al., 2011; Braat and de Groot, 2012) and was promoted after the publication of Millennium Ecosystem Assessment (MA; http://millenniumassessment.org/en/index.html) in 2005 (Gómez-Baggethun et al., 2010; Daw et al., 2011; Shackleton et al., 2016; Wangai et al., 2016). The MA was developed as a tool for informing the public and decision makers (Dooley, 2005) about the sustainable management of ecosystems for human well-being (Yang et al., 2013). The MA viewed ecosystems through the services they provided to humans, the impact of humans on the provision of these services and the consequences of ecosystem change for human well-being; subsequently developing a framework for understanding these interactions (Carpenter et al., 2009; Yang et al., 2013). The MA highlighted the importance of ES to the well-being of poor societies and the relevance of the ES concept in understanding issues on environmental conservation, socio-economic development and poverty alleviation (Daw et al., 2011; Whelan et al., 2015). Research on ES has been growing globally since the publication of the MA with the first studies on ES in Africa done in South Africa (2005), Kenya (2006) and Tanzania (2007); collectively these three countries account for 61.5% of all ES publications on Africa (Wangai et al., 2016).

Although the ES approach has been viewed as a tool for promoting the understanding of the biophysical environment (Ericksen et al., 2012); it has been criticised as being concerned only with the positive effects of ecosystems while ignoring negative and harmful ecosystem effects (Vaz et al., 2017). These effects are sometimes referred to as ecosystem disservices (EDS) and include ecosystem functions, processes and attributes which have perceived or actual negative impacts on human well-being (Shackleton et al., 2016; Vaz et al., 2017). The EDS concept stemmed from research on ES provided by large cities as well as the EDS associated with them such as allergens from plants and trees blocking sunlight (Vaz et al., 2017). Disservices can be caused by natural events such as wild fires, earthquakes and floods as well as anthropogenic actions such as release of toxic substances (Lyytimäki and Sipilä, 2009). However, the distinction between natural and anthropogenic causes of EDS is unclear (Lyytimäki and Sipilä, 2009), particularly because many EDS are aggravated by anthropogenically induced disturbances in natural environments (Shapiro and Báldi, 2014; Villa et al., 2014) and tend to be most acute when ecosystems are poorly managed (Hohenthal et al., 2015) such as in flash floods following forest clearance or in intensive fires in exotic plantations. The use of the EDS concept is, however, minimal and its analytical value can be challenged (Ango et al., 2014).

Africa has a highly varied and variable climatic regime with varying ecosystems types and human population settlement patterns leading to varying levels of ES dependence across the continent. Most communities in Africa live in rural areas where employment opportunities are limited and natural resources underpin livelihoods. Though the financial rewards from these household-scale rural activities may be relatively small, it may be sufficient to alleviate poverty, especially where social support structures are missing (Egoh et al., 2012). Consequently, due to their dependence on natural resources, and their associated vulnerability to natural disasters, many rural African communities are reliant on ES (Daw et al., 2011; Boafo et al., 2016) and their well-being is determined by the ES they can access. For example, communities in humid areas of west and central Africa rely on farming and harvesting non-timber forest products for their livelihoods while those in semi-arid areas of northern, eastern and southern Africa rely on tourism and grazing (Egoh et al., 2012). Conflict over resource management, interacting governance issues, climate and land use change can result in access to ES becoming challenging to communities that depend on them (Enfors and

Gordon, 2008). This is particularly so because areas providing ES, and the people benefitting from these, are unevenly distributed (Wangai et al., 2016).

Ultimately, the varying dependence, perceptions and uses of ES amongst different communities promotes or hinders the supply of ES. When the supply of ES is higher than their demand, their value goes down and when the demand is higher than supply, environmental degradation can occur (Wangai et al., 2016). The application of market forces to ecosystems has been continually debated. If threshold levels of ES are considered essential to human wellbeing, then marginal analysis and monetary valuation of ES is inappropriate (Farley, 2012). However, the ES concept allows for the consideration of natural capital stocks and flows of ES, alongside traditional measures of economic capital (Turner and Daily, 2008). As such, the cost of traditional economic activities via the degradation of ecosystems may become more apparent, leading to more sustainable decision-making.

2.5.1 Types of ecosystem services

Four categories of ES characterise most frameworks: provisioning, regulating, cultural, and supporting services. Provisioning ES are material benefits that can be harvested from ecosystems to be directly used by humans. In communities where most households do not have access to other assets besides what the ecosystem provides, provisioning ES are important livelihood assets and food sources (Boafo et al., 2016); especially during natural hazards such as floods and droughts. Provisioning ES include food, traditional medicine, bush-meat, raw materials, water, fuel-wood and timber among others, and they may be used for domestic purposes or sold and used as a source of income. For example, miombo woodlands in central, eastern and southern African cover an estimated area of 2.7 million km^2 (Kalaba et al., 2013) and directly support livelihoods of 39 million people through the provision of food, fibre, fuelwood and charcoal to a further 15 million people who live in urban areas (Sileshi et al., 2007). Miombo woodlands protect households from poverty by providing alternate food sources, fuel-wood and medicine from the woodland products (Jew et al., 2016) as well as food sources, largely fruits, during famines (Sileshi et al., 2007). Water is another provisioning ES and is regarded as an essential natural resource (Mulatu et al., 2014) but one that is highly distributed. For example, the Mara River basin extends from the headwaters on the Mau Escarpment in south-western Kenya through northwestern Tanzania into Lake Victoria. As the Mara river flows through the Maasai Mara and Serengeti protected areas the water supports wildlife and major economic activities such as pastoralism, agriculture, mining and tourism (Dessu et al., 2014). Other water sources like lakes also contribute significantly to national economies and support several livelihoods. For example, over half a million people in 11 countries in Africa are employed in fisheries with fishing alone in Lake Chilwa in Malawi valued at US$ 18 million per year (Kafumbata et al., 2014). Regulating ES contribute to an environment that humans and other organisms can live in by protecting them from extreme environmental events and facilitating ecosystem functions that allow them to live in that environment (Braat and de Groot, 2012). Climate regulation is an important regulating ES and is often performed via carbon storage and sequestration across vegetation types; e.g. miombo woodlands (Jew et al., 2016), as well as the fynbos and thickets in South Africa (Egoh et al., 2009). The carbon sequestered and stored in vegetation can have a significant impact on atmospheric concentrations of carbon dioxide. Agricultural expansion in eastern Tanzania resulted in an emission of 0.9 Pg C over the twentieth century, a rate of 0.3 Mg C ha^{-1} yr^{-1} (Willcock et al., 2016). Ecosystems also pay an important role in regulating the water flow across watersheds. In Kenya, the catchment area of the Tana River covers over one-sixth of the country, transports between 2.7 and 10.2 billion cubic metres annually and controls flooding (Leauthaud et al., 2013). Wetlands in sub-Saharan Africa, which occupy 4.7% of the area (with about 65% of the wetland area covered by four largest basins: the Chad, Congo, Niger River and Nile River basin) (Rebelo et al., 2010) are also associated with EDS like providing habitats for invertebrate vectors of parasites such as malaria, which is transmitted by female anopheles mosquitoes and causes 1.5 - 2.7 million deaths annually (Malan et al., 2009). The disease burden caused by malaria is huge; for example, half of all consultations that occur in Malawi there are classified as malaria (Mathanga et al., 2012). Other incidences of impacts of regulating EDS on human health include flooding events in Mozambique in the year 2000 that led to a rise in infectious diseases (Egoh et al., 2012) and the 1998 El Niño floods that led to an increase in cholera and typhoid as well as damage to food crops in Africa (Wangai et al., 2016).

Cultural ES are non-material benefits that humans get from ecosystems (Sileshi et al., 2007) and include recreational opportunities, spiritual importance and inspiration for art and music (Wenny et al., 2011) as well as natural sites used as protected areas, natural heritage sites and nature used for education purposes (Egoh et al., 2012). Africa holds about 40% of global biodiversity and some may be of cultural importance (Egoh et al., 2012). For example, some African communities consider certain tree species sacred. In Kenya, *Ficus natalensis* and *Ficus thonningii* (Mũgumo) are sacred to the Gĩkũyũ tribe, symbolising life, power and fertility with the most important sacrifices held under it being circumcision, transfer of traditional governments between generations, prayers for rains and burial of diseases (Karangi, 2008). In Tanzania, communities in Arusha place grass or flowers under *Ficus sycomorus* as an offering to God and ask for blessings while in the Bamileke region of Cameroon, figs are used as sites of family worship (Wilson and Wilson, 2013). Some culturally important sites in Africa are considered sacred and are protected from human interference by restricting their access to religious leaders. For example, in Kenya, Mount Kenya is regarded as a holy mountain by the Gĩkũyũ and Meru, in Malawi Nyika National Park has several sacred sites used for rainmaking ceremonies, in Nigeria the sacred Groves of Onshogbo have sacred spaces, worship points, shrines and two palaces and are considered a World Heritage Site and in Tanzania Misali Island has a shape that points towards Mecca and is considered sacred by Muslims (Dudley et al., 2009). The aesthetic value of wildlife influences the attitude and benefits people get from wildlife. In Uganda, elephants are seen as beautiful creatures which make people happy while pastoralists in Amboseli, in southern Kenya, find large wild herbivores, especially elephants attractive, intelligent, tender and powerful (Moss 1988; De Pinho 2016). On national levels, tourism contributes significantly to African economies. In 2011, tourism formed 2.7% of Gross Domestic Product (GDP) for sub-Saharan countries, directly and indirectly employed 12.8 million people, and directly contributed to 2.6% of GDP in Ghana, 5.4% in Kenya, 5% in Tanzania and 2.9% in South Africa (Christie et al., 2014).

Supporting ES provide processes, such as nutrient cycling, biomass production, and seed dispersal, which are necessary for the production of other ES and for ecological communities and agricultural ecosystems (Wenny et al., 2011). They are considered as a fundament basis for other categories of ES and as such often termed ‘ecosystem processes’ and not regarded as final services in their own right to avoid ‘double counting’ when final ES are evaluated (Fisher et al., 2008).

While regulating ES can function without human intervention, provisioning and cultural ES only reach and benefit humans with some form of energy investment such as labour (Braat and de Groot, 2012). Provisioning ES require harvesting and gathering while cultural ES, such as spiritual benefits, require sensory and intellectual abilities to absorb and process information conveyed by ecosystems. It is possible for communities to derive multiple benefits from several ES at the same time (termed non-rival), such as cultural value of scenic landscapes and provision of pasture for livestock, as well as for ES benefits to be mutually exclusive (termed rival) such as using forests for firewood/timber but depleting carbon stores.

Whilst the rationale of the four categories of ES have been criticised (Daw et al., 2011), and the process of studying ES is challenged by issues such as ES identification, quantification, interpretation and uncertainties (Wangai et al., 2016), ES are clearly important to people across Africa. Furthermore, with the current 2.7% annual rate of population increase in Africa (United Nations, 2013), the demand for ES will increase and trade-offs and synergies between ES are likely to occur with varying spatial and temporal scales and intensities.

2.5.2 Modelling and mapping ecosystem services

ES models and maps aim to understand the stocks, demands and flows of ES across space and time (Burkhard et al., 2013). Multiple ES have been mapped at numerous scales, including global (Naidoo et al., 2008), continental (Schulp et al., 2012), national (Bateman et al., 2011) and sub-national (Nelson et al., 2009). Historically, the majority of ES maps focus on the biophysical potential of the landscape to provide a service, more recent studies have shifted to include the demand and use of ES (Burkhard et al., 2012). A number of reviews have been produced summarising the availability of ES data (Martnez-Harms and Balvanera, 2012; Crossman et al., 2013; Laurans et al., 2013; McKenzie et al., 2014; Ruckelshaus et al., 2015; Wong et al., 2015) and the main findings can be generalised as follows:

- ES stocks have received more attention than ES flows.

- Provisioning and regulating ES are more commonly mapped than cultural ES. Specifically, services related to climate regulation (carbon storage and sequestration), food production, water provision and recreation are most commonly studied.
- Secondary data (e.g. remotely sensed land cover maps) are most commonly used to create ES maps. However, these proxy methods are known to have the highest potential for error (Eigenbrod et al., 2010).
- The most common scale of mapping ES is sub-national.

Broadly, ES models can be divided into a three "Tier" system, analogous to the reporting system used by the Intergovernmental Panel on Climate Change. Tier 1 is the simplest method, using global values via look-up tables (e.g. benefit transfer (Costanza et al., 1997). The intermediate Tier 2 level improves on Tier 1 by using country specific data and locally validated regression models. Tier 3 is the most rigorous approach, using a time series of local data to support processed-based models. The models are generally thought to become progressively more robust from Tier 1 to 3, however Tier 3 methods are more expensive and some nations may lack the capacity to adopt and apply such methods (Willcock et al., 2014). Depending on the objective addressed, Tier 1 methodologies are used for mapping ES in data deficient areas while Tier 3 can be used for mapping urban ES (Grêt-Regamey et al., 2015). Practically, it may be worthwhile to merge data and modelling activities from multiple tiers, using Tier 3 methodologies for highly variable and/or substantive ES flows, whilst Tier 1 and 2 methodologies may be sufficient for ES of lower importance. This flexible approach is particularly helpful when mapping complex nested social-ecological systems where locally relevant ES may be missed (Grêt-Regamey et al., 2015). Thus, the types of ES maps and models available may be highly constrained by data deficiency and a lack of understanding surrounding the unique local situation. However, there are several, widely available modelling frameworks designed to support the production of ecosystem maps and models to ultimately aid decision-making. Some of the leading ES modelling and mapping frameworks are described in Box 1.

2.5.3 Ecosystem services and decision making

Decisions and policy regarding land and water management can be improved through the provision of quantitative ES models and maps derived from robust, spatially-explicit data (Fisher et al., 2008; Bastian et al., 2012). This could be especially so in developing countries, where the rural poor are often highly dependent on ES for their livelihoods, especially as a safety net during crises (Enfors and Gordon, 2008; Shackleton et al., 2008). ES have the potential for reducing poverty as improved flows of ES lead to improved well-being of societies (Daw et al., 2011), although this notion may be vulnerable to threat multipliers such as climate change, population growth and poor governance and may be too simple for global application (Raudsepp-Hearne et al., 2010).

Globally, ES science has been relatively successful at gaining traction within society and as such has shown broad uptake into decision-making processes by a range of stakeholders. For example, some businesses (e.g. Unilever), development agencies (e.g. the World Bank), governments (e.g. China), and non-governmental organisations (NGOs; e.g. Conservation International) have incorporated ES into their practices (Ruckelshaus et al., 2015; Wong et al., 2015). This relatively rapid uptake into policies and management may indicate that ES science has a high potential to alter decision-making practices, leading to more ecologically sound decisions that value economic, social and natural capital.

One reason that ES science has been successfully incorporated into decision-making is derived from their human-centric focus and their ability to be economically valued. As described above, ES are the benefits that societies derive from the ecosystems comprising of the flow of materials, energy and information from the natural environment to societies and, as such, these services can be valued by calculating the relative contribution of ecosystems to the benefit received by societies. Valuation, either implicitly or explicitly, is a necessary step to aid decision-making as it allows the assessment of trade-offs in order to evaluate the path to a specified goal (e.g. the Sustainable Development Goals; https://sustainabledevelopment.un.org/). However, there are on-going challenges to overcome when valuing ES. For example, some of the methods used to derive value are based on individual's perceptions of the benefits they derive, but an individual's perceptions may be limited and biased, neglecting benefits to whole communities, or to future generations via increase sustainability and/or resilience. Thus, ES valuation studies combine stated and revealed preference methods to better capture the true value of each ecosystem (Costanza et al., 2014).

As with ES maps and models, ES valuation methods can be performed at multiple times and scales, and show large ranges of complexity. For example, benefit transfer assumes a constant unit value per hectare of ecosystem type and multiplies that value by the area of each type to arrive at aggregate totals (Costanza et al., 1997). As such, benefit transfer is analogous to a Tier 1 method and can be improved by adjusting to local conditions (Tier 2). As with other Tier 1 methods, benefit transfer fails to capture many of the complexities involved in the flows of ES to beneficiaries and more spatially explicit and dynamic approaches (Tier 3) are often preferable (e.g. (Bateman et al (2013)). The Tier required for ES valuation is partially dependent on the intended use for the valuation itself, with potential uses ranging from relatively simple raising of awareness to detailed analysis of various policy choices and scenarios (Table 2.2; (Costanza et al (2014). Payment for ecosystem services (PES) schemes aim to maintain ES through actors who are willing to transact and pay for particular ES (Daw et al., 2011) and often draws particular attention as a use for ES valuation due to these direct benefits on sustainability, conservation and development (Gómez-Baggethun et al., 2010; Mulatu et al., 2014). However, multiple methods are likely needed to achieve the goal of sustainable human wellbeing and sustainable provision of ES.

Whilst the valuation of ES has helped integrate ES science into some decision-making practices, there are surprisingly few documented examples demonstrating how ES concepts have changed decision-making outcomes (Laurans et al., 2013; Ruckelshaus et al., 2015). This ‘implementation gap’ between the potential impact of ES research and its utilisation in practice has recently been investigated within sub-Saharan Africa. Willcock et al (2016) surveyed decision-makers from across sub-Saharan Africa to estimate levels of use of ES data in decision-making, as well as current and future requirements of this information; the first and only time this have been performed for the African continent, although other more localised studies do exist (Sitas et al., 2013, 2014). Over 90% of those surveyed reported incorporating ES information into their decision-making, however the majority (over 70%) require additional data, indicating a need for demand-driven research across the continent (Willcock et al., 2016). The respondents used ES information for policy development, ES supply management, land use management, creating awareness and for understanding the link between humans and the environment. Reflecting data availability, respondents focus on provisioning and regulating services at national and sub-national scales (Willcock et al., 2016). The authors followed-up with technical experts who were unanimous in highlighting the importance of scenarios to the decision-making process, emphasising the need for Tier 3 models and maps that are able to reflect the dynamic nature of ES flows (Willcock et al., 2016). This study provides evidence that stakeholders within sub-Saharan Africa are actively engaging with ES research and using the information to support policy development. However, the stakeholders pointed out that they needed more reliable information across more ES to better support sustainable development efforts in Africa. Capacity building should be widely adopted amongst ES researchers, minimising ambiguity at the science-policy interface whilst maximising the ability of research to support sustainable policies and increase human well-being.

Table 2.2: Range of uses for ecosystem service valuation (adapted from Costanza et al. (Costanza et al., 2014)).

Use of valuation	**Appropriate values**	**Precision needed**
Raising awareness and interest	Total values, macro aggregates	Low
National income and well-being accounts	Total values by sector and macro aggregates	Medium
Specific policy analyses	Changes by policy	Medium to high
Urban and regional land use planning	Changes by land use scenario	Low to medium
Payment for ecosystem services	Changes by actions due payment	Medium to high
Full cost accounting	Total values by business, product, or activity and changes by business, product, or activity	Medium to high
Common asset trusts	Totals to assess capital and changes to assess income and loss	Medium

2.6 Conclusion

The concepts of ES flows and stocks are increasingly useful ways to highlight, measure, and value the interaction and interdependence between humans and ecosystems. The ES approach is complementary with other approaches to sustainable development, but provides conceptual and empirical tools that the others lack and it communicates with different audiences for different purposes. ES science may be particularly important in

Africa due to the high levels of poverty prevalent on the continent and, particularly in rural regions, the dependence on ES for wellbeing and sustaining livelihoods. Encouragingly, decision-makers across Africa are engaging with the ES concept and its ability to evaluate trade-offs through policy scenarios will be key if the Sustainable Development Goals are to be achieved.

Box 1 – An introduction to some of the leading ecosystem service modelling and mapping frameworks.

Integrated Valuation of Environmental Services and Trade-offs (InVEST; www.naturalcapitalproject.org/InVEST.html), is a set of models designed to map and value trade-offs between multiple ecosystem services. InVEST adopts a tiered approach to the modelling of ES using a GIS interface: Tier 1 models use globally available data to form first estimates of ES values; Tier 2 models, require additional local data; and Tier 3 models are increasingly complex and data-intense. Currently, InVEST is able to model a larger range of ES than the other leading modelling platforms, with several more in development. Additionally, beta versions of InVEST are in existence and are reviewed through an open-source community, so they are may be more reliable than other modelling systems. However, Tiers 2 and 3 (analogous to many of the ARIES models) are in early development. In summary, InVEST is well placed to capture changes in ES value and can represent alternative scenarios for identifying trade-offs. However, it has little functionality to explore feedbacks between ES and beneficiaries and so future estimates may be highly uncertain.

Co$ting Nature (www.policysupport.org/costingnature) is a web-based tool to quantify ES, identify beneficiaries and assess the impacts of proposed human interventions. The models are analogous to Tier 1 InVEST models but are available on-line, without the need for GIS skills. However, the software is only able to model a limited range of ES in comparison to the other leading frameworks. Co$ting Nature is well suited for scenario assessment of impacts on ES delivery, however the uncertainty associated with the simplistic models is not well understood nor is it communicated to the end user.

ARtificial Intelligence for Ecosystem Services (ARIES; http://aries.integratedmodelling.org/) is an open source technology, which has the ability to select and run models to quantify and map ecosystem service provision, including biophysical generation, flow and extraction by sinks and beneficiaries. ARIES can be applied in a broad range of physical, social and economic contexts, providing access to a library of ecosystem service models and spatial datasets at multiple scales ranging from global to local. Decision making rules using artificial intelligence enable addition or removal of components as appropriate, allowing accurate results to be accessible to users without extensive skills or training. ARIES also uses Bayesian network modelling and Monte Carlo simulation to supply uncertainty estimates for the model outputs. At present, the ARIES models are mostly limited to a few case-study locations. Thus, expert model development is required to run ARIES in most regions. However, global models, which run without user data, may be available by 2020. These will provide initial estimates of ES values in data-deficient regions. As with InVEST tiers 2 and 3, ARIES plans integration of existing ecological process models in future releases, so allowing complex relationships to be better described. As such, ARIES is well suited for scenario assessment for different future climate and land use/cover conditions.

The Economics of Ecosystems and Biodiversity (TEEB; http://www.teebweb.org/) model of ES was created under the United Nation Environmental Programme (UNEP) with an aim of assessing the importance of ecological systems to societies. It places natural science in one category and human, social and economic science in the other category with ES flowing from natural science components to social science category components with indications of relative importance of the links between various ecosystem components (Braat and de Groot, 2012). TEEB uses benefit transfer and as such are Tier 1 ecosystem service models.

Further ecosystem service mapping tools of note are the **Social Values for Ecosystem Services** (SolVES; https://solves.cr.usgs.gov/), and the **Global Unified Metamodel of the BiOsphere** (GUMBO). SolVES is a GIS tool to assess, map, and quantify the perceived social values for ecosystems, such as aesthetics, biodiversity, and recreation. GUMBO uses simulation modelling to model global dynamics and interactions of natural capital with built, social and human capital.

2.7 Chapter summary

This chapter discusses the coverage, drivers, ecosystem services and spatio-temporal changes of African savannas. The impact of savanna controls on vegetation has been discussed using specific savanna sites in Africa. The focus, however, is on East African savanna sites. Also discussed are the proposed theories for the coexistence between trees and grasses and how these theories are connected to the drivers of savanna vegetation.

Discussion of ecosystem services in Africa begins with the definition of the ecosystem services concept, the origin of the concept, categories of ecosystem services, available methods of mapping and modelling ecosystem services and the valuation and use of the ecosystem service in decision making. Also discussed are specific examples in Africa where the ecosystem services concept has been applied. The entire section on 'ecosystem services in Africa' (1.5-1.7) has been as a book chapter (Kariuki et al., 2018).

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3 Study Areas and Models Used

3.1 Preface

This chapter discusses the characteristics of the study areas used in this thesis. Discussion of the study areas includes their climatic and physical attributes as well as land use change in the areas. Also discussed in the chapter are the details of the simulation models used in chapters 6 and 7. A broad overview of modelling techniques used to study interactions between climate, ecosystems and people is given first. It is then followed with the specific modelling techniques used in this thesis.

3.2 Selection of study areas

All the study areas used in this thesis are located in the Kenyan drylands, which include grasslands, savannas, bushlands and woodlands. Drylands cover 88% of Kenya's terrestrial land surface (Mwaura and Kaburu, 2009) and are largely used for livestock production and wildlife conservation.

Several areas within the Kenyan savannas were selected and used to assess changes in vegetation along a rainfall gradient in Kenyan savannas' (chapter 4) while the Amboseli and Mara ecosystems in south Kenya were used to study 'grazing and sedentarisation patterns in Kenyan savannas' (chapters 5, 6 and 7). Selection and collection of vegetation data used in chapter 4 was done by the Department of Remote Sensing and Resource Survey (DRSRS), formerly known as Kenya Rangeland Ecological Monitoring Unit (KREMU), in Kenya between 1977 and 1981 as an exercise aimed to create baseline vegetation conditions across Kenyan savannas. Selection of the vegetation plots by DRSRS was based on the definition of ecoclimatic zones in Kenya as classified by Pratt et al (1996). According to Kuchar (1981), DRSRS classified Kenyan savannas into 44 ecounits and sampled vegetation on each ecounit based on the physiognomic characteristics of vegetation as described by Pratt et al (1996). In selecting the vegetation plots, DRSRS wanted to select vegetation that was representative of Kenyan savannas and that would be used to establish baseline conditions across Kenyan savannas with a goal of being monitored over time (Kuchar, 1981). The DRSRS vegetation data used in this thesis came from 46 vegetation plots distributed across ecoclimatic zones IV, V, VI in thirteen counties in Kenyan drylands namely: Samburu, Baringo, Laikipia, Nakuru, Narok, Kajiado, Taita Taveta, Kwale, Tana River, Kilifi, Kitui, Garissa and Lamu (Figure 3.1).

The Amboseli and Mara ecosystems are located in Kajiado and Narok Counties in southern Kenya (Figure 3.1) and were selected for studying grazing and sedentarisation patterns in East African savannas using land use change to show the changing patterns. The Mara ecosystem is expansive and includes the Loita Plains, which was also included in chapter 5 of this thesis. Amboseli and Mara were selected for study as both of them are arid ecosystems located in southern Kenya and have been used for livestock production and wildlife conservation for decades. However, they show differences in micro-climatic patterns, conservation management and human activities, in particular land use patterns.

3.3 Amboseli ecosystem

Amboseli is located in southeast Kenya, north of Mt Kilimanjaro, west of Chyulu Hills and east of the Mara ecosystem. It includes the Amboseli National Park (392km^2) and the surrounding community lands (known as group ranches), mainly Olgulului/Olorarashi, Kimana/Tikondo, Eselenkei/Lengisim, Kuku, Mbirikani, Osilalei, Mailua and other subdivided and farmed group ranches at the slopes of Mt Kilimanjaro (Okello et al., 2016). The Amboseli National Park was gazetted as a National Park in 1977 (Western and Lindsay, 1984) and was declared a UNESCO Man and the Biosphere Reserve in 1991 (Rucina et al., 2010). The community lands surrounding the National Park provide crucial wildlife corridors and dispersal zones that are used by wildlife for feeding, watering and as breeding grounds (Okello and D'Amour, 2008). The group ranches also link the Amboseli, Chyulu Hills and Tsavo government protected areas to community conservation areas, such as Kimana Wildlife Sanctuary (Okello et al., 2011) and provide wet season grazing for wildlife (Groom and Western, 2013).

The Amboseli Basin largely occupies the national park, it has an elevation of 1140 m and is filled with Pleistocene sediments (Stroessell and Hay, 1978; Hay et al., 1995). Its eastern side has spring-fed swamps while its western side has a 21km lake bed (Stroessell and Hay, 1978). To the north of the Amboseli Basin are low hills with an elevation between 1250 and 1400 m and to the south of the basin is Mt Kilimanjaro with an elevation of 5895 m. The hills at the north of Amboseli Basin are made up of metamorphosed Precambrian sediments whilst the southern and eastern parts of the

Amboseli Basin are formed by Pleistocene alkaline olivine basalts of Kilimanjaro (Stroessell and Hay, 1978). The Amboseli National Park has five swamps that are

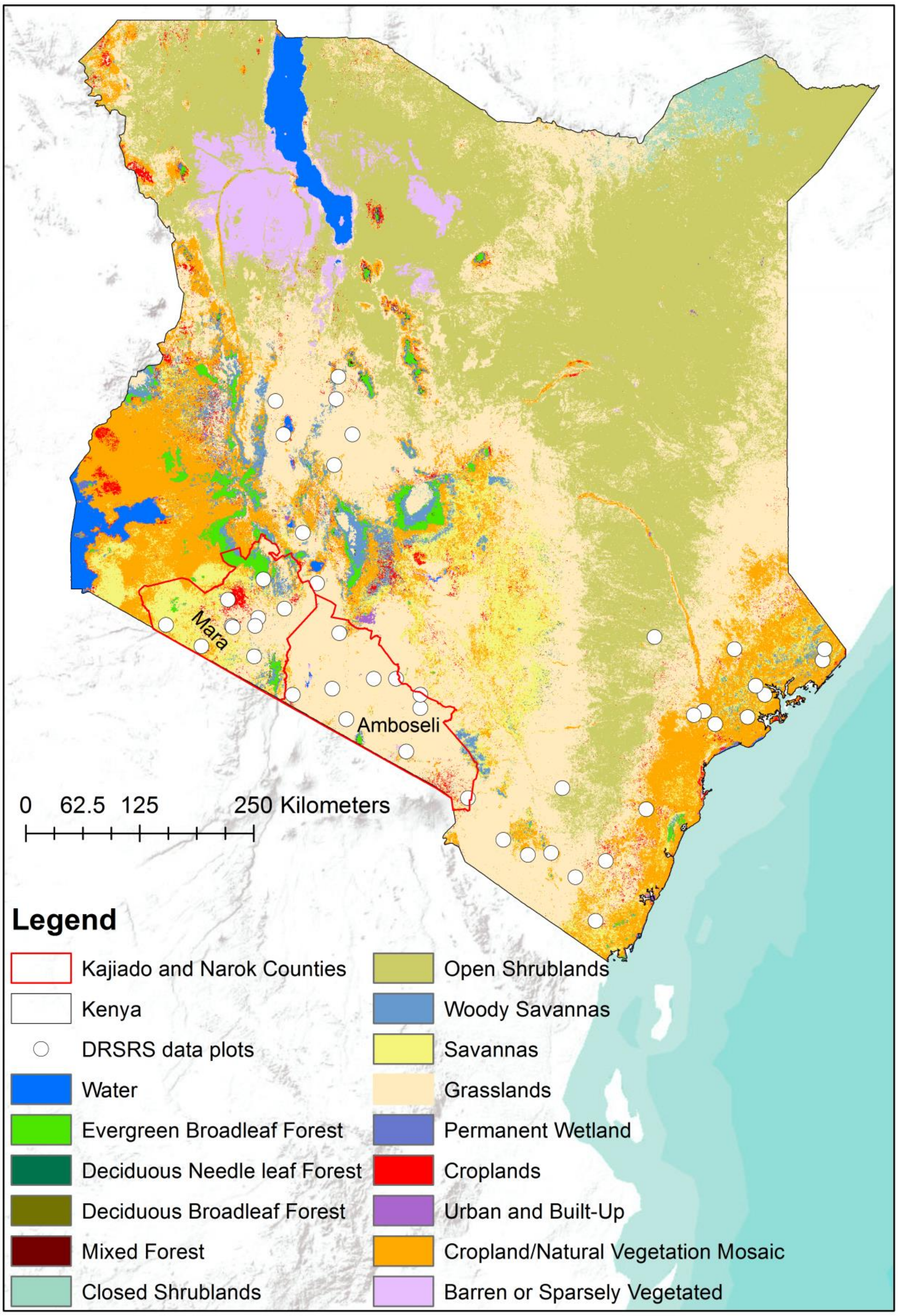

Figure 3.1: Map showing the location and distribution of sampled DRSRS vegetation plots across different types of savanna vegetation in Kenya. Also shown is the location and vegetation cover in Amboseli and Mara. Source – MODIS data (Channan et al., 2014).

remnants of the extensive lake that is now dried up (Rucina et al., 2010). The permanent swamps within Amboseli provide dry season grazing for migratory wildlife species (Western and Maitumo, 2004, Okello et al., 2016). The major ground water sources to the Amboseli Basin lie on the northern slope of Mt. Kilimanjaro, and flow to the basin as streams and ground water (Stroessell and Hay, 1978; Hay et al., 1995). Soils in Amboseli are mainly oxisols with low infiltration rates due to sparse vegetation cover, poor humus content and soil structure (Muchiru et al., 2008).

Ninety two percent of Amboseli is considered arid or semi-arid (Galvin et al., 2008) and droughts are frequent, occurring at least once per decade since the 1930s (Groom and Western, 2013). Rainfall in Amboseli is greatly influenced by altitude (Mwangi and Ostrom, 2009); it is variable and ranges from 350-500 mm yr^{-1} along a west-east gradient (Groom and Western, 2013). Rain falls in two seasons, the long (March-May) and short (October-December) rains seasons. Mean temperatures in Amboseli vary with altitude and season, and range from $12^{o}C$ in July to $34^{o}C$ in February to March (Altmann et al., 2002). Daily temperature ranges from $8^{o}C$ at night to $35^{o}C$ during the day (Altmann et al., 2002; Groom and Western, 2013).

Apart from the Amboseli Basin which is characterised by alkaline grasslands, woodlands and swamps (Western and Lindsay, 1984), the vegetation type in Amboseli is mainly Acacia and Commiphora scattered woodland and is categorized under ecological zone V (Pratt et al., 1996). Amboseli is a relatively dry area and livestock and wildlife depend on swamps for grazing and watering while pastoralists depend on them for irrigated agriculture (Reid et al., 2016). Between 1950-2002, *Acacia xanthophloea* and *Phoenix reclinata* woodlands, in the Amboseli basin, declined and was replaced by *Sueada-Salvadora* scrubland and alkaline grasslands while the two main swamps, Enkongu Narok and Longinye, expanded (Western, 2006). These habitat changes have been attributed to an increase in elephants inside the national park due to habitat fragmentation outside the park (Western and Maitumo, 2004; Western, 2006).

The semi-arid and arid lands of southern Kenya have been occupied by the Maasai pastoral community, their livestock and wildlife for several years. The pastoralists coped with spatial and temporal variability of resources using mobility to access the variable quality and quantity of pasture (Galvin et al., 2008). In early 20th century, Maasai pastoralists in Kenya lost grazing land to the British colonial government who forced them to sign treaties agreeing to reduce their grazing range (Galvin et al., 2008). The colonial government, and later, Kenya's independent government, considered pastoralism responsible for rangeland degradation as it maximized herd size rather than the quality and productivity of livestock leading to overgrazing (Western et al., 2009). In a bid to conserve natural resources and to promote a sedentary lifestyle for the pastoral Maasai community, the government created conservation areas in the 1940s and group ranches in the 1960s. The definition and formation of group ranches is discussed in chapter 2 of this thesis. Ownership of land in the group ranches was challenged by climatic variability, human population growth and poor management that led to further subdivision. As at the late 1990s, 40 out of the 52 group ranches in Kajiado County (formerly Kajiado District) had been subdivided (Galvin et al., 2008; Homewood et al., 2009) and currently, group ranches in Amboseli have different subdivision status where some are subdivided, some are not and some are in the process of being subdivided. With the rising land subdivision levels, human-wildlife conflict and habitat loss for wildlife, non-state protected areas called conservancies were established to conserve highly endangered species, to promote tourism and to increase financial returns to landowners for land used for wildlife initiatives (KWCA 2016). In Amboseli, the first conservancy to work with the Amboseli Ecosystem Trust (AET) was Kitirua established in 1984, and as at 2016, AET worked with 17 conservancies that occupy an area of 79,562 hectares (ha) and support 86,811 households (KWCA 2016).

3.4 Mara ecosystem

Mara is located in southwestern Kenya, east of the Lake Victoria Basin, west of the Amboseli ecosystem, south of the Mau uplands and north of the Serengeti ecosystem in northern Tanzania. Mara is made up of the Maasai Mara National Reserve (1510km^2) and the surrounding group ranches that were meant to be buffer zones between the national reserve and high-potential agricultural zones in the northern part of Narok County (Serneels and Lambin, 2001; Serneels et al., 2001). The national reserve was established in 1961 (Serneels et al., 2001) and, together with the group ranches, provides a dry season grazing refuge for wildebeest migrating from the

Serengeti (Reid et al., 2016). Loita Plains are part of Mara and are located northeast of Mara between the Nguruman - Magadi escarpment and the Maasai Mara National Reserve.

Mara is an open, lightly wooded savanna (Figure 3.2) interspersed with waterbodies, quartzitic hills, some inselbergs and has an elevation of 1600-1900 m above sea level (Robertshaw, 1990). Mara is underlain by extensive flows of Tertiary phonolitic lava (Vuorio et al., 2014) while the Loita Plains are covered by volcanic ashes (Robertshaw, 1990). To the northeast of Mara are sedimentary hills which are of Archaen Age (Robertshaw, 1990). The lowlands have black cotton soils that are dark, nutrient rich, deep clay vertisols with poor drainage while the hilltops have lighter shallow sandy loam soils (Robertshaw, 1990; Vuorio et al., 2014). The major rivers draining Mara are the Sand, Talek and Mara (Ogutu et al., 2009). All water courses in Mara flow into the Mara River, which arises from the Mau Uplands, flows south through the national reserve, eventually discharging into Lake Victoria. The largest tributary of Mara River is Talek which drains the northern Siana Hills and western Loita Plains through two tributaries, Kaimurunya and Ol Sabukiai while the Loita Plains are drained by the Ewaso Ngiro River and its tributaries whose course ends in the swamps north of Lake Natron in Rift Valley (Robertshaw, 1990). Besides the main rivers in the Mara and Loita plains, there are numerous ephemeral streams and permanent springs that arise from the bases of Lemek Hills (Robertshaw, 1990).

