SPATIO-TEMPORAL DYNAMICS OF LAND USE AND LAND COVER, WILDLIFE HABITATS AND POPULATIONS IN THE GREATER SERENGETI ECOSYSTEM, TANZANIA

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A THESIS SUBMITTED IN THE FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN WILDLIFE MANAGEMENT OF SOKOINE UNIVERSITY OF AGRICULTURE, MOROGORO, TANZANIA

2021

EXTENDED ABSTRACT

Land use and land cover (LULC) change is a common phenomenon and of great concern to conservation in many terrestrial ecosystems, including the Serengeti Ecosystem (SE) in Tanzania. LULC changes can pose profound impacts on wildlife habitats, abundance and spatio-temporal distribution of wildlife species. This situation needs close monitoring, as it is not clearly known how the future ecological conditions of the ecosystem might be, if these changes remain unchecked. Previous studies on LULC changes, drivers, wildlife habitats and species distributions in the ecosystem are fragmented, focused either on specific habitat types or only on predicting spatial distribution and habitat suitability for particular wildlife species inside the protected areas (PAs). The above-mentioned studies provided limited information on the long-term prediction, imposing difficulties to infer the causes of wildlife populations fluctuation and observed changes in distribution pattern.

Knowledge of dynamics of LULC and habitats quality, and the drivers of change is imperative for maintaining healthy wildlife populations and ecosystems integrity. In lieu of this, therefore, the study aimed to carry out a spatio-temporal dyamics of LULC, wildlife habitats and populations in the SE (1975-2015). Specifically, the study sought to: i) characterize LULC change; ii) assess drivers of LULC changes; iii) assess quality of wildlife habitat; and (iv) determine the dynamics of herbivore distribution and habitat selection.

For objective one, the random forest classification algorithm was employed to classify the Multispectral Scanner (MSS), Thematic Mapper (TM), Enhanced Thematic Mapper Plus (+ETM) and Operational Land Imager (OLI) was used to characterize LULC into eight

main classes and extracted quantitative data for assessing the corresponding changes during 1975-1995, 1995-2015 and 1975-2015.

For objective two, LULC data for 1995 and 2015 derived from Landsat imageries (objective 1), and nine predictors of change (human population density, precipitation, distance from rivers, soil moisture, fire frequency, distance from roads, elevation, slope and elephant density) were used to ascertain their negative and positive influence for the changes using Binomial Logistic Regression. Drivers of change in LULC, have implications for wildlife habitat quality and spatio-temporal dynamics of wildlife species, therefore, for objective three, we mapped and evaluated changes in habitat quality (1975–2015) using the Integrated Valuation of Environmental Services and Trade-offs (InVEST) model, whereas, in objective four, Bonferroni confidence interval, with the Chi-square goodness-of-fit test and kernel density were used to assess herbivores habitat selection and distribution for browsers (grant's gazelles and giraffe), grazers (wildebeest, zebra and buffalo) and mixed feeders (impala and elephant).

Results revealed that grassland, shrubland and woodland were the major LULC types throughout 1975-2015 with percentage coverages of 50.6%, 23.7% and 20.9% for 1975; 54.2%, 23.5% and 15.9% for 1995; and 57.0%, 23.8% and 8.9% for 2015. Woodland cover (-11.1%) was the most converted to other cover types during 1975-2015. Overall habitat quality declined over time (1975–2015) in unprotected and human-dominated areas surrounding the ecosystem, intermediate deterioration rates in less heavily PAs (Wildlife Management Areas (WMAs), Game Controlled Area (GCA), Game Reserves (GRs) and the Ngorongoro Conservation Area (NCA) and the least rate in the most heavily protected Serengeti National Park. Significant clustered distribution pattern was observed for all

herbivores across space and time, with contracted distribution ranges for browsers and an expanded one for grazers and mixed feeders for 2015 in comparison to 1995.

The obtained information on species distribution, habitat selection and use are useful in determining high priority areas for effective conservation practices. Generally, increasing human population size, agriculture, settlements and policy changes, fires and elephant browsing pressure are central to LULC and habitats quality dynamics in the ecosystem.

The study recommends a more protection effort to halter LULC changes and habitats degradations in order to enhance quality habitat conditions for both browsers and grazers in the ecosystem. For less PAs (e.g. WMAs and GCA) improvement strategies are needed to strengthen conservation and management practices. Effective management of the key drivers of LULC and habitats change in the SE are of paramount importance. Wet and dry season herbivores coverage is needed to examine species guild’s spatio-temporal changes.

DECLARATION

I, Hamza Khalid Kija declare to the Senate of Sokoine University of Agriculture that, this thesis is my own original work done and that it has neither been submitted nor being concurrently submitted in any other high learning institution (s).

_____ _____

Hamza K. Kija **Date**

The above declaration is confirmed by the following Supervisors:

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Prof. Emmanuel F. Nzunda **Date**

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ACKNOWLEDGEMENTS

I am very grateful to the Almighty God, the Beneficent, the Merciful for his endless blessings to my commitment towards successfully accomplish this PhD program. It is his blessings, that kept me strong, and heart-giving power during up and downs in my academic and professional journey. My deep and sincere thanks are devoted to Prof. E.F. Nzunda, Prof. J.R. Kideghesho and Dr. Y.S. Mohammed for their endless guidance, assistance and support during my study as well as Prof. J.O. Ogutu for his timely and endless support throughout the program. Their encouragement and heart-giving guidance are appreciated the most. I am highly indebted to my employer, the Tanzania Wildlife Research Institute (TAWIRI) for granting me a study leave and use of the wildlife census data for the Greater Serengeti Ecosystem. I thank as well my fellow staffs; Dr. John Bukombe, Mr. Machoke Mwita (PhD Candidate-The Nelson Mandela African Institution of Science and Technology, NM-AIST) and Mr. John Sanare for their support (MSc Candidate: NM-AIST). I extend my thanks to my SUA colleagues; Dr. John Bernadol and Dr. Alex Mayamba (Graduated in 2020). I thank staffs from the College of Forestry, Wildlife and Tourism as well as the Post Graduate Committee (Dr. Kitegile and Dr. Mgonja) for organizing routine seminars, which shaped our understanding. The Committee played a great role in critical reviewing my manuscripts before submitted to journals.

I would also like to thank the *AfricanBioservices Project (ABS)*, for funding my PhD program and the Friedkin Conservation Fund, for additional funding to complete my program as well as Rungwa Game Safaris Tanzania for the top up funding towards thesis compilation.

I appreciate the high-level encouragement and patience of my lovely wives Rukia Manyegule and Nayma Mneney and children Advera, Musa, Nasra, Fahad, Ibrahim and Ashura, who gave me moral support throughout the entirety of the study period. Ibrahim and his young sister Ashura have been always behind my tail, inspiring me to push over and over. Nasra has been very fun, always encouraging me to complete my study and resume to my office and back home to stay with the family (Thanks to Mama Nasra as well). Lastly, I express my sincere gratitude to all people who in one way or another contributed to the success of my study program, without forgetting my close friend Mr. Lazaro Mangewa (PhD Candidate-The Nelson Mandela African Institution of Science and Technology, NM-AIST).

DEDICATION

I dedicate this work to my lovely wives Rukia Manyegule and Nayma Mneney and my children Advera, Musa, Nasra, Fahad, Ibrahim and Ashura. My family has been always praying for my academic and professional success, I thank for their endless prayers!

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LIST OF ABBREVIATIONS

ASCII	American Standard Code for Information Interchange
AUC	Area Under the Curve
AVHRR	Advanced Very High-Resolution Radiometer (AVHRR)
CHIRPS	Climate Hazards Center InfraRed Precipitation with Station
DEM	Digital Elevation Model
ESRI	Environmental Systems Research Institute
ETM+	Enhanced Thematic Mapper
GCA	Game Controlled Area
GIS	Geographic Information System
GPS	Global Positioning System
GRs	Game Reserves
GSE	Greater Serengeti Ecosystem
InVEST	Integrated Valuation of Environmental Services and Tradeoffs
KIA	Kappa Index of Agreement
LGCA	Loliondo Game Controlled Area
LULC	Land use and land cover
MGR	Maswa Game Reserve
MODIS	Moderate Resolution Imaging Spectroradiometer
MSS	Multi Spectral Scanner
NBS	National Bureau of Statistics
NCA	Ngorongoro Conservation Area
NOAA	National Oceanic and Atmospheric Administration
OLI	Operational Land Imager
ROC	Receiver Operating Characteristic
SNP	Serengeti National Park
SRF	Systematic Reconnaissance Survey
SRTM	Shuttle Radar Topography Mission
SUA	Sokoine University of Agriculture
TANAPA	Tanzania National Parks
TANROADS	Tanzania National Roads Agency

TAWA	Tanzania Wildlife Management Authority
TAWIRI	Tanzania Wildlife Research Institute
TM	Thematic Mapper
TOA	Top of Atmosphere
USGS	United State Geological Survey
UTM	Universal Transverse Mercator
VIF	Value Inflation Factor
WCA	Wildlife Conservation Act
WGS	World Geodetic System
WMA	Wildlife Management Area
WRS	World Reference System

LIST OF PUBLISHED PAPERS AND MANUSCRIPTS

Paper I: **Kija, H.K.**; Ogutu, J.O.; Mangewa, L.J.; Bukombe, J.; Verones, F.; Graae, B.J.; Kideghesho, J.R.; Said, M.Y.; Nzunda, E.F. Land Use and Land Cover Change Within and Around the Greater Serengeti Ecosystem, Tanzania

Status: Published in *American Journal of Remote Sensing.* **2020,** 8 (1) 1-19.

Paper II: **Kija, H.K.;** Mangewa, L.J.; Bukombe, Ogutu, J.O.; J.; Kideghesho, J.R.; Said, M.Y.; Nzunda, E.F. Factors influencing land use and land cover changes in the Greater Serengeti Ecosystem (1975-2015), Tanzania.

Status: Submitted to *Journal of Sustainability, Environment and Peace*

Paper III: **Kija, H.K.;** Ogutu, J.O.; Mangewa, L.J.; Bukombe, J.; Verones, F.; Graae, B.; Kideghesho, J.R.; Said, M.Y.; Nzunda, E.F. Spatio-Temporal Changes in Wildlife Habitat Quality in the Greater Serengeti Ecosystem.

Status: Published in *Sustainability.* **2020,** 12 (6) 2440.

Paper IV: **Kija, H.K.;** Ogutu, J.O.; Mangewa, L.J.; Bukombe, J.; Kideghesho, J.R.; Said, M.Y.; Nzunda, E.F. Dynamics of wild herbivores distribution and habitat selection in the Greater Serengeti Ecosystem, Tanzania.

Status: Submitted to *Journal of Global Ecology and Conservation*.

CHAPTER ONE

1.0 GENERAL INTRODUCTION

1.1 Land cover and its implications on wildlife habitats and populations

Land use and land cover (LULC) is an important part of biodiversity management. LULC and its accelerating change can lead to species habitats decline and/or loss, and an altered distributional range (Yadav *et al.* 2012). LULC can provide feeds and habitats to wildlife species (Morrison *et al.* 2012). Nonetheless, it's interactions in human-dominated landscapes interfere with the natural biotic and abiotic factors and processes, resulting into adverse consequences to species' habitat, abundance and diversity (Sala *et al.* 2000).

LULC changes can impose profound impacts on the structure and function of terrestrial ecosystems. LULC changes are pervasive and pose threats to biological resources at local and regional scales, than any other forms of environmental change such as climate change (Sala *et al.* 2000). LULC changes can reduce the size of any PAs in terrestrial ecosystem (Hansen and DeFries 2007), thus loss of biodiversity and decreased species richness (Huerta 2007), introduction of invasive species (Mosher *et al.* 2009), loss of crucial species habitats and blockage of wildlife corridors (Jones *et al.* 2012), habitat fragmentation (Krauss *et al.* 2010) and species distribution and movement patterns (ITTO and RFD 2015).