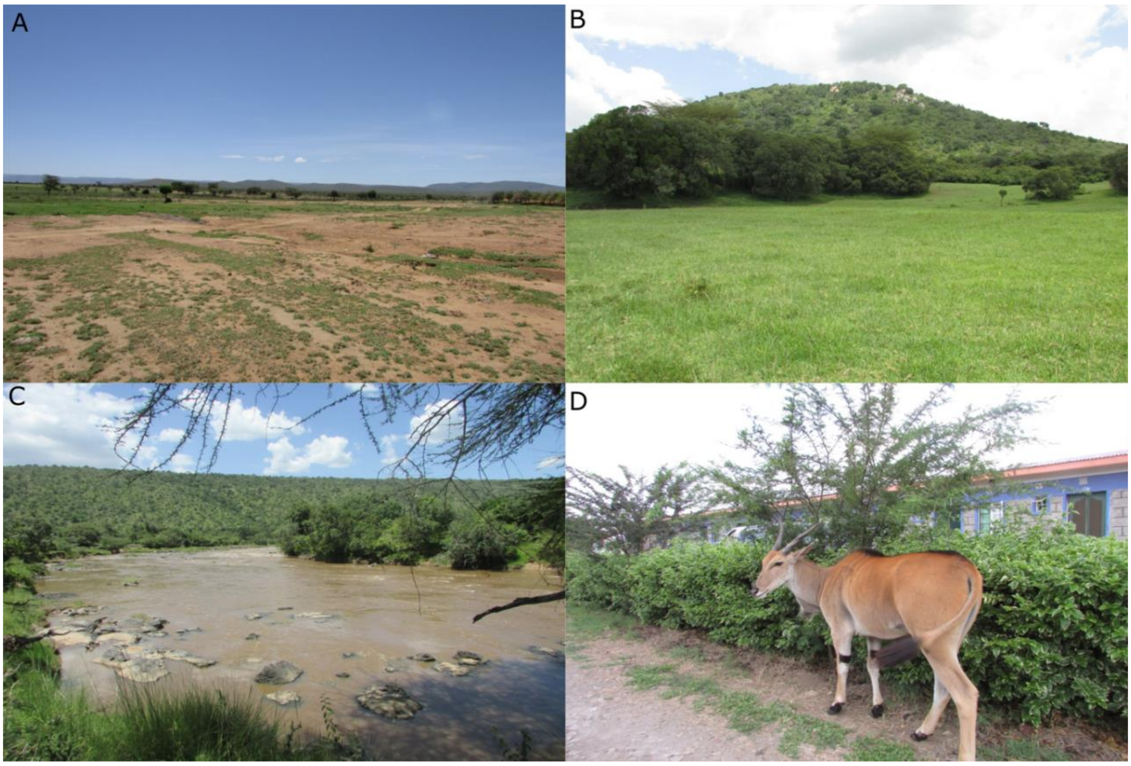

Figure 3.2: Mara during the wet season. Figure A shows a sparsely vegetated area, B) structure of grasses and trees in Mara, C) riverine vegetation along Mara River, D) an eland foraging near residential houses. Photos source: The author.

Average annual rainfall in Mara range between 600-1000 mm yr^{-1} (Lamprey and Reid, 2004) making Mara one of the wettest savannas in East Africa (Lamprey and Waller, 1990; Reid et al., 2016). Average temperature in Mara is 14^{o}C with a monthly range of 14.7^{o}C to 30^{o}C (Jandreau and Berkes, 2016). Rainfall is erratic, increases with altitude (Serneels et al., 2001) and creates a rainfall gradient from the dry southeastern plains to wet northwestern parts (Homewood et al., 2001). Loita Plains, located on the eastern side, receive 400 mm yr^{-1} (Serneels et al., 2001) and the western parts receive about 1000 mm yr^{-1} as their rainfall is strongly influenced by Lake Victoria's weather system and the orographic effect of the Siria Escarpment (Robertshaw, 1990). The short rains fall between November and December and may sometimes continue up to the long rain season between March and June (Vuorio et al., 2014). The influence of Lake Victoria and topography also leads to a diversity of local climates that support repeated vegetation types at different zones of Mara (Homewood et al., 2001).

Vegetation in Mara is dominated by *Themeda triandra* and *Pennisetum* sp. grasslands with patches of Acacia woodlands and riverine forests (Robertshaw, 1990; Lamprey and Reid, 2004; Vuorio et al., 2014). Loita Plains are covered by dwarf shrubs and

Acacia drepanolobium grassland (Serneels and Lambin, 2001). The *Acacia-Commiphora* woodland community was once extensive in Mara and provided a suitable habitat for tsetseflies but was destroyed by fires in the 1950s and 1960s and increased elephant immigration in Mara (Robertshaw, 1990). Three major ecological disturbances have affected Mara and Loita Plains vegetation in the recent past: 1) the eradication of rinderpest disease in 1963, 2) an increase in fire frequency and intensity between 1959-1963, 3) immigration of elephants into the Mara region in the early 1960s following widespread agriculture encroachment north and west of the Serengeti and Mara (Dublin et al., 1990; Robertshaw, 1990; Serneels and Lambin, 2001). This had led to a reduction in woodland species (Figure 3.3).

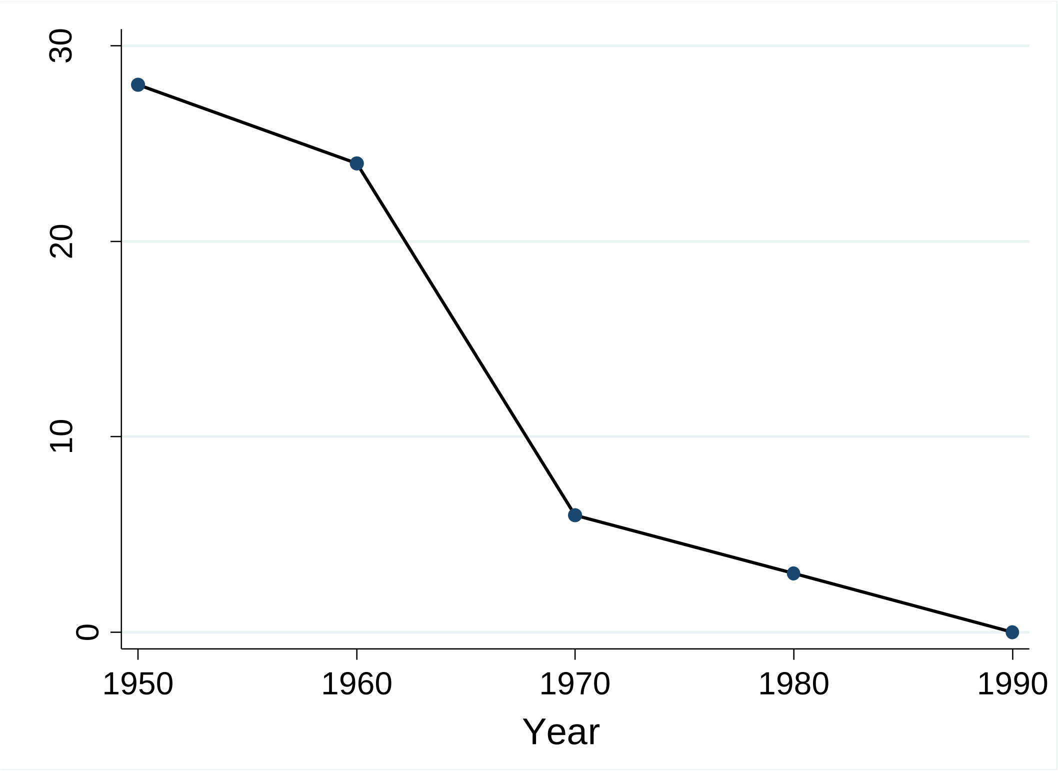

Figure 3.3: Percent cover of Acacia woodland in Maasai Mara (Shorrocks, 2007)**.**

Most wildlife in Mara are found in the community group ranches and moves seasonally between the ranches and the reserve following the variable quality and quantity of forage (Ogutu et al., 2009; Bhola et al., 2012). In addition, about one million wildebeest, zebra and Thomson's gazelle from Loita Plains and the Serengeti ecosystems migrate into Mara annually (Bhola et al., 2012). Of all wildlife found in Kenya, the Mara ecosystem has the highest wildlife density and accounts for 25% of all wildlife in Kenya (Western et al., 2009; Wishitemi et al., 2015). However, this wildlife population has declined in the recent years due to a number of reasons. First, tourism revenues from wildlife only get to wealthy pastoral elites and not the poorer pastoralists who live with the wildlife (Reid et al., 2016) leading to negative attitudes towards wildlife by the local communities. Second, land use change brought by human population growth, land subdivision, socio-economic changes, political changes and increased sedentarisation threatens the sustainability of wildlife and vegetation ecology in areas where pastoralists share their land with wildlife (Ogutu et al., 2009).

Maasai pastoralists are believed to have moved into Mara around 1750 (Lamprey and Waller, 1990; Vuorio et al., 2014). After the 1890 rinderpest pandemic, most of their animals, together with other wild animals, were killed (Lamprey and Waller, 1990; Vuorio et al., 2014). The rinderpest pandemic was followed by a severe smallpox epidemic and a tsetsefly outbreak that led to felling down and burning of the dense *Acacia-Commiphora* bushland in the 1960s and consequently, the opening up grazing areas (Vuorio et al., 2014). Since then human population as well as livestock numbers have soared (Lamprey and Reid, 2004; Vuorio et al., 2014) and by the end of 1970s most group ranches in Narok had been subdivided and were owned under private titles by registered group members (Serneels et al., 2001). Subdivision of group ranches continued throughout the 1980s (Serneels and Lambin, 2001) and continues to present leading to marked land use changes in the area. Large scale agricultural expansion is the most significant land use change in Mara (Serneels and Lambin, 2001; Ogutu et al., 2009) leading to the loss of wildlife habitats, livestock overgrazing and subsequently, habitat degradation (Ogutu et al., 2009). Conservancies have been established in Mara to promote tourism and halt agriculture encroachment and habitat fragmentation for wildlife. As at 2016, the Maasai Mara Wildlife Conservancies Association (MMWCA) worked with 16 conservancies which occupied 170,131 ha and supported 106,102 households (KWCA 2016).

3.5 Modelling techniques used

This research used a vegetation and a social-ecological model to understand the interactions between changing climate and human impact on the ecology of East African savannas. The first part of this ‘sub-section’ focuses on vegetation models and on LPJ-GUESS (the model that was used for this research), while the second part of this ‘sub-section’ discusses social-ecological models.

3.6 Models used for understanding climate, ecosystems and vegetation interactions

Global vegetation models are used to reconstruct vegetation distribution for an area and can be applied on any ice free land surface with clearly defined environmental conditions (Cramer et al., 2001). They use plant functional types (PFT) as the basic unit for classifying and predicting vegetation structure, composition and vegetation processes such as photosynthesis, respiration, carbon and nutrient allocation (Pavlick et al., 2012). Each PFT represents a group of plants distinguished by their physiognomic and morphological adaptation to climate, soil nutrients, topography and disturbances (Keane et al., 2004; Díaz et al., 2007; Weber et al., 2009; Pavlick et al., 2012) and several PFTs constitute a biome (Weber et al., 2009). Savanna PFTs are simulated as a mixture of tropical, broadleaved, deciduous trees and mainly C_4 grass species (Baudena et al., 2015). Biomes in DGVMs are demarcated according to the relative dominance of different PFTs (Moncrieff et al., 2015).

Bioclimatic units in a model describe the fractional coverage of populations of different PFTs in a grid cell and are used to determine the establishment and survival of a particular PFT in a particular environment (Melton et al., 2010). The PFT concept was developed in the first vegetation model, BIOME 1, and has been used in the subsequent models of the BIOME family as well as in other models with varying characterisation of PFTs (Prentice et al., 1992; Haxeltine and Prentice, 1996; Sitch et al., 2003). In most models, the PFT approach is seen to be effective in capturing vegetation distribution and productivity at the resolutions that are ideal for continental and global scale studies (Smith et al., 2001). This is because the applicability of the PFT approach in local ecosystem scales is challenged because it generalises the behaviour of individual species to few PFTs (Quillet et al., 2010).

In order to predict the potential effects of climatic change and human disturbances on vegetation distribution, two categories of vegetation models have been developed: the static (time independent) and the dynamic (time dependent) models (Peng, 2000). According to Peng (2000), static vegetation models relate the distribution of vegetation and geographic distribution of climatic parameters by assuming that both climate and terrestrial vegetation are in equilibrium. They do not simulate the temporal changes in vegetation due to rapid climate change as they do not integrate the gradual shifts of vegetation species in relation to climate change and other disturbances but they indicate probable directions of vegetation change and provide an important framework for modelling. Static biogeographical models provide estimates of the distribution of potential vegetation at large scales and they require less information compared to the dynamic models (Peng, 2000). For this reason, they provide a tool for converting past vegetation into palaeoclimatic patterns thus providing a means of comparing and understanding reconstructed past vegetation patterns (Haxeltine and Prentice, 1996; Cramer et al., 2001). Some limitations of static biogeographical models include nonexistence or simplified representation of disturbances and non-integration of biogeochemical cycles (Peng, 2000). Examples of static biogeographical models are climate-vegetation classification models such as the Koppen and Holdridge classification scheme, and the PFT models such as the Box models, Rule-based Biome Model (RBBM) and Ecophysiological-based Biome model (BIOME).

By contrast, dynamic vegetation models, also known as Dynamic Global Vegetation Models (DGVMs), are process based models that capture the temporal response of vegetation and biogeochemistry to a changing environment and also incorporate representation of key ecological processes such as tree growth, competition and nutrient cycling (Peng, 2000; Cramer et al., 2001; Sitch et al., 2003). DGVMs simulate vegetation, water and carbon dynamics using climate, soil properties and atmospheric CO_2 as input data (Cramer et al., 2001; Bond and Keeley, 2005; Bond et al., 2005). They were developed to overcome some of the limitations of the static biogeographical models, to avoid coupling different models and to promote the use of a single dynamic model which can incorporate and quantify biogeochemical processes on vegetation distribution (Peng, 2000). DGVMs enable the simulation of global ecosystem structure by simulating the growth of plants as limited by climate only (Bond and Keeley, 2005; Bond et al., 2005). However, for some DGVMs to simulate vegetation dynamics in relation to climate change, they are coupled with climate models using relationships between climate and biogeography change (Bonan et al., 2003), Additionally, coupling of DGVMs with general circulation models has been used to determine the impact of future climate changes on the carbon cycle (Cramer et al., 2001). Early DGVMs focussed on the response of plants to climate change and atmospheric CO_2 concentration and were successful in simulating the distribution of biomes and their contribution to the carbon cycle (Cramer et al., 2001; Sitch et al., 2003; Díaz et al., 2007). Current DGVMs vary in their complexities, abilities to perform different tasks (Sitch et al., 2003), temporal resolution and resolution of PFTs (Weber et al., 2009).

In DGVMs, simulation of processes such as competition and mortality, that influence the distribution of PFTs is done at grid scale of 0.25° and is based on a standard set of allometric relationships (Sitch et al., 2005; Scheiter and Higgins, 2009). DGVMs have been applied to various ecosystems and examples include the Sheffield DGVM used to investigate and compare the impact of fire and climate in driving the distribution of vegetation globally (Bond et al., 2005b) and to demonstrate changes in global woody biomass in savanna long-term burning experiments (Bond and Keeley, 2005) and the aDGVM (adaptive dynamic global vegetation model) which has been used to study tree-grass interactions in African savannas (Scheiter and Higgins, 2009; Baudena et al., 2015). The aDGVM integrates an individual based approach that allows it to model the effect of disturbances, such as herbivory and fire, as a function of plant height which gives an index of vulnerability (Scheiter and Higgins, 2009; Moncrieff et al., 2014). It simulates leaf phenology and allocations as a function of available resources and allocation rules that allow carbon to be allocated to roots when water is limiting and to stems when light is insufficient or when fire destroys above ground biomass (Scheiter and Higgins, 2009). This allows the plant to improve its water uptake and its body respectively. In addition, the phenology model of the aDGVM allows deciduous or evergreen vegetation to be defined by resource availability and not by moisture and temperature as is the case with other DGVMs (Scheiter and Higgins, 2009). Fire is modelled based on Higgins et al (2008) equations and it spreads when minimum fire intensity is exceeded and a fire ignition event occurs (Moncrieff et al., 2014). Other process based models such as Savanna Dynamics (SD) (Holdo et al., 2009) and SAVANNA (Boone et al., 2002) are specific to savannas and incorporate the effect of animals. The SD model is spatially explicit and investigates the combined effect of grazers, browsers and fire on savanna vegetation structure (Holdo et al., 2009). It also models key ecosystem processes that are influenced by rainfall such as vegetation growth, mortality, herbivore population dynamics and fire (Holdo et al., 2009). The SAVANNA is also spatially explicit and simulates ecosystem processes, such as primary production, and has been used to understand the carrying capacity and management options for ecosystems in Australia, South Africa, Tanzania and United States (Boone et al., 2002).

The Lund-Potsdam-Jena (LPJ) DGVM is a coupled biogeography-biogeochemistry model which integrates spatio-temporal terrestrial vegetation dynamics and biogeochemical cycling (Hickler et al., 2006; Doherty et al., 2010). It has several versions such as Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) (Smith et al., 2001) and the Lund-Potsdam-Jena managed Land (LPJ-ML) (Bondeau et al., 2007). The LPJ-DGVM (Sitch et al., 2003) is a process based biogeographic and biogeochemical model that originates from the BIOME (Prentice et al., 1992) family of models (Guodong and Mu, 2013). It is built on many features of the BIOME models using the same logic as that used in BIOME models to define its PFTs, their bioclimatic limits and the photosynthetic and water schemes used for calculating gross primary production for each PFT (Sitch et al., 2003). LPJ simulates vegetation patterns based on carbon and water fluxes (Bodin et al., 2016) where growth of PFTs in a grid cell is simulated by incorporating processes that shape the growth of plants in the area occupied by each PFT. Vegetation in a grid is described in terms of the fractional coverage of populations of different PFTs (Bonan et al., 2003; Sitch et al., 2003) and the major processes simulated by LPJ include growth, competition, fire and disturbance. LPJ is also used to study past, present and future terrestrial ecosystem dynamics, biogeochemical and biophysical interactions between ecosystems and the atmosphere (Sitch et al., 2003).

The LPJ-GUESS (Sitch et al., 2003) DGVM is an extended and detailed version of LPJ (Pachzelt et al., 2013). LPJ-GUESS is a regional to global DGVM that integrates a detailed, individual and patch based representation of vegetation structure, demography and resource competition with physiological and biogeochemical processes (Lindeskog et al., 2013; Pachzelt et al., 2013; Wu et al., 2017). It was developed to integrate the age structure of forest trees into LPJ and so can simulate vegetation dynamics amongst age cohorts (Baudena et al., 2015). LPJ-GUESS can also be used to simulate vegetation changes and ecosystem carbon and water cycling under future climate conditions (Doherty et al., 2010). Simulation in LPJ-GUESS utilises time series climate data, CO_2 concentration, nitrogen deposition rates and soil physical properties as input data (Wu et al., 2017).

Each PFT is described using its photosynthetic pathway, phenology, allocation patterns and responses to disturbances (Moncrieff et al., 2015). The fractional coverage of PFTs for each location is dependent on the net primary production and competition (for light, water and soil nutrients), based on environmental factors in that region (Smith et al., 2014; Moncrieff et al., 2015). In tropical regions, both grasses and trees utilize water at 0.5m deep but trees can access water better than grasses at deeper (1m) levels and thrive in high rainfall areas (Baudena et al., 2015). The height and diameter of woody vegetation are based on carbon allocation which is directed by a set of rules based on allometric relationships for each PFT (Lehsten et al., 2009). Competition for light and water is simulated among different age cohorts of several PFTs (Lehsten et al., 2016) and changes in population dynamics are simulated as competition between PFTs for light, water and space (Ahlström et al., 2015). Among individual plant species, growth and competition is simulated by focussing on individual plant traits and assessing how these traits influence plant processes such as turnover and carbon allocation (Smith et al., 2001). Establishment and mortality in LPJ-GUESS is simulated as a function of resources, the demography and life history trait of the PFT (Lindeskog et al., 2013; Smith et al., 2014). The spatial resolution for LPJ-GUESS grid cell is 0.25^o (Bodin et al., 2016). Plant process such as photosynthesis, respiration, phenology and water uptake are simulated on a daily time step while population dynamics, tissue turnover and carbon allocation are simulated annually (Knorr et al., 2012; Lindeskog et al., 2013; Smith et al., 2014). Results from LPJ-GUESS have been compared to net primary production satellite proxies, leaf area index and biomass from biomes around the world (Lindeskog et al., 2013).

Our study selected LPJ-GUESS to model vegetation dynamics because it integrates an individual based approach to simulate vegetation dynamics, biogeochemical and physiological processes (Smith et al., 2001; Sitch et al., 2003). An individual based approach provides a better representation of savanna vegetation structure and its underlying drivers. LPJ-GUESS has also been applied to African biomes and its modelled leaf area index and vegetation map validated using pollen, remote sensed data and existing vegetation maps (Hély et al., 2006). In East Africa, results simulated by LPJ-GUESS on the distribution of biomes have been validated with pollen data (Fer et al., 2016). Overall, model outputs show that LPJ-GUESS performs better in predicting potential natural vegetation in continents such as Europe and Africa, compared to LPJ-DGVM (Hély et al., 2006; Weber et al., 2009); perhaps because it uses an individual based approach compared to LPJ which uses an 'average individuals' approach (Lehsten et al., 2009).

3.7 Limitations of DGVMs

DGVMs have multiple uses (e.g. simulating land-atmosphere carbon and water exchanges, and simulating ecosystem processes such as primary production and resource competition), but, like all models, have certain limitations. These limitations include: Firstly, while DGVMs seek to represent the effects of global environmental change on the distribution of vegetation types and on biogeochemical cycles at regional or continental scales, they may simplify vegetation composition using irrelevant, inaccurate and incomplete plant functional types. This is because representation of vegetation as PFTs by DGVMs only uses a limited number of plant attributes to describe a number of PFTs (Scheiter et al., 2013). Secondly, the scale used by DGVMs when simulating the PFTs is coarse and may lead to a bias in representing vegetation dynamics. Simulation of vegetation dynamics by most DGVMs is done at a spatial resolution of 0.25^{o} which is coarse for representing vegetation interactions at local scale. Thirdly, some DGVMs use the average individual approach to simulate only one age-height class per PFT for every grid cell at any particular time and this surpasses some life cycle stages which might be important in shaping vegetation dynamics (Sitch et al., 2003). Also, they do not treat patch scale interactions among individual plants explicitly and might not perform well in simulating vegetation dynamics in conditions other than those they were calibrated and tested for (Smith et al., 2001). Fourthly, uncertainties in the use of DGVMs coupled with general circulation models in predicting impacts of future climate change on vegetation distribution and carbon cycle are large and arise from different land use and future emissions scenarios, parameterisation of primary ecosystem processes and climate projections by different general circulation models (Doherty et al., 2010). Although recent DGVMs have included the effects of land use change, the approach incorporates the effects of land use change rather than the processes responsible for the change (Díaz et al., 2007). Finally, the response of vegetation and biogeochemistry to changing climates may be nonlinear and DGVMs might not be able to simulate such relationships and in such instances, it is better to validate the model outputs with results from other historical sources such as palaeo proxies and remote sensed data. Beyond historical conditions, present day ecological data, such as leaf area index and existing vegetation maps, have been used to validate DGVM outputs (Hely et al., 2006; Lindeskog et al., 2013).

Application of DGVMs in savanna ecosystems is also limited. To begin with, while most DGVMs have successfully simulated vegetation distribution, carbon stocks and projected climate, the interactions between potential drivers of vegetation in savannas are complex and the combined influence of the savanna controls might not be accounted for by the DGVMs (Hirota et al., 2011; Moncrieff et al., 2014). In addition, when DGVMs are used to address the effects of climate change on future vegetation distribution (Sitch et al., 2003), they predict either grasslands or tropical forests in savanna regions, and most of them underestimate the extent of savannas as they were not specifically designed and tested for tropical grass-tree ecosystems (Scheiter and Higgins, 2009; Baudena et al., 2015). Also, besides the distribution of African savannas, there are other possible stable biomes that can occur over much of the African savanna range and this has been a major challenge to DGVMs (Cramer et al., 2001; Moncrieff et al., 2014) largely because the existence of alternate stable biomes implies that the favoured biome is determined by the initial conditions of the model (Moncrieff et al., 2014). Simulation of fire in DGVMs assume that fire frequency is determined by fuel loads and moisture content and that fire removes a predefined amount of biomass (Scheiter and Higgins, 2009). However, the effect of fire on woody vegetation depends on the stage of growth, bark thickness and stem diameter (Hoffmann and Solbrig, 2003; Lehmann et al., 2011) and DGVMs do not take this into account. Lastly, DGVMs rarely distinguish shrubs from trees functional types (Zizka et al., 2014) and this can be problematic particularly in shrub dominated savannas. As DGVMs underestimate the distribution of savanna biomes (Baudena et al., 2015), their simulation of future changes should be treated carefully (Moncrieff et al., 2015; Lehsten et al., 2016). This is particularly vital in land use change studies as most studies project that without incorporating the impacts of land use change, forest in Africa will increase compared to savannas and grasslands (Moncrieff et al., 2015).

3.8 Integrating human activities in DGVMs

Savannas are highly disturbed ecosystems, experiencing regular disturbances from people, fauna and fire. To accurately simulate modern day savanna ecosystems, the effect of humans in shaping the landscape needs to be understood. As most DGVMs were developed to simulate transient changes in biogeography and biogeochemistry in relation to changing climates, they are not able to simulate the effect of humans in shaping vegetation structure and composition. In particular, human impact, through land use change, is poorly represented in DGVMs and although land use changes have been included in later DGVMs, these models incorporate the effect of land use change and not the processes driving the change (Díaz et al., 2007).

Agent based models (ABM) have been coupled to process-based ecosystem models and used to simulate land use changes. They are preferred as they provide a flexible approach to represent interaction between people and their environment while integrating spatial heterogeneity (Matthews et al., 2007; Bithell and Brasington, 2009). They also have the advantage of incorporating decision making processes of components in a system at multiple scales (Matthews and Bakam, 2007). However, coupling and full integration of process-based ecosystem models and ABM is an area under development (Matthews and Selman, 2006) and that has potential to address changes in ecosystem functions (Rounsevell et al., 2012). For instance, (Rounsevell and Metzger, 2010), used BIOME-BGC to initialise biogeochemical state variables in an agent based model that aimed to estimate the ecosystem impact of exurban development and land management in south-eastern Michigan, USA. Pachzelt et al (2013) linked LPJ-GUESS to a general model for grazers, based on animal physiology, using herbaceous biomass which determined the growth of the grazer population. This thesis used grass biomass simulated by LPJ-GUESS to initialise grazer offtakes and animal densities in an ABM that aimed to understand the impact of rainfall regimes and socio-economic factors in driving land use change, human wellbeing and animal densities in southern Kenyan savannas.

3.9 Understanding and simulating the behaviour of Complex Adaptive Systems (CAS)

CAS are composed of heterogeneous subsystems, with autonomous entities characterised by nonlinear relationships and multiple interactions among them and their environment (An, 2012; North, 2014). The entities are decision makers, set up in an interactive environment, have an ability to learn from each other and to adapt to the conditions of a given environment (Macal and North, 2005; North, 2014). In CAS, these decision makers are modelled as individual agents in order to observe the differences brought about by decision makers with respect to their individual attributes and their individual contribution to the behaviour of the entire system (Macal and North, 2005; North, 2014). CAS are common in nature and in social settings (North, 2014) and modelling them involves a ‘bottom-up’ approach, such as ABM, which produce macroscale patterns that are shaped by local, spatially explicit autonomous decision makers (Schlüter et al., 2012).

Social-ecological systems (SESs) are CAS (Folke et al., 2005; Schlüter and Pahl-Wostl, 2007) made up of multiple subsystems with several internal variables interacting at multiple levels (Ostrom, 2009). They are characterised by non-linear interactions, uncertainty, potential regime shifts and an ability to self-organise (Schlüter et al., 2012). All resources used by humans are embedded in SESs (Ostrom, 2009) leading to numerous multi-scaled and strong interactions between the social and ecological components (Schlüter and Pahl-Wostl, 2007; Schlüter et al., 2012). Additionally, the feedback between available resources, actors and institutions interacting at multiple scales further drives these interactions and the complexity of SESs (Schlüter et al., 2012). In SES, the interdependent relationships between humans are mediated through interactions with the biophysical environment and the capacity of the SES to adapt and respond to stress is driven by the interactions between the social and biophysical processes (Schlüter and Pahl-Wostl, 2007). Humans are a main focus of SESs and they impact the system through decisions on resource use (Schulze et al., 2017). The individual humans that make up SESs have an ability to change, learn from experience and exploit what suits them best (Levin et al., 2013; Schulze et al., 2017). These individuals compete for limited resources and space making them have exploitative behaviours, competition and cooperation (Levin et al., 2013).

SES models are tools used for improving the understanding of factors and processes that shape the sustainable outcomes of SES of interest (Schlüter et al., 2012) such as grazing systems, fisheries and agriculture. SES models improve our understanding of SESs by analysing how the characteristics of ecological and social systems and interactions within and between them influence the overall behaviour of the system (Schlüter et al., 2012). SES models are also used for other purposes such as, integrating multidisciplinary approaches, developing frameworks for collecting empirical data, creating scenarios of the future and testing alternative policy and management interventions (Robinson et al., 2007). They provide alternative representation of human decision making and can be used to interrogate data deficient systems (Rounsevell et al., 2012). SESs are studied as coevolving systems and when modelling them, the dynamics of the social system influence the evolution of the bio-physical system, which in turn influences the evolution of the social system (Schlüter et al., 2012). Additionally, by taking into account the coevolving nature of SES, SES models provide effective guidance on the management of SES that can cope with their uncertainty (Schlüter et al., 2012).

ABM are tools used for improving the understanding of SES and the ability of modellers to predict and manage SES successfully (Grimm and Railsback, 2005; Schulze et al., 2017) by including individual decision making into SES model (Schlüter et al., 2012). ABM also have the advantage of representing the social and institutional relationships between humans at different scales (Schlüter and Pahl-Wostl, 2007). In science, the application of ABM to understand SESs is either through simple computer simulation experiments or as detailed representation of the real world (Ward et al., 2016). The discussion below expounds more about ABM with emphasis on their characteristics that are relevant to this thesis.

3.9.1 ABM: definition, application and simulation

An ABM is a computer simulation of the behaviour of virtual independent decision makers, called agents, that have the capacity to learn, interact and adapt to changes in other agents and in their environment (An, 2012). An agent is a computation unit that interacts with its environment and has the following qualities: independence, social ability (where it satisfies its objectives by interacting with other model entities) and reaction to environmental signals (Barbati et al., 2012). Agents represent real-world actors (Arneth et al., 2014) and can also be adaptive, static or dynamic and can recognize and distinguish the attributes and behaviour of other agents (Macal and North, 2005). ABM are sometimes used interchangeably with individual based models (IBMs) (Schulze et al., 2017), however, the difference between the two is that ABM simulate human agents and decisions while IBMs simulate non-human agents interacting in an ecological system (Polhill et al., 2013). ABM focus on explaining the behaviour of a system such as heterogeneity of and among agents, interactions between agents and adaptive behaviour of agents (Grimm et al., 2010). In ecology, the number of publications using ABM sharply increased from the 1990s because of the ability of ABM to address issues that other system-level models could not address, the evolution of theory and strategies for using ABM to perform science and development and the development of efficient computer softwares for running ABM (Railsback et al., 2006). Since the 1990s, when the IBM and ABM concept became widely used in ecology, general approaches for describing and implementing ABM have been developed and are increasingly used (Schulze et al., 2017). Specific uses of ABM include forecasting and exploring future scenarios of change, exploring possible alternative decisions by setting different values for the decision variables and assessing the effects of documented changes (Barbati et al., 2012).

Designing of ABM use a ‘bottom-up’ approach to incorporate the influence of agents and decisions at the micro-scale on macro-scale outcomes (Robinson et al., 2007). Micro-level processes simulated by ABM include the decision making process of agents and how agents are organized socially (Schlüter et al., 2012), which gives rise to macro-scale outcomes of a system (also known as emergent properties) (Janssen and Ostrom, 2006). The attributes of the agents enable them to interact with each other and with their environment following appropriate rules for a given environment (Barbati et al., 2012). An agent does not always have to be an individual but can represent any level of organization, such as a village or a cohort (Schlüter et al., 2012). The environment may be used to provide geographic information, such as the spatial location, of different agents (Macal and North, 2010). The heterogeneity of agents in an ABM is key because it influences adaptation and initiates different behaviour of agents (Robinson et al., 2007). However, the unique behaviour of ABM agents’ can change with the interaction of other agents in the system as well as with the slow evolution of macro-scale variables (Macal and North, 2010; Levin et al., 2013). The behaviour of agents is simulated in ABM using identified parameters and rules obtained from mathematical equations or artificial intelligence procedures (Ward et al., 2016) and agents can act independently or can join other agents in the system (Macal and North, 2010). In their interactions, agents are self-directed and active in initiating their action and acquiring information on which they base their decisions that enable them to achieve their goals (Galvin et al., 2006; Macal and North, 2010). Simulation in ABM usually begins with the set of assumptions and rules that are based on real world patterns (An, 2012) and simulating an ABM involves agents executing their behaviours and interactions repeatedly (Macal and North, 2010), ultimately producing data that can be analysed (An, 2012). When unexpected patterns emerge from the model outputs, they are used to explain the emergence behaviour of social-ecological systems. The multiple runs are important for covering different scenarios and accounting for stochastic variations (North, 2014). The outcomes of ABM are subjected to 'sensitivity analysis' which tests how reliable and robust the outcomes are (Filatova et al., 2013).

There are some differences between ABM and other models. First, ABM distinguish themselves from other modelling approaches, such as system dynamics and discrete event simulation, through their emphasis on modelling the heterogeneity of agents across a population and the emergence of self-organization in a system (Macal and North, 2010). Second, the ability of ABM to represent micro-level processes is lacking in other analytic methods such as time series and statistical procedures (Robinson et al., 2007; Ward et al., 2016). Third, in ABM simulation, the characteristics of individuals change through time whereas in other modelling approaches, the characteristics of individuals or populations are averaged and the model simulates changes in the behaviour of the averaged characteristics (Galvin et al., 2006). Lastly, ABM are important for theory and for management as, contrary to other analytical models, they allow researchers to study aspects that are sometimes ignored, such as local interactions, and the behaviour of individuals in adapting to internal and external changes in their environment (Grimm et al., 2006).

ABM have been applied in southern Kenyan savannas. Boone et al., (2011), created an household ABM called DECUMA, linked it to the SAVANNA ecosystem model and used the coupled model to explore the well-being of households in response to the impacts of droughts on grazing resources in southeastern Kajiado County (formerly District). Bulte et al., (2008), explored the potential of payments for ecosystem services to engage in land use types that are compatible with wildlife conservation while Thornton et al., (2006), quantified the impact of land subdivision to livestock numbers and food security of pastoral households in Kajiado County.

3.9.2 The Overview, Design concepts and Details (ODD) protocol used in ABM

Contrary to analytical models, which are formulated using a mathematical language that makes them easy to communicate, there was no standard method of communicating ABM and this made their published description vague and difficult to read and their outputs irreproducible (Grimm et al., 2006). The 'Overview, Design concepts and Details (ODD) protocol (Grimm et al., 2006) was designed as a tool that could facilitate the communication and re-implementation of ABM. The ODD protocol attempted to create a standard structure for documenting ABM that would make model descriptions understandable, more efficient, complete, easy to write, read and to reproduce (Grimm et al., 2010).

The ODD protocol aimed to always structure information about ABM in the same sequence (Grimm et al., 2006). It is made up of seven elements that can be categorised in three groups: Overview, Design concepts and Details (Table 3.1). The overview is made up of three elements namely: the purpose of the model, state variables, their scales, processes and schedules (Müller et al., 2013; Polhill et al., 2013). The overview is a statement of the intention of the model, the main variables used in the model and a discussion of the activities of the agents (North, 2014). Its intention is to have sufficient information to outline a model (Polhill et al., 2013). The 'purpose' sub-section of the overview explains what the model does while the 'state variables and scales' sub-sections outline the structure of the model including all the variables that constitute the model and their spatial and temporal scales (Polhill et al., 2013). The 'process overview and scheduling' sub-section of the model outlines the sequence of all model processes and the agents that will be implementing them at each modelling step (Polhill et al., 2013).