Serengeti ecosystem (SE) is one of the biodiversity hotspot in the world (Sinclair and Arcese 1995). This ecosystem has been registering significant and progressive stress on LULC change due to high human population growth to meet the demand for agriculture, livestock grazing, settlement and infrastructure development which diminish wildlife habitats and impairs habitats quality, consequently exerting negative ecological impacts on wildlife populations and the overall ecosystem integrity (Kideghesho *et al.* 2006).

These changes if continue in the inadequacy of data and information for appropriate interventions are likely to degrade or fragment areas that were once critical wildlife habitats and can change the ecological integrity of the ecosystem. LULC changes compromise the establishment purposes of many-core PAs to safeguard flora and fauna biodiversity (Hockings 2006, DeFries *et al.* 2007).

In the Serengeti ecosystem, LULC change has been studied by Estes *et al.* (2012) and Reed *et al.* (2009). Este's study covered within and outside the ecosystem boundaries, and only considered land cover change, in a span of two decades (1984-2003). Reed's study assessed only land cover (specifically vegetation types), covering one temporal scale (2000) and limited within PAs boundaries, excluding land use in the surrounding human dominating lands, which are believed to influence changes in land cover inside PAs boundaries. Both Estes and Reed's studies used narrow spatio-temporal scales and different approaches.

Changes in LULC have adverse effect on wildlife habitat quality and availability (Gaston *et al.* 2008). Wildlife habitats refer to the physical environment where an animal lives and obtains all necessary requirements for its survival (Hall *et al.* 1997). These habitats support a diversity of biological resources and provides breeding grounds, cover and space for wildlife species (Beerens *et al.* 2015). Wildlife habitats influence species diversity, density, distribution and movement patterns (Byrom *et al.* 2015, Dai *et al.* 2018, Zhang *et al.* 2019).

Changes in habitat quality have implications to wildlife, especially in savannah ecosystems, including the Serengeti. Savannah ecosystems are key habitats for wildlife and home to many iconic PAs and wildlife migrations (Sinclair *et al.* 2007, Bohm and

Hofer 2018). Change in wildlife habitats can cause; changes in species diversity (Rittenhouse *et al.* 2012), loss of wildlife species (Otuoma *et al.* 2009); and local or global species extinction (Davies *et al.* 2006).

Scientists elsewhere documented importance of habitat quality, quantity and threats (Wilson *et al.* 2015). For instance, Byrom *et al.* (2015) studied impact of LULC and climate change on avifauna in human-dominated landscapes in the western Serengeti, and characterized the influence of habitat types on species diversity and richness. Results indicated that under changing LULC, avifauna species with localized distributions are declining. Sinclair *et al.* (2002) study on human effects on bird abundances in the western Serengeti found that species diversity was declining in agricultural-dominated lands. Besides these studies, habitats quality and quantity were hardly determined, taking into account that the effects of LULC on wildlife habitats have been reported to intensify and exert effects on ecosystem functions globally (Sala *et al.* 2000).

Like many other areas in East Africa, LULC and wildlife habitats changes in the Serengeti ecosystem are particularly linked to increased anthropogenic pressures along its borders, mainly agriculture and settlements, and changes in various national policies (Veldhuis *et al.* 2019) thus altering habitats and ecosystem services (Zhang *et al.* 2019).

Un-regulated conversions of land cover types such as forests (including logging) for crop production, mining, urban, and infrastructure development, among other human-induced changes, have contributed to declines in high-quality wildlife habitats worldwide (Vermeulen *et al.* 2000, Santos and Tabarelli 2002, Otuoma 2004, Reid *et al.* 2004, Kideghesho *et al.* 2006, Prugh *et al.* 2008, Laurance 2010, Hanski 2011).

The study in Kenya showed that anthropogenic activities are significantly changing cover, resulting in an observable changing pattern of LULC and wildlife habitats over time (Nduati *et al.* 2013). Associated with humans, demand for settlement, grazing lands and infrastructure development are possible causes of change in LULC and can exert ecological disturbance to the ecosystem (Lambin *et al.* 2001, DeFries *et al.* 2007). These threats are likely to have continued effects on the ecosystem, as human population growth increase demand for agriculture, settlement and grazing lands (Estes *et al.* 2012).

LULC types, wildlife habitats and associated driving factors are dynamic in space and time (Nduati *et al.* 2013), and evidence suggests that there is no single driver attributed to LULC, rather a complex interaction of drivers (Serneels and Lambin 2001). Like LULC change, wildlife habitat quality is also influenced by multiple factors, mainly human-induced pressures, including over-utilization of biodiversity resources, poor land-use practices, and climate change (Kideghesho *et al.* 2006, Lindenmayer and Fischer 2013, Yan *et al.* 2016, Kija *et al.* 2020).

Kideghesho *et al.* (2006) reviewed major drivers for habitat change and ecological impacts on wildlife in the Serengeti ecosystem, focusing on the review of factors, and found that anthropogenic activities are the major cause of habitat degradation and wildlife loss. Homewood *et al.* (2001) assessed drivers for land cover and wildebeest population in the Serengeti-Mara ecosystem and found that agropastoralism and human population were not the main drivers for change. From the above studies, it is evident that, both LULC and wildlife habitats associated driving factors are threatening the survival of wildlife populations, thus impairing the ecological integrity of the ecosystem at large.

Furthermore, despite the existence of the above studies, little had been done particularly on linking the spatial and temporal aspects of LULC in relation to wildlife habitats quality and associated drivers of change in a spatial-explicit manner. The previously assumed changing pattern could not be inferred under current and likely future conditions without scientific studies. Hence, there was a need to conduct a study on spatio-temporal assessment of LULC and wildlife habitats and their drivers in the SE.

Likewise, despite the declining habitat quality in the ecosystem and its surrounding buffer area, no study had been conducted hitherto to quantify spatial and temporal changes in relation to protection status (Ngorongoro Conservation Area (NCA), National Park (NP), Game Reserves (GRs), Game Controlled Area (GCA) and Wildlife Management Areas (WMAs) and the buffer area (30 km). Consequently, the direction and magnitude of changes in habitat quality over time under contrasting levels of protection has not been examined in the ecosystem.

Habitat quality assessment has provided evidence-based information to inform management authorities to protect and improve habitats. The study mapped and quantified habitat quality in space and time using the Integrated Valuation of Environmental Services and Tradeoffs (InVEST). More precisely, we evaluated changes in habitat quality at three points in time (1975, 1995, and 2015) to provide a quantitative basis for improving wildlife habitat management and enhancing natural ecological processes in the ecosystem and possibly elsewhere.

1.2 Problem statement and Justification of the study

1.2.1 Problem statement

Serengeti ecosystem is one of the unique biodiversity hotspot ecosystem and a designated World Heritage Site and Biosphere Reserve (Sinclair *et al.* 2008). It is one of the sources of foreign exchange in Tanzania. Despite its ecological and economical importance in the country and the world at large, it faces progressive changes in LULC and wildlife habitats quality which threatens its ecological integrity (Estes *et al.* 2012).

The ecosystem changes are significant and progressive, possibly due to dynamic nature of drivers of changes such as climatic variability and human population growth with associated socio-economic activities (Ogutu *et al.* 2008, Estes *et al.* 2012). The recent increase in human and livestock populations in the ecosystem potentiates the negative changes in land use and land cover (Kideghesho *et al.* 2006, Estes *et al.* 2012) thus posing profound impacts on wildlife habitats, abundance and distribution. This situation needs close monitoring, as it is not clearly known how the future ecological conditions if remain unchecked.

Inadequate ecological data and information to monitor LULC changes, wildlife habitats quality dynamics and their impacts on wildlife populations impose difficulties in ecological monitoring of the ecosystem. Previous studies on LULC changes and wildlife habitats quality are fragmented and focused only on specific habitat types or habitats in proximity to human-dominated landscapes, excluding other habitat types (Sinclair *et al.* 2002, Sinclair *et al.* 2008, Byrom *et al.* 2015) whereas other studies only predicted spatial distributions and habitat suitability for particular species inside PAs. For example, a few studies focusing on land cover mapping, predicting spatial distribution, movement pattern and suitability of selected species (Fryxell *et al.* 2004, Gottschalk *et al.* 2007, Estes 2012).

The previous studies did not cover a wide array of LULC types, and habitats quality in the adjacent human-dominated lands, which are believed to entail ecological integrity of the ecosystem (Reed *et al.* (2009); Estes *et al.* (2012). These studies provided limited information on the long-term change prediction, imposing difficulties to infer the causes of wildlife populations fluctuation and changes in distribution pattern. For example, there have been on-going anthropogenic activities around the ecosystem that probably may have altered the spatial pattern and configuration of LULC.

The increase in human population has a direct relationship with the growing demand for agricultural production, space for human settlement and grazing lands, with ultimate change in spatial and temporal configuration of wildlife habitats (Kideghesho *et al.* 2006). Furthermore, changes in LULC alter wildlife habitats quality, species decline and distribution pattern (Campbell and Borner 1995, Ogutu *et al.* 2008).

This study noted a knowledge gap linking LULC changes, wildlife habitats quality and drivers of the changes in a spatial-explicit manner. It was not clearly known, prior to this study, which factors are most influencing LULC changes and wildlife habitats, given that drivers of change are dynamic, and are likely to have continued effects on the ecosystem (Kideghesho *et al.* 2006). Therefore, it was imperative to have an in-depth study covering the entire ecosystem and its surrounding buffer area close to the ecosystem boundary. The study thus investigated in detail the causes, processes and influences of LULC and wildlife habitat changes to wildlife populations and distribution.

1.2.2 Justification of the study

The Great Serengeti Ecosystem (GSE) is one of the best tourism destinations designated as World Heritage Site and Biosphere Reserve (Sinclair *et al.* 2008). The ecosystem is among the main sources of tourism foreign exchange in Tanzania. LULC changes and wildlife habitats quality influence the specie's spatio-temporal movements and distribution patterns and habitat's preferences. This affecting tourism activities because animals change movement and distribution patterns away from the previously determined tourist attractions. Therefore study findings intend to inform wildlife conservation and management practitioners, policy and decision-makers in the wildlife, tourism and related sectors to integrate and strengthen their efforts to address the various drivers of LULC change and wildlife habitats to ensure sustained ecological integrity and hence its economic importance through tourism.

Understanding of the spatial and temporal dynamics of habitat quality and associated drivers is fundamental to effective management of the GSE which is experiencing significant change in LULC and wildlife habitats quality. Since high habitat quality is a key determinant of vibrant wildlife populations in the ecosystem (Kideghesho *et al.* 2006), its decline hampers the ability of habitat to sustain diverse wildlife resources, resulting in altered species distributions, composition, and population abundance (Sutherland 1998), and ultimately loss of wildlife (Vermeulen *et al.* 2000, Hanski 2011) that are key tourists' attractions, hence loss of foreign exchange. In addition, the findings can provide the likely long-term trajectories and potential consequences for wildlife habitat and populations, which is crucial in planning for various conservation and management practices in the ecosystem. Generally, the study findings serves as baseline information for ecological monitoring and further studies.

1.3 Research Objectives

1.3.1 Overall objective

The overall objective was to carry out a spatio-temporal assessment of LULC change, wildlife habitats and populations in the Greater Serengeti ecosystem from 1975 to 2015.

1.3.2 Specific objectives

Specifically, the study sought to:

i) Characterize LULC change during the 40 years' study period (1975-2015);

ii) Assess drivers of the changes in LULC (1995-2015);

iii) Assess the spatio-temporal changes in wildlife habitat quality (1975-2015); and

iv) Assess spatio-temporal dynamics of herbivores and habitat selection (1995-2015).