Design concepts describe the general concepts used to design the model (Müller et al., 2013; Polhill et al., 2013; North, 2014). These concepts are based on those identified in the field of CAS such as emergence of system properties, type of interactions between agents, how agents adapt their behaviour, how stochasticity is treated in the model and how individuals predict the consequences of their decisions (Grimm et al., 2006; Polhill et al., 2013). The 'Details' part of the ODD is made up of three elements namely: initialisation, input and sub-models and it presents the details of the model that were excluded from the overview (Grimm et al., 2006; Polhill et al., 2013; North, 2014). It elaborates the outline of the overview and should enable complete replication of the model (Müller et al., 2013; Polhill et al., 2013). The 'initialisation' sub-section of the details provides references to any initial values of the data used (North, 2014). The 'input' subsection provides any other inputs used in the model while the 'sub-model' subsection explains the processes outlined in the overview subsection of 'Process overview and scheduling', including the selection criteria of parameter values and testing and calibrating sub-models (Polhill et al., 2013).

Table 3.1: The ODD protocol as described by (Grimm et al., 2010)**.**

Elements in the ODD protocol	
Overview	1) Purpose
	2) Entities, state variables and scales
	3) Process overview and scheduling
Design concepts	4) Basic principles
	○ Emergence
	○ Adaptation
	○ Objectives
	○ Learning
	○ Prediction
	○ Sensing
	○ Interaction
	○ Stochasticity
	○ Collectives
	○ Observation
Details	5) Initialisation
	6) Input data
	7) Submodels

Through the ODD protocol, the theoretical aspects of the model can be given a better and clearer description (Grimm et al., 2010) and though the protocol provides a useful standard that facilitates better communication of the model and comparison between models (Polhill et al., 2008) critics of the original ODD protocol (Grimm et al., 2006) include its focus on ecological dynamics and lack of a comprehensive description of human decision making processes (An, 2012; Müller et al., 2013). Consequently, Müller et al (2013) developed an extension of the ODD protocol and called it ODD + D (ODD + Decision) protocol. Its aim was to preserve the ODD as a standard for describing ABM but change the 'Design concepts' section of the ODD to include additional description of human decision making processes. they argued that human decision making is the key in socio-ecological ABM, thus these models are best represented using the ODD + D protocol (Schulze et al., 2017).

3.9.3 Modelling patterns and human decisions in ABM

In designing ABM, the development of a model is guided by, and compared to existing patterns of the system of interest that are indicators of the underlying micro-scale environment (Robinson et al., 2007). Through a process called 'pattern oriented modelling (POM)', the designing and structure of an ABM can be made more realistic by reproducing multiple patterns observed in a real system (Grimm et al., 2005; Schulze et al., 2017).

Patterns are defining characteristics of a system and they often indicate important underlying processes and structural organization in the system (Grimm et al., 2005). The purpose of POM is to decode these patterns by focussing on the most important information about the internal organization of a complex system with the understanding that using observed patterns in the design of the model links the model to the internal structure of a real system (Grimm et al., 2005). Thus it is important for the representation of micro-scale patterns and structures in ABM to be credible and defensible (Robinson et al., 2007). The observed patterns are also used to reduce uncertainty of parameters in ABM and to improve the ability of ABM to predict the behaviour of systems characterised by long-term periods of ecological change (Grimm et al., 2005; Schulze et al., 2017).

Human behaviour is unpredictable and its parameterisation is uncertain (Le et al., 2010). It is simulated using a set of rules which may be simple, such as in decision trees, or highly complex that needs to be programmed in computers (Galvin et al., 2006; Macal and North, 2010). It can also be based on different behavioural theories such as simple heuristics, optimisation, bounded rationality, satisficing and evolutionary processes (Robinson et al., 2007; Rounsevell et al., 2012; Schulze et al., 2017). The *ad hoc* heuristics are informed by empirical observation or rigorous theoretical approaches (Schlüter et al., 2012). For example, outputs from biophysical models can be used as inputs for human decision making in SESs (Galvin et al., 2006). Heuristics decision making behaviour includes all functions that transform a prompt into a response and simple 'IF….THEN' clauses are used to show the outcome behaviour of the agent in response to the prompt (Robinson et al., 2007; Rounsevell et al., 2012). In implementing the optimisation behaviour of agents, if an agent has complete information on the system and can select its behaviour to maximise its utility among all other possible options, then the model integrates rational agents and if the agents achieves the minimum utility or maximises its utility over limited options, then the model integrates satisficing or bounded rationality respectively (Robinson et al., 2007; Müller et al., 2013). The rational choice theory has been criticised for being simplistic while the conditional rules that the bounded rationality theory is based upon prompt action or a combination of the two theories (Müller et al., 2013).

Different disciplines base their SES models on different theories of human-environment interactions and human decision making leading to models with different assumptions, evaluation criteria, outcomes and interpretation (Schlüter et al., 2012). However, the agent attributes and knowledge support that represent human decision making processes require qualitative or quantitative empirical sources (Smajgl et al., 2011). Qualitative and quantitative data can be used directly or indirectly to parameterise ABM (Schulze et al., 2017). Empirical data is useful for setting rules and decisions on the sub-models in the ABM (An, 2012; Müller et al., 2013) and these rules are based on data that must be compiled, computed and analysed statistically to obtain the rules (An, 2012). Several approaches are used for collecting empirical data that can inform ABM. They include:

- Surveys and interviews - Responses from sample survey are used to parameterise the behaviour of models based on micro-economic theory or to produce statistical descriptions of the attributes of the agents used in the ABM (Robinson et al., 2007).
- Expert knowledge – it involves the formal or informal acquisition of the understanding of experts in their area of expertise and using that knowledge in models (Smajgl et al., 2011).
- Participant observation – it involves a researcher living with a group of people participating in and documenting their daily activities.

- Participatory modelling – it involves real people describing their local environments to the modeller and informing the modeller what they would do under certain conditions of change (An, 2012). Example of a participatory approach in ABM is role playing games that aim to understand decision making processes of stakeholders and to incorporate them in ABM (Castella et al., 2005; An, 2012; Schulze et al., 2017). This is done by analysing outputs, from games played by stakeholders in a virtual world created by the modeller, to modify or verify the processes described by the model and to code the behaviour of agents in a computer (Robinson et al., 2007). This approach, however, is faced by challenges such as in selecting a representative sample of stakeholders, stakeholder subjectivity and conflict between parties (Schulze et al., 2017).
- Field and laboratory experiment – They are designed to indicate how a change in a predictor variable affects a response variable (Smajgl et al., 2011). Laboratory experiments have been used in psychology, economics and geography (Robinson et al., 2007).
- GIS and remote sensed data - GIS has been used in studies of land use change and it involves using spatial data to get input variables for drivers of land use change (Robinson et al., 2007; Smajgl et al., 2011; Müller et al., 2013).

These approaches can sometimes be combined together to fully parameterise the behaviour of agents in an ABM (Smajgl et al., 2011) using methods such as Bayesian belief networks (Schulze et al., 2017). However, due to multiple challenges experienced in parameterisation and calibration of ABM (Robinson et al., 2007; Schulze et al., 2017), representation of decision making in different models is based on data availability, theoretical reasons or POM (Grimm et al., 2005; Müller et al., 2013).

3.9.4 Strengths and limitations of ABM

ABM have numerous strengths associated with them. First, they enable researchers to assess how the behaviour of a system is shaped by the adaptive behaviour of individuals and in turn, how the behaviour of the system influences individuals (Grimm et al., 2006). Second, as ABM have an ability to simulate individual decision making while integrating the heterogeneity and interactions of the agents (An, 2012), they help in understanding the general behaviour of a given system that cannot be deciphered by observing each agent (Barbati et al., 2012). Third, the flexibility of ABM allows them to incorporate multiple scales and multi-disciplinary knowledge in qualitative and quantitative forms when simulating the system of interest (An, 2012). Fourth, human behaviour in ABM is represented more realistically where heterogeneous interactions, learning and bounded rationality are well accounted for (Filatova et al., 2013; Müller et al., 2013) and through participatory modelling approaches, stakeholders and decision makers views are incorporated in socio-ecological ABM (Schulze et al., 2017).

Challenges faced by ABM include issues that involve parameterisation, decision making, type of data used and model validation. Due to the complexity of ABM, they tend to be difficult to parameterise and analyse (Smajgl et al., 2011; Schulze et al., 2017) and a major challenge they face is modelling how the decisions of agents are designed and parameterised to capture the interactions and behaviour of a real system (Filatova et al., 2013). In modelling human behaviour in ABM, the models are often not described in a transparent manner and the selection criteria of human decisions are poorly documented having insufficient empirical and theoretical foundations (Müller et al., 2013; Schulze et al., 2017). In addition, modelling individual decision making faces challenges in identification of decision criteria of agents or determining the social rules in individual decision making (Schlüter et al., 2012) and though social science theories and empirical observations are used to model decision-making of individuals in ABM, there is no accepted protocol that can guide these choices (Filatova et al., 2013). There is also no standard way of documenting and communicating the empirical support that modelling and design decisions in ABM are based upon (Smajgl et al., 2011) as well as those reporting the use of participatory approaches in ABM (Schulze et al., 2017).

In using empirical data to inform human decision making in ABM, it can be challenging to gather long term data for the behaviour of individuals or a group (Schulze et al., 2017). Also, survey data assumes individuals are independent and does not emphasise on the impact of interactions between people (Schulze et al., 2017). Because of problems associated with empirical data collection explicit inclusion of cognitive, institutional and social processes in ABM is challenging leading to a bias in achieving good statistical outputs (Janssen and Ostrom, 2006).

One way of evaluating ABM is by conducting sensitivity analysis which sequentially tests each parameter used in the model to measure its impact on the outcomes of the model (O'Sullivan et al., 2016). However, the sensitivity of ABM to stochastic elements, parameters used in the model and decision-making theories used can be challenging particularly when assessing the soundness of their construction and their ability to replicate real world situations (Filatova et al., 2013). In addition, though significant developments have been made in describing ABM in a standard manner, in linking observed real world patterns to simulated processes and in calibrating, verifying and valuation of ABM at all stages of their implementation (Grimm et al., 2005; O'Sullivan et al., 2016), issues related to evaluation of ABM, specifically in model calibration, verification and valuation, still remain a challenge (O'Sullivan et al., 2016).

The use of ABM to understand SESs is also challenged by the inability of ABM to properly address some aspects of SESs like the role of institutions, multi-level decision making and influences between attitude and behaviours (Schulze et al., 2017). In addition, social-ecological models sometimes involve coupling ABM focused on human behaviours with other biophysical or ecological models such that multiple feedbacks between them are incorporated. With the basic understanding of the non-linear behaviour of SES missing (Schlüter et al., 2012), identifying the variables that join human focused ABM to other biophysical or ecological models is challenging (Filatova et al., 2013) leading to uncertainty in SES outcomes. More so, because the validity, efficiency and accuracy in incorporating multiple feedbacks between human-focussed ABM coupled to biophysical or ecological models is rarely tested (Filatova et al., 2013). Even with all the theoretical and technical developments in ABM, the theory of CAS still requires further development as it currently lacks a clear conceptual framework as well as proper ontological and epistemiological representation of complexity (An, 2012).

3.10 Conclusion

This chapter discusses the study areas that were selected for this study. All study locations were located in the arid and semi-arid savannas of Kenya and though numerous sites contributed to the vegetation study (chapter 4) in this thesis, the focus of our study sites were Amboseli and Mara ecosystems in southern Kenya. The location, climate, geology, hydrology, conservation and human activities in Amboseli and Mara areas are discussed in detail. Also discussed are the modelling techniques used for research in this thesis. The chapter discusses the definition, development, application, strength and limitations of the vegetation and social-ecological models used. The reasons why the models were selected and the applicability of the models to simulate the dynamics of the social-ecological systems studied in this thesis are also discussed.

3.11 References

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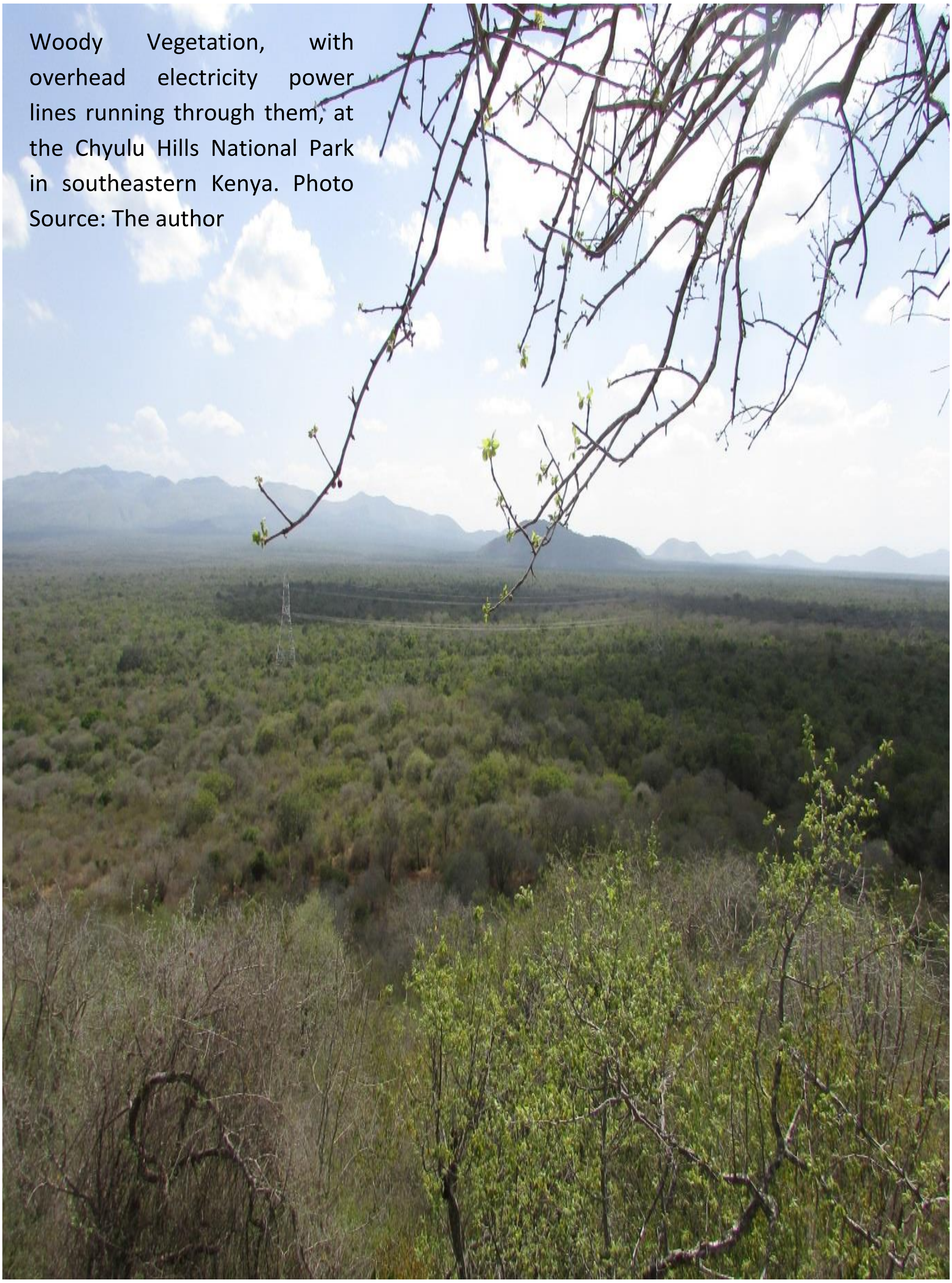
4 Influence of Rainfall on Woody Vegetation Structure



Woody Vegetation, with overhead electricity power lines running through them, at the Chyulu Hills National Park in southeastern Kenya. Photo Source: The author

Change in Woody Vegetation Structure and Function along a Rainfall Gradient in Savanna Ecosystems: a historical Kenyan case study

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4.1 Abstract

Savannas cover 88% of Kenya's land surface and account for two thirds of the woody biomass. Rainfall imposes an upper limit to woody vegetation growth in savannas and plays a primary role in shaping ecosystem composition, structure and function, secondarily modified by soil nutrients, fire, herbivores and human activity. We used historical data (collected prior to current high levels of sedentarization) to identify woody vegetation attributes in relation to rainfall in 46 vegetation plots in Kenyan savannas. We compare these attributes between two savanna ecosystems, Amboseli and Maasai Mara, which differ in human and herbivore activities. Woody structure was linearly related to rainfall, accounting for 20% of the variation in biomass, 20% in production and 21% in plant height. Woody biomass, production and composition was higher in Amboseli compared to Maasai Mara, corresponding to, differences in soil infiltration rates, increased elephant numbers and extensive burning of woodlands. The Amboseli and Maasai Mara comparison show a strong rainfall signature prevailing despite heavy environmental disturbances. These historic data are useful to separate abiotic drivers from human disturbance and assess the effects of other drivers once the effects of rainfall have been accounted for. These insights from Kenya have wider relevance for understanding abiotic and biotic controls on savanna ecosystems.

Key Words: Amboseli, data recovery, drylands, Maasai Mara, production, precipitation, vegetation structure

4.2 Introduction

Drylands, including savannas, bushlands and open grasslands, are characterized by mean annual rainfall (MAR) from 150 to 1100 mm yr^{-1}, high daily temperature variability (Mwaura and Kaburu, 2009) and severe wet and dry seasons (Mlambo et al., 2007). They occupy 30% of all terrestrial land, 50% of the vegetated surface of the African continent (Franz et al., 2010) and 88% of the land surface area in Kenya (Mwaura and Kaburu, 2009). Due to differences in climate, soils and disturbances, savanna vegetation structure is highly heterogeneous (Dong et al., 2016). Drylands support most pastoralist societies (Franz et al., 2010) and in Kenya it is estimated they support about 30% of the human population (Mwaura and Kaburu, 2009; Dong et al., 2016), as well as high biomass of livestock and wildlife (Muchiru et al., 2008). Thus it is important to understand the key role played by woody plants in these ecosystems and the effect of rainfall in regulating their structure and function.

Rainfall in Kenya is influenced by the seasonal north-south movement of the Intertropical Convergence Zone (ITCZ) that results in a bimodal rainfall pattern characterised by the long rainy season (March-May) and the short rainy season (October-December). Seasonal variability in rainfall is considered the most important variable in shaping the dynamics of grassy and woody layers in savanna ecosystems (Bobe, 2006; Bond, 2008; Levick and Asner, 2013) acting as the main environmental filter over large spatial scales (Murphy and Bowman, 2012; Toledo et al., 2012). Consequently, most plant species are morphologically and physiologically adapted to deal with variable rainfall and a range of other disturbances (such as fires, humans and herbivory) (Dong et al., 2016).

Woody species comprise a significant proportion of savannas and contribute to regulating ecosystem functions such as hydrology (Sankaran et al., 2008; Otieno et al., 2011), biodiversity, primary production and transpiration. Additionally, woody cover is the most common description of savanna vegetation structure as it shows differential water use among functional groups (Franz et al., 2010) particularly in dry savannas where competition between trees and grasses is to a large extent attributed to water availability (Van den Koppel and Prins, 1998).

Woody biomass tends to increases with rainfall and infiltration (Georgiadis, 1989) and woody species have been shown to have differential responses to rainfall in tropical forests and savannas in Africa, Australia and South America (Hirota et al., 2011). For example, Murphy and Bowman (2012) showed a strong relationship exists between woody cover and dry season soil water availability in Africa and Australia while in South America this relationship is weak. While the importance of rainfall on woody species has been well documented for different savanna ecosystems in Africa (Sankaran et al., 2005; Bond, 2008; February et al., 2013), a study showing the explicit effect of rainfall on woody species across space in different savanna ecosystems in Kenya has not been done. This data deficiency is important because Kenya holds ~0.5 million km^2 (Mwagore, 2003) of savanna, over 3 % of the savanna area in Africa (Grace et al., 2006; Mworia, 2011).

The resilience of savanna ecosystems decrease towards drier and wetter areas; in the former, the probability of the ecosystem turning to a tree-less state increases, and in the latter, the probability of the ecosystem turning into a forest increases (Hirota et al., 2011). Thus, an evaluation of vegetation structure across different environmental gradients provides important insights into the interactions between different vegetation controls (Morrison et al., 2016). Fire is considered second in importance after rainfall in shaping tree structure of African savannas followed by the effect of soil nutrients and herbivory (Sankaran and Ratnam, 2013). Generally, fire intensity and frequency is higher in more humid savannas, reoccurring every one to three years, due to availability of high biomass of grass fuel compared to semi-arid areas where the fire frequency is more than three years (Tomlinson et al., 2012). Soils in arid areas range from clayey rich soils to poor sandy soils with the effect of soil properties on vegetation increasing with rainfall and being less important than rainfall in dry areas. The impact of herbivory on primary production is explained by the grazing optimization theory (Georgiadis, 1989) where herbivores promote or suppress tree cover depending on their size, density and mobility. For example, small browsers have been shown to suppress shrubs and the large browsers the structure and density of woodlands (Bond, 2008). Moreover, the interaction between herbivores and vegetation has been shown to cascade into other communities of plants and animals (Franz et al., 2010). Elephants and humans are keystone species in regulating savanna patch dynamics (Dublin et al., 1990; Western and Maitumo, 2004; Beale et al., 2013) with humans transforming savannas through their pastoral, farming, fire patterns and settlement activities. Additionally, through their varied choices of land use types, humans alter the structure, function and ecosystem service type and quantity produced (Higgins et al., 1999).

To quantify the factors that regulate the structure, function and diversity of woodlands, we need to better understand the structure and composition of woody species along environmental gradients. Such insights not only provide much needed knowledge on the relationships between woody vegetation structure, function and composition in savannas, but can also be used to validate outputs from Dynamic Global Vegetation Models (DGVMs) that simulate changes in vegetation distribution and physiological processes as a function of changing climates.

Our study had two objectives. 1) To assess the variance in structure and function of woody vegetation along an environmental gradient in Kenya’s savannas by assessing the structure, biomass, primary production and turnover rates of woody vegetation in relation to rainfall. 2) To compare woody community functions and composition in two areas in southern Kenya: the Amboseli and Maasai Mara ecosystems. These two areas have supported pastoralists, their livestock and wild animals for many years but vary in the degree of human influence especially in land use practices, land tenure types and conservation models with community-based joint management plans established across a number of conservancies in both areas having varying resources and challenges which they address using varying management strategies

4.3 Study areas and methods

Woody vegetation information on 120 vegetation plots (Appendix I) located in Kenyan rangelands was collected by the Kenya Rangeland Monitoring Unit (KREMU), subsequently renamed as the Department of Remote Sensing and Resource Survey (DRSRS), between 1977 and 1981. Historical data such as these are useful in determining the impact of environmental variables (e.g. rainfall) as they were collected prior to high levels of human disturbance which may mask the processes linking abiotic drivers with vegetation characteristics (Hannah et al., 1995; Ward, 2005; Willcock et al., 2016). KREMU classified Kenyan rangelands into 44 eco-units, based on three eco-climatic zones (IV, V and VI) defined by Pratt et al. (1996). Data used in this paper came from 10 x 10 km plots (Figure 4.1) distributed across the three eco-climatic zones and was recovered through collaboration with the African Conservation Centre (Amboseli Conservation Program) in Kenya.

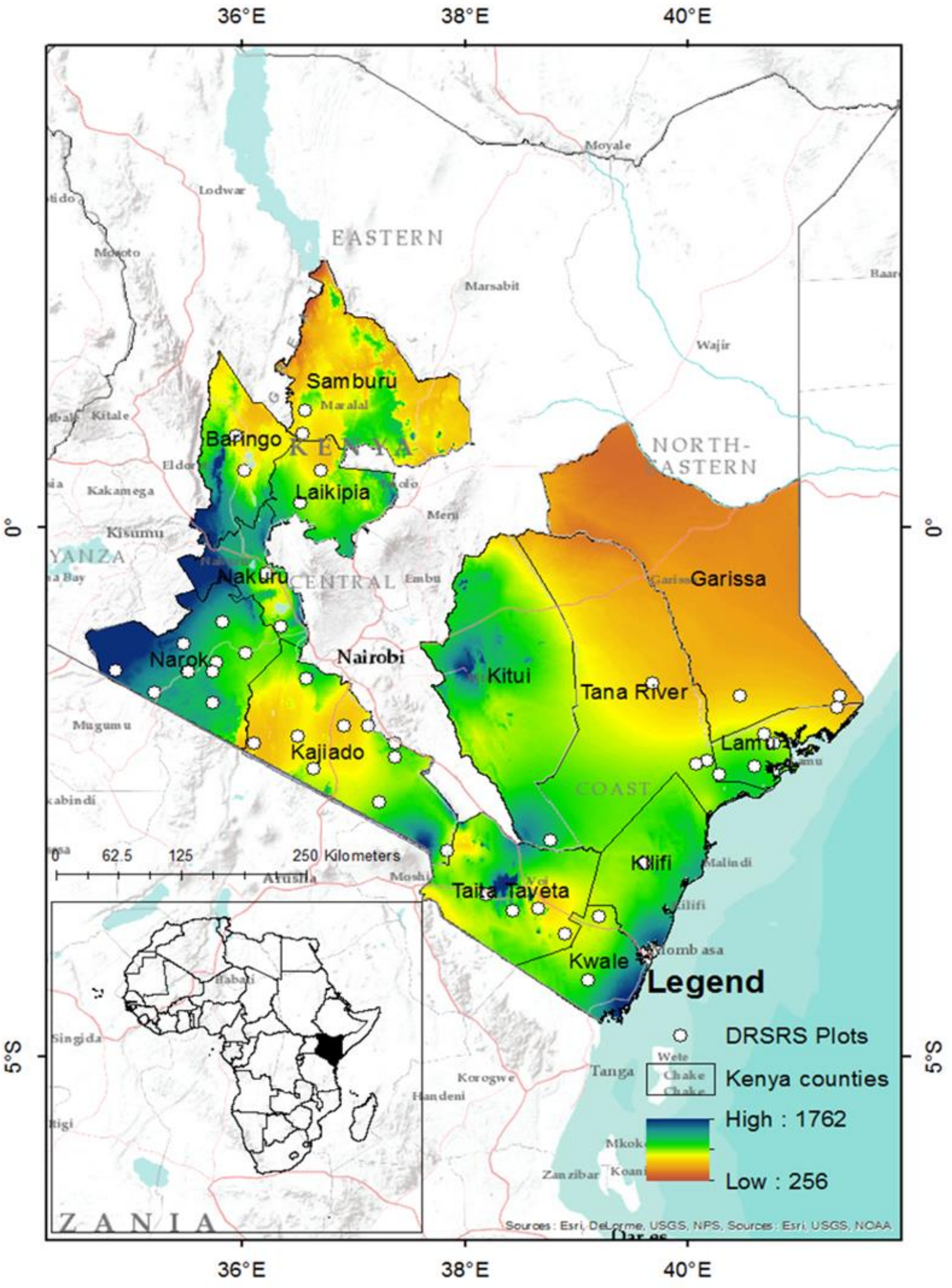

Figure 4.1: Location of 46 vegetation plots sampled by DRSRS in Kenyan savannas in the late 1970s/early 1980s and used in this study and their distribution across a rainfall gradient in Kenya savannas. The source of the mean annual rainfall (mm yr^{-1}) is WorldClim

Amboseli and Maasai Mara are located in southern Kenya within Kajiado and Narok counties. The Amboseli ecosystem contains the Amboseli National Park, receives an average annual rainfall of 350-400 mm yr^{-1} (Western and Van Praet, 1973) and its vegetation is sparse bushed-grassland except the Amboseli basin which has alkaline grasslands, woodlands and swamps (Western and Lindsay, 1984). Maasai Mara contains the Maasai Mara National Reserve and receives an annual mean rainfall of 600 mm yr^{-1} on the eastern side while the western side, which is closer to Lake Victoria, receives an annual mean rainfall of 1000 mm yr^{-1} (Lamprey and Reid, 2004). Its vegetation type is classified as semi-arid to semi-humid (Serneels et al., 2001).

Of the 120 vegetation plots sampled (of which all GPS coordinates are known), we fully recovered woody vegetation data from 46 plots, with data from the other vegetation plots either fully or partly missing. Thirty-nine plots were used to estimate woody vegetation functions while ten and nine plots estimated woody structure and function in Amboseli and Maasai Mara respectively. Each plot was 10 x 10 km and was randomly selected to represent an eco-unit's local terrain, climate and vegetation (Kuchar, 1981). The selection of the vegetation plots in each ecounit was based on the physiognomic characteristics of vegetation in the area as defined by Pratt et al. (1996). The plots were established as representative of vegetation structure and composition of Kenyan rangelands. A Within each 10 x 10 km plot, one or more representative subplots (rarely exceeding three per plot) were identified for sampling. The subplots were plant communities representative of the area and representing the slope, topography and plant cover of the area. The total area surveyed per subplot was 4 hectares (ha), usually 200 x 200 m; where vegetation occurred along a narrow strip the dimension of the surveyed area was 100 x 400 m. The 4 ha subplot sampled within each plot resulted in at least 184 ha of vegetation sampled in all the 46 vegetation plots with 40 ha and 36 ha being sampled in Amboseli and Maasai Mara.

In each vegetation plot, herbaceous and woody vegetation data was collected. We focussed on woody plants > 0.7 m tall including epiphytes and succulents > 1 m tall. The point centred quarter (PCQ) method (Mueller-Dombois and Ellenberg, 1974) was used to measure woody vegetation variables (Figure 4.2). It is a plotless vegetation sampling technique whereby four or multiples of four woody individuals are sampled at each point. A baseline transect is marked and the first sampling point is selected randomly 5 – 15 m along the baseline. Using a compass to maintain direction, sampling points are chosen along the ensuing transect where four quarters are established, at a sampling point, through an intersection between the baseline and line perpendicular to it. The distance from the sampling point to the mid-point of the nearest woody species is then measured in each quarter (Mueller-Dombois and Ellenberg, 1974). Vegetation variables collected at each subplot were species names for each individual plant, height, stem diameter, diameter at breast height and canopy dimensions.

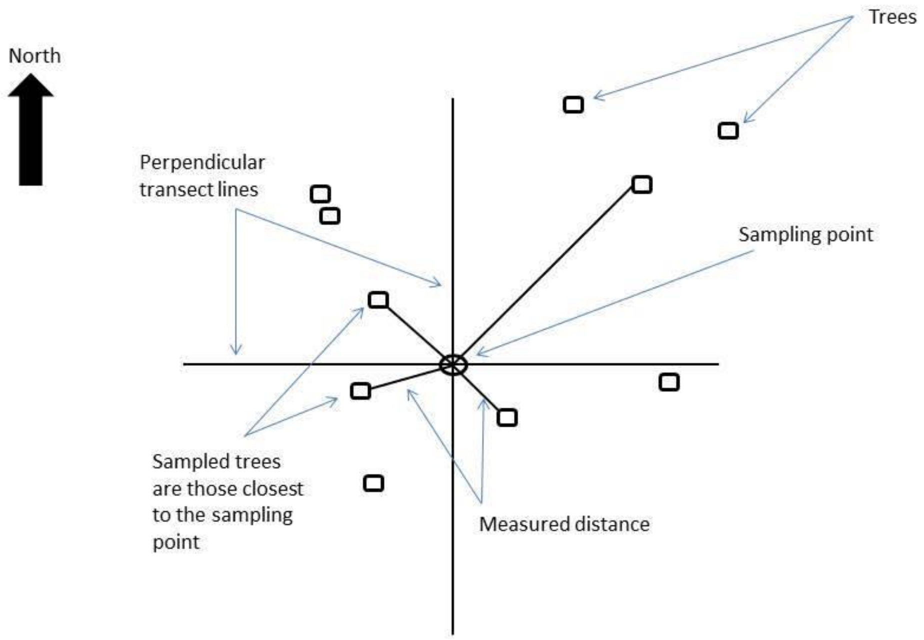

Figure 4.2: Point centred quarter technique (modified after Mueller-Dombois et al., (2003).

To get the minimal sampling size that is representative of the vegetation community, the relevé nested plot technique was used (Mueller-Dombois and Ellenberg, 1974). Plant height was divided into five possible layers: tall woody (> 6 m), medium woody (2 – 6 m), low woody (0.7 - 2 m), dwarf shrub/herb and vines and epiphytes (Kuchar, 1981). As sampling was non-repetitive, plots were selected based on Pratt et al. (1996) and the relevé nested plot technique. This ensured that regional vegetation type and vegetation important to large herbivores was well represented. Height stratification was done such that there were two, sometimes three, different height classes at each sampling point. First, where there was one clear layer of woody vegetation with a height of < 4 m, it was taken as a stratum. Second, where there were two distinct layers of woody vegetation with one layer being taller or where the woody plants ranged across all height categories, two layers of strata were sampled: a lower (0.7 – 2 m) and an upper (> 2 m) layer. Third, where there were very tall trees, three layers were sampled: a lower (0.7 – 2 m), middle (> 2 m) and an upper (> 15 m) layer. In sparsely populated vegetated areas where the nearest plant was > 30 m from the sampling point, their measurements were not taken. Where vegetation was dense, the vegetated area was divided into clumps and two perpendicular lines inserted into the clumps dividing the plot into four quarters where vegetation sampling was done (Kuchar, 1981).

4.3.1 Estimation of vegetation biomass

Woody species biomass can be estimated indirectly using allometric regression equations which use easily measurable variables such as stem height and canopy diameter that are measured non-destructively (Sawadogo et al., 2010). Though stem diameter is commonly used as an independent variable when predicting woody vegetation biomass (Shackleton and Scholes, 2011); it can be challenging to use it in areas with high densities of multi-stemmed woody species. Other variables such as canopy dimensions and plant height can be used independently or jointly to predict biomass. Western (unpublished data), conducted a survey for analysing available and utilizable wood fuel in the savannas of Kenya and developed allometric equations to estimate biomass and production based on height, canopy dimensions and diameter at breast height of at least 30 single stemmed individuals for 23 woody species from the Amboseli ecosystem. For each species, the height, canopy dimensions and diameter at breast height were measured and recorded before oven drying and weighing proportions of different plant parts; by using canopy diameter and depth the volume and area of the canopy could be calculated. Western then used best fit regression relationships (Equations 1 and 2) to estimate woody vegetation biomass using canopy dimensions. Equation 2 was used for woody species that did not have canopy depth. Western also estimated production and turnover rates of woody vegetation for these plots by relating net primary production to total biomass where turnover rates were estimated as a ratio between production and biomass.

$$\log m_t = 1.11 \times \log (CV \times 0.07) \qquad \text{'Equation 1'}$$

$$\log m_t = 1.53 \times \log (CA \times 0.04) \qquad \text{'Equation 2'}$$

Where $m_{t,}$ CV and CA are woody vegetation biomass, canopy volume and canopy area respectively.

These two allometric equations have been used to estimate woody biomass elsewhere in Kenya (Lindsay 1994; Western & Ssemakula 1981) and we used them to estimate woody biomass in the vegetation plots used in this study as, to the best of our knowledge, they are the only locally derived allometric equations available.

4.3.2 Determining rainfall and woody vegetation relationships

Due to challenges in deriving accurate rainfall estimates for each vegetation plot; three sources of rainfall data were used; the Kenya Meteorological Department (KMD), Tropical Rainfall Measuring Mission (TRMM) and WorldClim (http://www.worldclim.org/). The Kenya Meteorological Department and WorldClim data were used to estimate long term rainfall averages while TRMM values were used where KMD and WorldClim over-estimated rainfall as KMD data was not spatial and the resolution of WorldClim data was coarse. Vegetation biomass, production and turnover rates for different vegetation plots were related to long-term average rainfall. Further, the relationships between rainfall and stem diameter, height and canopy width of woody species were analysed.

4.3.3 Data analysis

For each vegetation plot we estimated i) the biomass, ii) production, iii) turnover rates and iv) long-term average rainfall. We used log-transformation of woody vegetation biomass, production, turnover and rainfall to reduce variance. Biomass was estimated in kg ha^{-1} while production was estimated in kg ha yr^{-1}. As turnover (in years) was a ratio between production and biomass, the years were converted to days for ease of interpretation. The relationship between woody vegetation functions and rainfall were examined using a linear regression and non-linear fits while analysis of variance tests were used to establish the differences between vegetation function across rainfall zones. To establish the difference in woody vegetation function and composition between Amboseli and Maasai Mara, we used independent samples t-test. All tests were performed using R studio statistical software and the level of significance was set to $P < 0.05$.

4.4 Results

4.4.1 Mapping vegetation plots across rainfall gradients

Mean rainfall ranged from 200 to 1100 mm yr^{-1} across the vegetation plots sampled (mean ± SE; 607.86 ± 40.7 mm yr^{-1}) and was categorized into three zones: i) arid zones receiving MAR between 200 to 450 mm yr^{-1}; ii) semi-arid zones receiving MAR of 450 to 750 mm yr^{-1} and iii) sub-humid zones whose MAR was 750 to 1100 mm yr^{-1}. The semi-arid zones were largely located in southern Kenya while the sub-humid zones were located in south-east Kenya near the coast and near Lake Victoria in western Kenya. Arid zones covered all the other areas (Figure 4.1). The lowest annual mean rainfall estimate (226 mm yr^{-1}) was recorded on a vegetation plot in Kajiado while the highest estimate (1060 mm yr^{-1}) was recorded on a vegetation plot near the coastal region. Of the vegetation plots sampled, 48% were found in the semi-arid zone, 29% in the arid zones and 23% in the sub-humid zones.

4.4.2 Comparative analysis of woody vegetation biomass, production and turnover amongst savanna rainfall zones

The mean biomass of woody species for arid zones was 16.99 ± 4.47 t ha^{-1}, while in the semi-arid and sub-humid zones it was 20.64 ± 2.6 t ha^{-1} and 36.64 ± 7.7 t ha^{-1} respectively. There was a significant difference ($F_{2, 28} = 4.48$, $P < 0.05$) between biomass in the three zones and a subsequent Bonferroni test showed the difference was between the arid and the sub-humid zones ($P < 0.05$) as well as between the semi-arid and the sub-humid zones ($P < 0.05$). However, the difference in biomass between the arid and semi-arid zone was not significant ($P > 0.05$; Figure 4.3).

Mean woody vegetation production for all the plots was 1.16 ± 0.16 t ha^{-1} yr^{-1}. The sub-humid zones recorded the highest mean production levels of 1.93 ± 0.45 t ha^{-1} yr^{-1}, followed by the semi-arid zones at 0.99 ± 0.14 t ha^{-1} yr^{-1} and the arid zones at 0.82 ± 0.23 t ha^{-1} yr^{-1}. There was a significant difference ($F_{2, 28} = 4.76$, $P < 0.05$) between woody vegetation production in the three zones, and a further post-hoc test established that the difference was between the arid and sub-humid zones as well as between the semi-arid and the sub-humid zones. However, there was no difference ($P > 0.05$) between the arid and semi-arid zones. The turnover rate of woody vegetation decreased as rainfall increased. Arid zones had the longest turnover rates, followed by the semi-arid and sub-humid zones. There was a significant difference in turnover rates among the three zones ($F_{2, 27} = 42.42$, $P < 0.05$); with all the zones being different from each other.

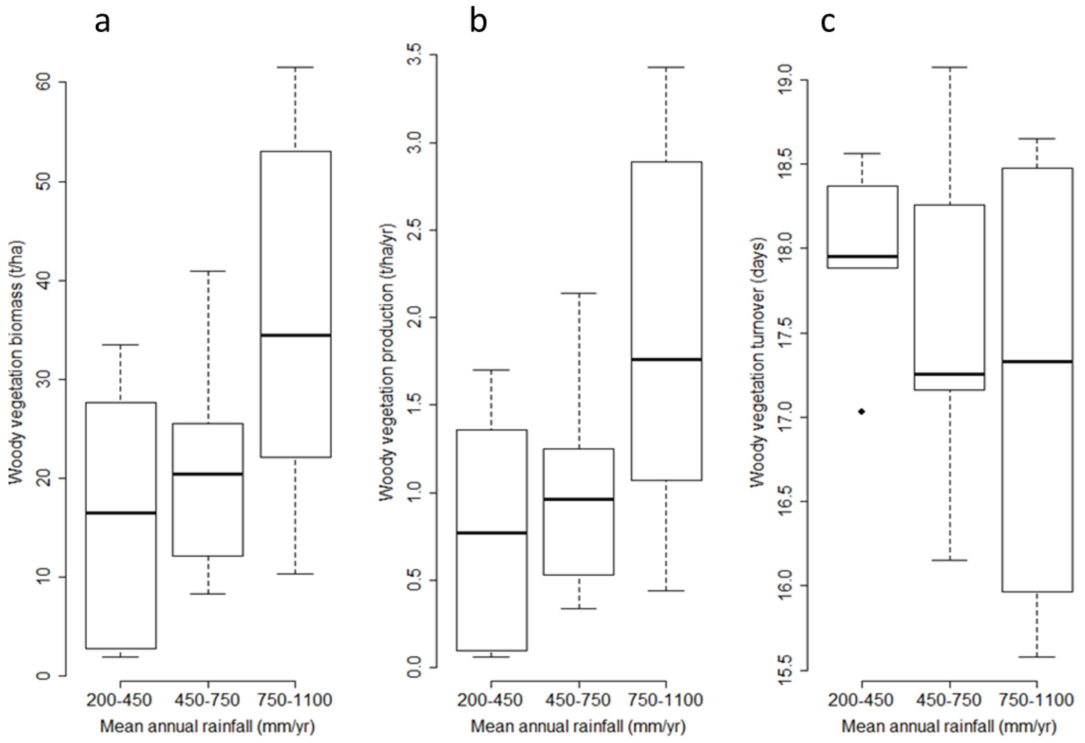

Figure 4.3: Woody vegetation biomass (a), production (b) and turnover (c) among rainfall zones in savanna ecosystems in Kenya. Biomass and production increased with rainfall while turnover rates decreased as rainfall increased.

4.4.3 Relationship between woody vegetation structure and function and rainfall

The relationship between log of rainfall and height of woody species was significant ($F_{1, 19} = 5.03$, $P < 0.05$, $n = 21$, $R^2 = 20.92\%$). However, the relationship between rainfall and stem diameter and canopy width was insignificant ($P > 0.05$; Figure 4.4). Woody species biomass and production were directly related to rainfall while the turnover rate was inversely related to rainfall. The relationships between biomass and production were significant with rainfall explaining 19.7% of the variation in biomass ($F_{1, 36} = 8.88$, $P < 0.05$, $n = 38$) and 19.5% of variation in production ($F_{1, 36} = 8.73$, $P < 0.05$, $n = 38$). However, the relationship between woody vegetation turnover rates and rainfall was insignificant. Non-linear fits between rainfall and woody vegetation biomass and production showed a linear increase at low rainfall that slows down as the rainfall increases. Rainfall, in the non-linear regression, explained 21.2% and 20.9% of biomass and production of woody vegetation in Kenyan savannas.

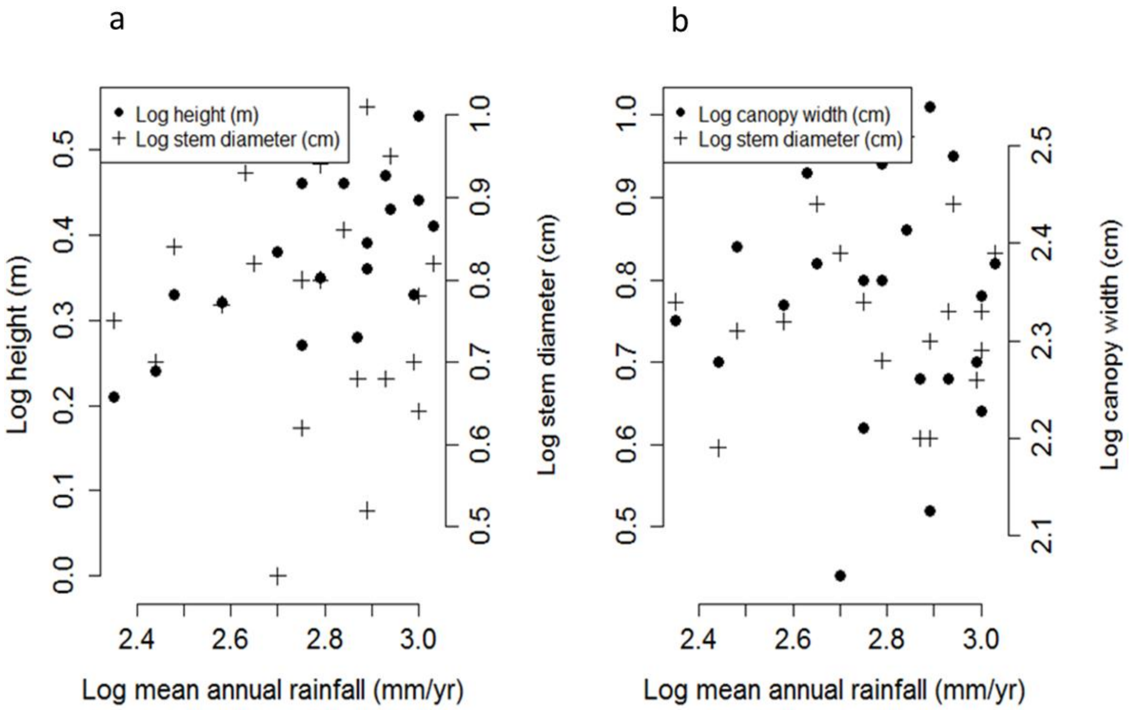

Figure 4.4: Relationships between mean annual rainfall, height and stem diameter (a); and between mean annual rainfall, canopy width and stem diameter (b) of woody species in savanna ecosystems in Kenya.

4.4.4 Comparing woody vegetation production and composition in Amboseli and Maasai Mara

Mean biomass of woody species was not significantly higher in Amboseli (19.6 ± 4.94 t ha^{-1}) compared to Maasai Mara (9.8 ± 1.9 t ha^{-1}). Similar trends were observed in vegetation production with Amboseli having higher production that was not different ($P > 0.05$) to Maasai Mara (Figure 4.5). Woody species richness was insignificantly ($P > 0.05$) higher in Amboseli with 69 species compared to Maasai Mara with 57 species. Species diversity, calculated using Shannon-Weiner Index, in Amboseli was higher (2.31 ± 0.15 H) than in Maasai Mara (1.05 ± 0.42 H) and the difference between these two areas was found to be significant ($t_{2, 8} = 2.31$, $P < 0.05$). Woody species dominance was higher in Maasai Mara compared to Amboseli; however, the difference was not significant ($P > 0.05$).

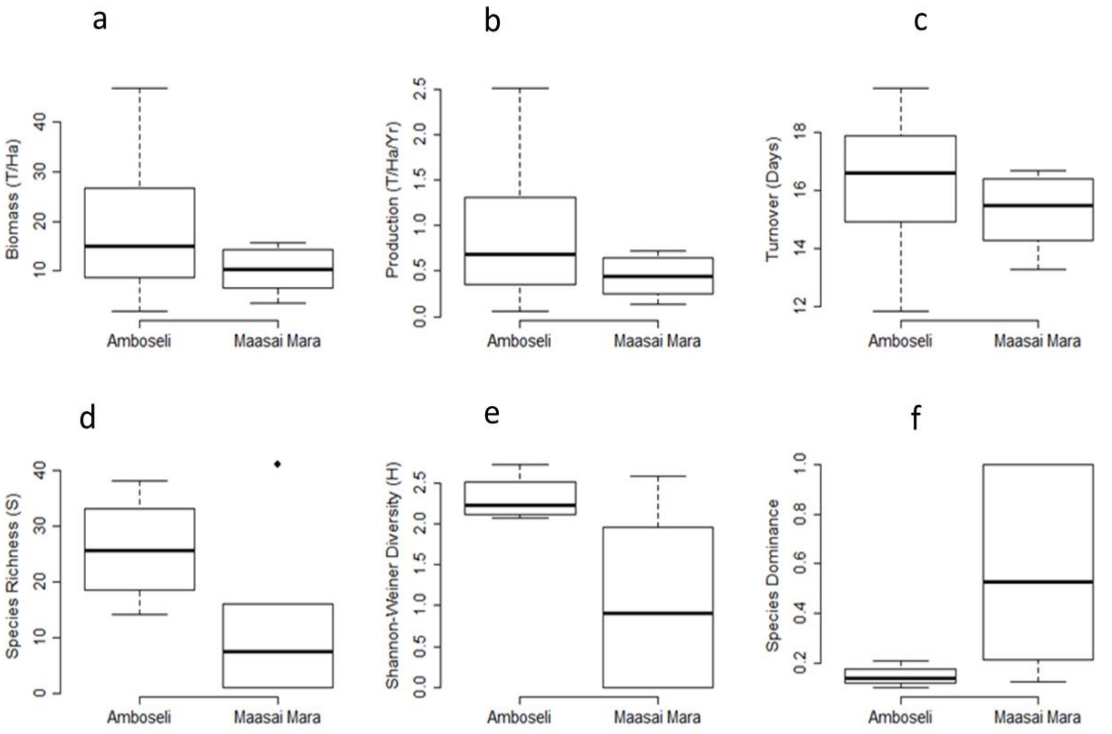

Figure 4.5: Comparison between woody vegetation biomass (a), production (b), turnover (c), species richness (d), species diversity (e) and species dominance (f) between Amboseli in Kajiado County and Maasai Mara in Narok County in southern Kenya.

4.5 Discussion

In this study, we quantified the influence of rainfall on woody structure and function under background conditions of free-ranging pastoralism and wildlife activity that represent long-standing interactions. We used recovered, historical data (that was initially collected by DRSRS in late 1970s / early 1980s) as the data was collected prior to the high levels of land subdivision and sedentarization levels that characterise savannas presently (Western and Nightingale, 2003; Galvin et al., 2008; Western et al., 2009). The selection, sampling and marking of vegetation plots by DRSRS was thoroughly done as it was envisioned that these plots would establish baseline vegetation conditions for Kenyan savannas and would be used for subsequent monitoring (Kuchar 1981), which was unfortunately never done. However, the study presented here 1) highlights the usefulness of historic data to detect underlying processes that may be masked by modern-day anthropogenic disturbance (Willcock et al., 2016; Marchant et al., 2017) and 2) provides the opportunity to conduct a resurvey on the sampled vegetation plots creating 40 years of unprecedented long-term data of savanna ecosystem change.

Drylands, in particular savanna ecosystems, are highly variable in their structure and composition (Serneels et al., 2001); particularly in response to rainfall (Franz *et al.* 2010). In our study, MAR explained 21% of variance in woody biomass and production, hence it is a factor affecting primary production across Kenya (Hempson et al., 2007; February et al., 2013). Although other factors contribute to this variance, their role varies with other ecosystem properties. For instance, the impact of fire on tree cover is less important in dry savannas with < 1000 mm yr^{-1} rainfall but becomes important in areas with rainfall between 1000 and 2000 mm yr^{-1} (Staver et al., 2011). Soil nutrients are known to be more scarce in moist savannas when compared to drier savannas (Otieno *et al.* 2011). In addition, the impact of rainfall on vegetation in dry areas is also influenced by soil water reserves which are dependent on topography, soil depth and soil texture (Toledo et al., 2012). The impact of humans and large herbivores, elephants in particular, is very high across savannas and brings far more variation in woody cover than would be expected from rainfall (Guldemond & Van Aarde 2008; Holdo 2007; Morrison *et al.* 2016). However, despite these perturbations and the extensive shrub encroachment observed in rangelands across the United States, Australia and South Africa (Asner et al., 2004); the persistent effects of rainfall on woody species are evident.

Woody cover is commonly used to describe the vegetation structure of drylands (Franz *et al.* 2010). We found woody biomass and production to be higher in the sub-humid zones compared to the arid and semi-arid zones; implying that in high rainfall areas, most of the plant mass is fixed in large trees. In contrast, trees in dry areas have very slow growth rates (Birkett and Stevens-Wood, 2005; February et al., 2013). February et al. (2013) showed that rainfall promotes growth of trees through increased water infiltration and this may explain the significant linear relationship between plant height and rainfall found by our study. Furthermore, stem diameter at breast height (dbh) is positively but nonlinearly related to height and linearly to canopy radius mainly for structural reasons (Cruickshank and Filipescu, 2012), perhaps explaining why we did not observe a significant linear relationship between both stem diameter and canopy width with rainfall. We found the turnover rate to be higher in drier areas probably because grass, which grow in drier areas, have higher turnover rates compared to long-lived trees, which grow on wetter areas (Grime, 1977).

Spatial dissimilarity in vegetation can occur in small geographic scales within similar rainfall regimes in savanna ecosystems due to micro-landscape and land use patterns. In our comparison between Amboseli and Maasai Mara, we show that despite the former area being relatively drier, its woody vegetation biomass and production was relatively higher than Maasai Mara in the late 1970s / early 1980s, highlighting the influence of varying soil texture in shaping woodlands in the two areas. The north-western parts Mara are characterised with clay-based soils (Walpole et al., 2004) while soils in Amboseli have a sandy loam topsoil and a clay loam subsoil (Maskall and Thornton 1991). In addition there exist differences in herbivore and human activities between the two areas. Firstly, in Maasai Mara, woody biomass may not have recovered from the massive transformation of woodlands to grasslands in Serengeti prior to 1980s (Sinclair et al., 2007) and in Maasai Mara in the 1960s (Dublin et al., 1990). These transformations were promoted by elephants which had moved into the Maasai Mara ecosystem due to an increase in settlements in areas outside the Serengeti-Mara conservation area (Dublin, 1991; Serneels et al., 2001; Lamprey and Reid, 2004); secondly, this period followed a period of tsetse fly infestation in Maasai Mara which occurred in the first half of the twentieth century which had expanded massively following the rinderpest epidemic in late 19th century leading to active tsetse-fly control by the local Maasai community and the government using fire to clear dense woodlands (Dublin, 1991; Serneels et al., 2001); thirdly, differences in management of livestock grazing areas, conservation initiatives and other natural resources between the two areas where Amboseli National Park is managed by Kenya Wildlife Services and Maasai Mara National Reserve is managed by Narok County Council and finally there are more fires in Maaasai Mara compared to Amboseli which suppress woody vegetation (Dublin et al., 1990; Lamprey and reid 2004; Walpole et al., 2004).

The combined influence of rainfall and disturbance can also change the species composition of dry areas. For example, in northern Burkina Faso in the West African Sahel an increase in rainfall and change in land use patterns led to an increase in drought tolerant tree and shrub species (Hänke et al., 2016). Our results show that

Massai Mara contains lower woody species diversity than Amboseli, despite the former being wetter than the latter and rainfall being directly related to plant diversity in most tropical semi-arid grasslands, including Serengeti National Park (Anderson, 2008). Woody vegetation species dominance in Maasai Mara was higher than in Amboseli and could be related to its low species diversity. Further monitoring of the DRSRS vegetation plots can elucidate the long-term impact of rainfall and human activities on species diversity of woody species in Kenyan savannas and particularly in Amboseli and Maasai Mara where tree cover has been known to change rapidly. The Maasai Mara-Serengeti ecosystem changed from open grassland to a dense woodland and back to open grassland within one hundred years (Dublin, 1991; Serneels et al., 2001; Birkett and Stevens-Wood, 2005) while vegetation communities within the Amboseli basin changed within fifty years from a hydrophytic dense woodland characterised by *Acacia xanthophloea* to a halophytic vegetation community with an increase in swamps (Altmann et al., 2002; Western and Maitumo, 2004; Western, 2006).

The extent to which rainfall regulates vegetation growth is particularly important when conducting vegetation modelling. For example, in arid and semi-arid areas, Dynamic Global Vegetation Models must be parameterized and validated by downscaled data for a given local ecosystem and the relationship between vegetation and biophysical factors such as rainfall and soil characteristics (Sankaran et al., 2005). Under climate change, East Africa is expected to become warmer and wetter, and our results indicate increased biomass and turnover of savanna trees under these conditions, supporting Dynamic Global Vegetation Models (Thonicke et al., 2001; Bond et al., 2005; Doherty et al., 2010). East Africa future climate prediction means that as it becomes warmer and wetter, potential evapotranspiration rates, soil texture and soil water infiltration abilities the will play a key role in shaping woodland structure in Kenyan savannas. However, the variability of precipitation in the region is also predicted to increase (Franz et al., 2010; Platts et al., 2015), and so it is important to understand the dynamics of woody species and both rainfall amount and seasonality to accurately predict their future trends based on future climatic forecasts.

4.6 Conclusion

This study has provided a foundation for understanding the relationship between woody species and rainfall in Kenyan savannas under relatively free ranging wildlife and pastoralism activities, finding that the structure and function of woody communities change significantly along a rainfall gradient. This trend is exhibited by some woody vegetation attributes such as plant height. Furthermore, a comparison of the structure and function of woody communities, and the controls on these between Amboseli and Maasai Mara provides useful insight into the importance of the micro-habitat variabilities and management control on shaping the vegetation dynamics of the two areas. Together, these findings can be used to inform coupled vegetation-climate-land use models that simulate transient changes in vegetation distribution and plant physiological processes in relation to changing climates and human activities. Finally, our study has demonstrated the usefulness of historical data, and also provided potential for revisiting and resurveying the DRSRS vegetation plots and reanalysing current vegetation trends against changing climate and land use types in Kenyan savannas. This potential perspective of measured vegetation change over a 40-year period can be used to provide a direct evidence base to inform our understanding of savanna ecosystem dynamics and response to recent historical land use management, conservation, changing land uses and global climate change.

4.7 Authors Contributions

R.K., D.W. and R.M. conceived and designed the study; D.W. provided the data from DRSRS; R.K. analysed the data; R.K. led the writing of the manuscript with substantial feedback from D.W., S.W. and R.M. All authors contributed critically to the development of ideas and drafts and gave their final approval for publication.

4.8 Acknowledgements

We would like to thank the personnel of DRSRS for selecting the vegetation sampling plots, collecting data and writing reports on their research design. We are grateful to the Government of Kenya for funding the DRSRS study and to Frank Msafiri of DRSRS for retrieving the missing data after many years. We appreciate the support received from African Conservation Centre (ACC) and from Caroline Mburu of Amboseli Conservation Program (ACP) on cleaning up the DRSRS data. This study was funded by a European Commission Marie Curie Initial Training Network grant to R.M. (FP7-PEOPLE-2013-ITN project number 606879).

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5 Social Perspectives of Trade-offs in Land Use Change

A pastoralist in Amboseli looking after his cows. Photo source: The author.

Trade-offs between Agriculture, Pastoralism and Conservation: Community perspectives from Southern Kenya

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5.1 Abstract

Despite mobile livestock grazing being recognised as the most viable and sustainable land use for semi-arid savannas, the levels of pastoral sedentarisation and transitions to agriculture continues to rise in many pastoral communities across the world. Using insights on long-term (from 1960 to present) land use changes from semi-structured interviews with local community elders we compare trends in livestock grazing, conservation and sedentarisation levels across three locations in southern Kenya. Our results highlight a 30% decline in livestock grazing over the latter half of the 21st century, due to expansion of agriculture and conservation. Despite this, livestock grazing remains the preferred land use type in subdivided and private lands in southern Kenya. The proportion of private land used by pastoralists did not vary across sites. However, the proportion of private land allocated for conservation activities varied significantly, ranging from 23% in Mara to 3% in Loita Plains. This disparity arises as, over the past 50 years, conservation activities have increased in Mara but have dramatically decreased in Loita Plains, despite being geographically close. Although the Loita Plains are largely a wet season dispersal area and support far less wildlife than Mara, we recommend that successful conservation activities from Mara (e.g. the formation and monetary support of more conservancies) should be undertaken in

Loita Plains, especially along wildlife migratory corridors and other lands with high conservation value.

Key words: Amboseli, climate, community perspectives, Maasai Mara, historical ecology, post-colonial, rangelands, sedentarisation, savanna

5.2 Introduction

The relationship between pastoralists, their livestock, and conservation in East African savannas, as with the rest of the world, is complex due to highly variable climates and rapidly changing socio-economic and political factors. While mobile livestock grazing in pastoral areas is deemed viable, sustainable (Kirkbride and Grahn, 2008; Zinsstag et al., 2016) and compatible with wildlife conservation (Bedelian and Ogutu, 2017), many pastoralists in East African savannas are increasingly becoming sedentary and changing their land use (Worden et al., 2003; Groom and Western, 2013; McCabe et al., 2014; Reid et al., 2014). In addition, in Kenya, despite 70% of livestock production and 75% of wildlife areas being located in the savannas (Kirkbride and Grahn, 2008; REGLAP, 2012; UNCCD and World-Bank, 2016), pastoral communities remain poor and have the lowest access to social services and infrastructure (REGLAP, 2012; UNCCD and World-Bank, 2016). The viability of these pastoral communities are crucial to the sustainability and resilience of the open savanna rangelands and the continued coexistence of livestock and wildlife in the face of land pressures and climate change (Githumbi et al., 2018). Thus understanding the interlinkages between pastoralism, land health and biodiversity is crucial to the future of large migratory populations of herbivore and carnivores in and beyond national parks (Western and Ssemakula, 1981).

Pastoralism first emerged in East Africa approximately 4500-4000 years ago (Marchant et al., 2018) though it was characterised by shifting livelihood patterns between agriculturalists, hunter-gatherers and other subsistence strategies (Smith, 1992; Prendergast, 2011; Courtney-Mustaphi et al., 2015; Marchant et al., 2018). It gradually spread to the mainland at different times. For example, in Amboseli, the earliest evidence of pastoral activities was found on the slopes of Mt. Kilimanjaro and is dated to 4100 years ago (Githumbi et al., 2018) while in the Tsavo ecosystem, the emergence of pastoralism is dated to 3370 years (Wright, 2011). Through livestock grazing and the use of fire, pastoral activities shaped savanna ecology for millennia and determined the structure, composition and nutrient levels of plants, and consequently, of wildlife (Lankester and Davis, 2016). Historical wildlife numbers were also shaped by other human activities such as hunting and ivory trade. For example, c.1860-1890, hunting in the Serengeti Plains of Tanzania accounted for a huge decline in elephant numbers (Courtney-Mustaphi et al., 2018). Additionally, since the late 1800s, the coexistence between pastoralism and wildlife in East African savannas was challenged by wildlife management concepts that encouraged separation of people and wildlife (Lankester and Davis, 2016). The sustainability of present day seasonally mobile pastoralism is threatened by climate change and land use change, which is driven by changing government policies, land tenure types and socio-economic factors (Franz et al., 2010; Hailegiorgis et al., 2010; Kariuki et al., 2018). With unpredictable rainfall in the savannas, mobile pastoralism has been used as an efficient land use type that ensures livestock has access to high quality forage during the dry season and diseases are avoided (Galvin, 2009; Homewood et al., 2009; Sundstrom et al., 2012). Pastoralists maximise their herds' grazing based on the changing distribution of rainfall patterns that allow them to access dry season grazing reserves and maximise digestible energy intake (Russell et al., 2018). To mitigate the effects of unfavourable climatic and socio-economic conditions, pastoralists use various adaptive strategies such as mobility, changing herd composition, improving livestock breeds by cross breeding and livelihood diversification (Kirkbride and Grahn, 2008; Lind et al., 2016).

Over the late twentieth and early twenty-first centuries, there has been a shift from specialised pastoralism to more sedentary and diversified livelihoods in East African savannas. For example, since the mid-1980s, the pastoral Pokot community of north-western Kenya has moved from pastoralism to sedentary honey production, agropastoralism, goat and camel herding (Bollig, 2016; Greiner and Mwaka, 2016), while the pastoral Maasai community in the Tarangire-Manyara area of northern Tanzania have gradually been changing from pastoralism to commercial and subsistence agriculture (Kiffner et al., 2014). Pastoralist sedentarisation has a diverse range of drivers. Among the Turkana community of northern Kenya, sedentarisation and livelihood diversification has been driven by the effects of droughts, high insecurity and famines (Kibet et al., 2016). Influence from immigrant non-pastoral communities often drives pastoralists to adopt agriculture or waged employment, with those who chose to maintain pastoralism being pushed further into drier and more marginal lands (Greiner and Mwaka, 2016). Sedentarisation often begins in wetter and fertile areas (Campbell et al., 2000; Greiner et al., 2013), denying pastoralists and their livestock access to the most productive dry season grazing reserves and creating conflict between competing land uses (Campbell et al., 2000; Serneels and Lambin, 2001; Little et al., 2008; Okello et al., 2011; Greiner and Mwaka, 2016). Conservation efforts further reduce the grazing resources available to pastoralists as relatively recently created protected areas may encompass historic grazing lands (Pas, 2018). Such subdivision of grazing land has led to declines in livestock and the resilience of pastoralism to drought (Campbell et al., 2000; Seno and Shaw, 2002; Sundstrom et al., 2012).

Despite human impact on the ecology of savannas being significant (Western and Maitumo, 2004) and human development linked to environmental sustainability (Sanz et al., 2017), the contributions of humans to savanna dynamics is poorly understood (Mograbi et al., 2015). Present day pastoralism is not just a function of herd size and number of households practicing pastoralism but also depends on diverse forms of pastoralism as well as other investments in pastoral areas (Lind et al., 2016). For pastoralism to be developed sustainably, decentralised governance with active integration of the views of local communities and stakeholders should be promoted (Zinsstag et al., 2016). Among the pastoralists, traditional ecological knowledge is centred around their perceptions on human-environmental interactions and historical knowledge of resource use (Butz, 2009). Tapping into this knowledge is important as it influences their decisions on how they utilise and manage natural resources (Kaye-zwiebel and King, 2014). Thus, utilising community perceptions is important for planning of local development and sustainable management of ecosystem services trade-offs (Cuni-Sanchez et al., 2016).

Using the perceptions of local community elders, our study develops an understanding of the drivers behind land use changes across southern Kenyan savannas through the postcolonial era. These savannas are characterised by a gradient that spans a range of rainfall, elevation and vegetation structure with marked overlaps of land use types that have developed over the recent past. These overlaps are observed in relatively dry areas where livestock grazing and agropastoralism are practiced or wet areas where agriculture and wildlife conservation are practiced. Our paper has three objectives: 1) To quantify changes in land use types from 1960 to present using the perceptions of local community elders in three study areas in southern Kenyan savannas. We quantify the overall trends in land use change in the three study areas and across land tenure types with a focus on private land tenure; 2) To establish and compare the drivers of land use changes and group ranch land subdivision across the three study areas; and 3) To compare community perceptions on use of subdivided private land across the three study areas, particularly in reference to conservation activities.

5.3 Study areas

We focus on three areas: Amboseli, Mara and the Loita Plains (Figure 5.1). The Amboseli ecosystem includes the Amboseli National Park (392 km^2) and the surrounding community ranches. Mean annual rainfall in Amboseli is 350 mm yr^{-1} and falls in two seasons: the short rains (November to January) and the long rains (March to May). Temperature in Amboseli ranges from lows of 12 ^{o}C in July to highs of 35 ^{o}C in February (Okello et al., 2011). Vegetation is characterised by sparse bushed grassland (Western and Lindsay, 1984) that is dominated by *Acacia* and *Commiphora* species. Over the last fifty years, woodland species in the Amboseli basin have declined and halophytic species and wetlands have increased (Altmann et al., 2002; Western, 2006).

The Mara ecosystem encompasses the Maasai Mara National Reserve (1510 km^2) and the surrounding pastoral lands. The pastoral lands surrounding the reserve were intended to act as wildlife buffer zones between the national reserve and the highly fertile agricultural lands in the northern part of Narok County (Serneels and Lambin, 2001; Serneels et al., 2001). Climate and vegetation in Mara is categorised as semi-arid to sub-humid (Serneels et al., 2001). Rainfall is highly variable with an average of 600 mm yr^{-1} on the eastern part and 1000 mm yr^{-1} on the western part where climate is influenced by Lake Victoria weather patterns (Lamprey and Reid, 2004; Ogutu et al., 2005). It is bimodal with short rains from October to December and the long rains from March to May. Mean annual temperature is 18°C (Waithaka, 2004). Mara is a grassland with scattered woodlands. Over the last 100 years, its vegetation has undergone changes from grassland to dense woodland and to grassland largely due to climate change, land use change, tsetse-fly and tick infections (Dublin, 1991; Serneels et al., 2001). Maasai Mara National Reserve accounts for 25% of Kenya's wildlife (Western et al., 2009) and is ranked first of all Kenyan protected areas because of high wildlife density, beautiful landscape and its annual wildebeest migration between the Serengeti and Mara ecosystems (Wishitemi et al., 2015).

The Loita Plains are approximately 30 km east of the Mara ecosystem (Figure 5.1) at an elevation of 1800 m and a mean annual rainfall of 400 mm yr^{-1} over two rainfall seasons (Serneels et al., 2001; Lamprey and Reid, 2004). The plains are covered by a dwarf shrubland and *Acacia drepanolobium* grassland (Ottichilo et al., 2000). The low-rainfall nutrient rich Loita Plains provides the wet season grazing range and the main breeding zone for Kenyan wildebeest population (Serneels and Lambin, 2001; Løvschal et al., 2017).

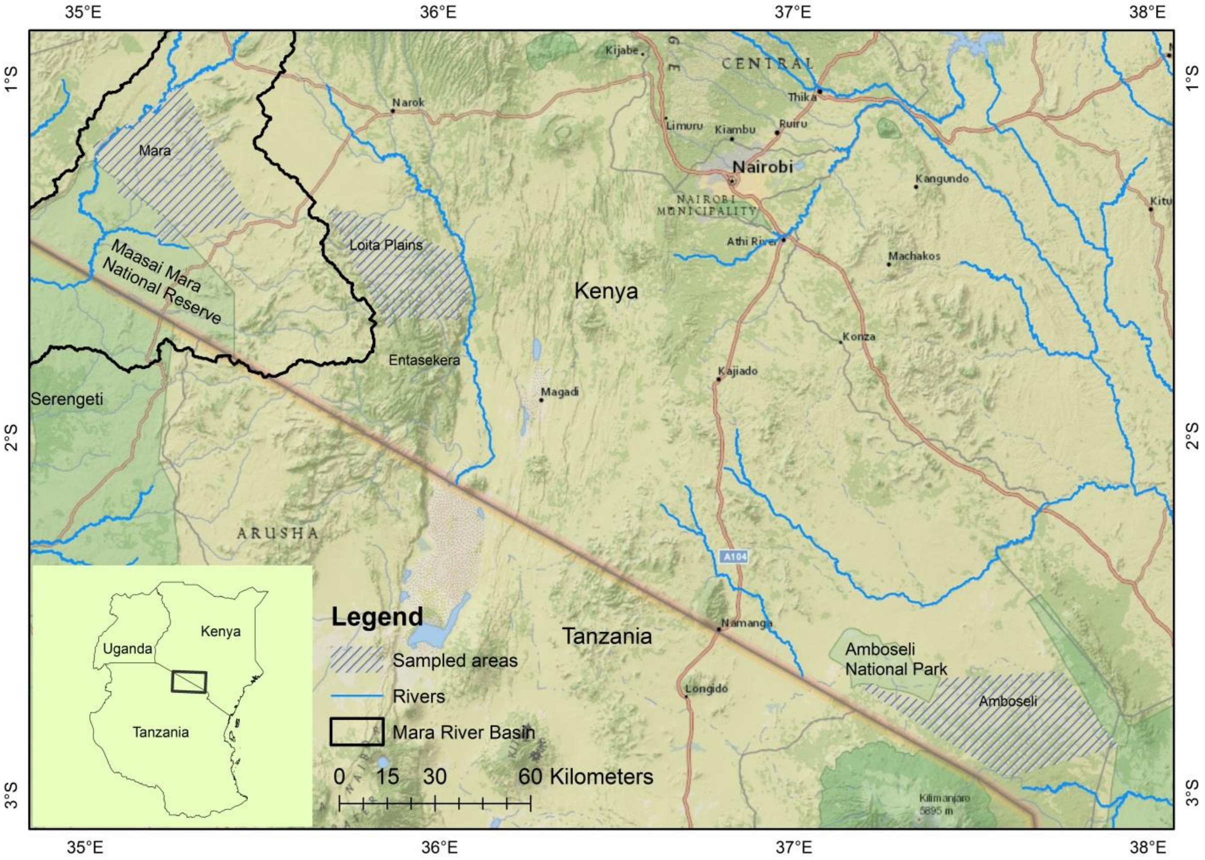

Figure 5.1: Location of the study areas and the surrounding ecosystems in southern Kenya. Base Layer Source: National Geographic.

5.4 Methods

To understand the long-term changes in land use types and the drivers of change among the three study areas, we compared the views of elderly community leaders by conducting 83 semi-structured interviews (Appendix 2) across the three sites. Thus, we consider ‘long-term’ to equate to the social memory of this group (approximately five to six decades). The interviews were conducted in January and February 2016 and the questions focussed on the history and drivers of land use types, land tenure, livelihood strategies and land management. We selected interviewees who had lived in the same area for five to six decades and the spatial boundary for the views of each interviewee was based on the boundary of the group ranch they lived in. Before conducting an interview, we explained the purpose of our interview to the respondent and each interview took between one and two hours. As the questions were written in English, and most elders could not understand English, the questions were translated by research assistants to Maasai or Swahili language and communicated to elders. The views from the elders were then recorded quantitatively and qualitatively.

Given the existing variations in land use types, land tenure types, water sources and conservation initiatives in our study areas, we selected our respondents using proportional stratified random sampling where selected respondents owned land that was representative of the different socio-economic and natural factors observed (Table 5.1). We were only able to interview resident landowners in the study areas and therefore did not capture the views of non-resident landowners. The interviewees included men (69) and women (14) who had lived in the same area for at least five decades and held land near community or national protected areas. Their land tenure varied from communal land, private land and community land that was in the process of privatisation. They had varying levels of education and livelihood sources.

Together with the interviewees, we categorised the current local land use into five types: livestock grazing, agriculture, livestock grazing with conservation, settlements and built-up areas. The livestock grazing land use was defined as land used for pastoralism alone while the agriculture land use consisted of small-holder rain-fed and irrigated agriculture. Conservation land was pastoral land that had been subdivided into individual and titled parcels of land and the landowners had decided to allow wildlife to forage on their land. Settlements and social facilities were not classified as a single category because the former comprised of pastoralist homesteads while the latter comprised of social facilities such as churches, health centres and schools.

Where land use types overlapped, such as agropastoral zones, the percent cover of each overlapping land use type was determined.

To capture the changing perceptions of land use change over time, we asked the pastoralists to state how the percent coverage of a given land use type, in their area, has changed over five decades. This provided us with insight spanning from the 1960s (when Kenya obtained its independence from the British government) to the present day. Also, most respondents could recall changes in land use patterns within this time frame; though not to the same degree. We only recorded land use events that respondents could recall and did not record those they were uncertain about, such as the beginning of subdivision of their group ranch or specific government policies that drove their land use options.