1.4 Conceptual Framework

The conceptual framework (CF) is presented in figure 1.1. CF provides a working strategy as it presents key components and depicts relationships and feedbacks. The CF is framed to provide an understanding of the processes and impacts of change in LULC, drivers of change, habitat and spatio-temporal distribution of wildlife. LULC and wildlife habitats are influenced by direct and indirect drivers of changes such as; biophysical, physical, socio-economic, and climatic factors.

Basically, in terrestrial ecosystems, there is a complex interaction between LULC and drivers of change. Drivers of change can influence wildlife habitats either through reduced habitat patch sizes or degrading the quality of habitat patches or altering wildlife populations and the way they are distributed within the landscape, with respect to time.

Drivers of change can either act in single or multiple scales to influence changes, direct or indirect. For instance, GSE is comprised of conservation areas with differed protection

statuses, therefore, because ecosystems do not exist as isolated lands, LULC changes within the human-natural interface may disrupt ecological processes (Hansen and DeFries 2007).

The human population around the ecosystem can cause expansion of agriculture and settlement, negatively reducing habitat patches as lands will be cleared for settlement and cultivation to sustain the growing population (Nduati *et al.* 2013). Precipitation is positively associated with LULC change as it influences plants productivity (Ogutu *et al.* 2008). Proximity to water sources and roads obviously impact LULC as well as wildlife habitats in different magnitude.

The effect of fire on vegetation is important to the ecosystem as it can change vegetation state. Similarly, soil moisture determines the spatial distribution of LULC and habitat types (Canute *et al.* 2015). Slope and elevation affect LULC cover and wildlife habitats as steeper and elevated areas are hardly accessed (Bakker *et al.* 2005). Elephant density shape woody vegetation of any terrestrial ecosystem. These drivers either in single-or-multiple interaction can exert impacts on habitats, taking in account wildlife population and distribution are determined by habitats which provide ecological attributes for species survival (Mtui 2014).

LULC change and its influence on habitat and wildlife population is a key aspect in ecological science (Houet *et al.* 2010). Therefore, it is important to model the ecosystem conditions to provide information for the management authorities and decision-makers to understand which Pas are influenced by a particular LULC or habitat change and set strategies to intervene deleterious impacts in the ecosystem, if there is any.

To this end, the study is guided by the questions; how LULC are characterized? where the change occurred?, what are the drivers of LULC changes and how these changes affects wildlife habitat quality and species' distribution and dynamics in the study ecosystem.

1.5 Thesis Structure

This thesis is prepared according to "*Published papers*" format under section 7.2 (7.2.1-7.2.2 of the Regulations and Guidelines for Higher Degrees, 6th edition (2018) of the Sokoine University of Agriculture. It is organized in six chapters arranged coherently, preceeded by an extended abstract that summarizes the objectives, materials and methods, principal research findings, conclusion and recommendations. Chapter one is the general introduction of the study theme, which details the background information on land use and land cover (LULC), drivers of change, and how these changes affect habitat quality, and the spatio-temporal distribution of wildlife. The chapter contain as well study justifications and objectives. Chapters two to five are comprised of published papers (chapters two and four) and submitted publishable manuscripts (chapters three and five). Chapter two (paper 1) characterized LULC change. Chapter three (manuscript 1) make use of data and information from the previous published paper. The manuscript explored drivers for LULC within and around the study ecosystem. Chapter four (paper 2) modelled wildlife habitat quality, using the InVEST Model. Chapter five (manuscript 2) provides insights on herbivore spatio-temporal distribution and habitat selection of wildlife species. The published papers and publishable manuscripts are articulated to the main study theme. Chapter six presents key contributions, general conclusions and specific recommendations of the study for better conservation and management of wildlife in the ecosystem. The format and writing style of published papers (and manuscripts 1 and 2 in chapters four and five respectively) are according to the requirements of the target journals.

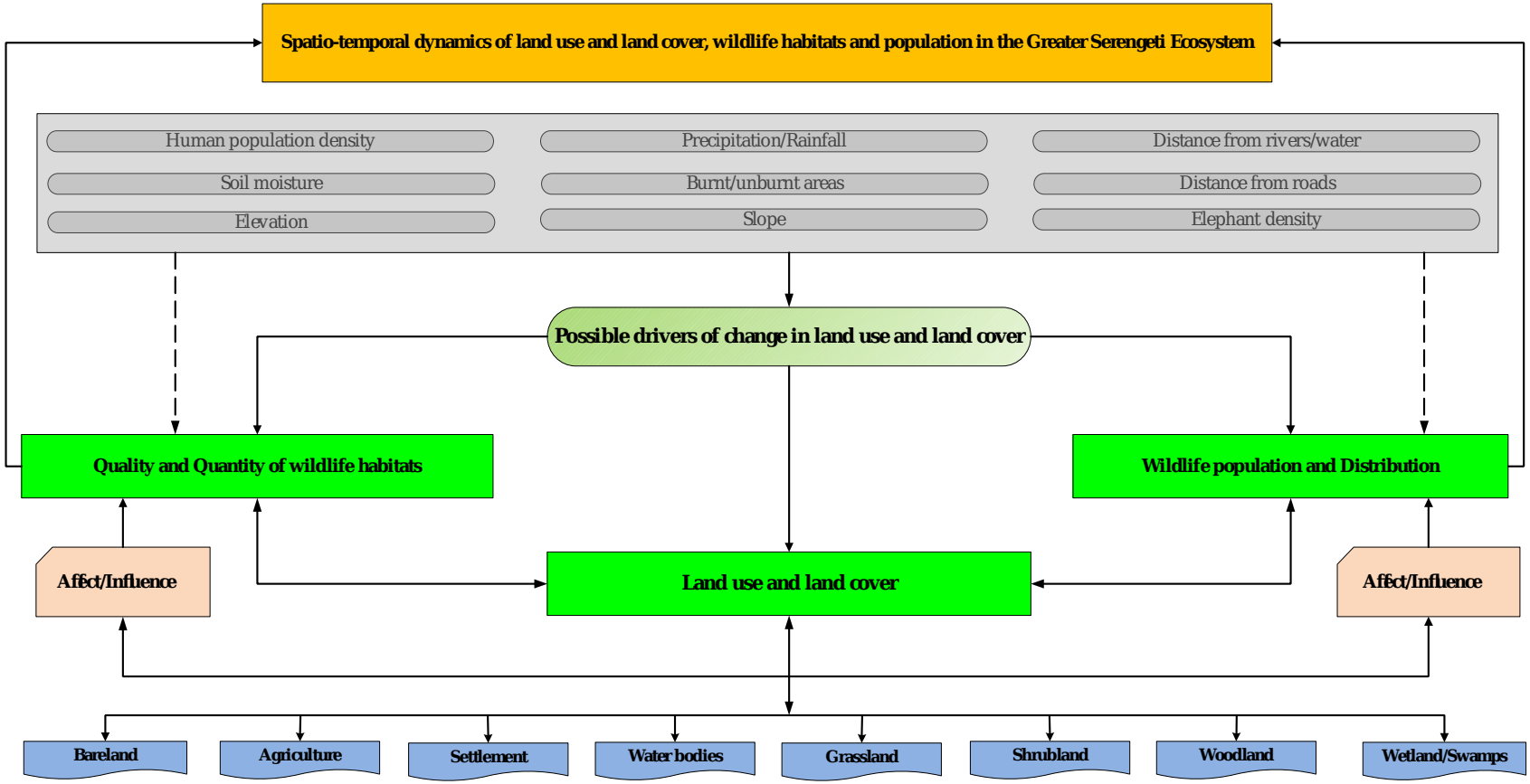

Figure 1.1: Conceptual framework of the study (Source: Student perspective)

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CHAPTER TWO

Land use and land cover change within and around the Greater Serengeti Ecosystem, Tanzania

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Status: Published in the *American Journal of Remote Sensing.* **2020,** 8 (1) 1-19.

American Journal of Remote Sensing
2020; 8(1): 1-19
http://www.sciencepublishinggroup.com/j/ajrs
doi: 10.11648/j.ajrs.20200801.11
ISSN: 2328-5788 (Print); ISSN: 2328-580X (Online)

Land Use and Land Cover Change Within and Around the Greater Serengeti Ecosystem, Tanzania

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To cite this article:
Hamza Khalid Kija, Joseph Ochieng Ogutu, Lazaro Johana Mangewa, John Bukombe, Francesca Verones, Bente Jessen Graae, Jafari Ramadhani Kideghesho, Mohammed Yahya Said, Emmanuel Fred Nzunda. Land Use and Land Cover Change Within and Around the Greater Serengeti Ecosystem, Tanzania. *American Journal of Remote Sensing*. Vol. 8, No. 1, 2020, pp. 1-19. doi: 10.11648/j.ajrs.20200801.11

Received: March 3, 2020; **Accepted**: March 20, 2020; **Published**: April 29, 2020

Abstract: Land use and land cover (LULC) changes can pose profound impacts on wildlife habitats, abundance and distribution and on human-dominated landscapes. We investigated LULC changes in the Greater Serengeti ecosystem, Tanzania, for a period of 41 years from 1975 to 2015. Specifically, we mapped LULC types for 1975, 1995 and 2015 and assessed the corresponding changes during 1975-1995, 1995-2015 and 1975-2015. We used the random forest classification algorithm to classify Multispectral Scanner (MSS), Thematic Mapper (TM), Enhanced Thematic Mapper Plus (+ETM) and Operational Land Imager (OLI) into eight main classes. We obtained accuracies of 88.4%, 90.6% and 93.4% with Kappa Indices of Agreement (KIA) of 0.86, 0.87 and 0.91 for 1975, 1995 and 2015, respectively. Grassland, shrubland and woodland were the major LULC types throughout 1975-2015 with percentage coverages of 50.6%, 23.7% and 20.9% for 1975; 54.2%, 23.5% and 15.9% for 1995; and 57.0%, 23.8% and 8.9% for 2015, respectively. Overall, woodland cover (-11.1%) was converted to most of the other cover types during 1975-2015. The loss of woodland cover is due to increasing human population size, agriculture, settlements and policy changes fires and elephant browsing. Effective conservation policies and regulation of socio-economic activities in the ecosystem and its buffer area are essential to ameliorate declining vegetation cover, especially along the protected areas boundaries.

Keywords: Land Use and Cover Change, Land Cover Transformation, Random Forest Classification, GIS and Remote Sensing, Serengeti Ecosystem, Wildlife Habitats

1. Introduction

Land use and land cover (LULC) are important components of natural ecosystems. Land cover provides habitats for wildlife, while land use shapes the land cover, and consequently, alters the habitat types and wildlife species [1].

annual average of 500 mm in the southeast to 1150 mm in the northwest and from 500 mm in the East to 950 mm in the west [25, 26]. Part of the spatial variation in rainfall is due to topographical gradients in the ecosystem. Temperatures are generally warm year-round and averages 27 °C [25].

The ecosystem supports a mixture of diverse vegetation types, ranging from grassland plains in the south-eastern and western regions of Serengeti and northern Ngorongoro [27], to north of Grumeti river and woodlands in Maswa and a mosaic of woodlands and closed gallery forests along major rivers in Ikorongo-Grumeti Game Reserve [16, 28]. Other vegetation types include riverine forests, swamps, grasslands, woodlands and open-woodlands [27], with woodlands, covering 60% of the ecosystem, being the dominant vegetation type [28]. It is home to abundant herds of diverse ungulate species, including the migratory wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga burchellii*), Thomson's gazelle (*Gazella thomsoni*), and other species, such as buffalo (*Syncerus caffer*) and elephants (*Loxodonta africana*) [7, 29].

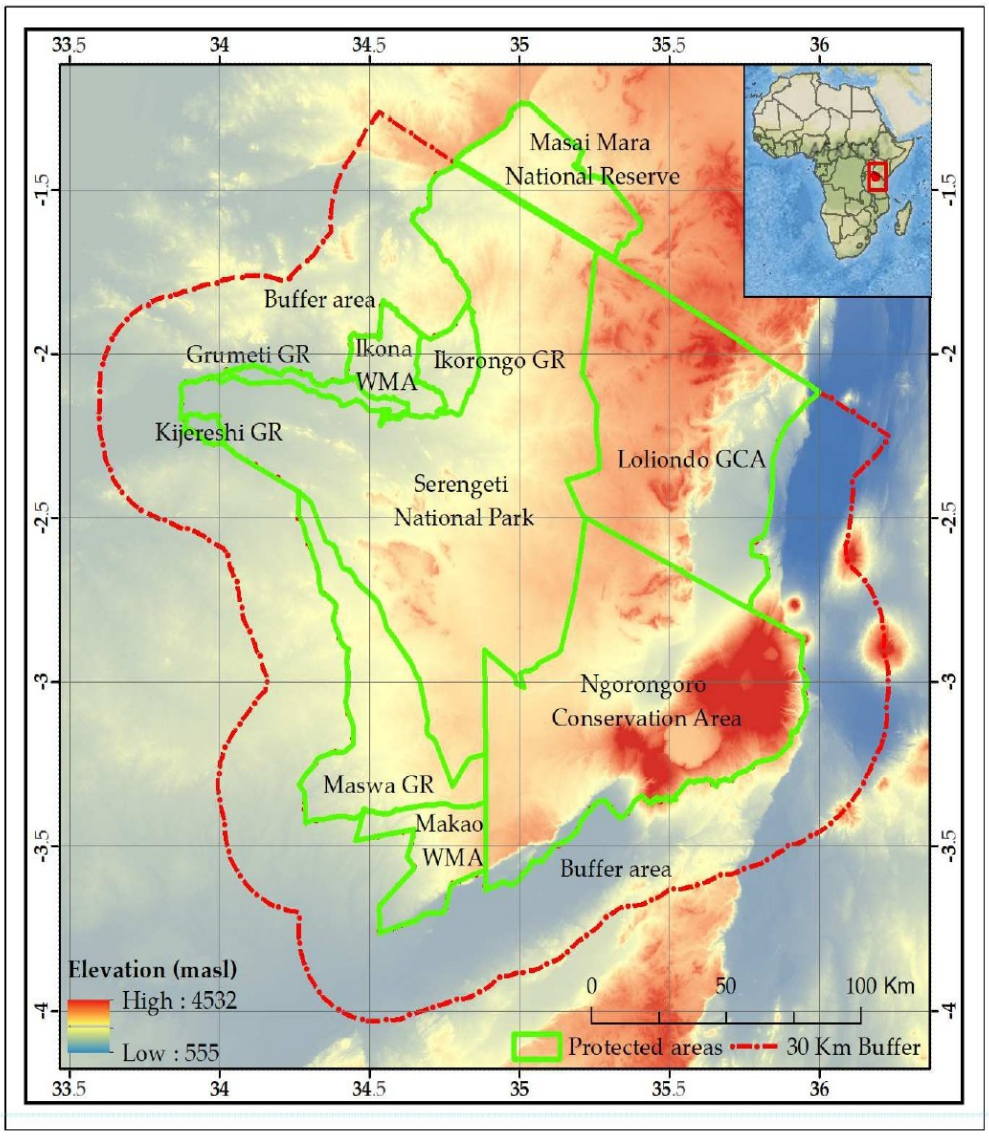

Figure 1. *Map of the study area showing the protected and buffer areas.*

2.2. Image Acquisition and Pre-processing

Landsat Multispectral Scanner (MSS), Thematic Mapper (TM) and Landsat-8 (Operational Land Imager) time series images for the years 1975, 1995 and 2015 that correspond to paths 168, 169 and 170 and rows 61, 62 and 63 of the Landsat Worldwide Reference System (WRS) were downloaded from the Earth Explorer (https://earthexplorer.usgs.gov/) web platform. The effect of seasonal differences in vegetation phenology between study windows was minimized by downloading image scenes captured on similar satellite overpass times or seasons (Dry periods spanning January-February, July-August and October-November). Dry season images have relatively lower cloud cover than wet season images. Details of the Landsat images used are summarized in Table 1.

Table 1. *Details of the Landsat images used for LULC mapping.*

Image date	Image type	Resolution	Path and Row	Data Source
	Landsat MSS	57 × 57 m	168/61-62	United States Geological Survey
1975	Landsat MSS	57 × 57 m	169/61-63	United States Geological Survey
	Landsat MSS	57 × 57 m	170/61-62	United States Geological Survey
	Landsat TM	30 × 30 m	168/61-62	United States Geological Survey
1995	Landsat TM	30 × 30 m	169/61-63	United States Geological Survey
	Landsat TM	30 × 30 m	170/61-62	United States Geological Survey
	Landsat (OLI)	30 × 30 m	168/61-62	United States Geological Survey
2015	Landsat (OLI)	30 × 30 m	169/61-63	United States Geological Survey
	Landsat (OLI)	30 × 30 m	170/61-62	United States Geological Survey

Prior to analysis, images were corrected for geometric and radiometric effects [30-32]. Such pre-processing is useful to remove false indication of objects and facilitates comparison of multi-temporal images and field-based data [33, 34], and ensures that the corrected images are of sufficiently high quality for analysis [31]. Image and/or sensor differences within and between scenes were normalized by converting the brightness values of each pixel (Digital Number (DN) to actual reflectance (Top of Atmosphere Reflectance (TOA)), in order to obtain the actual ground reflectance [35]. Topographic normalization is a crucial part of atmospheric correction [36-38] as it enhances representation of the original image, hence improving spectral signatures, classification and overall accuracy [35, 39].

A Digital Elevation Model (DEM), covering the entire study area at a spatial resolution of 30 m, derived from the Shuttle Radar Topography Mission (SRTM) was used to correct images that are acquired from undulating, mountainous or hilly (topographic effects) and/or rugged terrain lands [40]. Topographic correction is an important pre-processing stage as it improves accuracy of thematic maps [41]. Geometric correction was not performed as Landsat Level-1 products are terrain-corrected [32]. Atmospheric effects on the images were corrected through haze removal and masking clouds in the scenes using the Atmospheric Correction Tool [42].

2.3. Cloud Removal

Satellite images tend to have clouds. It was almost impossible to get cloud-free image scenes that covered the entire study area. Therefore, sections of a scene with clouds were first removed and the resulting gaps filled with corresponding sections of cloud-free images for the same scene taken closely in time, or in the same season and the gap-filled using the Smart GeoFill tool [42].

2.4. Image Mosaicking and Sub Setting

The geometric and radiometric corrected scenes were seamlessly stitched in PCI Geomatica [42] to obtain one image covering the entire ecosystem. Image scenes were then clipped to individual strata (the various protected areas plus the buffer area) for minimizing the spread of classes to other areas that do not belong to it, and to speed up the classification process.

2.5. Sampling Design

i. Sample Size and Distribution of Samples

The study area was stratified into 10 strata, each corresponding to one of the nine protected areas and the surrounding 30-km wide unprotected buffer area on the Tanzanian side of the Greater Serengeti-Mara ecosystem (Figure 1). LULC variability was high in each stratum, implying a high likelihood of having different classes for LULC. Based on Congalton [43] and the principle of binomial distribution, a minimum of 75-100 validation samples per class are suggested for analysis. However, due to logistical and financial constraints, terrain features and legal prohibition of driving off-road within protected areas, approximately 30% of the required sample size was validated for a total of n=1918 sampling points.

Despite these constraints, the sample sizes for the collected test and validation data are higher than the minimum recommended sample size [43] and thus were considered sufficient for reliable classification. Samples were randomly allocated in proportion to the area of each LULC type represented in each stratum, using a pre-defined baseline map. However, for infrequent classes (water, wetland/swamps, and bareland), the estimated sample size was adjusted upwards by selecting additional samples using Google Earth and Bing images.

ii. Collection of Sample Points

The selected random samples were traced on the ground using hand-held Garmin CSX GPS. Sample points falling in inaccessible areas (due to terrain features or absence of roads), and restricted off-road access were replaced with samples from nearby pixels with similar reflectance or overlaid on high resolution Google Earth (https://www.google.com/intl/de/earth/)

and Bing (https://www.bing.com/maps) images and the corresponding object and/or LULC identified [44]. In order to minimize the likelihood of misclassifying the sampled LULC, spectral signatures for the selected sample points were inspected in scatter plots. Opportunistic observations made while travelling from one sampling point to another supplemented the training and testing data sets.

For historical images, the Herlocker (1976) and Reed [13] maps were used to obtain the training and testing sets for the 1975 and 1995 imageries, respectively. A minimum of 75-100 samples per category (Table 2) were extracted. Less covered class samples were supplemented by collecting additional manually extracted samples from the imageries using spectral characteristics.

iii. Digitization and Selection of Training and Test Sets

Multi-resolution segmentation was performed in E-Cognition [45] on each strata image to obtain polygons (area representing a land cover feature of regular, irregular, circular or elliptical shape) which reflects different ground objects based on image spectral characteristics, shape and tone. Segmentation parameters were set as follows: scale=1, shape=0.1 and compactness=0. Field samples were overlaid on to the segmented image and corresponding polygons extracted.

The spatial join tool (ArcGIS 10.5) was used to overlay the LULC on to corresponding classes in the field samples (Table 2). Then, a research tool (random selection within subsets*)* in QGIS 3.10 was used to randomly partition the samples into training (50%) and testing (50%) sets for classification and accuracy assessment, respectively, based on the LULC categories.

iv. Signature separability

The training and test samples were evaluated for class spectral signature separability. This is the statistical measure of the distance between two object signatures that can be correctly assigned to proper LULC patterns that do not overlap with one another. Signature separability was tested in PCI Geomatica [42] using the Bhattacharyya distance (BD) using bands 3, 4 and 5. BD is a separation index, with values ranging from 0 to 2, with 0 indicating total overlap and 2 indicating purely separable signatures. Two objects are separable if the separation distance between them is statistically significant and sufficient to produce a successful classification. Thus, to enhance classification, signatures with good separability ($1.9 < x < 2.0$) were retained, and the poorly separated signatures ($1.0 < x < 1.9$) were either merged or edited until a reasonable separability level was attained, where x is the separability distance between two samples.

v. Image Classification

Image classification was performed using the Random Forest (RF) coded script [46] that is run in the R software package. RF is a powerful machine learning classifier that is widely used in land-based remote sensing because it has a high classification accuracy, is more robust to noise than many other competing classifiers and is a non-parametric classifier [47, 48]. Furthermore, it is able to impute missing values and rank variables in order of their importance, and allows reliable assessment of the predictive accuracy of classification [48, 49]. Shuttle Radar Topography Mission (SRTM) derivatives (Digital Elevation Model, Slope and Topographic Wetness Index) were combined with the spectral multi-temporal data to improve the classification and accuracies of the classified LULC maps [50, 51]. To increase precision and accuracy, images scenes that are part of different strata were first classified independently and then merged.