Table 5.1: General characteristics of the sampled sites in the study areas

Study area	**Number of interviewees**	**Sampled locations**	**Main livelihoods**
Amboseli	30	Olgulului/Ololorashi	Pastoralism
		Kuku	Pastoralism
		Namelok	Pastoralism, agropastoralism, agriculture
		Kimana	Pastoralism, agropastoralism, agriculture
Mara	27	Enonkishu	Community conservancy, limited pastoralism
		Mara North	Community conservancy, limited pastoralism
		Maji Moto	Pastoralism
		Naboisho	Community conservancy, limited pastoralism
		Talek	Pastoralism, conservation
		Motorogi	Community conservancy, limited pastoralism
Loita Plains	29	Narosura	Pastoralism, agropastoralism, agriculture
		Elangata	Pastoralism
		Kanukha	Agropastoralists, agriculture
		Osupuko	

5.5 Data analysis

Both descriptive and inferential statistics were used to assess patterns and relationships in land use types in the three study areas. Data analysis was performed in R studio. The level of significance was set to P = 0.05 throughout. Analyses of variance tests were used to assess differences in percent cover of land use categories in different decades, study areas and land tenure types. To assess the relationship between land use categories and the study areas as well as between land use categories and land tenure, chi-square tests (X^2) were used. As published remote sensing results do not cover the same areas as our study areas, it was difficult to compare the views of temporal land use change from the elders with published remote sensing results. Thus, we include the standard error of the mean to the percent land use change that the elders estimated.

5.6 Results

5.6.1 Changes in livestock grazing, agriculture and conservancies over time across the study areas

Changes over time in livestock grazing and agriculture in the three areas were inversely related. While livestock grazing has been decreasing, small holder agriculture has been increasing. On the whole, in all the areas, the interviewees were of the opinion that the area of land used for livestock grazing had decreased from 81% in the 1960s to 51% by 2016 while that used for agriculture had increased from 1% in the 1960s to 22% in 2016 (Table 5.2). The total proportion of private land used for conservation activities in the three areas was perceived to increase from 4% in the 1960s to 24% in 2016. However, the increase in private land allocated for conservation activities was dominated by Amboseli and Mara (which both increase) and, in fact, was perceived to have decreased in the Loita Plains from 15% to 2% over the same period (Table 5.2).

Overall, significant differences were established in the proportion of land used for livestock grazing across the decades ($F_{5,\ 480} = 33.68$, $p<0.001$) and the study areas ($F_{2,\ 483} = 28.04$, $p<0.001$; Table 5.2). However, a two-way ANOVA did not establish any difference in the proportion of livestock grazing land use type in the interaction terms between the decades and the study areas ($F_{10} = 0.74$, $p = 0.69$, $R^2 = 0.35$).

Expansion of agriculture in Mara was not perceived to be as high as in Amboseli and Loita Plains. There was a significant difference in the proportion of land used for agriculture among the decades ($F_{5,\ 465} = 32.25$, $p<0.001$) and among the three study areas ($F_{2,\ 468} = 22.55$, $p<0.001$; Table 5.2). Additionally, a significant difference ($F_{10} =$

6.254, $p<0.001$, $R^2=0.4$) in the proportion of land used for agriculture was shown in the interaction between decades and study areas.

The proportion of private land perceived to be used for conservation activities was significantly different across decades ($F_{5, 203} = 14.24$, $p<0.001$) and among the three study areas ($F_{2, 206} = 7.57$, $p<0.001$; Table 5.2). However, the interaction between the decades and study areas did not establish any difference ($F_{10} = 7.57$, $p = 0.25$, $R^2 = 0.34$) in the proportion of land used for conservation activities.

Table 5.2: Percent area change and percent standard deviation (in brackets) in livestock grazing, agriculture and conservancies from 1960s to 2016, as estimated by community leaders in Amboseli, Mara and Loita Plains.

	Livestock grazing (percent cover and standard deviation)					
	1960s	**1970s**	**1980s**	**1990s**	**2000s**	**2010s**
Amboseli	91 (6.6)	90 (7.4)	87 (7.2)	81 (11.6)	73 (14.7)	55 (23.2)
Mara	72 (23.9)	74 (20.2)	69 (23.6)	68 (21.2)	59 (22.9)	50 (26.2)
Loita Plains	77 (12.6)	76 (13.1)	72 (10.6)	65 (10.9)	57 (12.7)	47 (13.9)
	Agriculture (percent cover and standard deviation)					
	1960s	**1970s**	**1980s**	**1990s**	**2000s**	**2010s**
Amboseli	0 (0)	1 (3.7)	3 (5.9)	6 (9)	13 (12.6)	29 (21.44)
Mara	0 (0)	0 (0)	0 (0)	1 (3.1)	1 (2.3)	3 (10.5)
Loita Plains	1 (6)	2 (8)	5 (9.7)	9 (12.5)	17 (17.3)	30 (23.2)
	Private conservation areas/conservancies (percent cover and standard deviation)					
	1960s	**1970s**	**1980s**	**1990s**	**2000s**	**2010s**
Amboseli	1 (2.8)	2 (3.4)	3 (5.5)	5 (5.6)	8 (6.9)	16 (11.7)
Mara	5 (13.6)	5 (13.6)	7 (14.8)	10 (15.8)	20 (19.2)	33 (20.3)
Loita Plains	15 (21.2)	10 (14.1)	5 (7.1)	4 (4.9)	3 (3.5)	2 (2.1)

5.6.2 Drivers of land use change

In Amboseli and Loita Plains, rainfall variability was perceived to be the most important cause of change from pastoralism to other livelihoods while in Mara, land subdivision and increase in education levels were the leading causes of livelihood change (Table 5.3). Presence of animal diseases, such as respiratory diseases, was mentioned as a factor of land use change in Amboseli and Mara but was not mentioned in Loita Plains. Additionally, increase in agriculture and influence from immigrant communities were perceived to be influential in pastoral land use change decisions in Amboseli and Loita Plains but not in Mara.

Table 5.3: Drivers of land use change as perceived by pastoralists in southern Kenyan savannas

Site	Drivers of land use change	Views (%)
Amboseli	Rainfall variability	19%
	Population growth	19%
	Socio economic development	18%
	Tertiary education level	11%
	Land subdivision	11%
	Animal diseases	7%
	Conservation has more money	5%
	Increase in agriculture	4%
	Little benefit from conservation	3%
	To secure financial stability	2%
	Immigrants influence	1%
Mara	Land subdivision	21%
	Tertiary education level	15%
	To secure financial stability	15%
	Conservation has more money	12%
	Population growth	12%
	Rainfall variability	11%
	Socio economic development	10%
	Animal diseases	2%
	Little benefit from conservation	1%
Loita Plains	Rainfall variability	24%
	Tertiary education level	18%
	Land subdivision	16%
	Population growth	15%
	To secure financial stability	13%
	Socio economic development	10%
	Increase in agriculture	3%
	Immigrants influence	1%

5.6.3 Drivers of land subdivision

Land subdivision as a factor of land use change was mentioned by 11%, 21% and 16% of pastoralists in Amboseli, Mara and Loita Plains respectively. The reasons for land subdivision varied across the three study areas with the desire to have personal ownership of land being the most common reason (Figure 5.2). The fear of losing land was mentioned by more people in Mara compared to Amboseli and Loita Plains, and agricultural expansion was mentioned only in Amboseli. Influence from subdivided group ranches across Kenyan rangelands and high population growth had more mentions in Loita Plains compared to Amboseli and Mara (Figure 5.2). Views from Amboseli were more diverse compared to those from Mara and Loita Plains probably because the interviewers in Mara and Loita Plains were different from those at Amboseli.

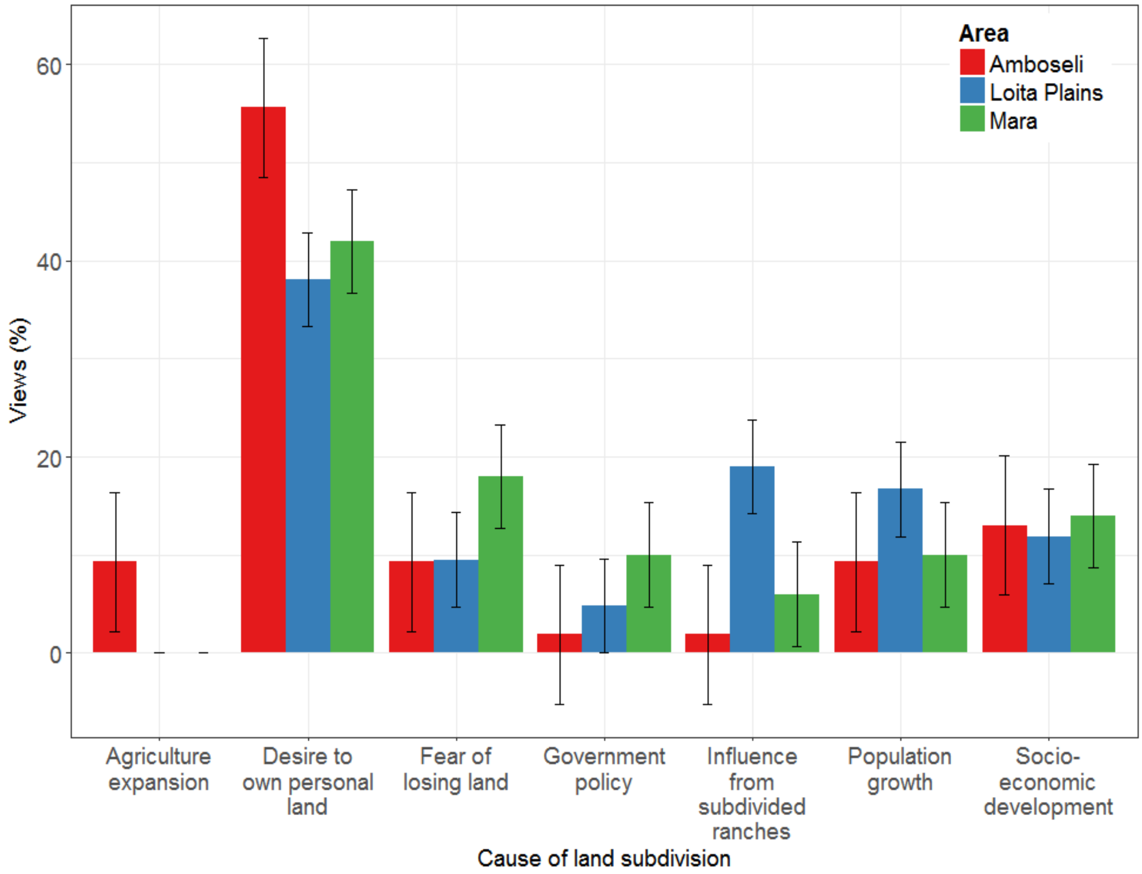

Figure 5.2: Causes of land subdivision in Amboseli, Loita Plains and Mara in southern Kenyan savannas. The error bars represent the standard error of the mean.

5.6.4 Changes in land use types in relation to land tenure types

Across the three study areas, communal lands were perceived to be used mainly for extensive livestock grazing while private lands were perceived to be used for both agriculture and livestock grazing. Government lands (though not widespread) were largely used for social facilities, conservation and livestock grazing (Figure 5.3). In Amboseli, livestock grazing and agriculture were perceived to be dominant on private land. In Mara, elders perceived that there was no agriculture and low levels of conservation on communal lands while private lands had low levels of agriculture but high levels of conservation. By contrast Loita Plains had higher agriculture levels and lower conservation activities in communal and private lands when compared to both Amboseli and Mara. The relationship between land use type and land tenure was significant (X^2=118.27, df=8, n=362, p<0.001) as well as that between land use types and study areas (X^2=38.55, df=8, n=362, p<0.001).

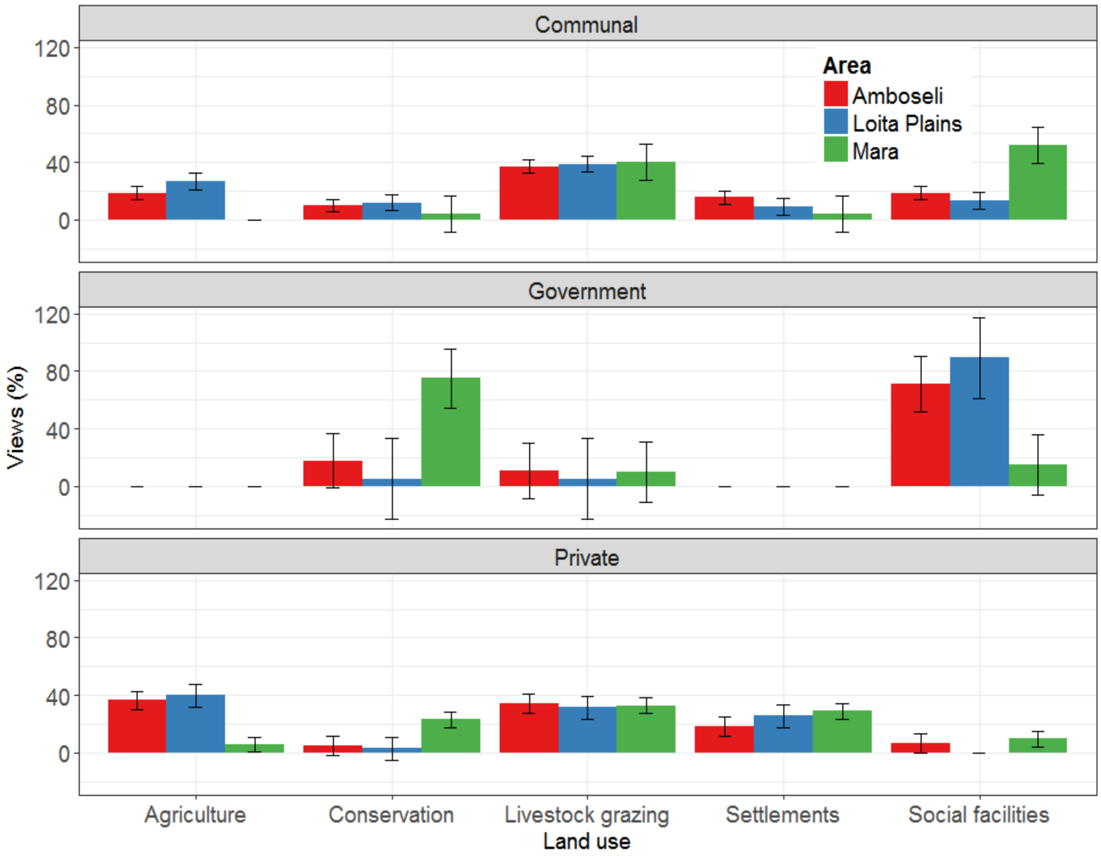

Figure 5.3: Land use within land tenure types in southern Kenyan savannas. In all the graphs, the error bars represent the standard error of the mean

5.6.5 Allocation of private land use to agropastoral activities

The proportion of private land used by pastoralists either for livestock grazing, subsistence agriculture or a combination of subsistence and commercial agriculture did not vary significantly ($F_{2,237}$ = 0.01, p=0.99) across the three study areas. The mean (± SE) percentage of land used by pastoralists in the three study areas for livestock grazing, subsistence agriculture and subsistence agriculture together with commercial agriculture was 61.38 (± 3.6) %, 21.5 (± 3.4) % and 20.04 (± 2.0) %. Of the three land uses, livestock grazing was perceived to be more widespread in the Mara compared to Amboseli and Loita Plains where both subsistence and commercial agriculture were higher (Figure 5.4). The difference in the proportion of land allocated by pastoralists to the three land use types was significant ($F_{2,237}$ = 75.67, p<0.001).

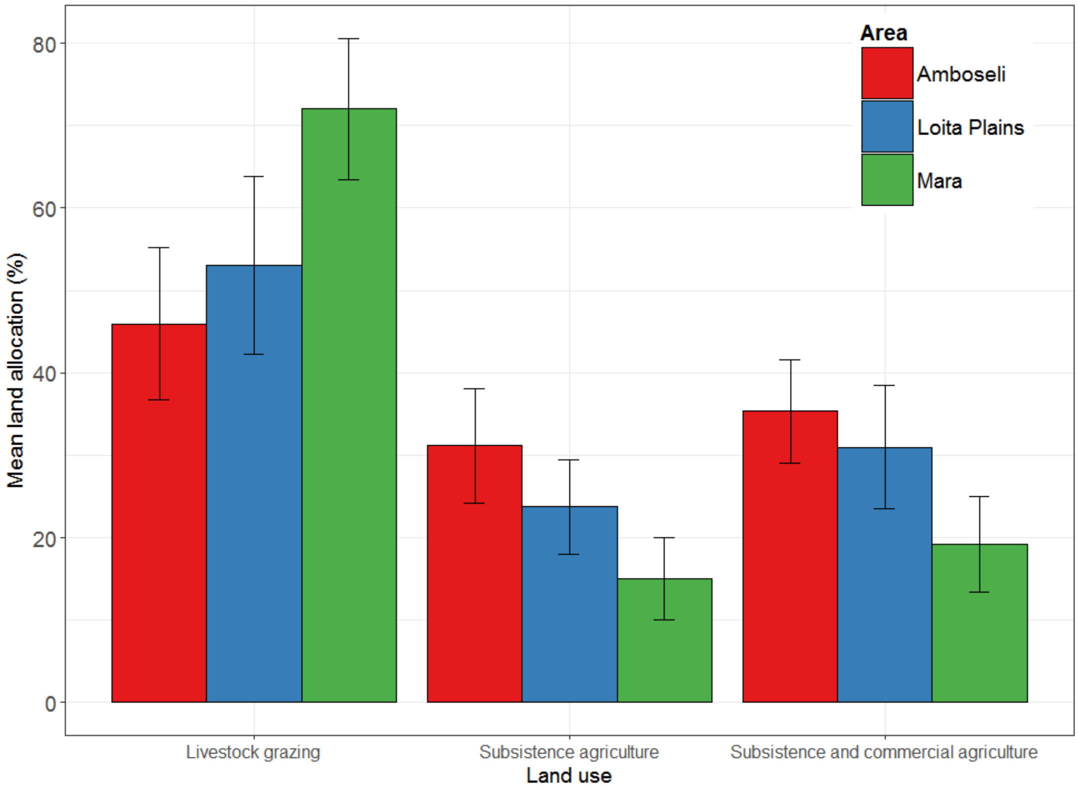

Figure 5.4: Proportion of agricultural and livestock grazing land use on private land in Amboseli, Loita Plains and Mara. The error bars represent the standard error of the mean.

5.7 Discussion

The interaction between pastoralists, their livestock, and both conservation and agriculture in East African savannas is complex. However, our results provide interesting insights, highlighting that: 1) conservation activities in Mara and Amboseli have been more successful over the long-term than in Loita Plains, and 2) agricultural expansion has occurred at all three sites at the expense of pastoral land.

5.7.1 Pastoralism and conservation

The increase in pastoral land used for conservation initiatives has been substantially higher in Mara than in Amboseli and Loita Plains, primarily because Mara has higher wildlife densities which attract tourism. Community lands close to protected areas in Amboseli and Mara are largely pastoral and support wildlife that migrates between protected areas and community lands. These lands have been used to form ‘community’ and ‘group’ conservancies whereby a community conservancy is formed by a community on community land and a group conservancy is formed by pooling land owned by private landowners for wildlife conservation (KWCA, 2016). Conservancies are set up primarily to attract tourism and to generate a cash income. In the process they discourage fragmentation of wildlife habitats and ensure that humans, livestock and wildlife utilise available resources and human-wildlife conflicts are reduced. The growth of community and group conservancies in Kenya escalated in the 2000s. In Mara, there were only two conservancies in 2006 covering a total area of 14,576 hectares (ha) and by 2010, they had increased to eight covering a total area of about 100,000 ha (Osano et al., 2013); by 2016 16 conservancies cover 170,131 ha, supporting 106,102 households and employing 300 rangers (KWCA, 2016). In contrast, by 2016 Amboseli had 17 conservancies under the Amboseli Ecosystem Trust (AET), covering 79,562 ha and employing 476 people as rangers, while in the Loita Plains, the South Rift Association of Land Owners (SORALO) only works with six conservancies, occupying 38,850 ha, in the area connecting Mara, through Loita Plains, and Amboseli (KWCA, 2016). Mara has many wildlife conservancies because it has so much wildlife outside the reserve and supports over 150 lodges while Amboseli has a far lower wildlife density, but sufficient to support some 20 lodges. Loita Plains has very low and seasonal wildlife densities and is not a major attraction for tourists. It is no wonder elders in Loita Plains noted a marked decrease in the land used for conservation over the past 50 years (Table 2).

Besides wildlife-based benefits received from rent paid by tourism investors to land owners who lease their land for wildlife conservation (Boone and Lesorogol, 2016; Jandreau and Berkes, 2016; Bedelian and Ogutu, 2017), other wildlife benefits are in forms of fees from cultural bomas, training and employment of local community members as game scouts. The nature, distribution and perceptions of wildlife benefits often vary across different ecosystems. In Amboseli, group ranches around the national park have been supported by the park, which since 1977 has contributed a portion of gate receipts, largely for scholarships, to the group ranches, making this the largest source of wildlife income for these communities. However, unequal distribution of benefits from wildlife has been reported as most individual pastoralists do not receive any direct or indirect benefits from wildlife conservation (Bulte et al., 2008). On the other hand, in the Mara, wildlife is an important source of income for most households (Homewood et al., 2009) and has increased since the mid-1980s with both the local Maasai pastoralists and the local government being involved in it (Lamprey and Reid, 2004). Also, the conservancy concept may have gained momentum in Mara because the local community is involved and the payment system for land leased is efficient.

In Loita Plains, pastoralists deemed pastoral land used for conservation had declined over time. This is probably accounted for by the vast areas in the Loita Plains that have been converted to agriculture since early 1970s (Serneels and Lambin, 2001). Between 1977-1997, there was large scale conversion of rangelands in Loita Plains to wheat farms leading to the displacement of wildebeest from their wet season grazing areas and a 70-80% reduction in their numbers (Ottichilo et al., 2001; Serneels and Lambin, 2001). In addition, the areas we sampled in Loita Plains neither had conservancies nor tourism investments. The absence of wildlife enterprises in Loita Plains reflects the historical concentration of tourism in parks in general, and their dry season concentrations of wildlife in particular. This is especially so in Mara with annual migrations into the reserve and surrounding group ranches. These areas have a high population density and a wide range of ungulates and predators year-round. The Loita Plains have far less habitat diversity and largely supports wet season migrations of wildebeest and zebra which have declined steeply in the last 30 years (Ogutu et al., 2016). So the historical disparity between Mara and Loita Plains has grown and there is little to attract tourists today, given the high subdivision and sedentarisation levels.

5.7.2 Pastoralism and agriculture

Community elders across the three study areas were of the opinion that the land available for livestock grazing had declined significantly over time. While the number of cattle in southern Kenyan savannas has decreased, the number of sheep and goats have increased sharply since the 1990s (Western and Nightingale, 2003; Lind et al., 2016). Consequently, the grazing pressure has not decreased but has increased heavily due to land loss and sedentarisation (Western et al., 2015; Kimiti et al., 2016). The elders further noted that land used for livestock grazing was declining from the 2000s, while that used for agriculture, especially in Amboseli and Loita Plains, had expanded. Reduction of livestock herds at this time were driven by the 2006 and 2009 droughts that led to the loss of 90% of cattle and 70% of sheep and goats in southern Kenya (Lind et al., 2016). It could also be due to declining per capita livestock holdings which is the key point driving a transition from a subsistence to cash economy and diversification of livelihoods.

Agriculture levels in all our sampled areas were perceived to have increased significantly over time. Pastoralists turn to agriculture as a means of supplementing their income from livestock grazing (Seno and Shaw, 2002). Increase in rain-fed agriculture towards the close of the twentieth century may have been a result of the 1997/1998 El Niño rains. In Amboseli, both highland rain-fed agriculture and irrigated agriculture expanded from the 1970s (Galvin et al., 2008). By the late 1980s, most fertile areas in Amboseli had already been settled with most Maasai pastoralists actively practicing agriculture on their own farms from the 1980s and 1990s (Western and Nightingale, 2003). At the turn of the twenty-first century, agriculture expansion in Amboseli was driven by economic growth and improved market access in Kenya and overseas (Campbell et al., 2000). Presently, it continues to be enhanced by local pastoralists who rent out large portions of their land to non-pastoral farming communities (Bulte et al., 2008). Irrigated agriculture in Amboseli is driven by the many large swamps which have been tapped for irrigation and have attracted a large immigrant population of farmers as well as local Maasai. Income from irrigated agriculture is used to supplement and offset the shortfall in the pastoral economy. However, with swamp basins, where most irrigation in Amboseli occurs, being predominantly saline (Worden et al., 2003) and highly susceptible to erosion (Okello and Kioko, 2010); irrigation agriculture is not sustainable. Furthermore, it reduces water access to people, livestock and wildlife and is a cause of human-wildlife conflict.

From satellite imagery of the Mara River Basin, land use change, especially small-scale agriculture peaked during 1995-2003 (Mwangi et al., 2018). Expansion of smallholder agriculture in Mara and Loita Plains is driven by changes in population density, socio-economic factors and proximity to permanent water sources (Serneels and Lambin, 2001). The areas we sampled in Mara were close to the Maasai Mara National Reserve and tended to have very low agriculture levels. Additionally, as a result of failed agricultural harvests every year in Mara, subsistence rainfed agriculture tends to be restricted to poorer households who have no other livelihood opportunities (Homewood et al., 2009). By contrast, smallholder agriculture has been documented to expand on northern Loita Plains (Lamprey and Reid, 2004) where cropland has been expanding since the 1970s (Serneels and Lambin, 2001). Smallholder agriculture is common along rivers in Loita Plains, and is sometimes practiced together with dairy farming, especially among landowners whose land is close to roads and markets.

5.7.3 Drivers of land use change and land subdivision

The elders perceived the main drivers of land use change were rainfall variability, land subdivision, population growth and socio-economic development. Drivers of land use change are known to be interlinked and work together to drive pastoral land use decisions. Rainfall variability was considered the primary factor shaping land use change in Amboseli and Loita Plains. This is probably because these areas are generally dry (350 – 400 mm yr^{-1}) as they lie in rain shadows. Livestock numbers rise and fall with rains and droughts leaving pastoralists vulnerable to the erratic weather experienced in semi-arid savannas (Western and Nightingale, 2003). Pastoralists with land in proximity to permanent water bodies change to irrigated agriculture as they rebuild their herds after droughts or periods of disease (Mwangi and Ostrom, 2009; Greiner and Mwaka, 2016). Some elders in Amboseli mentioned agriculture expansion and influence from immigrant non-pastoral communities as factors responsible for driving land use change decisions. In Amboseli, irrigated agriculture along swamp edges is seen as a favourable land use to adapt to because of the availability of water from swamps and pastoralists willing to lease their land to immigrant agricultural communities (Okello et al., 2011). Additionally, agriculture is perceived to be beneficial as it provides subsistence foods and higher individual returns compared to wildlife (Bulte et al., 2008; Okello et al., 2011). In the Mara, while the demand for leasing land for agriculture is still high, agriculture is declining in some areas partly because of local conservation initiatives (Homewood et al., 2009).

The leading causes of land subdivision identified by the elders within our three study areas (in order of impact) were: need for individual land ownership rights, population growth, socio-economic development, influence from subdivided group ranches and government policy. Group ranch subdivision in Kenyan savannas has been promoted by government policies aimed at promoting land privatisation and intensification of livestock production as mobile pastoralism was perceived to be inefficient (Mwangi and Ostrom, 2009; Osano et al., 2013). These policies were a potential tipping point, as they commenced a positive feedback cycle resulting in further subdivision. That is to say that the failure of group ranches to manage livestock grazing, to provide security in land rights and to provide better economic options for pastoralists amidst changing climates, rising human population and national development further enhanced the desire by pastoralists to subdivide the group ranches (Majule et al., 2009; Sundstrom et al., 2012; Osano et al., 2013). Agriculture expansion and the lack of benefit from conservation were also mentioned as factors leading to land subdivision. When land gets subdivided, pastoralists, particularly those in wetter areas, turn to agriculture (Lamprey and Reid, 2004). This is highlighted by the responses from the elders in Amboseli and Loita Plains who felt agriculture levels were higher in private lands. Generally communities do not invest in agriculture on group ranches until they have been allocated individual plots, hence the high agriculture levels on private lands. In Mara, subdivided and private lands were perceived to have higher conservation levels compared to Amboseli and Mara. This could be attributed to the growing number of group conservancies in the area in the last decade (Osano et al., 2013). Interestingly, livestock grazing across the three areas was perceived to be practiced at almost similar levels in both communal and private lands. In addition, in all the three areas, the area allocated for livestock grazing in subdivided and privatised lands was perceived to be higher than that allocated for subsistence or commercial farming. This shows that pastoralists never stop practicing livestock grazing as it remains a huge part of their livelihood and culture (Homewood et al., 2009; Sundstrom et al., 2012).

Sedentarisation of pastoralists and land use change has implication on the ecological, social and economic components of savannas. Sometimes pastoralists prefer sedentarisation as it enables their families to attend school and use available social facilities. However, sedentarisation around key resource areas has negative consequences on savanna ecology. The combined impact of increased sedentarisation, land subdivision and land use change is the reduction of the spatial scale of ecological and social connections (Western et al., 2009; Lind et al., 2016). The immediate impact of sedentarisation on pastoralists is the year-round non-mobile livestock grazing patterns which degrades the grasslands and reduces its productivity per unit of rainfall (Western et al., 2015). In Mara, movement of wildlife has been restricted by settlements and urban centres that have been developing near the national reserve and in the group ranches (Ogutu et al., 2009). In Loita Plains, decline in wildebeest numbers has been attributed to agriculture expansion which narrows the migratory corridor between grazing lands (Serneels and Lambin, 2001). Land use change in the Mara has also been attributed to increased sedimentation in the Mara River as well as a 97% change in the streamflow of the Nyangores River, which is a tributary of the Mara River (Mwangi et al., 2018).

Though recent policies and legislation in a number of African countries, including Kenya, formally recognise mobile pastoralism as an efficient and viable land use, the practice lacks support in its implementation (Pas, 2018). Pastoralism is still challenged by changing climatic and socio-economic conditions. Going by the predicted climate change scenarios for East Africa, which forecast a warmer and wetter future; pastoralism may become attractive as the impact of rainfall variability on pasture, and consequently on livestock numbers, will be reduced. Addressing the sustainability of savannas should utilise social, ecological and economic perspectives which should integrate science-based management strategies and indigenous knowledge from rangelands communities. As the key land use change negatively affecting rangeland sustainability is agricultural encroachment, particularly in sub-arable rangelands; searching for science-based solutions should integrate views from rangeland ecologists and agriculturalists. The focus on the sub-arable rangelands should be on what it will take to sustain their productivity and resilience. This can be addressed by answering important questions such as: How can continued mobility and maintenance of wet and dry season grazing reserves be promoted in the rangelands in the face of rising human populations? How can improved livestock breeds, extensive marketing and income diversification through wildlife enterprises improve the well-being of pastoralists? Where a location is important to conservation and the costs of wildlife are insufficient, the opportunity costs to land owners can be offset by leases and payments for ecological services. In addition, stratifying wildlife areas relative to their importance and focusing on those with greatest potential and least alternative demand would address rangeland sustainability issues. This would probably mean ignoring the Loita Plains and focussing on the Loita Hills which connects wildlife populations across the Rift Valley.

5.8 Conclusion

This study shows the importance of utilising the views of local community elders to understand land use change in East African savannas. By comparing three study areas the similarities and differences in perceptions of land use across in rangelands are unveiled. Our respondents across the three study areas deem the main land use changes have been the decline of livestock production and the expansion of agriculture. However, the trends of wildlife conservation land use differed. In Amboseli and Mara, pastoral land used for conservation was reported to increase, with the formation of conservancies being the driving force behind the increase. However, in the Loita Plains, pastoral land used for conservation was reported to be declining with increasing climatic variability, increase in education levels and land subdivision mentioned as the leading drivers of land use change. Our study presents insights from combined community voices from across rangelands of southern Kenya. These voices provide historical insights into the interactions between climate, livelihood and conservation that are relevant to developing sustainable pastoral livelihoods while maintaining space for conservation and enhancing resilience in the face of increasing variable climate and land use change.

5.9 Acknowledgement

We would like to thank the National Commission for Science, Technology and Innovation (NACOSTI) for granting us a research permit to conduct field work. We are grateful to the pastoralists who patiently talked to us and filled in our questionnaire. We thank the field assistants in Amboseli, Mara and Loita Plains: Rebecca Muriuki, Daniel Letee, John Lembakuli, Francis Sopia and Saitoti Silantoi. This work was funded by the European Union under the Resilience in East African Landscapes (REAL) Marie Curie Initial Training Network Project 606879 grant given to RM.

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6 ABM Insights on Climate Change, Land Use Change and Conservation

Amboseli during the dry season in July 2017. Photo source: The author

Rangeland Livelihood Strategies under Varying Climate Regimes: Model Insights from Southern Kenya

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Received: 31 January 2018; Accepted: 10 April 2018; Published: 12 April 2018

6.1 Abstract

Rangelands throughout sub-Saharan Africa are currently undergoing two major pressures: climate change (through altered rainfall and seasonality patterns) and habitat fragmentation (brought by land use change driven by land demand for agriculture and conservation). Here we explore these dimensions, investigating the impact of land use change decisions, by pastoralists in southern Kenya rangelands, on human well-being and animal densities using an agent-based model. The constructed agent-based model uses input biomass data simulated by the Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) dynamic vegetation model and parameterized with data from literature. Scenarios of land use change under different rainfall years, land tenure types and levels of wildlife conservation support were simulated. Reflecting reality, our results show livestock grazing as the predominant land use that changes with precipitation and land tenure leading to varying livelihood strategies. For example, agriculture is the most common livelihood in wet years and conservation levels increase with increasing support of wildlife conservation initiatives. Our model demonstrates the complex and multiple interactions between pastoralists, land management and the environment. We highlight the importance of understanding the conditions driving the sustainability of semi-arid rangelands and the

communities they support, and the role of external actors, such as wildlife conservation investors, in East Africa.

Keywords: agent-based-model; climate change; conservation; grazing; pastoralists; precipitation; savannas; social-ecological systems

6.2 Introduction

Rangelands occupy 45% of the earth's land surface and 61% of the African continent [1] with 35% of African rangelands under permanent pasture [2]. They include grasslands, shrublands and savannahs used largely for livestock production and wildlife conservation that are often characterized by low productivity, sparse human population and common land use [2,3]. About 60% of global rangelands are relatively dry [1] with water scarcity common during certain months of the year [4,5], leaving any local human populations who are dependent on their ecosystem services at risk that is often mitigated by migration.

In East Africa, ecosystems are shaped by long term interactions between changing climates and human activities [6,7]. Human impact, through land use change, is one of the strongest factors changing rangelands and is driven by the demand for ecosystem services [3,8]. However, rainfall is a major control of human land use options [9]. Rainfall seasonality affects pasture production independent of mean annual rainfall [10]. Rainfed agriculture is only viable in areas receiving at least 700 mm yr^{-1} of rainfall [9,11]; thus, pastoralism is the main livelihood strategy in areas of low and/or highly variable rainfall [12]. Wildlife and livestock utilize rangelands in complementary ways [13–15] where livestock grazing maintains the rangelands for wildlife by keeping them open and as hotspots of biodiversity [16,17].

In arid and semi-arid areas of Kenya, the pastoral economy accounts for 90% of all employment opportunities and 95% of household income [18]. Pastoralists in Kenyan rangelands were organized in group ranches to allow members to own land communally, to improve livestock production and encourage socio-economic development [19]. To reduce their vulnerability to unfavourable climates and socio-economic factors, pastoralists use various adaptation and coping mechanisms such as movement of livestock, changing livestock herd composition and selling stock to get money [18,20,21]. In the 1970s, the Kenyan Government deemed pastoralism as an inefficient land use type [22] and encouraged sedentarization and/or land subdivision, commercialization and privatization of communal group ranches [23,24]. Furthermore, leadership in the group ranches was ineffective and did not provide equitable distribution of resources to all group ranch members leading to their dissatisfaction and prompting further subdivision [19,25]. As a result, by the end of the twentieth century, the future of exclusive pastoralism in East African rangelands was uncertain [10,26]. With increasing sedentarization and subdivision; land tenure became an important driver of pastoralists land use change decisions, agriculture expanded in wet areas and near permanent water bodies [22,27,28] and wildlife conservancies were formed in response to changing climatic, socio-economic and political factors [3,17,29].

The sustainability of pastoralism is primarily threatened by climate and land use change [30] and its success depends on rainfall patterns, land availability, forage availability and socio-economic changes. About 65% of the pastoral population living in arid and semi-arid areas in Kenya live below the poverty line [31]. With low income, decreasing livestock numbers and increasing climate variability, the number of pastoralists that can rely entirely on livestock reduces making livelihood diversification and/or intensification a necessity [1,10,11]. Pastoralists who can no longer sustain themselves by livestock grazing use their land for agropastoralism, agriculture or real estate. These land use transformations cause rangeland fragmentation through the loss of connectivity between landscapes [23].

In contrast to some other parts of Africa, diverse wildlife species still coexist with pastoralists and agropastoralists within East Africa [1,11]. The rapidly growing human population, multiple socio-economic and political factors and the interaction between pastoralist activities and wildlife pose a challenge on how best the sustainability of East African rangelands can be addressed. This unique interaction between humans and rangeland ecosystem services make them complex social-ecological systems where adaptations between the social and ecological components need to be understood. Additionally, it is by understanding the interactions between pastoralist livelihoods and the environment that more sustainable management of pastoral lands futures in East Africa can be developed. As the interactions between components in social-ecological systems are complex, nonlinear and adaptive, perspectives from social and natural environments have been used to understand them [32]. However, integrating these perspectives is challenged by the difficulty of understanding the interactions between multiple ecosystem services and trade-offs in human impact [33] making simulation modelling a potential tool to quantitatively address the response of pastoral activities to changing socio-economic and environmental factors [34]. As such, integrated modelling could contribute to answering important questions of interest to conservation researchers and practitioners, including: Which driver (biological, climatic, or anthropogenic) is more important in driving livelihood strategies in rangelands? How can payment for ecosystem services enhance conservation activities in rangelands? How can trade-offs between conservation and national development be addressed to promote sustainable development? Who are the likely “winners” and “losers” in rangelands under climate change scenarios?