For each classification run, three outputs are produced, namely; the *classImage*, *probImage* and *threshImage*. The *classImage*, is an output of the classified image. The *probImage* that shows the probability of correct classification of the *classImage* layer. On the other hand, *threshImage* identifies classified pixels with inter-class confusion by highlighting pixels with a probability of correct classification that is lower than a user-specified threshold. Besides the three optional raster outputs, a point vector file, "*Margin file*", is file that reports assessment of the quality of sample data. Positive margin values represent correct classification, and vice versa, and provide a basis for removing poorly classified samples or relabeling sample data. Moreover, it helps to determine which classes need additional training signatures. Before the final RF classification, 2-3 runs were performed and the run with the best accuracy, i.e., above 85%, selected as the final classification. Procedures for image pre-processing, processing and post-processing are summarized in Figure 2.

vi. Accuracy Assessment and Error Matrix

The agreement between the ground truthing data and the classified map (accuracy assessment) was assessed by an error matrix [52, 53] using the test dataset (50% of the full sample). The error matrix (cross-tabulation) table for each thematic image was generated. Kappa Index of Agreement (KIA) that measures how well the classified map matches the reference data [54] was also computed.

In thematic classification, an overall accuracy of $\geq 85\%$ is considered acceptable, provided the per-class accuracy is at least 70% [44]. Accuracy assessment is accompanied by KIA, a measure of how well the classified map matches the reference data. KIA values greater than 0.8 indicate perfect classification whereas values lying between 0.6 and 0.8 indicate good classification [55]. Therefore, the KIA values we obtained indicate acceptable classification [56, 57].

vii. Post-classification: Change Detection Analysis

A majority filter (3×3 pixels) as recommended [58] was applied to the thematic maps to eliminate the salt-and-pepper effects (Figure 2). Consequently, the smallest mappable unit (MU) for the classified map in the ecosystem was about 1 hectare. In order to identify the type, magnitude and spatial aspects of LULC changes between the images for 1975 versus 1995, 1995 versus 2015 and 1975 versus 2015, a post-classification change detection was performed in the Semi-Automatic Classification Plugin in QGIS software [59]. In order to enable multi-temporal comparison with the rest of the images, a Nearest Neighbor Sampling Algorithm (NNSA) was used to re-sample the MSS classified images to 30×30 m pixel. Post-classification comparison or change detection was used to estimate the percentage change between two images.

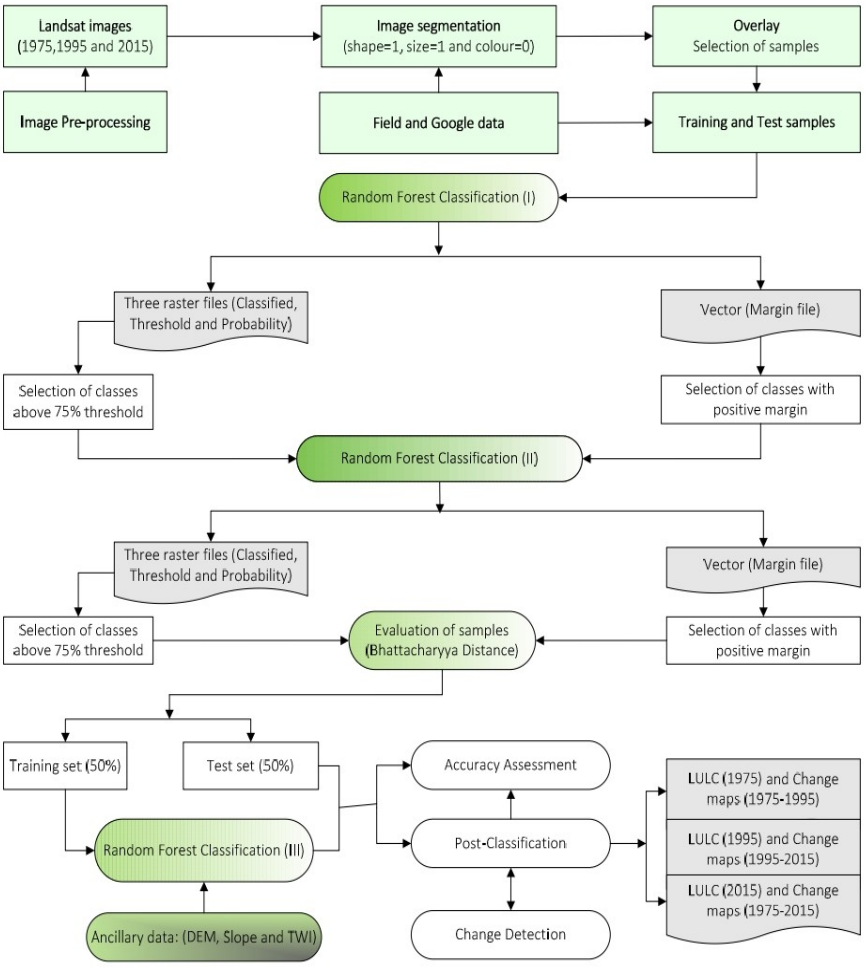

Figure 2. *Flow chart for image classification.*

Table 2. *Description of LULC classes.*

Land use and cover	Land use and cover class descriptions
Bareland	Any area with vegetation cover between 0 and 2%, and includes areas that are barren land, bare rocks and/or soil that are exposed due to burning of trees and shifting cultivation
Cultivation	Consists of land parcels that are used for subsistence or commercial farming
Settlement	Areas that are designated as small towns, villages and roads
Water	Areas that are covered by water bodies, such as rivers, dams and lakes
Grassland	Areas with non-woody vegetation, comprised of short and tall grasses, used primarily for wildlife and livestock grazing. Rice fields, plantations, and non-irrigated land are excluded from this class
Shrubland	Woody vegetation, with multi-stem and height of 3-5 m
Woodland	Areas with woody vegetation with a height between 6 -15 m
Wetland and Swamps	Areas covered by water and other vegetation types

Source: Modified from Tekle, K. and Hedlund, L. [60].

3. Results

3.1. Land Use and Land Cover Types

The spatial distributions of LULC types in the Serengeti ecosystem and its surrounding buffer area in 1975, 1995 and 2015 are illustrated in Figures 3-5, respectively. The overall accuracies of the classified maps were 88.4%, 90.6% and 93.4% and the corresponding Kappa Indices of Agreement were 0.86, 0.87 and 0.91 for 1975, 1995 and 2015, respectively. The areal

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and percentage coverages of the individual LULC classes are summarized in Table 3.

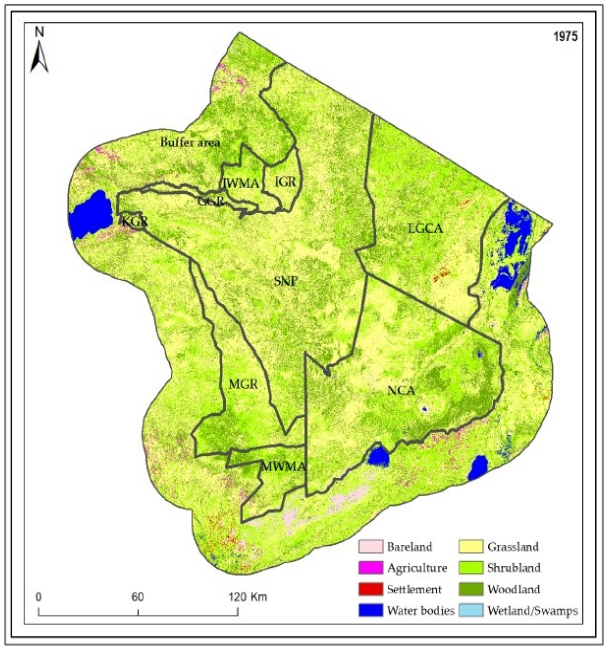

Figure 3. *Distribution of LULC types in the Serengeti ecosystem and surrounding buffer zone in 1975.*

Where: LGCA=Loliondo Game Controlled Area, MWMA=Makao Wildlife Management Area, IWMA=Ikona Wildlife Management Area, NCA=Ngorongoro Conservation Area, MGR=Maswa Game Reserve, IGR=Ikorongo Game Reserve, KGR=Kijereshi Game Reserve, GGR=Grumeti Game Reserve, SNP=Serengeti National Park.

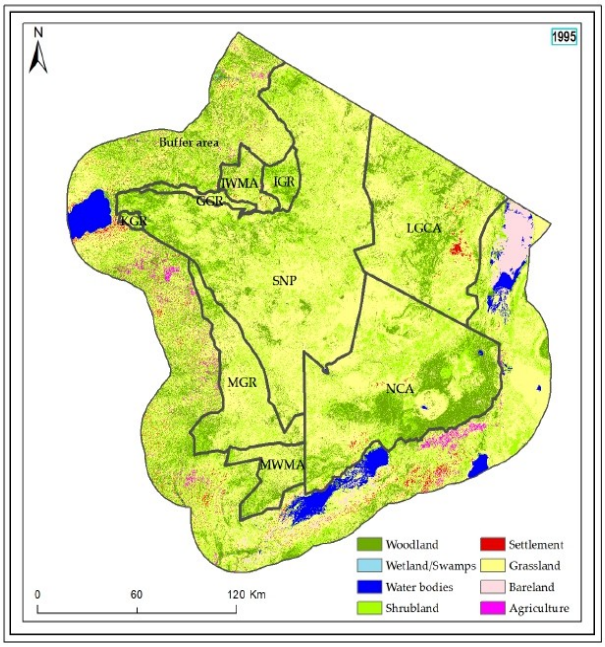

Figure 4. *Distribution of LULC types in the Serengeti ecosystem and surrounding buffer zone in 1995.*

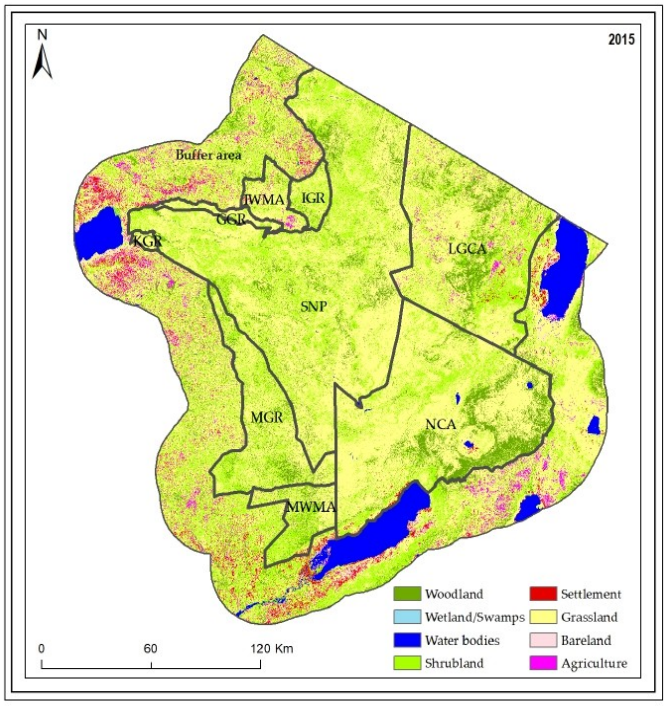

Figure 5. *Distribution of LULC types in the GSE and surrounding buffer zone in 2015.*

Across the entire ecosystem and its buffer area, grassland was the major land cover class, followed by shrubland and woodland whereas wetland/swamps, settlement, agriculture and bareland had relatively low coverages during 1975-2015 (Table 3).