Our study aims to understand grazing and sedentarization levels in southern Kenyan rangelands using an agent-based model to simulate pastoral land use decision making criteria and the impact it has on animal densities and pastoral livelihoods. Two objectives were used to address this research. First, we aim to show land use change across different rainfall years and land tenure scenarios. These land use change types are simulated over varying levels of wildlife conservation support in form of maximum annual income per land use type. Second, we aim to establish the impact of land use change on livestock densities, wildlife densities and pastoralist income. These impacts are simulated over nine different scenarios of rainfall and land tenure. We hypothesize that rainfall variability and socio-economic changes influence pastoral land use change decisions as pastoralists select the land use type that remains most profitable despite changing rainfall and socio-economic patterns. We also hypothesize that the land use selected by pastoralists drives their well-being and animal densities in rangelands.

6.3 Study areas

The Amboseli and Mara ecosystems in southern Kenya were selected for study as their ecologies, historical land use types and conservation use have broadly been similar but have changed over the recent past due to varying pastoral sedentarization levels, social-economic development, and conservation initiatives. The Amboseli ecosystem consists of the Amboseli Basin, which is mainly the Amboseli National Park, and the group ranches surrounding the park (Figure 6.1). The park provides a dry season grazing reserve for wildlife while the group ranches surrounding the national park provide wildlife dispersal zones. For instance, the Kimana group ranch provides a migratory corridor for wildlife migrating between the Amboseli, Chyulu Hills and Tsavo National Parks/Reserves. The group ranches were formed under the Land Act of 1968 which aimed to incorporate landowners in collective management of pastoral land and resource use [35]. The group ranches were meant to encourage pastoralists to maintain a sizeable herd and to limit livestock grazing within their group ranch boundaries [36]. However, the group ranches were ineffectively managed and the pastoralists neither reduced their herds nor restricted grazing to their ranches leading to group ranch subdivision from the mid-1980s to present [1,36].

Rainfall in Amboseli is influenced by altitude [31] where higher rainfall areas occur along the northern foothills of Kilimanjaro (>800 mm year−1) and Chyulu Hills (500–600 mm year^{-1}) [1] while lower points such as the Amboseli receive an average rainfall of 350 mm year^{-1} [37,38]. There are two annual rainfall seasons (November–January and March–May) and sometimes one or both of the rainfall seasons fail [1]. The ecosystem is characterized by a series of swamps, streams and rivers that are supported by the underground flows from Mt. Kilimanjaro [35,39]. Grasslands in Amboseli are dominated by *Chloris rocksburghiana, Eragrostis tennuifolia* and *Sporobolus* spp., woodlands are dominated by *Commiphora* and *Acacia* spp., swamps and flooded areas are dominated by *Acacia xanthophloea, Cyperus immensus, Psilolemma jaegeri* and *Salvadora persica* and the slopes of Kilimanjaro and Chyulu Hills are dominated by broad leaved dry tropical forests [38,40,41]. Our study was only interested in the drier parts of Amboseli and covered the Amboseli National Park and the surrounding pastoral group ranches (Figure 6.1).

The Mara ecosystem is north of the Serengeti ecosystem in Tanzania and provides dry season grazing reserve for wildebeests migrating from the Serengeti [42]. It consists of the Maasai Mara National Reserve and the surrounding group ranches which form wildlife dispersal zones (Figure 6.1). These group ranches also act as a buffer between the national reserve and the agricultural lands in the north of Narok County that are largely under mechanized agriculture [27,40,43]. The Mara is characterized by two rainfall seasons (November–December and March–May) with a gradient from the dry south eastern parts with an average rainfall of 500 mm year^{-1}, to the wet north-western parts with an average rainfall of 1200 mm year^{-1} [40,44]. The average temperature is 18 °C [45]. There are several permanent and seasonal rivers and streams in the Mara and they all flow into the Mara River [46]. Vegetation in the Mara is characterized by open woodlands and forests along river and water courses [46]. Our study area in Mara covered the Maasai Mara National Reserve and the surrounding group ranches (Figure 6.1).

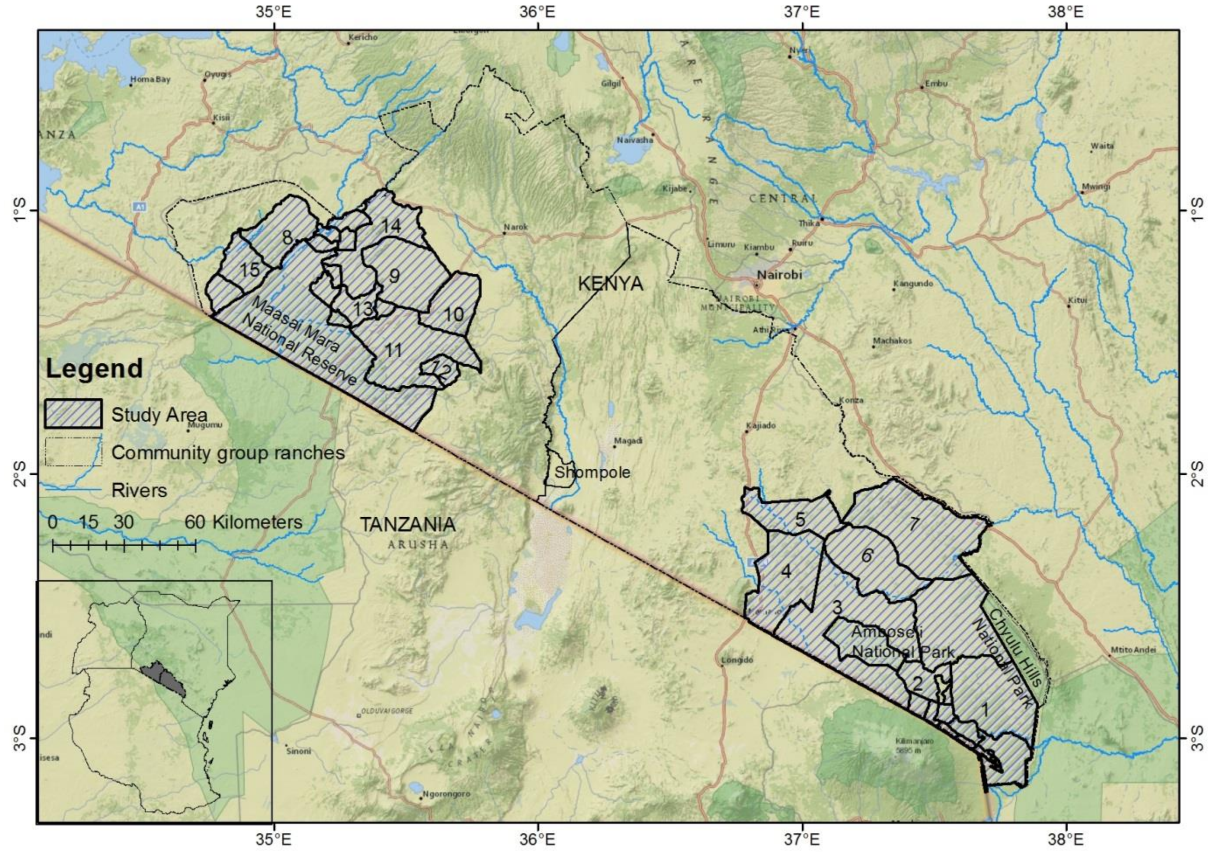

Figure 6.1: Amboseli and Mara ecosystems in southern Kenya and the surrounding group ranches (numbered 1–15). Group ranches 1 to 7 are in Amboseli while group ranches 8 to 15 are in the Mara. The name for the numbered group ranches are as follows: 1—Kuku, 2—Kimana, 3—Olgulului/Ololorashi, 4—Mailua, 5—Osilalei, 6—Lengesim, 7—Kaputei South, 8—Kimintet, 9—Ol Kinyei, 10—Maji Moto, 11—Siana, 12—Naikara, 13—Naboisho, 14—Lemek and 15—Oloirien. Those areas specifically modelled in this investigation are shaded. Group ranches in Amboseli were digitised by the International Livestock Research Institute (ILRI) while those in Mara were digitised by Benson Maina. Base layer Source: National Geographic.

6.4 Methods

Agent-based models (ABMs) are used to study complex adaptive systems made up of interactive, autonomous agents which give the system an ability to adapt, self-organize and show emerging patterns [47–50]. They simulate the behavior of agents from bottom-up to show the influence of individual agents in explaining the emergent patterns of a system [51–54]. ABMs can be used to link biophysical and socio-economic components of a system by incorporating outputs from biophysical process-based models as input data and linking them to other socio-economic factors simulated in the model [34,51,55].

The Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) dynamic global vegetation model [56,57] is a deterministic, process-based dynamic global vegetation model that simulates changes in vegetation dynamics and biogeochemical cycles as a function of changing climates [58–62]. LPJ-GUESS uses gridded time series climate data, atmospheric carbon dioxide (CO2) concentrations and soil physical properties as input data [62]. Vegetation is described as plant functional types (PFT) distinguished by bioclimatic limits, morphological, phenological, life history traits and photosynthetic pathway [60]. Simulated vegetation dynamics arise from competition for light, space, and soil resources among plant functional types [57,63]. Validation of LPJ-GUESS has been done by measures of vegetation structure, composition and productivity [61], and with vegetation maps, remote sensed and pollen data [64,65].

We apply an ABM to a social-ecological system [66] in Amboseli and Mara ecosystems in southern Kenya to understand the feedback between pastoral land use activities and natural resources. We link our custom-build ABM (details below) to LPJ-GUESS dynamic global vegetation model.

6.4.1 Our model description and dataset

We developed a novel ABM in NetLogo (version 6.0.2) [67]. To the best of our knowledge, this is the first model that integrates a process-based dynamic global vegetation model and an ABM to assess the interaction between climates, livelihoods, and conservation in East African rangelands. The description of the model follows the ODD (Overview, Design concepts and Details) protocol (S1 Appendix 1) [68,69] formulated to make models complete, reproducible and easy to communicate [70]. The period for the ABM is from 1950 to present. To parameterize ecological and socio-economic variables used in the ABM, we used data on animal densities, grazing rates, income levels, household densities and irrigation probabilities from literature focused on pastoralists/agropastoralists in the study areas [39,71–73] and from the 2009 Kenya census [74] (Table 6.1).

Table 6.1: Model variables, their descriptions and data sources. Variables are divided into two types: fixed variables are constant throughout the model run, while updated variables are continually altered throughout the model based on other parameters.

State variables	**Description/Units**	**Variable type**	**Data source**
Land tenure – type of land ownership	Communal, government and private	fixed	Randomised (see method)
Land use – current land use in the land area	Livestock grazing, irrigated agropastoralism, agriculture, livestock grazing with conservation activities and built-up	updated	Assigned via the NetLogo model
Households – the density of homes found in the land area	Number per kilometre squared (#/km^2)	fixed	[74]
Distance to the road – the closeness of a grazing land to the nearest all-weather road	Km	fixed	[73]
Irrigation-probability – the likelihood that a pastoralist will irrigate his/her land based on the overall likelihood of irrigation in the study areas	Probability of 0-1	fixed	[75]
The annual income earned from specific land uses practiced in 1 km^2 land area	Dollars per year ($ yr^{-1})	updated	[40]
Income – the highest income from different land uses practiced in 1km^2 land area	$ km^{-2} yr^{-1}	updated	Calculated by the NetLogo model
Grass biomass – the amount of grass available for livestock and wildlife grazing in 1km^2 of land area	Kilograms per kilometre squared (kg/km^2)	Updated	LPJ-GUESS [56,57]
Livestock density – the number of tropical livestock units (TLU) in 1km^2 of land area	TLU	Updated	[40]
Wildlife density – the number of wildlife found in 1km^2 of land area	#/km^2	Updated	[39]

To represent the density of livestock in the ABM, we used tropical livestock units (TLU). TLU are a composite index used to standardise livestock species according to their body weight whereby one TLU is equivalent to 250 kg which is the weight of a female zebu cow [13,40,76,77]. TLU as a measure allows comparison of livestock species and wealth across pastoral households [78] whereby a cow is approximately 1 TLU and one goat or sheep is 0.125 TLU [13]. Other ABM studies that use TLU to understand the behaviour of pastoral systems in Africa include [34] who simulates the decision making system of household heads with regard to ecosystem services and [49] who studied the role of herd numbers and stochastic events on the growth of herds. For each parameter we used the mean and standard deviation to incorporate stochasticity in the ABM. To capture multiple land use change behaviours observed in the ABM, we applied the principle of pattern oriented modelling [79] in the model design. We used insights from semi-structured interviews conducted with pastoralists in the study areas in January and February 2016. The interviews focussed on questions on the history and drivers of land use patterns, land tenure, livelihood strategies and land management. In the model, the important role of government policy in advocating for land subdivision in the study areas is reflected through the land tenure variable that has three land tenure scenarios (communal, government and private).

Long term mean rainfall and temperature estimates from Climatic Research Unit TS 3.0 dataset, [80] were used in LPJ-GUESS to simulate vegetation biomass for the Amboseli and Mara ecosystems for the period between 1950–2005. As LPJ-GUESS simulations are run at both daily and annual time steps over a spatial resolution of 0.5 degrees [81], we simulated grass biomass annually and converted the output to kg/km^2. Grass biomass from three representative years in Amboseli (1990, 1993 and 2001) and Mara (1983, 1987 and 1994) were used to represent dry (low biomass), normal (medium biomass) and wet (high biomass) years respectively. Grass biomass was then used as input data for the ABM and used to simulate grass biomass that was available to wildlife and livestock based on their feeding rates and the land use practiced on a given cell (S1 Appendix 1). The model assumed an animal of 250 kg (equivalent of one tropical livestock unit) grazes on 2500 kg of dry matter per year [72]. It also assumed that all cells used for livestock grazing land use were grazed by livestock alone, half of the cells used for irrigated agropastoralism land use were grazed by livestock, one-third of the cells used for livestock grazing with conservation land use were grazed by livestock while two-thirds were used by wildlife and all the cells used for agriculture and urban land use types had no livestock or wildlife grazing.

From the grass available for grazing, wildlife and livestock densities were simulated for each cell. Animal densities, together with the likelihood of irrigation, type of land tenure, distance to road, household density and the price of livestock were then used to simulate the potential income a pastoralist can earn from different land uses in a given cell. From each cell, the land use type that had the highest income was then selected as the preferred land use type. In addition, the wildlife and livestock density in that cell were simulated as model outputs. Though other factors, such as culture, are key in driving land use changes, our model was interested in simulating the influence of income on pastoral land use change decisions, thus it considered income as the most important factor.

As our model was interested in understanding land use change types and their impacts on animal density and pastoralists' income, it was not spatially explicit. However, the patterns underlying the designing and implementation of our model are based on patterns observed and documented for Amboseli and Mara.

6.4.2 Simulation experiments

6.4.2.1 Scenarios

We used repeated scenario experiments to explore a range of possible behaviours of the system from changing interactions between model variables. In the model, the variables used for computing different scenarios are the types of rainfall years (dry, normal and wet), and land tenure (communal, government and private), combined with modification on the amount of money available to support pastoralists who are willing to rent their land to be used for wildlife conservation (ranging 0 – 1000 \$ km^{-2} yr^{-1}) (See S1 Appendix 1 for full details). Simulation of each scenario was done independently from the start to the end and there was no alteration between scenarios when running the model.

6.5 Results

Our main findings were: 1) with no conservation subsidies, livestock grazing remains the main land use type on dry, normal and wet years across all land tenure scenarios, 2) agriculture levels increase on subdivided and privatised land on all rainfall years, 3) provision of conservation subsidies heightens livestock grazing with conservation land use and 4) livestock numbers, wildlife numbers and pastoralist income go up with higher conservation subsidies and decline with low conservation subsidies. Broadly, our findings were consistent across both Amboseli and Mara, and so we focus on Amboseli here, highlighting any differences with Mara throughout. For further details on the results for Mara please see the supplementary information.

6.5.1 Land use change in normal rainfall year

Our model assumed the normal rainfall year formed the baseline conditions in the rangeland. The levels of irrigated agropastoralism land use under all the different scenarios was negligible while livestock grazing with conservation was not practiced when there were no conservation subsidies.

In a normal rainfall year, the three land tenure scenarios are dominated by livestock grazing when there is no budget to support conservation initiatives. However, when the conservation budget increases, livestock grazing with conservation becomes the predominant land use type (Figure 6.2) highlighting the importance of conservation support in discouraging agriculture and enhancing pastoralism and conservation in dry rangelands. Compared to communal and government land tenure scenarios, the private land tenure scenario had higher levels of agriculture.

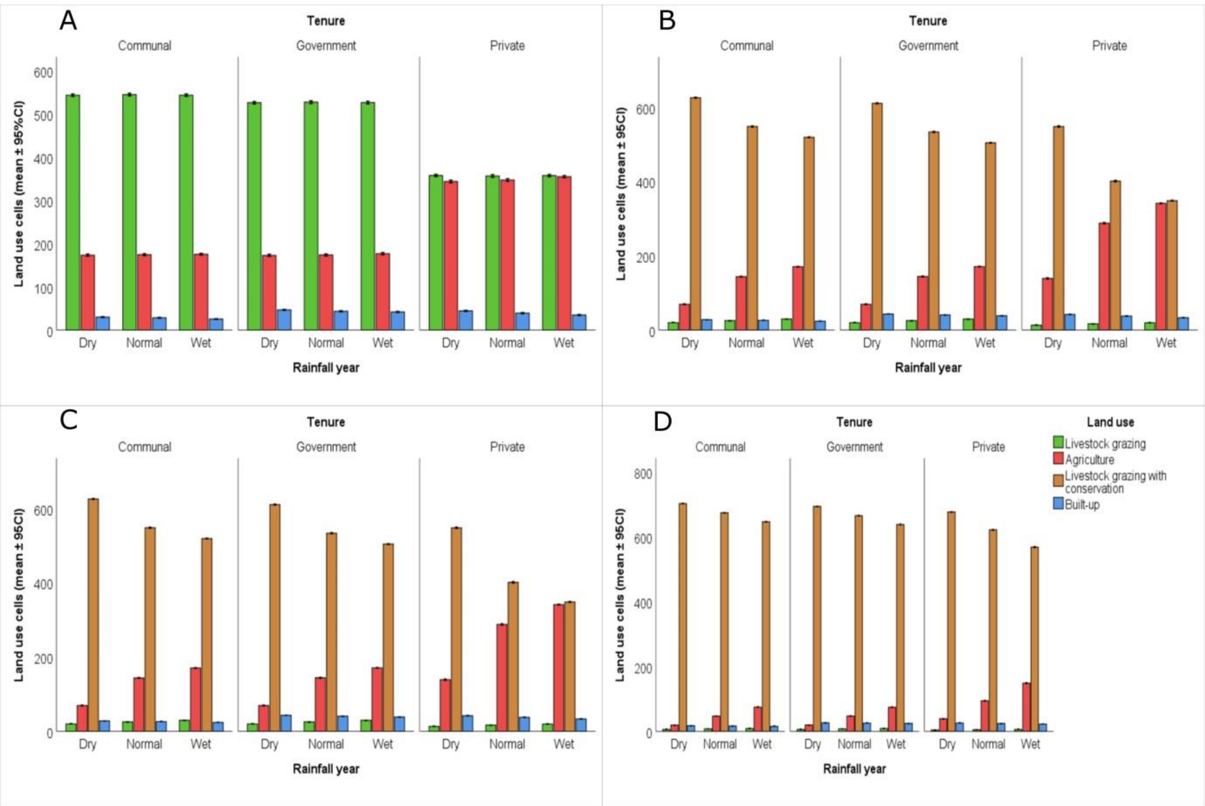

Figure 6.2: Comparison of land use types at different levels of conservation subsidies in Amboseli. In A there is no conservation subsidy, in B the conservation subsidy ranges from 10 – 100 \$ km^{-2} yr^{-1} while in C and D, the conservation subsidy ranges from 110 – 200 \$ km^{-2} yr^{-1} and 210 – 1000 \$ km^{-2} yr^{-1}. In all the graphs, the three land tenure scenarios are labelled as ‘Tenure’. The error bars represent 95% confidence interval.

6.5.2 Land use change in dry and wet rainfall years

Land use trends during the dry rainfall year are mainly similar to the normal rainfall year apart from the private land tenure scenario where increase in agriculture levels is higher (Figure 6.2). One key difference between Amboseli and Mara in a dry rainfall year is that in Mara, under the private land tenure scenario, livestock grazing decreases as agriculture increases while in Amboseli livestock grazing does not decline as agriculture increases.

In a wet rainfall year, livestock grazing is the main land use type in communal and government land tenure scenarios. However, under the private land tenure scenario, both livestock grazing and agriculture levels are high.

6.5.3 Land use change over different conservation budgets

In a normal rainfall year, as the conservation budget increases, livestock grazing with conservation dominates and all other land uses decline leading a wide margin between the levels of livestock grazing with conservation land use and other land use types. Under the private land tenure scenario, between 10 and 90 $\$ \mathrm{km}^{-2}\ \mathrm{yr}^{-1}$ of conservation budget, agriculture is the main land use type after which livestock grazing with conservation dominates as the conservation budget increases.

In a dry rainfall year, under communal and government land tenure scenarios, livestock grazing is the predominant land use type at conservation budget of 10 $\$ \mathrm{km}^{-2}\ \mathrm{yr}^{-1}$. However when the budget increases to 20 $\$ \mathrm{km}^{-2}\ \mathrm{yr}^{-1}$, livestock grazing with conservation becomes the main land use type followed by agriculture, livestock grazing and built-up in that order with the built-up areas surpassing livestock grazing as the conservation budget continues to rise. Similar trends are observed in the Mara. However, unlike Amboseli, overall trends in the Mara show agriculture levels declining faster as conservation budget increases. During a wet year, under the communal land tenure scenario, a provision of 10-20 $\$ \mathrm{km}^{-2}\ \mathrm{yr}^{-1}$ of conservation budget raises the level of livestock grazing with conservation. Similar trends are observed under the government land tenure scenarios. However, land use trends differ between Amboseli and Mara under the private land tenure scenario. In Amboseli, below a conservation budget of 150 $\$ \mathrm{km}^{-2}\ \mathrm{yr}^{-1}$, the private land tenure scenario has high levels of agriculture and livestock grazing with conservation and low levels of the built-up and livestock grazing land use. At 160 $\$ \mathrm{km}^{-2}\ \mathrm{yr}^{-1}$, livestock grazing with conservation and agriculture are practiced in somewhat equal levels after which agriculture decreases as the conservation budget increases. In Mara, when a small budget (<20 $\$ \mathrm{km}^{-2}\ \mathrm{yr}^{-1}$) is available for conservation, agriculture increases as livestock grazing diminishes and at 30 $\$ \mathrm{km}^{-2}\ \mathrm{yr}^{-1}$ of conservation budget, livestock grazing with conservation land use overtakes agriculture and increases proportionally with increasing conservation budget.

Under all three land tenure scenarios, in a wet rainfall year, the level of livestock grazing with conservation in Mara is higher than in Amboseli while the levels of agriculture and built-up land are higher in Amboseli than in the Mara.

6.5.4 Impact of land use change on wildlife, livestock and pastoralist income

Overall, wildlife density was higher in a wet rainfall year compared to normal and dry rainfall years (Table S1). It was also higher under communal and government land tenure scenarios than under the private land tenure scenario. In all rainfall and land tenure scenarios, as the conservation budget goes up, livestock grazing with conservation land use predominates leading to higher wildlife density (Figures 6.3 and S2). The highest wildlife density was recorded in a wet rainfall year under the communal land tenure scenario while the lowest wildlife density was recorded in a dry rainfall year under the private land tenure scenario (Table S1).

For all rainfall and land tenure scenarios, when there is no support for conservation, livestock grazing is the main land use type leading to higher livestock density relative to wildlife (Figures 6.3 and S2). Livestock density follows similar trends to wildlife where livestock density is higher in the wet rainfall year compared to the normal and dry years and private land tenure scenarios have less livestock density when compared to communal and government land tenure scenarios.

Income earned by pastoralists from different land use types was higher during the wet year and under private land tenure scenario. Income increased as the conservation budget increased since land use types such as agriculture and livestock grazing with conservation earned pastoralists more income than livestock grazing or using land for building business or residential properties to let.

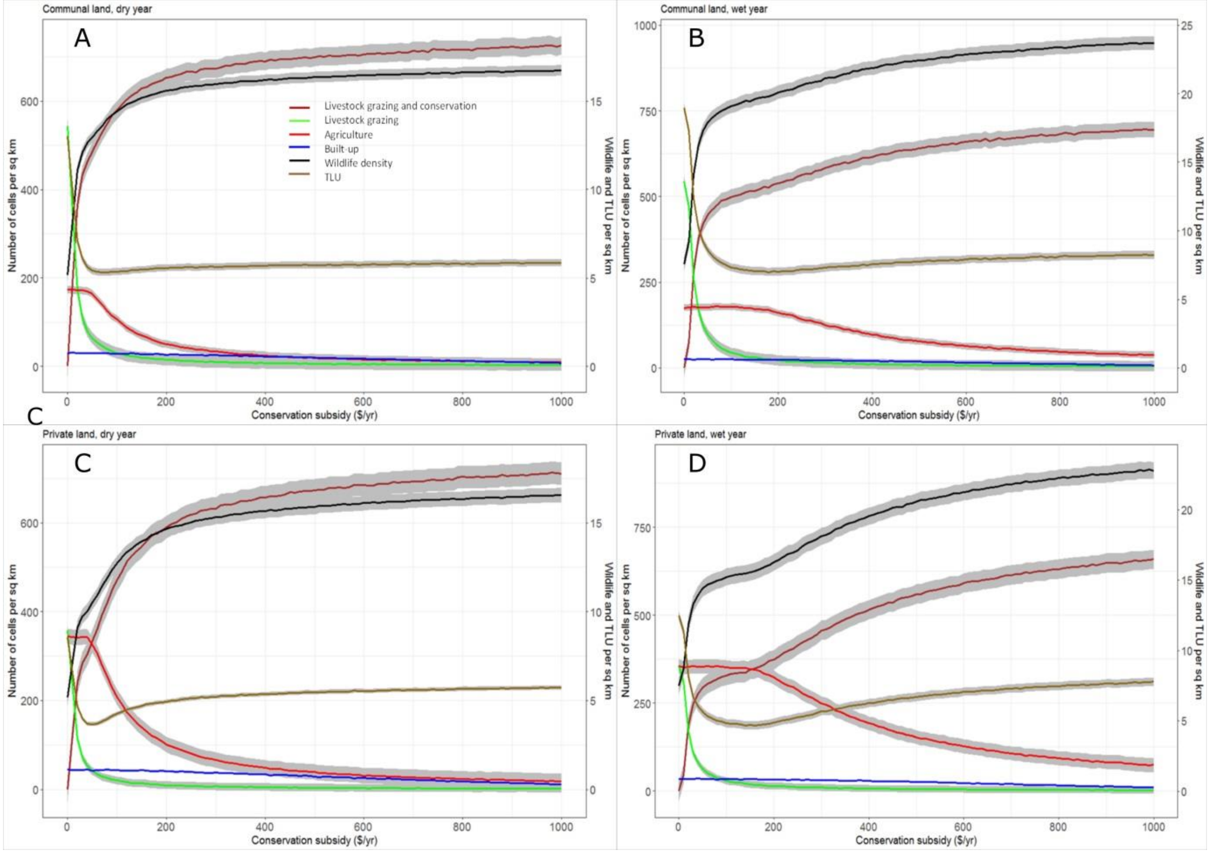

Figure 6.3: Trends in the relationship between land use types, wildlife and livestock density (TLU) in Amboseli. Figure (A,B) show dry and wet year trends under the communal land tenure scenario while figures (C,D) show dry and wet year trends under the private land tenure scenario. In all the figures, the grey zones represent the 95% confidence interval. From the figures, animal density increases with conservation subsidies though at different levels under different rainfall years and land tenure scenarios.

6.6 Discussion

By combining LPJ-GUESS with the land use change ABM, we aimed to integrate the impact of natural and social factors in pastoral land use decisions. Other studies in southern Kenyan rangelands that have integrated ABMs and biophysical models have been used to study: 1) the well-being of pastoralists in response to drought by simulating scenarios of lack of access to grazing resources and compensation for loss of grazing resource [34], 2) to explore the possibility of payment for ecosystem services to pastoralists whose land use types are compatible with wildlife conservation [82] and 3) to quantify the impact of land subdivision to livestock numbers and food security of households in Kajiado [83]. Our modelling work has shown the feedbacks between pastoral land use change decisions, their economic well-being and animal densities. With trends in land use, droughts and rainfall seasonality in East Africa expected to change in the future these land use change insights will improve our understanding of potential impacts of land use change on ecosystem services in East African rangelands.

The relative importance of livestock grazing, as the dominant land use type across southern Kenyan rangelands, change as rainfall, land tenure and conservation benefits change. Although land use changes have been attributed to multiple interactions between bio-physical and socio-economic factors, these interactions are complex, non-linear and difficult to include in land use analysis [84]. Livestock grazing is the most viable land use type in arid and semi-arid savannahs as it allows seasonal movement of livestock between dry and wet season grazing reserves [39,85,86]. It is also compatible to wildlife conservation [17], promotes cultural diversity [86] and supports many livelihoods thus making a significant contribution to the gross domestic product (GDP) of many East African countries [87]. However, climatic variability, manifested as delayed/failed rains, unreliable intensity of rainfall and increased frequency of droughts, drives rangeland conditions and impact on fodder available for livestock [88-90]. There is an increase in livestock grazing and agriculture during wet years in both Amboseli and Mara (S2 Appendix 2). This is because when adequate forage and water is available for livestock during wet years, pastoralists tend to maintain their livelihoods. Pastoralists also tend to practice agriculture where irrigated or rain-fed agriculture can be supported [88] leading to agricultural expansion in wet years and contraction in droughts or when there is intensified competition with wildlife [40].

Trends in the levels of irrigated agropastoralism, conservation and built-up land use are not different across the three rainfall years. This is probably because our model only considers three representative (dry, normal and wet) rainfall years and not rarer extreme events. Also, despite rainfall being a key determinant of the main land use types in rangelands [35], and pastoralists using different adaptive strategies to droughts, it is extreme droughts that lead to rapid pastoral land use change and sedentarisation [1]. This means that even the best land management techniques used to mitigate the effects of drought can fail under extreme droughts [91].

The influence of land fragmentation is modelled through land tenure scenarios in which the communal and government land tenures scenarios are largely un-subdivided and are used jointly by community members. On the other hand, the private land tenure scenario is largely divided into individual titled parcels of land and land use decisions are individual based. Our model results show that the levels of livestock grazing land use were high under communal and government land tenure scenarios compared to private land tenure scenarios. In contrast, agriculture levels were higher under private land tenure scenarios compared to the other land tenures. These trends are synonymous to the increasing smallholder agriculture and sedentarisation levels that have occurred in pastoral areas in southern Kenya following land subdivision [38,43,92,93]. Agriculture compartmentalises rangelands components by introducing fences and water canals and utilising dry season grazing lands as farms [88]. Changes in land tenure are driven by internal and external factors and lead to different land use change choices. Pastoralists, sometimes, encourage land subdivision when they are interested in controlling their land by keeping off agriculturalists and conservationists from gaining access to their lands [88]. Other times, when there is uncertainty over the leadership and effectiveness of communal land tenure, land privatisation is encouraged and pastoralists decide how to use their land. The outcome of land privatisation is a decline in exclusive pastoralism, increased sedentarisation and livelihood diversification [22].

Though our results show livestock grazing and agriculture levels increasing in the wet years, agricultural expansion during wet years under private land tenure scenarios is higher than the expansion of livestock grazing. As opposed to mechanized agriculture which is driven by land suitability and economic factors like market accessibility; smallholder agriculture is driven by changes in demographic and socio-economic factors [27]. The goal of government policies that supported the privatisation of communal lands was to promote intensive livestock production [25,31,94]. However, privatisation promoted land fragmentation that discouraged pastoral mobility [1,25,94] and encouraged agriculture and settlements expansion, land privatisation and sedentarization [1,42,95].

Besides rainfall and land tenure, the impact of external drivers such as conservation investors and politics are equally important in shaping pastoral land use change decisions [96]. Our results show the potential impact of conservation subsidies. In our model, conservation land use is not practiced when there is no conservation budget but increases with the conservation support provided. This is because pastoralists view conservation as a livelihood that complements pastoralism, rather than as a main livelihood [17]. When they receive wildlife related economic benefits, their perception towards conservation is positive consequently leading to an increase in wildlife numbers [24,97]. Wildlife and livestock densities from the model are also correlated with conservation support. National parks and game reserves in Kenya cover 8% of the land surface and account for 35% of wildlife [14,98]. However, between 65 and 70% of wildlife is found in communal lands surrounding protected areas [14,99]. Thus, it is important that income from conservation is extended to pastoralists nearby protected areas to encourage a more permeable matrix outside of protected areas [82]. Such conservation-orientated income could provide an important safety-net for pastoralists, especially during dry years [3,17,76]. To help manage this matrix, fragmented rangelands across Kenya are being merged and managed together in form of wildlife conservancies [3,100]. Conservancies are lands set aside for wildlife and tourism with controlled livestock grazing to promote wildlife conservation and pastoral well-being through partnerships between tourism operators and landowners [17,29,40,101]. The tourism operators manage the conservancy and pay landowners fixed land lease payments (maximum of 50 dollars per hectare per year) to voluntary vacate their land and refrain from putting up settlements, overgrazing and practicing agriculture [17,102]. As the conservancies discourage agriculture, due to its unsustainability and the human wildlife conflicts it brings [22,103], they encourage controlled livestock grazing which is seen to be compatible to wildlife conservation [82,103] leading to higher livestock grazing levels and no agriculture in conservancies. These community based wildlife conservancies have been documented as successful in enhancing wildlife populations compared to other non-community based wildlife zones [24]. For instance, formation of Nakuru Wildlife Conservancy, in central Kenya, is attributed to increasing the numbers of 32 wildlife species [99].

Our model results also highlight the impact of climate on wildlife and livestock, both of which show an increase in their densities during a wet year. Herbivore biomass has been associated with rainfall and food availability implying that it goes up in wet seasons and declines during droughts [99]. Simulation of wildlife and livestock densities across different land tenure scenarios showed both their densities were higher on communal and government land tenure scenarios compared to private land tenure scenario. This is because land subdivision and sedentarisation disrupts the distribution and mobility of wildlife and livestock and may lead to their decline [15,24,104]. Over the late twentieth century and early twenty first century, wildlife densities in East African savannahs have declined [15]. Initial wildlife declines were recorded on wet pastoral areas where agriculture had expanded while drier pastoral areas where land was communally owned and not subdivided recorded relatively high wildlife density [24]. Similar wildlife trends have also been observed in southern Kenya where subdivided group ranches have lower wildlife densities compared to ecologically similar un-subdivided group ranches [24,104].

With increasing pastoral sedentarisation, livestock density has also been declining in East African rangelands. To a great extent the wealth of Maasai pastoralists is associated with livestock and the number of TLU per person is used for estimating the wealth of households [78]. Per capita number of TLU needed by a pastoral family for subsistence and survival during droughts is six [77]. With per capita livestock numbers in East African rangelands having reduced from 10 in the 1960s to four in the 1980s [10], the ability of pastoral communities to depend entirely on livestock grazing for their subsistence is declining leading to diversification and intensification of pastoral livelihood strategies on and off the land [40,92]. However, our model shows that provision of conservation subsidies increases livestock density, particularly under the private land tenure scenario. This is because conservation land use is normally practiced together with controlled levels of livestock grazing. It also shows that the influence of conservation subsidies in driving livestock density is key when subsidies are <200 \$ yr^{-1} and further increases in the subsidies maintains wildlife and livestock density levels. This means that average conservation subsidies of 200 \$ yr^{-1} for $1km^2$ grazing land can allow pastoralists to practice livestock grazing, thus maintaining their cultural heritage, and promote wildlife conservation.