Table 3. *The areal and percentage coverages of LULC classes in the GSE and surrounding buffer area in 1975, 1995 and 2015.*

LULC Class	Area coverage (km^2)			Percentage (%)		
	1975	1995	2015	1975	1995	2015
Bareland	781	1,003	371	1.38	1.77	0.65
Agriculture	381	643	1,789	0.67	1.14	3.16
Settlement	144	498	982	0.25	0.88	1.73
Water	1,403	1,456	2,664	2.48	2.57	4.71
Grassland	28,649	30,685	32,278	50.62	54.21	57.03
Shrubland	13,384	13,273	13,442	23.65	23.45	23.75
Woodland	11,812	9,005	5,046	20.87	15.91	8.92
Wetland/Swamps	37	28	18	0.06	0.05	0.03
Total	56,590	56,590	56,590	100	100	100

Protected areas had higher proportions of grassland, shrubland and woodland coverages than the buffer area throughout 1975, 1995 and 2015. The buffer had high proportions of grassland, shrubland and woodland in 1975 and 1995 but was dominated by grassland and shrubland in 2015. The other LULC classes had relatively low proportional coverages in both the protected and buffer areas in 1975, 1995 and 2015 (Figure 6).

Grassland was the most dominant land cover type in all the protected areas and the buffer area throughout 1975-2015. It had the highest proportional coverage in the buffer area followed by the SNP, NCA and the LGCA. Grassland coverage varied little in the buffer area but increased slightly in the NCA, LGCA and SNP during 1975-2015 (Figure 7). Shrubland coverage similarly varied little in the buffer area, decreased in the NCA and GCA but increased in the SNP during 1975-2015 (Figure 7). Woodland coverage decreased persistently and strikingly in the buffer area and all the protected areas from 1975 to 2015 (Figure 7). The coverages of water, agriculture and settlement expanded in the buffer area from 1975 to 2015 (Figure 7).

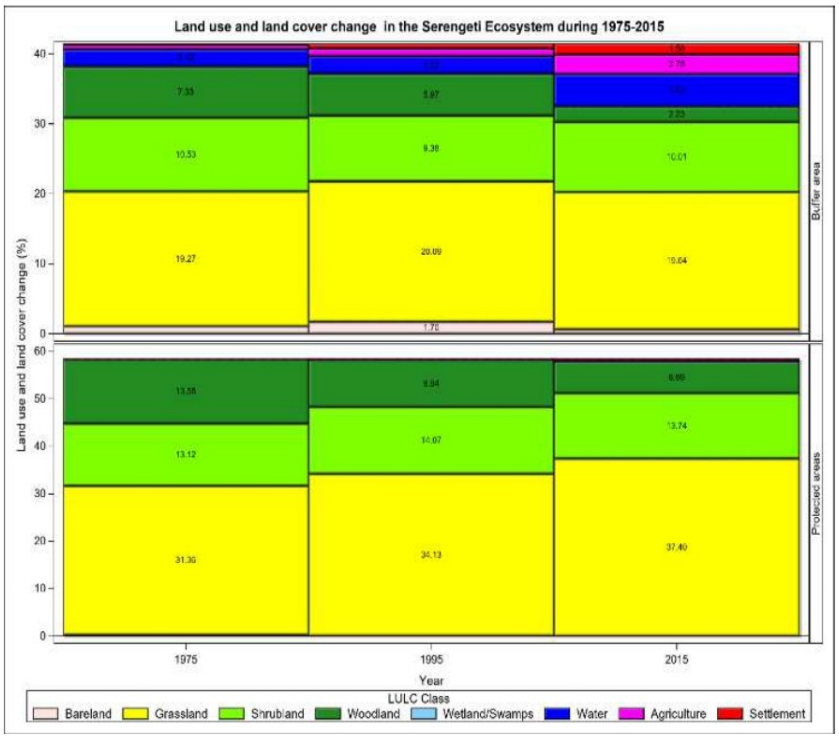

Figure 6. *Percentage coverage of LULC classes in all the protected areas in the GSE and surrounding buffer area in 1975, 1995 and 2015.*

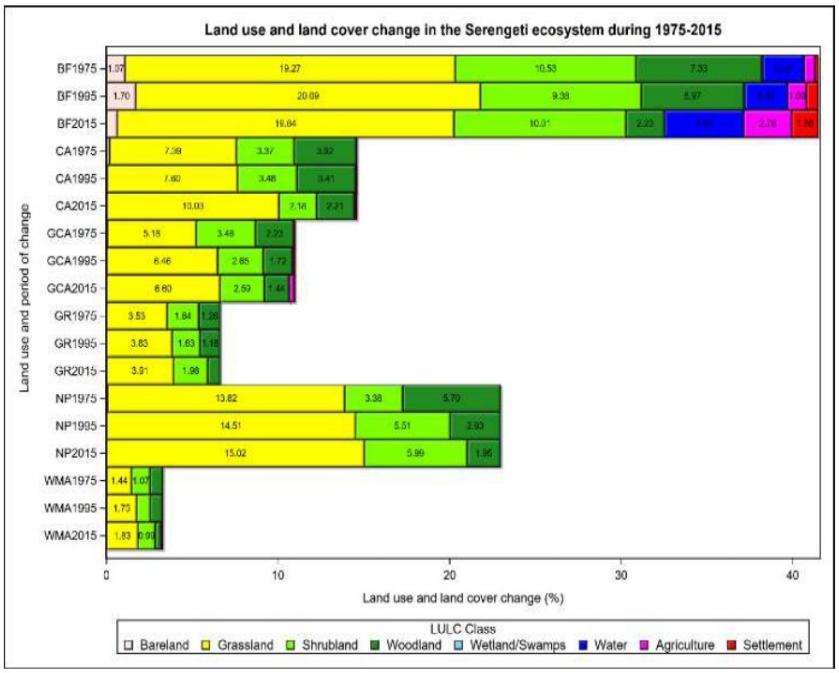

Figure 7. *LULC change (%) in different protected area categories in the GSE and surrounding buffer zone during 1975-2015.*

3.2. LULC Cover Change (1975-2015)

Between 1975 and 1995, woodland and shrubland coverages had the largest net declines in the ecosystem and its buffer area. Wetland/swamps coverages also declined. But grassland coverage expanded the most followed by settlements, agriculture and bareland (Figure 8). During the 1995-2015 period, the coverages of grassland, shrubland, settlement, bareland and wetland/swamps increased but those of woodland and bareland declined (Figure 8).

Woodland declined drastically and had the highest annual rate of change during 1975-2015. Bareland and wetland/swamps coverages also contracted during the 41-year study period (Figure 8). But coverages of grassland, shrubland, water, agriculture and settlements all expanded during 1975-2015 (Figure 8).

Grassland increased significantly in the buffer area and in all the protected areas except in the SNP where shrubland was more dominant than grassland during 1975-1995 (Figure 9). Bareland, water, agriculture and settlement increased notably in the buffer area (Figure 9). In contrast, woodland and shrubland coverages contracted in the buffer area and in all protected areas except in the NCA and the SNP where shrubland increased during 1975-1995 (Figure 9). Loss in woodland cover was more noticeable in the national park and the buffer area whereas the loss in shrubland cover was most marked in the buffer area and GCA (Figure 9).

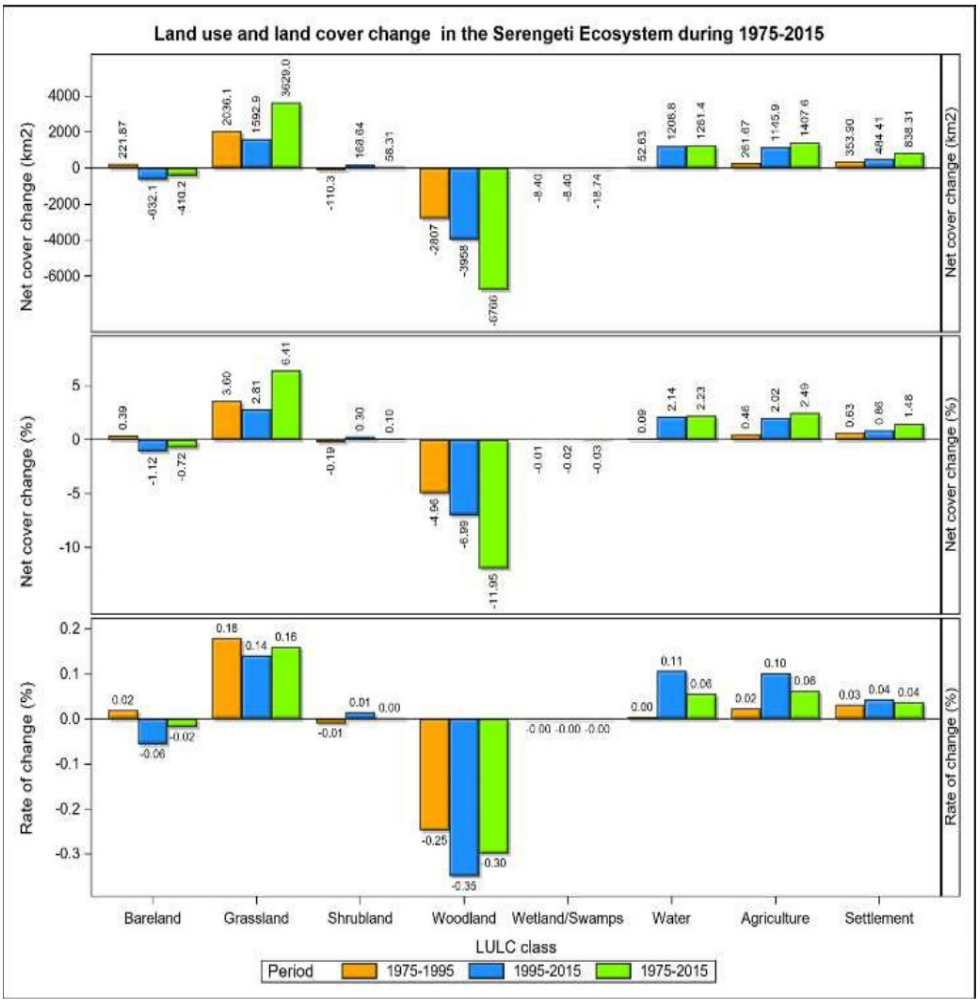

Figure 8. *Net absolute (km^2) and percentage LULC changes and rate of change (%) in the GSE and surrounding buffer area during 1975-2015.*

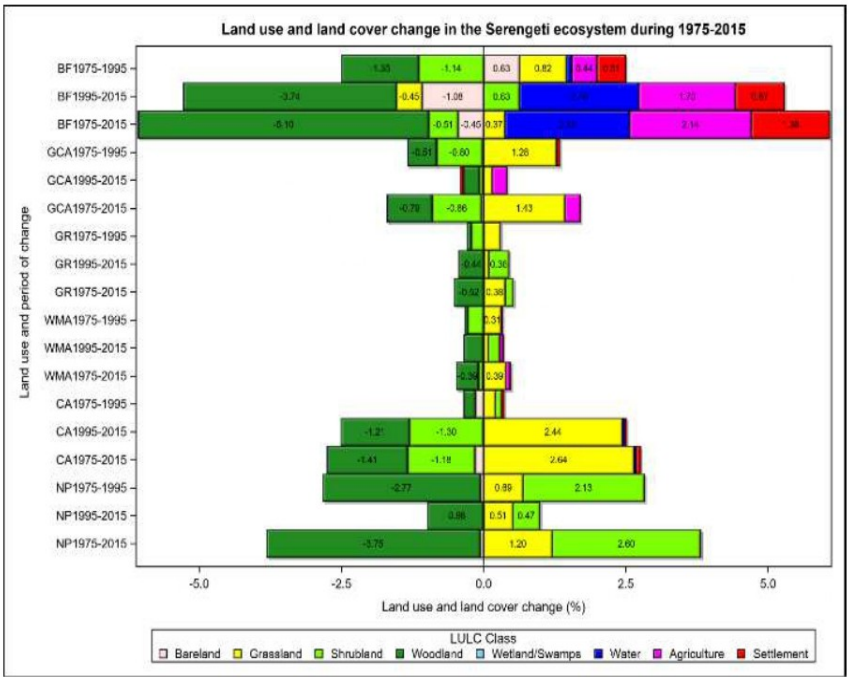

Figure 9. *LULC change (%) in each protected area category in the GSE and surrounding buffer zone during 1975-2015.*

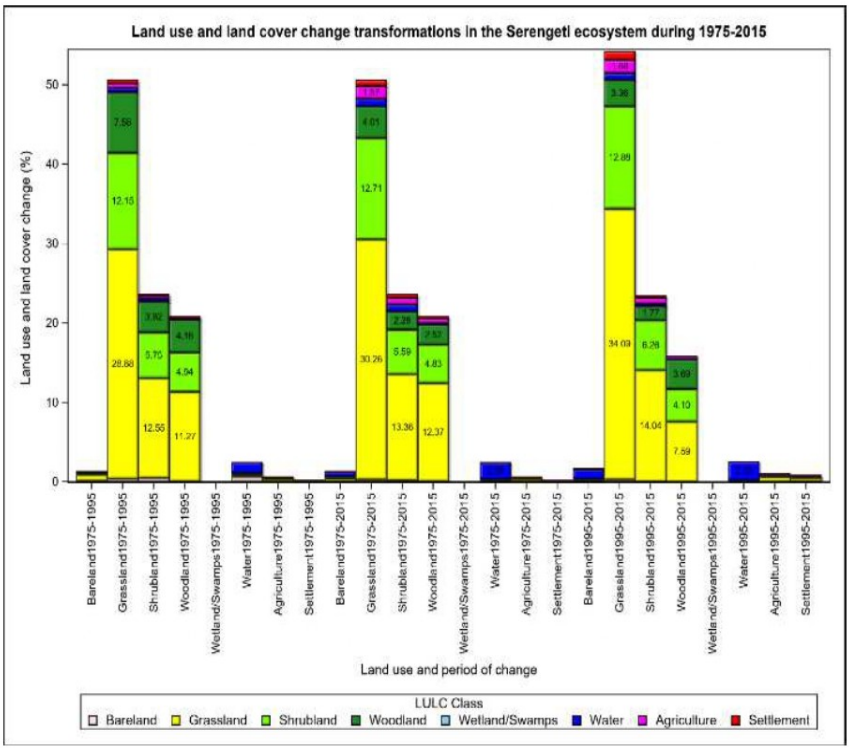

Figure 10. *Transformations between LULC classes in the GSE and surrounding buffer zone during 1975-2015.*

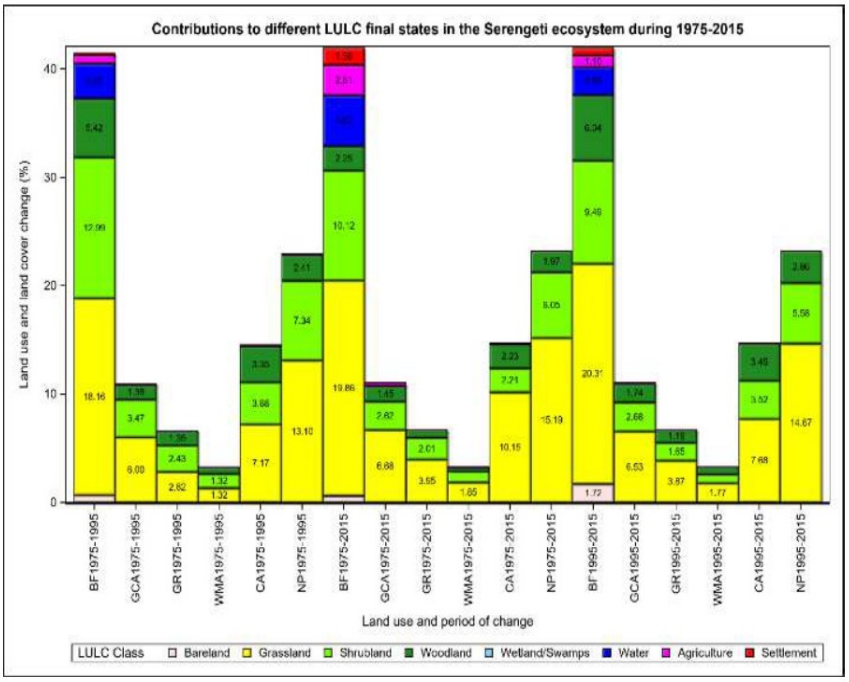

Figure 11. *Contributions from different conservation categories to LULC final states during 1975-1995, 1995-2015 and 1995-2015.*

During 1995-2015, woodland and bareland coverages declined the most, particularly in the buffer area, NCA and the SNP. However, shrubland cover declined mainly in the NCA but bareland cover contracted significantly in the buffer area (Figure 9).

Overall, during the entire period of assessment (1975-2015), decrease was more prominent for woodland followed by shrubland. The greatest loss of woodland occurred in the buffer area and national park. Shrubland increased in the NP but declined in the buffer area and GRs (Figure 9).

3.3. LULC Cover Change Trajectories (1975-2015)

During the 1975-1995 period, substantial woodland was converted to grassland and shrubland. Shrubland to grassland and woodland. Likewise, other cover types, mainly grassland were also converted to woodland and shrubland (Figure 10). The conversions of woodland, shrubland and grassland to other cover types occurred mainly in the buffer area, NCA and the NP (Figure 11). In the GCA, grassland registered the greatest conversion to other land cover types. Nevertheless, grassland, shrubland and woodland cover classes were the most persistent whereas swamps and settlement the least persistent cover classes (Figure 10).

During 1995-2015, shrubland and grassland underwent the greatest conversion to other LULC types but little woodland was converted to other types. Much of the shrubland was converted to grassland while some grassland became shrubland. Furthermore, substantial woodland cover was transformed to shrubland and grassland (Figure 10). The largest conversions of these LULC classes occurred mainly in the buffer area, SNP and NCA (Figure 11). Despite the various conversions, grassland was the most persistent cover type followed by shrubland (Figure 10).

Across the 1975-2015, the greatest transformations occurred in grasslands followed by woodlands and shrublands. Much of the grassland was converted to shrubland while considerable woodland was transformed to grassland and shrubland. Notably, most of the remaining LULC classes showed little transformations below 2% (Figure 10). The greatest transformations of grassland and woodland were recorded for the buffer area, SNP and NCA. In addition, much of the shrubland transformations occurred in the GCA and GRs (Figure 11). Shrubland was the second most persistent cover class during the 1975-2015 period (Figure 10).

4. Discussion

4.1. LULC Cover Types

Throughout the 41 years of assessment from 1975-2015, grassland, shrubland and woodland had the highest proportions across the entire ecosystem and buffer area. The high coverages of these land cover types in the protected areas, especially in the SNP, NCA, GRs and LGCA, can be attributed mainly to their savanna characteristics and geological formation [13, 61-63]. The volcanic hard pans extending from the NCA westwards through the SNP favor grasslands, with some areas towards the west supporting grasslands interspersed with shrublands and woodlands. In the buffer area,

the observed LULC cover changes can be attributed to anthropogenic activities, primarily agriculture, human settlement, fire and livestock grazing [64].

4.2. LULC Cover Change

Across the ecosystem and its surrounding buffer area, settlements, agriculture, grassland and water increased throughout 1975-2015 at the expense of woodland cover. Bareland declined during the 1975-1995 but increased during the 1995-2015. During the 1975-2015 period, grassland increased in all the protected areas unlike shrubland which increased in the NP and GRs during 1975-2015. In contrast, shrubland contracted in the GCA, where livestock grazing and agriculture are practiced, and in the NCA where pastoralism is pursued along with wildlife conservation. The expansion of grassland and shrubland cover in the Serengeti is likely the outcome of conversions from other cover types, particularly woodlands; herbivory (grazing and browsing) and fire [65, 66]. The increase in bareland coverage was coincident with human population growth and the associated expansion of agriculture and settlements, development of infrastructure and intense livestock grazing [8, 6].

The expansion in agriculture and settlements can be linked to human population growth and consequently increased demand for more food and income in rural Tanzania. Agriculture is the economic mainstay of the rural populations and a key source of national revenue and foreign exchange in Tanzania. The increase in settlements during the 1975-2015 was contemporaneous with increased cultivation and bareland and human population size inside the buffer area [12]. The expansion in settlement and agriculture in the ecosystem and the buffer area can be linked not only to human population growth but also to the 1974 villagization policy which involved forceful resettlement of people in nucleated villages and the policy encouraged people to cultivate the land in order to ensure to ensure food security and income for families [67, 68]. The expansion of cultivation between 1995 and 2015 was also partly driven by liberalization policies, such as the Promotion of Investment Policy of 1992 that advocated for expansion of agriculture, and consequently clearing of natural vegetation [67]. These policies also encouraged livelihood diversification, for example, from pure pastoralism to agro-pastoralism among the Maasai of LGCA and NCA in northern Tanzania [69]. However, agriculture has since then been banned to allow habitat recovery in the NCA [6]. Furthermore, socio-economic opportunities from tourism activities, livestock grazing and agriculture attracted people to the lands adjacent to the protected areas [70-73] and accentuated LULC changes. The activities aggravate the vulnerability, degradation and loss of wildlife habitats [74], adversely affecting biodiversity conservation [12]. Similarly, tourism opportunities and land suitability accelerated agricultural expansion in the adjoining Kenya's Narok County [75].

The increase in settlements around the protected areas in the Serengeti ecosystem is similar to patterns observed elsewhere [76-79], particularly in the pastoral ranches adjacent to the Masai Mara National Reserve [64] and in the Athi-Kaputiei Plains adjoining the Kenya's Nairobi National Park in Kenya [80, 81]. Our findings reinforce and expand upon these previous studies in this [12] and other ecosystems in Tanzania, including in the Tarangire and Katavi ecosystems [12, 82, 83, 109]. Furthermore, the expansion in agriculture at the expense of natural vegetation fits in a worrying contemporary worldwide trend [74, 76-78, 84, 85-87, 88, 89].

The decline in woodland cover throughout 1975-2015 in the ecosystem and buffer area was partly due to conversion of woodlands to other cover types. Woodland vegetation is also cleared for agriculture and settlements, often resulting in shrubland and other cover types. The declining trends in woodland cover can amplify land degradation, soil erosion, salinity and loss of quality [90], leading ultimately to wildlife habitat degradation and loss. The striking decline in woodland cover in the buffer area portrays weak protection [68]. Woodland decline inside the protected areas was also concurrent with increasing elephant numbers in the ecosystem [91, 92]. Similar findings have been reported for other protected areas in Tanzania, including the Loliondo Game Controlled Area [11], Rungwa Game Reserve [93, 94], Ruaha National Park [94], Tarangire-Manyara ecosystem [95] and the Selous wildlife corridor [74]. The African elephant also often destroys woody vegetation in many African savanna ecosystems, including in Tanzania [96, 97, 91], Kenya [98, 99], Malawi [100], Zimbabwe [87], Botswana [101], as well as Ethiopia [102] and South Africa [103, 104]. Besides elephant browsing, woodland declines in the Serengeti ecosystem have been associated with frequent fires and wildebeest population growth [97]. The conversion of woodland to grassland or shrubland can create habitats favorable to grazers and some browsers but unfavorable to the elephants themselves [105, 106] and to other browsers. This can reduce the diversity and abundance of woodland-dependent species [99].

The increase in water bodies was concurrent with increasing rainfall in the Mara-Serengeti ecosystem associated with the intensification of the El Niño Southern Oscillation (ENSO) [107] and the Indian Ocean Dipole [65]. The increasing availability of water can fundamentally reshape wildlife and livestock abundance, distribution and movements in the ecosystem [108]. A protracted drought spanning 1971-1975 [107] almost certainly reduced surface water availability in the ecosystem in 1975.