Though our model simulations provide useful trends on land use change, pastoral well-being and animal densities, it has some limitations. Firstly, it was not spatially explicit and the location of pastoralists land, though randomly assigned, could not be linked to environmental and socio-economic conditions. A spatially explicit ABM would have enabled the agents to make decisions based on the prevailing environmental and socio-economic conditions [34]. Secondly, to reduce the complexity of interpreting the model output, our model did not use time series data of changing rainfall and biomass amounts. Instead, we used three representative rainfall years and biomass available for animals was related to these years. Utilising time-series data would provide detailed information that is useful for predicting the behaviour of the system [105,106]. Thirdly, our model is sensitive to conservation subsidies because pastoral land use change decisions are primarily driven by income. Thus, as the subsidies increase, more pastoralists change to livestock grazing with conservation land use because it gives them higher income. However, our model shows that pastoralists will rely on conservation income only when conservation subsidies supplement their livestock grazing income. Similar trends have been documented in southern Kenyan rangelands where conservancy payment is ranked second or third income earner and is an important source of cash that prevents pastoralists from selling their herds when they need cash [17]. As climate variability and risk increase, if secure resource access is maximized, pastoralism is likely to continue. However, if resource availability is not assured, other land use types, besides pastoralism, are likely to be practiced. With rainfall variability in Africa expected to increase [89,107], how pastoralists respond to harsh weather patterns and ecosystem changes will challenge the resilience of rangelands and their ability to adapt to fast, slow, broad scale or fine scaled drivers of change [11]. Previous studies [17,88,108] have demonstrated the resilience and adaptive capacity of pastoral social-ecological systems in East Africa, and insights from modelling studies complement and inform the potential behaviour of pastoral systems under changing climates, development and political factors. These insights not only help in understanding the sustainable management of other rangelands across East Africa but can be used to inform appropriate policy and practice. Based on our model results, we recommend the use of stakeholders' perceptions in informing land use change modelling studies. The results from modelling studies can then be shared with the stakeholders who should also be involved in developing future scenarios of sustainable land use policy and practices. Furthermore, we recommend the development of policies that support and manage the provision of conservation subsides in rangelands as this provides adaptation strategies to climate change as well as prevents land fragmentation and consequently, land use change in rangelands.

6.7 Conclusions

In this study, we combine a process based model to an agent based model to understand the impact of interacting biophysical and socio-economic factors in driving land use patterns across two rangelands in southern Kenya. By using grass biomass estimates, simulated by LPJ-GUESS dynamic global vegetation model, as input to the agent based model, we show how biophysical and agent based models can be integrated. From the model outputs we discuss the implication of land use change on pastoral well-being, by simulating changes in pastoralist income and livestock density, and on rangeland ecology, by simulating changing trends in wildlife density. We show the role of conservation subsidies, in form of annual income, in enhancing livestock grazing and conservation land use type across the rangelands. Our model shows that this land use type not only increases pastoralists' income, livestock and wildlife density; but also promotes rangeland connectivity across fragmented rangelands as it emerged the main land use type when conservation subsidies are provided under the private land tenure scenario. By simulating land use trends across two study areas, our model was able to simulate similarities and differences in land use trends across two ecological similar rangelands. It also showed changing landscapes and livelihoods patterns in Kenyan rangelands and the factors that drive these changes. These insights are useful in highlighting the impact of multiple, interacting climatic, socio-economic and political factors in shaping livelihood strategies and ecological responses across semi-arid rangelands in East Africa. They can also be used to better understand the changes and the challenges faced by these social-ecological systems. Thus providing ways of developing practical solutions that will enhance environmental sustainability and human well-being, particularly in addressing questions on the longevity of pastoralism and the trade-offs between land use types.

6.8 Acknowledgement

We are grateful to the local community experts we interviewed and whose views informed the designing of the agent based model. We thank Rebecca Muthoni, Francis Sopia, Daniel Letee and John Lembakuli for their help in conducting the interviews. We appreciate the support in model development granted by the SES-LINK project at the Stockholm Resilience Centre (SRC), Sweden. The research permit for this study was issued by the National Commission for Science, Technology and Innovation (NACOSTI) in Kenya. This research was supported by the European Commission Marie Curie Initial Training Network grant to RM for the Resilience in East African Landscapes (REAL) (FP7-PEOPLE-2013-ITN 606879) project. Finally, we would like to thank the anonymous reviewers, whose comments improved the manuscript.

6.9 Author contribution

RK and SW developed the model. RK led the writing of the manuscript with substantial feedback from SW and RM. All authors contributed to the development of ideas and drafts and gave their final approval for publication.

Conflict of Interest: The authors declare they have no conflict of interest.

6.10 Supplementary materials:

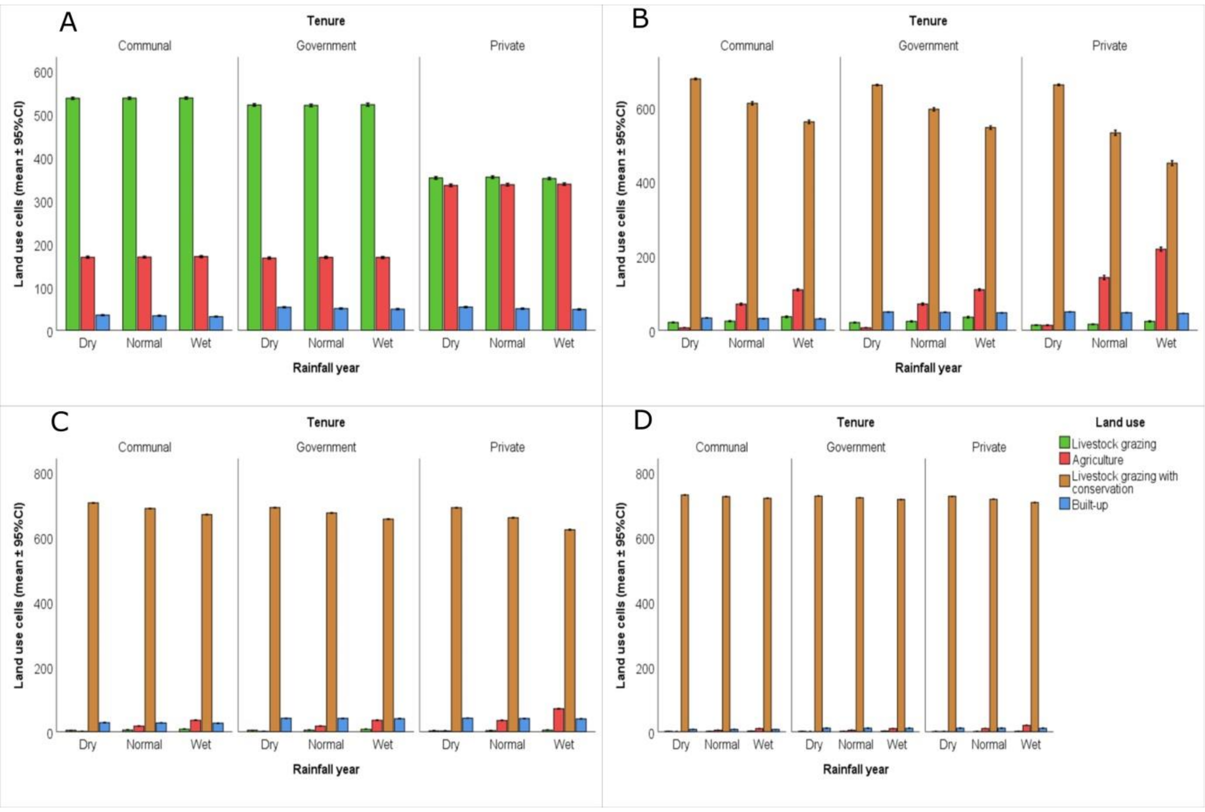

Figure S1: Comparison of land use types at different levels of conservation subsidies in Mara. In A there is no conservation subsidy, in B the conservation subsidy ranges from 10 – 100 $\$\ \mathrm{km}^{-2}\ \mathrm{yr}^{-1}$ while in C and D, the conservation subsidy ranges from 110 – 200 $\$\ \mathrm{km}^{-2}\ \mathrm{yr}^{-1}$ and 210 – 1000 $\$\ \mathrm{km}^{-2}\ \mathrm{yr}^{-1}$. In all the graphs, the three land tenure scenarios are labelled as ‘Tenure’. The error bars represent 95% confidence interval.

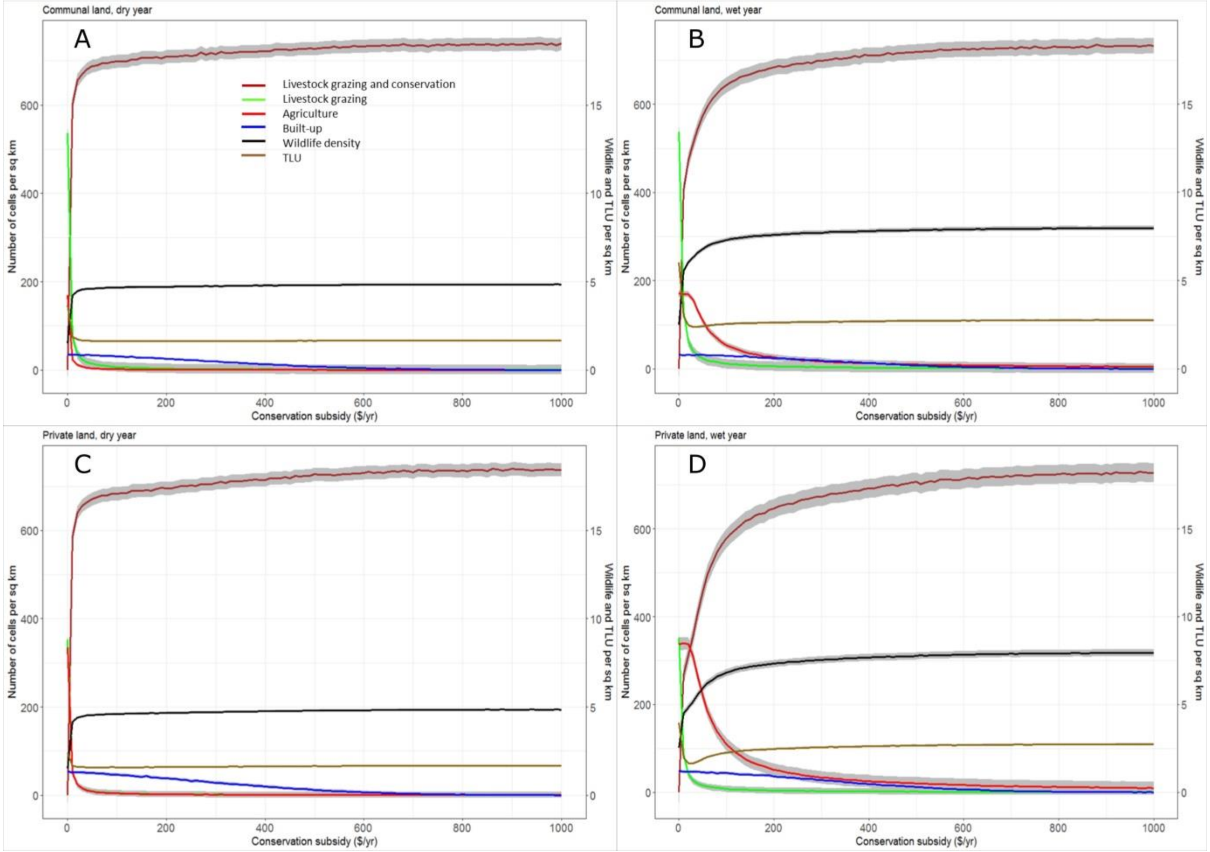

Figure S2: Relationship between land use types (shown as number of cells per km^2) and wildlife and livestock density (TLU) in Mara. Figures A and B show trends between the dry and wet years under communal land tenure scenario while figures C and D show trends between dry and wet years under the private land tenure scenario. The shaded grey areas represent the 95% confidence interval.

Table S1: Mean standard deviation levels of land use, animal densities and incomes per rainfall year and land tenure type for Amboseli and Mara

Amboseli means and standard deviation

Rainfall year	Tenure	Livestock grazing	Irrigated agropastoralism	Agriculture	Livestock grazing with conservation	Built-up	Wildlife density	TLU	Income
Dry	Communal	21.81(66.14)	0.07(0.27)	38.65(44.42)	664.62(105.95)	19.74(8.30)	15.78(1.68)	5.83(0.87)	539.99(322.36)
	Government	21.34(64.25)	0.08(0.28)	38.67(44.33)	654.83(106.57)	30.00(12.15)	15.63(1.70)	5.74(0.84)	545.04(309.43)
	Private	14.41(43.66)	0.14(0.39)	77.31(88.03)	623.53(129.13)	29.33(11.72)	15.13(2.05)	5.32(0.63)	616.30(354.74)
Normal	Communal	26.04(72.03)	0.03(0.18)	70.44(51.64)	629.77(113.17)	18.57(7.66)	19.08(2.26)	7.08(1.26)	647.92(379.18)
	Government	25.44(69.71)	0.04(0.2)	70.60(51.87)	620.13(114.31)	28.68(11.41)	18.89(2.28)	6.97(1.21)	655.19(364.24)
	Private	17.12(47.26)	0.07(0.26)	141.05(102.78)	559.41(141.36)	27.00(10.38)	17.68(2.83)	6.11(1.02)	817.56(426.62)
Wet	Communal	29.25(76.25)	0.02(0.15)	95.37(51.36)	603.12(114.17)	17.39(7.05)	21.55(2.65)	8.03(1.60)	756.67(417.38)
	Government	28.59(73.81)	0.02(0.14)	95.05(51.27)	593.67(115.16)	27.60(10.82)	21.34(2.67)	7.90(1.54)	763.63(412.30)
	Private	19.31(50.18)	0.05(0.21)	190.07(101.51)	510.66(139.31)	24.81(9.23)	19.41(3.24)	6.61(1.28)	1010.41(473.24)

Mara means and standard deviation

Rainfall year	Tenure	Livestock grazing	Irrigated agropastoralism	Agriculture	Livestock grazing with conservation	Built-up	Wildlife density	TLU	Income
Dry	Communal	8.98(53.46)	0.21(0.47)	2.80(16.91)	714.93(75.47)	2.31(12.20)	4.74(0.34)	1.68(0.2)	415.05(264.79)
	Government	8.79(51.96)	0.21(0.48)	2.80(16.72)	709.21(76.52)	18.36(17.97)	4.72(0.34)	1.67(0.19)	415.77(247.52)
	Private	5.91(35.15)	0.41(0.67)	5.61(33.48)	708.69(76.39)	18.45(18.07)	4.72(0.34)	1.65(0.09)	423.98(274)
Normal	Communal	9.57(53.67)	0.26(0.51)	14.35(29.11)	702.84(82.84)	12.00(11.78)	5.36(0.43)	1.89(0.23)	447.43(306.8)
	Government	9.31(52.04)	0.26(0.5)	14.42(29.13)	696.91(84.61)	18.13(17.63)	5.33(0.43)	1.88(0.23)	451.85(317.86)
	Private	6.31(35.46)	0.54(0.74)	28.83(58.09)	685.61(96.80)	17.99(17.50)	5.27(0.5)	1.82(0.16)	486.06(355.62)
Wet	Communal	11.53(54.67)	0.26(0.52)	23.85(36.46)	691.77(89.12)	11.75(11.48)	7.67(0.66)	2.72(0.35)	471.87(324.74)
	Government	11.30(53.15)	0.26(0.51)	23.84(36.32)	686.07(91.38)	17.82(17.30)	7.63(0.68)	2.70(0.34)	482.79(346.61)
	Private	7.59(35.78)	0.51(0.72)	47.81(72.39)	665.82(110.15)	17.45(16.82)	7.48(0.82)	2.58(0.28)	539.07(408.97)

6.10.1 S1 Appendix 1

ODD Protocol

The ODD protocol used to simulate the model is described below.

A) Overview

A1) Purpose

The ABM seeks to understand the feedback between pastoral land use change and the ecology of southern Kenya by exploring the role of rainfall, socio-economic and governance factors in driving land use types and the impact of adopted land use types on livestock densities, wildlife densities and pastoralists' annual income. Land use change by pastoralists mean changes from livestock grazing to other land use types such as agricultural expansion and urbanization as a result of shifting livelihood strategies.

This model is developed for researchers and decision makers to improve understanding of the influence of climate change, government policy and socio-economic development on pastoral land use decisions and the impact of land use change on pastoral well-being and wildlife.

A2) Entities, state variables and scales

The model has one agent; 'cells', which represents areas of land that can be used. The state variables for cells are listed in Table 1. Climatic variability, social-economic and political factors are the main reasons pastoralists in semi-arid rangelands change to other land use types [1,10,22,38,85,92,96,109].

From our field observations and literature, the main land use changes and livelihood diversification in the study areas are expansion of agriculture, urbanization and ecotourism [40,93]. Consequently, our model distinguished five land use types and for each 1 km^2 'cell' more than one land use could be practiced. Our model only simulates small-holder agriculture that is dependent on rainfall and is practiced in wildlife dispersal communal grazing lands. We do not simulate mechanized agriculture as it was rare in our study areas.

The environment is composed of amount of rainfall per year (low, normal and high) and budget available to pastoralists from investors and non-governmental conservation organizations to support wildlife conservation. The temporal setting for the model simulations is based on biophysical and socio-economic conditions from the 1950s and is simulated on an annual time step over 200 model runs. The spatial resolution for a single cell is 1 km^2 and a single cell can have multiple households, land tenure and land ownership types.

A3) Process overview and scheduling

The processes in the model are simulated in five steps related to natural and social-economic events that influence land use change decisions by pastoralists. Changes in rainfall influence the grass biomass available for livestock and wildlife to graze on. The density of livestock and wildlife, together with other socio-economic factors, drives the income pastoralists can earn from different land use types. In turn, the land use types that pastoralists choose have implications on their income and the density of livestock and wildlife.

The five processes and the order they are modelled in are listed below. The state variables are updated in each process.

i. Grass is assigned to every cell. The grass biomass depends on the rainfall year. A wet year produces more grass and a dry year produces less grass.
ii. Animal grazing: The current land use type and grass biomass on each cell is checked and used to simulate the livestock and wildlife density that can graze that given cell.
iii. Income calculation: For each cell, the income earned for each land use type was calculated. This depends on: the number of households on that cell, the rainfall year, available grass biomass for animals, probability of irrigation, land tenure, household density and distance to the road.
iv. Land use change: In each cell, the land use type with the highest income is selected as the preferred land use type by pastoralists.
v. In each cell, the number of selected land use type, the income, the mean wildlife and livestock density is calculated and updated for every time step.

B) Design concepts

B1) Basic Concepts

The basic principles underlying the model design are based on real world patterns observed in the study area. Land use change choices by pastoralists are based on what is most rewarding financially at each time step. The potential income for each land use type in each cell is calculated and the land use that gives the highest income is selected.

B2) Emergence

Feedback between social-economic and biophysical variables emerge from the interactions between grass biomass, animal density and land use types. Land use change to agriculture mainly occurs in wet rainfall years among pastoralists with private land ownership. Change to irrigated agropastoralism largely occurs near permanent water bodies while livestock grazing with conservation activities is preferred in areas where pastoralists derive monetary benefits, mainly through land rents, from investors or organizations supporting wildlife conservation initiatives.

B3) Adaptation

The land use type with the highest income is adopted.

B4) Objectives

In each cell, the objective is to select the land use type that maximizes profitability by using available natural resources and favourable weather and socio-economic patterns. If this is impossible, the land use and livelihood type that can easily be practiced based on existing infrastructure is selected.

B5) Prediction

There is no foresight of rainfall or the trends in other socio-economic variables. In the cell, if livestock grazing is hampered by low water availability, low income and high human population, then it is likely that the land use will shift to a more profitable land use.

B6) Sensing

Before a different land use type is selected, the potential income of all land uses can be sensed and are used to inform land use change decisions.

B7) Interaction

None.

B8) Stochasticity

The state variables for each cell are randomly assigned when the model starts.

B9) Observation

Observed variables per annual time steps are: land use types, annual income, average livestock (tropical livestock units) and wildlife density in each cell.

C) Details

C1) Initialization

When the model begins, livestock grazing is the main land use type. The household density, distance to road, grass biomass, livestock and wildlife density have a normal distribution centred around the mean and standard deviation of each variable in Amboseli and Mara ecosystems (Table 2). The probability of irrigation is randomly allocated to the cells and range between zero and one. Income for each land use type is set to zero. For the land tenure scenarios:

- In the communal scenario, land tenure it is randomly allocated a 50% chance of being communal, 25% of being government and 25% of being private.
- In the government scenario, land tenure is randomly given a chance of being 50% government, 25% communal and 25% private.
- In the private scenario, land tenure is randomly allocated a 50% chance of being private, 25% of being communal and 25% being government.

Table 6.2: Initialization state variable values

Variable	**Amboseli**	**Mara**	**Source**
Mean household density	13.18 / km^2	15.55 / km^2	[74]
Mean distance to road	9.4 km	9.4 km	[73]
Mean grass biomass	93000 kgkm^2	2958 kgkm^2	LPJGUESS DGVM
Mean TLU	61.3 / km^2	71.06 / km^2	[40]
Mean wildlife density	33.33 / km^2	138.94 / km^2	[39]

C2) Submodels

Animal grazing

The amount of grass grazed is a function of available grass biomass and the annual amount of dry matter (kg) grazed by one TLU of livestock per year. The model assume wildlife grazing habits are similar to those of livestock hence their annual grass offtake amounts are similar. One TLU feeds on 2500 kg/km^2 of dry matter per year [72] thus the formulas used for calculating livestock and wildlife density that can graze on a given cell in the three land use type are as follows: Note: agricultural and urban land use types have no livestock or wildlife grazing.

i. Livestock grazing land use where all the land is exclusively used for livestock grazing

$$TLU = \left(\frac{Grass\ biomass}{2500}\right) \tag{1}$$

ii. Irrigated agro-pastoralism where half of the land is grazed by livestock and the other half is used for agriculture.

$$TLU = \left(\frac{Grass\ biomass * \frac{1}{2}}{2500}\right) \tag{2}$$

iii. Livestock grazing with conservation activities where one third of the land is used for livestock grazing and two-thirds of the land is rented out for wildlife conservation.

$$TLU = \left(\frac{Grass\ biomass * \frac{1}{3}}{2500}\right) \tag{3}$$

$$Wildlife\ density = \left(\frac{Grass\ biomass * \frac{2}{3}}{2500}\right) \tag{4}$$

Calculation of income for each land use type in each grazing land

Income earned in each land use type differs. It depends on the interactions between social and the biophysical components of the system. Though each land tenure scenario has varying proportions of each land use type, livestock grazing is largely practiced in communal and government land while irrigated agropastoralism, agriculture and built-up areas are largely found on private land. The probability of irrigation is calculated as a ratio between irrigated area [75,110] and the total area studied resulting in a probability of 0.013 and 0.1389 for Amboseli and Mara respectively.

In suitable areas, potential income for each land use type in each grazing land is calculated as follows:

i. Income from livestock grazing =

$$\left(\frac{Grass\ biomass}{2500}\right) * \left(\frac{Cost\ (\$)\ of\ one\ TLU}{households}\right) \tag{5}$$

ii. Income from irrigated agropastoralism =

$$(\left(\frac{Mean\ household\ density}{households}\right) + \left(\frac{Grass\ biomass * \frac{1}{2}}{2500}\right) * \left(\frac{Cost\ (\$)\ of\ one\ TLU}{households}\right)) \tag{6}$$

iii. Income from irrigated agriculture =

$$(Agriculture\ income\ from\ literature * \frac{Mean\ household\ density}{households}) \tag{7}$$

iv. Income from livestock grazing and conservation =

$$(Amount\ of\ conservation\ subsidy + \left(\frac{Grass\ biomass * \frac{1}{3}}{2500}\right) * \left(\frac{Cost\ (\$)\ of\ one\ TLU}{households}\right)) \tag{8}$$

v. The only built-up areas that earn pastoralists income are those < 2km from all-weather roads with the income earned based on the mean income earned from urban areas in the study sites.

6.10.2 S2 Appendix 2

Comparison between Amboseli and Mara

In Amboseli, although land use types are a result of long term changes in physical and cultural interactions, current trends of increasing sedentarisation, agricultural expansion and development of conservation based initiatives are more recent [38]. These land use trends are a result of infrastructure access, economic opportunities, land tenure changes and settlement patterns [40]. Access to physical infrastructure such as roads, schools, markets and health centres vary considerable across Amboseli and depend on the location of pastoral settlements [1]. Agriculture expanded on swamps and the slopes of Mt. Kilimanjaro which are dry season animal grazing zones [38,112].

In Mara, subdivided group ranches that receive adequate rainfall that can support agriculture have been converted to agriculture [40,92] leaving only 25-35% livestock available to maintain a nomadic livelihood [45]. When pastoralists in Mara are selecting land use types, they consider trade-offs between increasing the size of livestock or maintaining income from wildlife conservation activities and between expanding land for small scale farming or leasing land for mechanized farming [92]. In areas close to the Maasai Mara National Reserve, residents are involved in wildlife related and tourism activities. The national reserve accounts for 25% of the total national wildlife population in Kenya [14]. This makes wildlife conservation initiatives an integral component of the land use systems in Mara and contribution from wildlife conservation to most households is higher than livestock and agriculture income [40,45]. However, livestock still supports many livelihoods as integrating pastoralism with conservation has been challenging [92].

Wildlife declines in the rangelands have been attributed to agriculture expansion that results to habitat loss and fragmented landscapes of wildlife dispersal areas [14]. From the model, general wildlife trends show lower wildlife density in private land tenure compared to communal and government land and higher wildlife density in wet years relative to dry years. In Amboseli, the consequence of agricultural expansion in swamps in Amboseli has been fragmentation of wildlife dispersal zones, decline in dry season pasture, loss of wildlife habitat and intense human-wildlife conflicts [38,109]. The Mara rangelands have shown huge resilience in supporting large biomass of resident and migratory herbivores for years [92]. However, conversion of large tracts of rangelands on the Loita plains (north of the national reserve) to large scale commercial farms has led to habitat loss for wildlife, and consequently their decline [27,44,92].

6.11 References

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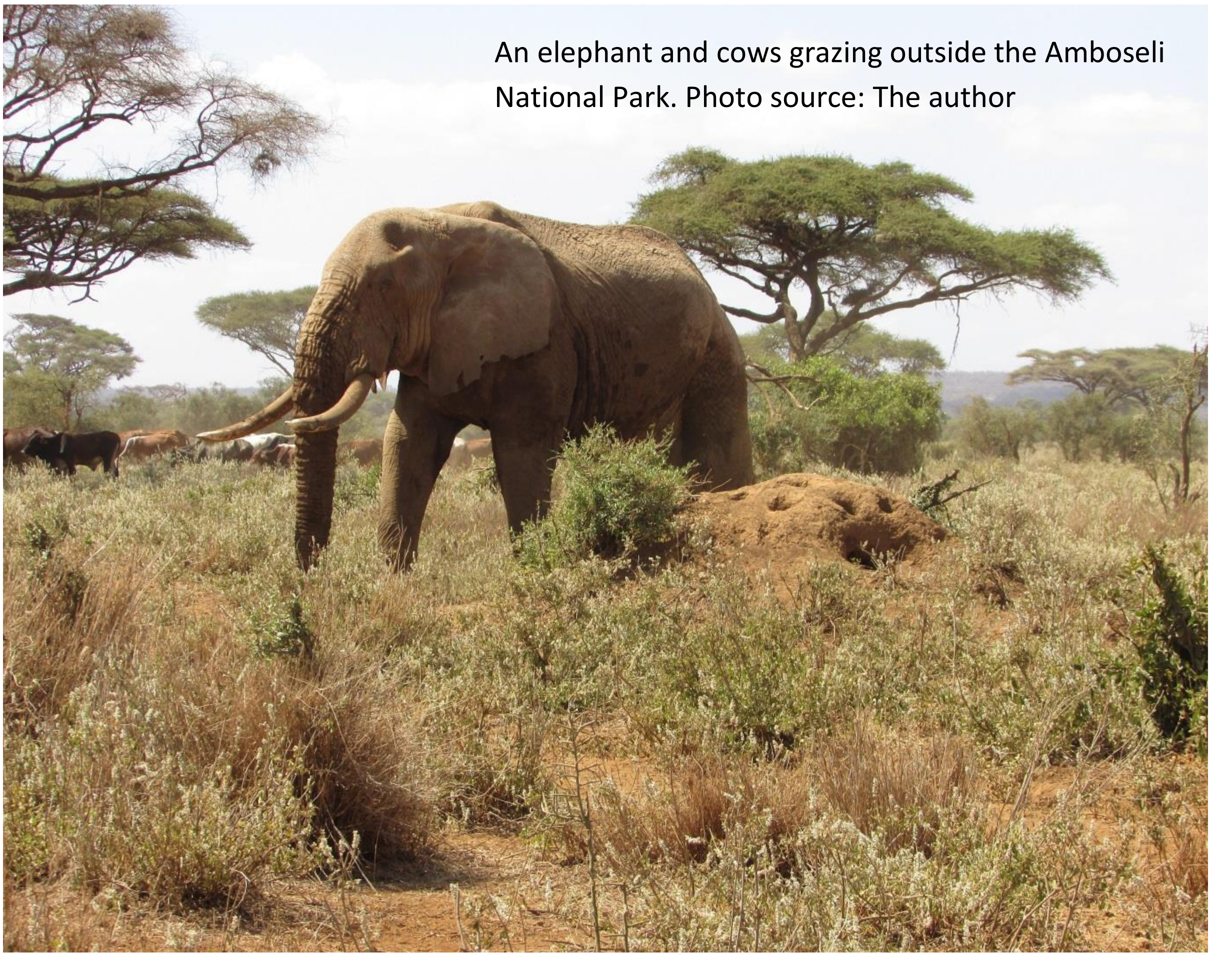
7 Synthesis



An elephant and cows grazing outside the Amboseli National Park. Photo source: The author

Interdisciplinary Social-Ecological Perspectives on Interactions between Pastoralists, Woody Vegetation Structure, Land Use, Conservation and Climate Change from Southern Kenya.

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7.1 Abstract

Assessing land use change patterns in East African savannas requires understanding the complex relationship between the biophysical, ecological, political and socio-economic factors that shape these ecosystems. We combine ecological, social and modelling approaches to assess interactions between climate, vegetation, animals and changing land use types in two semi-arid savanna ecosystems in southern Kenya. Woody vegetation data was collected using the point centred quarter (PCQ) technique, social data was collected using interviews with community elders, and climate and management scenarios were tested using an agent based model (ABM). From the ecological survey it is clear that woody vegetation attributes vary with rainfall and management interventions and the nature of these interactions vary between the two research sites. Community elders confirm that rainfall enhanced variability is an important cause of land use change in the Amboseli landscape while socio-economic factors and conservation are the key factors driving land use change in the Mara landscape. The ABM shows livestock grazing and agriculture as the predominant land use types under private land tenure scenario. The ABM also shows an inverse relationship between agriculture land use and wildlife under this scenario. These findings can inform the management and planning of savanna ecosystems and have relevance to plant ecologists, natural resource managers, social-ecological modellers, conservation biologists and pastoral communities globally.

Keywords: Amboseli, community perspectives, Maasai Mara, modelling, function, sedentarisation

7.2 Introduction

Globally, savannas occupy 20% of the land surface (Grace et al., 2006; Stevens et al., 2017), supporting 20% of human population (Lehmann et al., 2014) and high biomass of wildlife and livestock (Scholes and Archer, 1997; Augustine et al., 2003; Bond and Keeley, 2005; Kimuyu et al., 2017; Stevens et al., 2017). Of the people supported by the savannas, most depend on livestock production (Boone et al., 2018) and how they manage their environment impacts the functioning of savannas. Thus it is important to understand changes that occur in savannas through time and how this influences vegetation, wildlife, livestock and land use patterns.

The relative importance of biotic and abiotic variables in driving vegetation structure in savannas is debatable (Aleman et al., 2017), however, there is consensus on the influence of some variables. Primary production is shown to be positively related to annual rainfall in semi-arid (<650 mm yr^{-1}) savannas making rainfall the most significant driver of woody cover in dry savannas (Sankaran et al., 2005; Bucini and Hanan, 2007; Buitenwerf et al., 2011; Shorrocks and Bates, 2015; Aleman et al., 2017). In high rainfall (>650 mm yr^{-1}) areas, disturbances are required to maintain the system as a savanna. Together with variable rainfall, disturbances are associated with the high turnover rates characteristic of savanna vegetation (Anderson et al., 2015). Where vegetation structure is largely shaped by fire, the impact of inter-annual rainfall variability on woody cover reduces and the impact of land use becomes more significant than that of climate change (Synodinos et al., 2018). Generally, fire and herbivory are associated with humans because most fires are human induced and the main land use type in the savannas has been livestock grazing (Riginos et al., 2012; Kamau and Medley, 2014). Woody cover, in particular, is the most common descriptor of savanna vegetation structure and functionality (Franz et al., 2010; Aleman et al., 2017), and is the most affected by land use change because trees get cut first to make room for land use change. However, despite land use being significant in shaping vegetation patterns, transformation of woodlands to open savannas in many parts of Africa has been linked to fire and large herbivores, (Dublin et al., 1990; Leuthold, 1996;

Western and Maitumo, 2004; Anderson et al., 2015), and not to management policies and land use changes (Mutiti et al., 2017).

The relationship between wildlife conservation and pastoralism in the savannas is also highly debatable. In some cases, the relationship is seen to be complementary (Galvin et al., 2006; Kiffner et al., 2014), in others cases rising livestock numbers are associated with declining numbers of large mammalian wildlife species (Ogutu et al., 2009; Riginos et al., 2012), while in others, wildlife is seen to reduce livestock productivity through forage competition, diseases and predation (Riginos et al., 2012). Pastoralism has been the most suitable livelihood in arid and semi-arid savannas because it allows pastoralists to follow the changing rainfall patterns (Kirkbride and Grahn, 2008; Pricope et al., 2013). However, the high levels of agriculture expansion experienced in the recent past in pastoral areas (Sanz et al., 2017) has led to changes in the integrity of rangelands, the flows of ecosystem services (Reid et al., 2014) and consequently the structure of animal populations. As production of ecosystem services and the structure of savanna vegetation depends on the interactions between social and ecological systems (Bennett et al., 2015), it is necessary to understand trends in land use change and the potential impact they could have on savanna ecology. This is because savannas are the most converted biomes, from natural land to human land uses (Newbold et al., 2017), and their vegetation dynamics are best explained by the combined influence of climate change and land use change (Aleman et al., 2016). The impact of climate on vegetation becomes predominant when there is intensive land use change (Moore et al., 2015) while additional human impact, through resource acquisition or policy intervention, makes human impact in these ecological systems of great interest.

Interactions between humans and their environment in savannas can best be assessed by integrating ecological knowledge on resource use from indigenous communities with scientific approaches (Dabasso et al., 2012). Indigenous knowledge on environmental issues is fairly comprehensive and can be valuable to researchers developing sustainable natural resource management options (Angassa et al., 2012). Furthermore, the perceptions of land managers and local communities on land use often vary and compete (Fox et al., 2017) and when social capital and the perceptions of rangeland communities are undermined by policy makers and funders, who may prefer measurable economic or environmental outcomes, the adaptive capacity of community based conservation initiatives may be missed (Reid et al., 2014). In addition to natural resource planning, perceptions of indigenous communities on social-ecological issues can also be used for setting parameters or establishing statistical distributions of entities used in modelling social-ecological systems (Robinson et al., 2007). As it can be challenging to fully integrate the multiple nonlinear interactions in social-ecological systems using conventional statistical techniques, simulation models are often utilised (Schlüter et al., 2012; Miller and Morisette, 2014). This often involves combining process-based biophysical models with agent-based models (ABMs). The biophysical models provide ecological information which is used as input data for the ABM (Matthews and Bakam, 2007; Matthews et al., 2007; Boone et al., 2011). Ultimately, the combined models incorporate human decision making processes and ecological response to human activities to provide better understanding of the complex interactions between biophysical and social factors in the social-ecological systems (Galvin et al., 2006). Applications of ABMs in pastoral social-ecological systems in Africa include Boone et al. (2011), Martin et al. (2016) and Moritz et al. (2017).

In this study, we compare and contrast the interactions between climate, animals and changing land use types across two savannas in southern Kenya. We first assess.land use change using perceptions from local community elders. The perceptions are then used to design an ABM aimed at understanding the impact of changing land use types on wildlife densities. The study had two main objectives: 1) to assess perceptions of land use change trade-offs by pastoralists in southern Kenya; and 2) to integrate the impact of biophysical and socio-economic factors to simulate the impact of changing land use on wildlife conservation and livelihoods.

7.3 Study areas

Due to multiple interactions in driving ecosystem structure and land use change in pastoral areas, we were interested in comparing two pastoral sites in southern Kenya. Amboseli and Mara were selected as they are both dry areas used for pastoralism and conservation. Amboseli is located north of Mt Kilimanjaro on the Kenya-Tanzania border (Figure 7.1). It comprises the Amboseli National Park and the surrounding community group ranches. Average rainfall in Amboseli is 350 mm yr^{-1} (Altmann et al., 2002) and falls in two seasons; the short rains (November-January) and the long rains (March-May). Amboseli has a series of swamps, springs and rivers that are fed by underground seepages from Mt Kilimanjaro (Okello et al., 2016). Common grassy and woody plant species in Amboseli include *Chloris rocksburghiana, Eragrostis tennuifolia*, *Sporobolus* spp., *Commiphora* and *Acacia* spp. Mara is located north of the Serengeti ecosystem. It is made up of the Maasai Mara National Reserve and the surrounding community lands that provide wildlife dispersal zones. The eastern parts of Mara are drier (average rainfall of 600 mm yr^{-1}) while the western parts are influenced by Lake Victoria and are wetter (1000 mm yr^{-1}) (Lamprey and Reid, 2004). There are two rainfall season; the short (November-December) and the long (March-May) rains season. Vegetation in Mara is open woodlands with forests along rivers and seasonal water courses (Robertshaw, 1990; Vuorio et al., 2014). The main rivers in the Mara are the Sand, Talek and Mara (Ogutu et al., 2009) that all flow into the Mara River which begins its course in the Mau Escarpment and flows into Lake Victoria.

7.4 Methods

7.4.1 Data Collection and Analysis

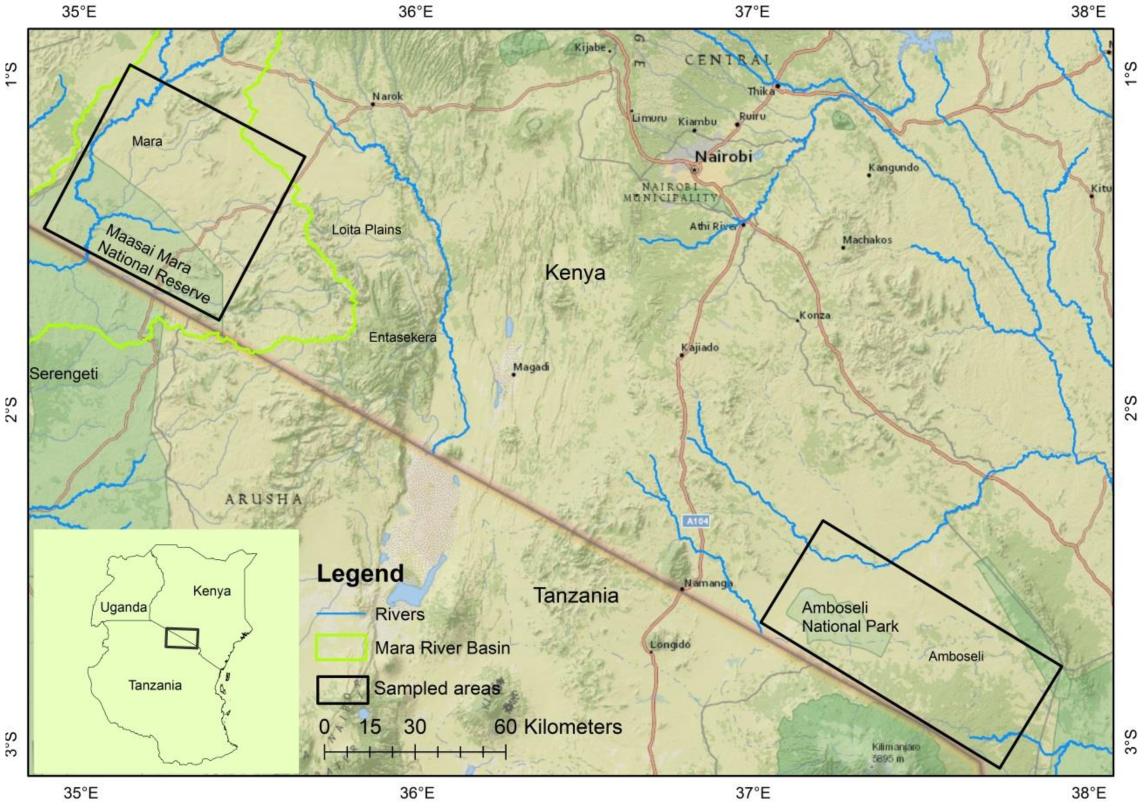

Figure 7.1: Location of Amboseli and Mara study sites and the delimitation of the protected areas in southern Kenya and northern Tanzania.

To understand historical land use changes and their drivers, semi-structured questionnaires were administered in different group ranches in Amboseli and Mara in

January and February 2016. The questionnaire was similar across the two areas and the selection of sampling areas was based on land tenure status, proximity to protected areas, roads and permanent water bodies. To ensure that the differences in the sampling areas were captured, we used proportional stratified random sampling to select respondents whose land was representative of the natural and socio-economic differences between the group ranches. The interviewees comprised of male and female land owners who had varying levels of education and diverse livelihood sources. Thirty pastoralists were interviewed in Amboseli and 27 in Mara. As the questionnaire was focussed on the history of land use changes, it targeted elderly pastoralists who had lived in the area for the most part of their adult life and could recall land use changes that have occurred in their group ranch in the last few decades. Themes that the questionnaire focussed on were on changes in land use types, drivers of land use change, impacts of land subdivision and land management.

We developed an ABM using NetLogo version 6.0.2 (Wilensky, 1999) and run it in Amboseli and Mara including on the vegetation plots sampled by DRSRS and the areas our questionnaire was administered. The description of the model variables and simulated processes followed the Overview, Design Concepts and Details (ODD) protocol (Grimm et al., 2006, 2010). The time resolution for the model was from 1950 to present and the spatial resolution is kilometre square (km^2). The ABM was linked to a dynamic global vegetation model, Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) (Smith et al., 2014), which provided input in form of grass biomass for the ABM. LPJ-GUESS dynamic global vegetation model used long-term rainfall data from Climatic Research Unit (Jones and Harris, 2008). It simulated grass biomass for Amboseli and Mara in annual time steps for the years between 1950 to 2005 at 0.5 x 0.5^o resolution. The biomass was converted to kg/km^2 and used as input in the ABM.

In designing the ABM, we used the pattern oriented modelling (POM) approach (Grimm et al., 2005) to incorporate the behaviour of Amboseli and Mara that we had observed during fieldwork and had been informed by our questionnaires. POM involves using multiple patterns observed in real world systems to calibrate the model and to accept/reject the decisions of agents that do/do not reproduce these patterns (Bert et al., 2014; Schulze et al., 2017). POM is utilised to overcome challenges in parameterising human decision making within ABMs and to make the model structure realistic and less sensitive to uncertainty of model parameters (Schlüter et al., 2012). The ecological and socio-economic variables used in the model were parameterised using data from literature. In addition, the mean and standard deviation of the variables was used to introduce stochasticity into the model. The simulated model outputs included changes in land use types and wildlife density under dry and wet rainfall regimes and under communal and private land tenure scenarios. Communal land tenure scenario assigned 50% of the land use cells in the model to be used as communal land, 25% as private land and 25% as government land. Private land tenure scenario assigned 50% of the land use cells to private land, 25% to communal land and 25% to government land. Both descriptive and inferential statistics were done to establish differences in the ecological and social-ecological interactions between the two study sites. The level of significance was set to P<0.05.

7.5 Results

Using our interdisciplinary methods, we found that: 1), 1) livestock grazing remains the main land use type in southern Kenyan savannas despite rainfall variability and land subdivision, 2) pastoralists turn to agriculture as a means of supplementing their income from livestock grazing, 3) provision of financial support to land owners discourages land subdivision and promotes livestock grazing with conservation land use, consequently enhancing livestock and wildlife numbers. Further details on our results from each individual method are provided below.

7.5.1 Suitability of land for specific land use types

In Amboseli, closeness of land to settlements and infrastructure development was considered important while pastoralists in Mara considered disease free areas as suitable for livestock grazing (Table 7.1). The leading factors perceived to make land suitable for agriculture were water availability, fertile soils, infrastructure development and lack of wildlife. The proportions vary between Amboseli and Mara: 50% and 4% of respondents in Amboseli viewed water availability and lack of wildlife as key factors compared to 11% and 16% in Mara. Five percent of elders in Amboseli and 40% in Mara perceived high wildlife numbers as important in determining the formation of wildlife conservancies. Woody areas, availability of pasture and tourist infrastructure were also viewed as key in determining the formation of conservancies. The presence of social facilities, water, pasture and flood-free zones were important in determining land that was suitable for settlements.

7.5.2 Periods when land use changes heightened

Periods of intensified land use change were defined as times when the levels of land use change were the highest. Overall, most pastoralists (44% in Amboseli and 56% in Mara) were of the opinion that there were periods of intensified land use changes. Periods of intense land use changes ranged from the 1960s to 2000s and were driven by climatic, socio-economic and political factors. The reasons varied in timing and frequency between Amboseli and Mara. For instance, rainfall variability was suggested as a key driver of land use changes in Amboseli from the 1960s to 2000s while in the Mara it was only mentioned as being important from 2000s (Table 7.2). Socio-economic and political factors were suggested as key factors driving land use change from the 1990s in Amboseli; whereas in Mara, human population and socio-economic growth were suggested as key land use change drivers a decade earlier (1990s) than in Amboseli (2000s). In the 1990s and 2000s, there were more pastoralists in Mara than in Amboseli who perceived land subdivision as a key driver of land use change. The influence of agricultural expansion was only mentioned in Amboseli while development of wildlife conservancies was only mentioned as a key driver of land use change in Mara.

Table 7.1: Comparison between pastoralists views on the best land for livestock grazing, agriculture, conservation and settlements in Amboseli and Mara.

Suitable land for livestock grazing			**Suitable land for agriculture**			**Suitable land for conservation**			**Suitable land for settlement**		
Amboseli	Pasture availability	46%	Amboseli	Water availability	50%	Amboseli	Pasture availability	26%	Amboseli	Social facilities and other settlements	35%
	Water availability	21%		Fertile soils	30%		More trees	15%		Water availability	22%
	Near settlements	7%		Depressed and flooded areas	8%		Arid soils	11%		Elevated and flooding free areas	14%
	Arid soils	7%		Infrastructure	4%		Rocky areas	11%		Pasture availability	10%
	Infrastructure	7%		Land availability	4%		Water availability	11%		Rocky areas	8%
	Land availability	4%		No wildlife	4%		Land after other uses	11%		Infertile land	5%
	No floods	4%			**100%**		Compatible to livestock grazing	5%		Near farms	3%
	Salty soils	4%	Mara	Fertile soils	58%		High wildlife numbers	5%		Near trees used for fencing and fuel	3%
		100%		No wildlife	16%		Investor influence - Lodges	5%			**100%**
Mara	Pasture availability	49%		Water availability	11%			**100%**	Mara	Water availability	25%
	Water availability	22%		Abandoned cattle corrals	5%	Mara	High wildlife numbers	40%		Social facilities and other settlements	28%
	No diseases	17%		Flat areas	5%		More trees	12%		Elevated and flooding free areas	19%
	Salt lake	9%		Infrastructure	5%		Vast land	16%		Pasture availability	13%
	Land availability	3%			**100%**		No settlements	8%		Flat areas	6%
		100%					Investor influence - Lodges	8%		No bushes	6%
							Water availability	8%		Fuel availability	3%
							Compatible to livestock grazing	4%			**100%**
							Tourist availability	4%			
								100%			

Table 7.2: Periods of peak land use change in Amboseli and Mara and the main reason for the land use change.

Peak of land use change	**Cause of land use change peak**	**Percent of mentions**	
		Amboseli	**Mara**
1960s	Rainfall variability	20%	
1980s	Rainfall variability	31%	
1990s	Agreement by community		5%
1990s	Rainfall variability	7%	
1990s	Education	7%	10%
1990s	Land subdivision	7%	10%
1990s	Population and economic development		15%
2000s	Agriculture expansion	7%	
2000s	Development of conservancies		20%
2000s	Rainfall variability	7%	5%
2000s	Education		5%
2000s	Population and economic development	7%	
2000s	Land subdivision	7%	30%
	Total	**100%**	**100%**

7.5.3 Pastoralism, Agriculture and Wildlife Densities

The model outputs for Amboseli and Mara were broadly similar and complemented the results from the vegetation plots and from the interviews. From the plots and the interviews, Amboseli was shown to have more variable climate. From the model, trends in livestock and wildlife are similar whereby their numbers increase in a wet year and decline in a dry year. Agriculture levels decrease with increasing wildlife both in dry and wet seasons. Under the communal land tenure scenario, there were high levels of livestock grazing land use compared to agriculture land use while under the private land tenure scenario, there were higher levels of agriculture. Consequently, wildlife density was higher under communal land tenure scenario compared to private land tenure scenario (Figure 7.2 A and B).

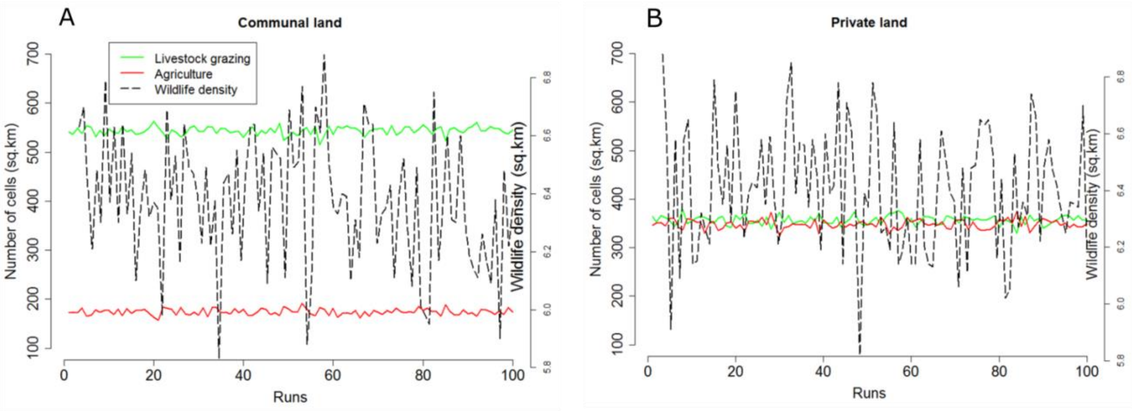

Figure 7.2: Trends between livestock grazing, agriculture and wildlife density under communal and private land tenure scenarios in Amboseli.

7.6 Discussion

Our interdisciplinary results help provide holistic insight into 4 real-world problems: 1) water and variability, 2) agricultural expansion, 3) wildlife, livestock and conservation interaction and 4) periods and nature of land use change.

7.6.1 Water and variability

Since the last half of the twentieth century, cyclic droughts in Kenya have become unpredictable with their frequency increasing from once every ten years in the 1960s to once every five years in the 1980s and once every two-three years in the 1990s (Opiyo et al., 2015). Severe droughts hinder the progress of pastoralism by causing widespread social and economic disruption to pastoralists (Western and Nightingale, 2003) especially in very arid areas where mobile pastoralism presents a resilient and potentially economical land use compared to sedentary livestock grazing (Riginos et al., 2012). Pastoralism in Kenyan rangelands has been regarded as ineffective (Campbell et al., 2000; Mwangi and Ostrom, 2009) and has been encroached by land use types seen as more productive, such as commercial agriculture, ranching and conservation (Nassef et al., 2009). For all land use types in the rangelands, water availability is key in determining potential land use and is considered the most important determinant of land use choices in southern Kenyan savannas (Okello et al., 2016). The erratic rainfall patterns and frequent droughts in pastoral areas have a huge impact on pasture production (Galvin, 2009; Pricope et al., 2013; Martin et al., 2016); this clearly comes through the elders perspectives and the ABM outputs. When adequate water and pasture are available for livestock, pastoralist maintain their livelihoods, otherwise they are forced to adopt drought management strategies or to diversify their livelihoods (Galvin et al., 2008; Homewood et al., 2009). Water variability is an important determinant of land use types in Amboseli compared to Mara mainly because Amboseli is drier (average rainfall of 350 mm yr^{-1}) than Mara (average rainfall 600-1000 mm yr^{-1}) (Altmann et al., 2002; Lamprey and Reid, 2004). As a result of this aridity, irrigated agriculture in Amboseli is more extensive along swamps (Worden et al., 2003; Okello et al., 2011) with its continued production dependent on the availability of adequate water (Campbell et al., 2000).

7.6.2 Agricultural expansion

The key land use change in East African rangelands, and often focused on key resource areas, such as swamps and forests, is the conversion to agriculture (Reid et al., 2004). These areas become centres of competing land uses, between agriculture, pastoralism and conservation (Campbell et al., 2000) with agriculture being a significant threat to wildlife conservation (Seno and Shaw, 2002). Agriculture expansion in Amboseli is significant as it began on the fertile and wet slopes of Mt Kilimanjaro in the 1930s (Campbell et al., 2000). Later on, irrigated agriculture, along riparian zones, was promoted by economic growth and improved market access in Kenya (Campbell et al., 2000) and presently is deemed as more profitable than pastoralism or conservation (Okello et al., 2011). Agriculture expansion is also driven by land subdivision as shown by the ABM outputs with agriculture levels being low under communal land tenure scenario, and rising under private land tenure scenario. To fulfil the food demands of its growing population, it is expected that agriculture will expand in Africa and will have a high impact on trade-offs between land use patterns such as in urban development and biodiversity conservation (Schaldach et al., 2009). This calls for interdisciplinary perspectives in finding solutions that address agriculture expansion in sub-arable rangelands and that would take into account the increasing human population and urbanization expected in the rangelands. It is also worth taking into account that investment in irrigated agriculture in pastoral areas in Kenya is estimated to be capable of profiting only 3% of the population by 2020 (REGLAP, 2012) and sedentary pastoralists in pastoral areas are largely poorer than mobile pastoralists (Little et al., 2008).

7.6.3 Wildlife, livestock and conservation interaction

In the later twentieth century, pastoralism has been threatened by land subdivision and sedentarisation which leaves pastoralists with the option of either maintaining mobile pastoralism on disconnected rangelands or settling on subdivided land and losing access to common resources (Reid et al., 2014). The impacts of land fragmentation on pastoralism are severe in arid areas. This has resulted in some pastoralists in very arid areas whose land is subdivided, collectively consolidating their lands and managing them in common (Reid et al., 2014) while others diversify their livelihoods as a last resort (Little et al., 2008) though the bulk (more than 50%) of their income comes from livestock production (Homewood et al., 2009). The absence of diseases as a factor that determines suitable areas for livestock grazing was mentioned as being important in Mara and not in Amboseli; this possibly relates to widespread tsetse fly infestation that occurred in the Mara in the first half of the twentieth century and the concerted efforts to eradicate the epidemic in the 1960s (Dublin et al., 1990; Serneels et al., 2001).

Specialisation in pastoralism and maintenance of a viable livestock herd requires about 4.6 to 6 per capita Tropical Livestock Units (TLU) (Little et al., 2008), where one TLU is equivalent to 250 kg (Osano et al., 2013; Kibet et al., 2016). When pastoralist herd sizes diminish below a certain threshold, they are not protected from the impact of droughts and diseases and might be forced to sell reproductive animals that would potentially increase their herds (Moritz et al., 2017). Below this threshold, 'poverty traps' exist amongst them and makes them unable to afford a decent life even in periods of high rainfall and adequate pasture (Little et al., 2008). To avoid reaching this threshold, conservation managers can set aside dry season grazing reserves within community lands. They should also control livestock numbers and grazing pressure to ensure that there is no overgrazing by practicing rotational grazing. Conservation managers should also encourage merging of fragmented land especially in the very dry areas where other land use type cannot be practiced. This is also beneficial to wildlife as protected areas account for only 35% of Kenya's wildlife population (Western et al., 2009) and 65-70% of wildlife populations are found in community lands surrounding protected areas (Ogutu et al., 2017). Land subdivision and sedentarisation negatively impacts wildlife and savanna productivity by reducing vegetation biomass, animal mobility and the recovery rates of grass after droughts (Groom and Western, 2013; Kiffner et al., 2014).

From the elders, high wildlife density makes land suitable for conservation land use. Higher wildlife biomass in Mara, relative to Amboseli, explains why more pastoralists regarded high wildlife density as a key determinant of suitable conservation areas. While elders in Amboseli associated conservation with arid and rocky areas, those in Mara associated conservation with land availability. These contrasting views explain the varying attitudes towards wildlife conservation in the two areas. It was also important to the elders for conservation areas to be compatible with livestock grazing. This is being implemented by the formation of wildlife conservancies across Kenyan rangelands that aim to promote wildlife tourism by discouraging wildlife habitat fragmentation, improving pastoral well-being and controlling land use in the rangelands (Vuorio et al., 2014; Boone and Lesorogol, 2016; Bedelian and Ogutu, 2017). Moreover, pastoralism in the Mara is perceived to be more widespread than in Amboseli probably because higher wildlife numbers in Mara favour pastoralism and conservation and discourage agriculture.

As land privatisation in pastoral areas may be inevitable, one way of ensuring livestock mobility across fragmented landscapes is land use zoning that will provide specific areas for livestock grazing, conservation, agriculture and settlements (Kimiti et al., 2018). Where pastoralism continues unrestrained by changes in land use or land tenure; livelihoods, biodiversity and sustainable land management practices are promoted (Kirkbride and Grahn, 2008). With pastoralism in Kenya contributing 10% of Kenya’s gross domestic product and supplying 50% of the meat consumed in the country (Kirkbride and Grahn, 2008); sustainable management of pastoral land will alleviate poverty among the 65% (Mwangi and Ostrom, 2009) of pastoralists who live below the poverty line in Kenyan dry lands. It will also prevent national government from losing 4-8% of their gross domestic product to degradation of drylands (United Nations, 2011).

7.6.4 Periods and nature of land use change

The periods of intensified land use changes often vary between areas and are characterised by micro-habitat factors. Socio-economic and political factors drove land use changes in Mara from the 1990s following the rapid human and cattle population growth in the late 1980s that was a result of active tsetse fly control measures by the government and pastoralists in the early 1960s, (Dublin, 1991; Lamprey and Reid, 2004). The high human population in Mara, compared to Amboseli (Kenya National Bureau Statistics, 2010) may also explain why there were more pastoralists in Mara who thought land subdivision, driven by population growth, accounted for land use change in the 1990s and 2000s. Development of wildlife conservancies in Mara is associated with the increase in conservation land use in Mara in the 2000s.

Competing land uses call for sustainable land use practices, otherwise ecosystem services trade-offs will occur. These trade-offs, where the supply of one ecosystem service diminishes as a result of the increase of another ecosystem service, can be prevented if we understand the interactions among ecosystem services (Rodríguez et al., 2006). Policies designed for managing social-ecological systems should aim at minimising ecosystem services trade-offs at multiple temporal and spatial scales (Rodríguez et al., 2006). Solutions to challenges brought by land use change should also integrate methods that address trade-offs between the role of ecosystems in providing ecosystem services to current populations and maintaining the integrity of the ecosystem for future populations (Foley et al., 2005). As Africa is recognised as potentially vulnerable to climate change, (Egoh et al., 2012) and the risk of droughts over much of the continent is projected to increase by 2050 (Opiyo et al., 2015); land use types will play an important role in shaping climate patterns, maintaining ecosystem integrity and in ensuring secure livelihoods and food security (Sanz et al., 2017).

7.7 Recommendation for future studies

Our study used social insights drawn from interviews with local community elders in southern Kenyan rangelands to understand and develop a social-ecological model for pastoral ecosystems in southern Kenya. Our study can be improved by incorporating the following suggestions:

- Results from our study suggests that livestock grazing remains the predominant land use type in southern Kenyan savannas despite variable climate and changing land tenure. We also discuss the value of conservation support to landowners in promoting livestock grazing and conservation land use type as well as in improving pastoral wellbeing. Of the land use types in savannas, pastoralism is the most resilient to variable and unpredictable climate characteristic of savannas (Nassef et al., 2009). However, pastoralists in Kenya have the highest poverty rates and poorest access to basic social facilities (Kirkbride and Grahn, 2008). If further research could focus on identifying solutions to land use change trade-offs that could enhance human wellbeing, national development and wildlife conservation; then solutions will help meet Sustainable Development Goals 1 (no poverty), 8 (decent work and economic growth) and 15 (life on land). The solutions proposed should take into account that 1) higher short rains seasons is predicted to fall over much of Kenya from the 2020s with an increase of up to 60% by 2050 (Kirkbride and Grahn, 2008; Nassef et al., 2009); 2) agriculture in developing countries is projected to expand in the future to meet the food demands of a growing population (UNCCD and World Bank, 2016); 3) ecosystem services trade-off decisions across the Millennium Ecosystem Assessment (MEA) categories, show a preference to provisioning followed by regulating and cultural services (Rodríguez et al., 2006) and 4) Kenya’s development blueprint, Vision 2030.

- In modelling SESs, there is no single and exclusive model that can address a given problem, rather a variety of models are developed using different perspectives and used to provide multiple insights to any given problem (Schlüter et al., 2012). The modelling technique we used was agent based modelling. Agent based models that are used for studying complex social-ecological systems have a human behaviour component that should be tested by continuous reviews with multiple criteria rather than with a numerical fit between model outcomes and observed patterns (Miyasaka et al., 2017). This is because agent based models outputs are based on multiple, heterogeneous nonlinear interactions at various scales among autonomous components and their environment. These multiple criteria involves how suitable the model addresses its objectives, the soundness of the model assumptions and theories and the validity of the sub-models, input data and model outputs (Macal and North, 2010; Le et al., 2012; Miyasaka et al., 2017). As our model was not spatially explicit, further studies can develop a spatially explicit land use change agent based model that uses high resolution land use and climate maps as input data. The simulated outputs can be a combination of maps and numerical data which can be tested using multiple criteria to establish their validity.

- SDG 15 focusses on the management of land resources and aims for each country to stop land degradation by 2030. Sustainable land management is important for ensuring current and future demands for crop and livestock production are met (UNCCD and World-Bank, 2016). However, the development of suitable natural resource management plans for the future is challenged by the uncertainty of most climate projections and the complexity of interactions between social and ecological factors (Miller and Morisette, 2014). In discussing tools that can guide natural resource management, Miller and Morisette (2014) propose the integration of species distribution models, scenario planning and simulation models drawing on their complementary strengths. This is because species distribution models may provide estimates of the future distribution of species, but their output is insufficient to guide social and economic components of natural resource management decisions. Scenario planning is effective in predicting potential futures of given systems under great uncertainty, but cannot predict the characteristics of complex systems, such as emergence and adaptation while simulation tools, such as agent based models, can effectively explore climate and management scenarios, however, they are not suitable for developing scenarios. This study proposes an integration of different models to simulate the past, present and future land use trends in Kenyan savannas.

7.8 Conclusion

In this study, we combine social and modelling insights to understand interactions between climate, land use types and wildlife. From the views from community elders, the Mara environment has only recently become variable whereas rainfall variability has been high in Amboseli since the 1960s. From the model outputs, the influence of climate and land tenure shows wildlife and livestock have similar trends when responding to climate and land tenure changes. We also show the roles of biophysical and socio-economic factors in driving land use change in pastoral areas in East Africa: insights that can guide land use planning, poverty alleviation and climate change mitigation in a world where pastoralists are facing multiple challenges from climate and land use change, population growth, conservation and policy shifts.

7.9 Acknowledgements

We thank the Department of Remote Sensing and Resource Survey (DRSRS) in Kenya for collecting woody vegetation data in Amboseli and Mara. We are grateful to the local community elders we interviewed and whose opinions were used to develop the agent based model. The research permit for this study was issued by the National Commission for Science, Technology and Innovation (NACOSTI) in Kenya. This research was supported by a grant from the European Commission to the Marie Curie Initial Training Network project titled 'Resilience in East African Landscapes (REAL) (FP7-PEOPLE-2013-ITN 606879) to RM.

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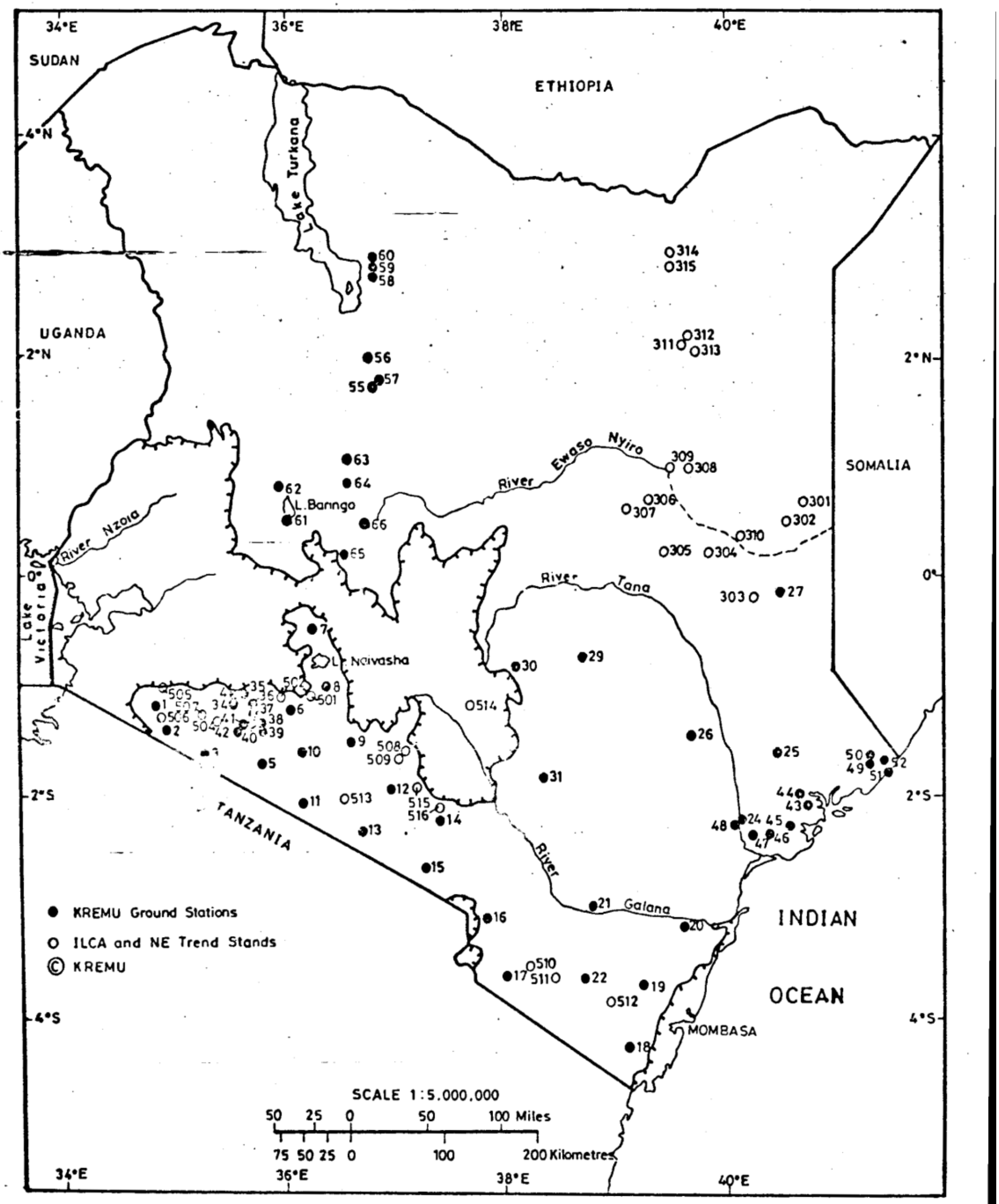
Appendix 1

FIG 2



Appendix 1: Distribution of all DRSRS vegetation plots sampled in late 1970s and early 1980s in Kenyan savannas. On the figure, the KREMU ground stations (circles with solid black fill) and the ILCA and NE trends stands (circles with transparent fill) illustrate the location of the vegetation plots that were sampled in late 1970s/early 1980s.

Appendix 2

Appendix 2: Questionnaire Survey

PART A -Land-use and livelihoods

1. What has been the percent cover of the following prevalent land uses in Mara?

Land use type	**1960s**	**1970s**	**1980s**	**1990s**	**2000s**	**2010s**
Livestock grazing						
Agriculture						
Conservation						
Forest						
Natural features (Swamps,rivers)						
Settlements						
Urban/built up areas/social facilities						
Fallow						

2. What land use types are observed in the following land tenure systems?

Land tenure type	**Land use type**
Communal land	
Private land	
Trust land	

3. What land makes good land for the following land uses and how is it allocated?

Land use type	**Why is it ideal for the land use type?**
Livestock grazing	
Agriculture	
Conservation	
Forest	
Natural features (Swamps,rivers)	
Settlements	
Urban/built up areas/social facilities	
Fallow	

4. What percent of available communal land used by communities for farming is allocated for:

Subsistence food provision? ------------------------

Income generation activities such as commercial farming--------------------

Livestock keeping? ---------------------------------

PART B: Changes in land use types

5. What are the main causes of land use change in Mara?
6. i) Was there a peak in land use change? Yes……………..No……………..

   ii) When was the peak?

   iii) What was the cause of the peak?
7. i) What are the main factors affecting livelihood patterns in Mara?

   ii) In what ways have climate change, availability of natural resources and human population growth affected livelihood patterns observed in Mara?

Social or environmental situation	**Livelihoods types practiced**	
	Males	**Females**
Increase in droughts		
Increase in rainfall		
Availability of natural resources e.g. wildlife, forests		
Human population increase		
Increase in education levels		
Increase in infrastructure and built-up areas		
Increase in land subdivision		
Increase in community based natural resource management		

iii) Do these patterns vary according to literacy levels or income levels?

Social or environmental situation	**Livelihoods practiced/Livelihood pattern**	
	Primary education	**Secondary or tertiary education**
Increase in droughts		
Increase in rainfall		
Availability of natural resources e.g. wildlife, forests		
Human population increase		
Per capita decrease in livestock		
Increase in infrastructure and built-up areas		
Increase in land subdivision		
Increase in community based natural resource management		

iv) Are there any seasonal, monthly or yearly variations in livelihood patterns?

8. Were there major climatic, cultural or economic events in the history of Mara that changed people's livelihoods? What coping strategies were used?

Historical events that changed people's livelihood	**Livelihood changes that occurred**	**Coping strategy used**
Climatic event(s)		
Cultural events		
Economic events		
Government policy		
Other		

9. What local organizations/public programmes have the greatest influence on the choice of livelihood patterns?

10. Which natural resource is most important for income generation/accessing adequate food?

11. i) What is the percent prevalence of pastoralism compared to other livelihoods in Mara after Kenya's independence in 1963?

High 65-100%)? -------------------

Medium (30-65%)? ----------------------

Low (0-30%)? ----------------------------

ii) What makes pastoralists change to other livelihoods? Rank the reasons below from highest to lowest with 1 and 7 being the least and most important reasons for change respectively.

Reason of changing from pastoralism to other livelihoods	**Rank**
Droughts	
Human population growth and socio economic development	
Land subdivision and fear of losing land	
Little income from pastoralism	
Government policy	
Livestock competition for pasture and water with wild animals	
Livestock competition for pasture and water with agriculture	
Other	

ii) What livelihood types do pastoralists prefer to adapt to?

Part D: Land management

12. What drivers of land use change can be addressed through better management of land/natural resources, policy intervention and community institutions?

	Intervention			
Driver of land use change	Better management of resources	Community benefiting from available resources	Formation of community institutions	Government policy
i)				
ii)				

13. What are the main causes of land subdivision in Mara?
14. Is land rotation system for farming and livestock practised in Mara?

    Yes -----------------

    No ------------------

15. i) Is there enough land for all?
    Yes -----------------
    No ------------------

    ii) What currently happens in cases of land scarcity?

    iii) What currently happens in cases of human migration?

16. Based on observed trends of land use/livelihood change over time: please indicate possible future land use scenarios when changes in the following aspects occur.

Human population/socio-economic development	**Livestock density**	**Wild animal density**	**Rainfall**	**Possible land use that will be practised**
Increase in human population	Decrease in per capita livestock density	Decrease in density of wild animals	Increase in rainfall	
Increase in human population	Increase in per capita livestock density	Decrease in density of wild animals	Decrease in rainfall	
Increase in human population	Decrease in per capita livestock density	Decrease in density of wild animals	Decrease in rainfall	
Increase in infrastructure and literacy levels	Increase in per capita livestock density	Increase in density of wild animals	Increase in rainfall	
Increase in infrastructure and literacy levels	Decrease in per capita livestock density	Decrease in density of wild animals	Decrease in rainfall	

Appendix 3

Appendix 3: Contribution to other articles during PhD studies

During my PhD studies, I co-authored the following articles.

1. Courtney-Mustaphi, C., Oliver, B., **Kariuki, R**., Capitani, C., Newman, R., Munishi, L., Lane, P. and Marchant, R. (2018) 'Informing land management policy dialogues with evidence of past, present, and future land use and land cover changes at the Kenya-Tanzania borderlands'. Manuscript submitted for publication.
2. Marchant, R., Richer, S., Boles, O., Capitani, C., Courtney-Mustaphi, C. J., Lane, P., Prendergast, M. E., Stump, D., De Cort, G., Kaplan, J. O., Phelps, L., Kay, A., Olago, D., Petek, N., Platts, P. J., Punwong, P., Widgren, M., Wynne-Jones, S., Ferro-Vázquez, C., Benard, J., Boivin, N., Crowther, A., Cuní-Sanchez, A., Deere, N. J., Ekblom, A., Farmer, J., Finch, J., Fuller, D., Gaillard-Lemdahl, M. J., Gillson, L., Githumbi, E., Kabora, T., **Kariuki, R**., Kinyanjui, R., Kyazike, E., Lang, C., Lejju, J., Morrison, K. D., Muiruri, V., Mumbi, C., Muthoni, R., Muzuka, A., Ndiema, E., Kabonyi Nzabandora, C., Onjala, I., Schrijver, A. P., Rucina, S., Shoemaker, A., Thornton-Barnett, S., van der Plas, G., Watson, E. E., Williamson, D. and Wright, D. (2018) 'Drivers and trajectories of land cover change in East Africa: Human and environmental interactions from 6000 years ago to present', *Earth-Science Reviews*, 178, pp. 322–378.
3. Githumbi, E. N., **Kariuki, R**., Shoemaker, A., Courtney-Mustaphi, C. J., Chuhilla, M., Richer, S., Lane, P. and Marchant, R. (2018) 'Pollen, People and Place: Multidisciplinary Perspectives on Ecosystem Change at Amboseli, Kenya', *Frontiers in Earth Science*, 5(January).
4. Courtney-Mustaphi, C. J., Shoemaker, A. C., Githumbi, E. N., **Kariuki, R**., Muriuki, R. M., Rucina, S. and Marchant, R. (2015) 'Historical ecology perspectives of changes in Amboseli, Kenya.', *GLP*, 12, pp. 26–29. Available at: https://glp.earth/how-we-work/glp-newsletters/glp-newsletter-issue-no-12-november-2015.