The increase in wetland/swamps between 1975 and 1995 is associated with rapid land cover transformations. Thereafter (1995-2015), wetland/swamps declined as land transformation progressed. Similar declines in swamps with progressing land transformations have also been reported for the Katavi National Park in Tanzania [109].

Generally, the declines in land cover near the protected areas jeopardize conservation initiatives run in the Wildlife management Areas (IKONA and Makao WMAs) and Outreach programme or Community Conservation Services (CCS) in the SNP. The WMAs promote community involvement in conservation through benefit-sharing schemes while reducing activities which are incompatible with conservation. The community-based conservation initiatives

enhancing timely and adaptive conservation interventions. Conservation spatial planning and effective implementation of the plans are also crucial. For example, community-based conservation initiatives, such as establishment of Wildlife Management Areas, Forest Reserves (Village forest reserves, community forest reserves and private forest reserves) and land use planning, and rangeland management) should be encouraged in the buffer area to regulate unsustainable resource extraction, which adversely impacts conservation and human wellbeing. The Wildlife Conservation Act No. 5 of 2009 and other related pieces of legislation (e.g., land, forest, and water) should be effectively implemented. Environmental and conservation policies should also be effectively implemented to minimize vegetation loss in the ecosystem and its buffer area. The declining vegetation cover in the buffer area should be ameliorated by planting more indigenous tree species that can also provide fuel wood, building poles and timber and relieve pressure on natural vegetation in the buffer and protected areas.

Generally, upgrading the protection status of conservation areas improves their conservation effectiveness in the Serengeti ecosystem. The substantial loss of land cover in areas of low protection status signifies the need to strengthen conservation in such areas and their buffer zones. In addition, the recorded declining trends of the LULC types call for policies, conservation and management actions that are able to control fires, regulate land use and tree felling, promote replanting trees and effectively manage elephant-tree interactions at high elephant densities. Equally important is the formulation and effective implementation of sound policies and far-sighted spatial land use plans to safeguard the future integrity of such iconic ecosystems as the Serengeti and human wellbeing in their surrounding buffer zones.

Author Contributions

HK, EN, MS and JK conceptualized and designed the research, HK collected the data, HK, EN, MS and JO and analyzed the data, and drafted the manuscript, MS, EN and JK supervised the research work, EN, MS, JO, JK, LM, BJ, BG, and FV reviewed and edited the manuscript for critical intellectual content.

Funding

This research work is a part of the Ph. D study of HKK and was funded by the European Union's Horizon 2020 research and innovation grant number 641918 through the AFRICANBIOSERVICES PROJECT and by the FRIEDKIN CONSERVATION FUND (FCF). JOO was also supported by a grant from the German National Research Foundation (DFG; Grant # 257734638).

Acknowledgements

We thank the Tanzanian Wildlife Research Institute (TAWIRI) for granting study leave and permission to HKK to conduct the research work, Tanzania National Park (TANAPA), Ngorongoro Conservation Area (NCAA), Tanzania Wildlife Management Authority (TAWA) and Wildlife Management Area Authorities (WMAs) for granting access to their areas of jurisdiction for data collection. We sincerely thank Ned Horning of the American Museum of Natural History, Centre for Biodiversity and Conservation, for guidance on using his R coded Random Forest Script. We also thank Eivin Roskaft (NTNU), Robert Fyumagwa, Janemary Ntalwila, and Machoke Mwita (TAWIRI) and Nsajigwa Mbije (SUA) for their support.

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CHAPTER THREE

Factors influencing land use and land cover changes in the Greater Serengeti Ecosystem (1995-2015), Tanzania

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Submitted to *Journal of Sustainability, Environment and Peace*

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Abstract

Land use and land cover (LULC) change is of great concern in many terrestrial ecosystems, including the Serengeti. Binomial Logistic Regression was used to analyze and inform possible drivers of LULC in the ecosystem, using LULC change data (1975-1995 and 1995-2015) and nine predictors of change (human population density, precipitation, distance from rivers, soil moisture, fire frequency, distance from roads, elevation, slope and elephant density). We evaluated model performance using the Receiver Operating Characteristic (ROC) and Area Under the Curve (AUC). Both consistent (consistent means the same positive or negative effect of a driver in both slices) and mixed effects of drivers on LULC manifested across the study slices. Human population density consistently affected negatively shrubland whereas agriculture was positively affected. Positive influence was on agriculture whereas negative was manifested to shrubland. Soil moisture had a negative significant effect on agriculture and positive on woodland. Fire showed negative effect on agriculture and settlement. Distance from roads had a negative effect on shrubland and positive on grassland. High elevation category showed a significant negative effect on grassland whereas both medium and high elevations had a positive effect on woodland. Interestingly, slope did not show any consistent effect. Low elephant density showed a significant positive effect on agriculture and settlement. Elephant density across all levels positively influenced shrubland. For significant mixed effects (±), only human population density (bareland, settlement, water bodies, grassland and woodland) and medium elevation (shrubland) were registered. Generally, human population density seems to be the main possible driver of LULC in the ecosystem. We recommend for: i) protected area (PAs) managers avoiding

roads constructions in shrubland, ii) integrated efforts to ensure appropriate human populations around the ecosystem to reduce its unpreferred effects on the various land cover types in the area, iii) an effective management of both prescribed and wild unplanned fires, iv) study and manage availability and distribution of key resources for elephants, and v) effective PAs management plans.

Keywords: Drivers of change, regression, cover types, wildlife distribution, buffer, protected areas

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1. INTRODUCTION

Land use and land cover (LULC) changes are of great concern to conservation in many parts of the world. These changes are due to different drivers and can fragment the continuous habitats into small patches, affecting the quality and quantity of habitats, species distribution and composition (Sala *et al.* 2000, Butchart *et al.* 2010, Atickem *et al.* 2011). Habitat loss, fragmentations and degradation attributed to LULC changes threaten wildlife within and adjacent PAs (Li *et al.* 2016). For example, human population density can cause expansion of agriculture and settlements, as lands will be cleared for socio-economic activities to enhance livelihoods (Nduati *et al.* 2013). Soil moisture influences distribution pattern of land cover types (Canute *et al.* 2015). Similarly, precipitation influences plants productivity (Ogutu *et al.* 2008). Highly elevated and steeper areas are hardly accessed (Bakker *et al.* 2005). Combination of these drivers can exert deleterious impacts on wildlife habitats, and if unchecked, can lead to species decline or loss as wildlife distribution is determined by land cover types which provide habitats requirements for their reproduction and survival (Mtui 2014). Furthermore, LULC changes tend to reduce habitat sizes within and adjacent PAs resulting in poor ecological integrity and resilience with ultimate biodiversity loss (Hansen and DeFries 2007, Giam *et al.* 2010, Hilty *et al.* 2012, Hamilton *et al.* 2013).

According to the Millennium Ecosystem Assessment (MEA), LULC changes are directly or indirectly related to natural or human-induced drivers (Nelson *et al.* 2006) and are caused by a complex interactions of proximate and underlying drivers. These drivers modifies the landscapes at different spatio-temporal scales, and are broadly categorized into proximate and biophysical (Briassoulis 2009, Minale 2013). Proximate driving forces are the immediate human activities and biophysical factors, whereas the underlying driving forces comprise important societal processes driving the proximate/direct drivers

(Serneels and Lambin 2001, Geist and Lambin 2002, Nelson *et al.* 2006, van Vliet *et al.* 2015).

The proximate drivers are factors driving expansion of farming areas, overgrazing, infrastructure such as roads and social services (Nelson *et al.* 2006, Odada *et al.* 2009) and distance to water sources, roads and settlement (Canute *et al.* 2015). Biophysical drivers include rainfall, topography (slope and elevation), landforms and soil types (Chopra *et al.* 2006, Briassoulis 2009, Ogutu *et al.* 2011), societal drivers (human population growth, economic development, technological and political issues) while the natural factors entail wildfire, drought and floods (Canute *et al.* 2015).

These drivers are frequently cited to influence changes in LULC and wildlife habitats and can exert profound ecological disturbances to ecosystems (DeFries *et al.* 2007, Souza *et al.* 2015). Their influences on the environment are eminent and rapidly increasing (Sala *et al.* 2000) to modify wildlife habitats (Kimanzi and Wishitemi 2003), leading to degradation and fragmentation of habitats (Reid *et al.* 2004) or changing the distribution pattern (Shaw *et al.* 2010), consequently, species loss (Kuussaari *et al.* 2009). Habitat degradation, change of species population and distribution and decline as a consequence of LULC and wildlife habitats changes are few common cited examples to this scenario (Kidane *et al.* 2012, Hamilton *et al.* 2013).

The Serengeti ecosystem, that straddles the northern Tanzania Kenya boarder has tremendously been undergoing progressive and significant changes in LULC over the past four decades. LULC change was quantitatively assessed (Kija *et al.* 2020) prior to this study, that updated and expanded the previously LULC reported for small areas in the ecosystem (Reed *et al.* 2009, Estes *et al.* 2012). The study reported

mixed directions of LULC change (1975-2015). Nonetheless, despite the recorded changes in the ecosystem, the few studies conducted did not explore the drivers broadly as the approach we sought.

The commonly cited factors driving such changes include conversion of natural habitats to agricultural lands to provide food for the increased human population around PAs (Estes *et al.* 2015). Study by Estes *et al.* (2012) included settlement and elephant density, and had a narrower geographical coverage.
In our understanding, this is the first broader and long-term study in the ecosystem that attempts to establish multiple factors responsible for LULC change for the past 20-years period. During 1995-2015, human population around the ecosystem has increased four-folds (Estes *et al.* 2012). The spatial extent of agriculture activities is increasing in line with livestock grazing. Settlement and associated activities have been expanding in and around the ecosystem (Estes *et al.* 2012).

Therefore, it is important to explore the possible drivers of LULC change because LULC are differently affected by drivers of change. In addition, the driving forces of LULC change are dynamic in nature at spatio-temporal scales. Understanding the underlying factors and their integrative effects on LULC changes is critical in conservation as serve as an alerting signals of the future impacts to terrestrial ecosystems (Chopra *et al.* 2006, Bansal *et al.* 2016, Li *et al.* 2016). Furthermore, LULC have high resilience to the effects of change, partly due to sprouting characteristics of the plant compositions (Nzunda 2008), while other have less effect to fire resistance, mainly due to types of barks and physiological characteristics (Brando *et al.* 2012). Some plant species are much prone to human-related threats, and may not recover, leading change of LULC types (Mugo *et al.* 2020).

The driving forces tend to control some socio-economic and environmental variables, the understanding which is useful in the

management of LULC changes (Hansen and Rotella 2002, Hansen and DeFries 2007). Importantly, if these changes continue unchecked, can undermine the overall values of any PAs (Giam *et al.* 2010, Hilty *et al.* 2012, Hamilton *et al.* 2013). Therefore, the main objective is to analyze and inform main drivers for LULC change in the Serengeti ecosystem (1995-2015). The drivers analyzed are; human population density, precipitation, distance from rivers, soil moisture, fire, distance from roads, elevation, slope and elephant density. It is expected that, the findings will contribute to a better understanding of the drivers and will assist managers and ecologists to appropriately prioritize, an important approach in conservation and ecological science (Houet *et al.* 2010).

2. MATERIALS AND METHODS

2.1 Study area

The Serengeti Ecosystem (SE) covering an area of 33,106 km^2, is located in northern Tanzania. The ecosystem and its surrounding buffer (Figure 3.1) have diverse and conspicuous variations in vegetation. It includes large PAs, traditional pastoralism, agro-pastoralism, cultivation, forest and wildlife conservation (Thirgood *et al.* 2004). According to Jones *et al.* (2009) and Veldhuis *et al.* (2019), habitats and resources influencing ecological processes inside PAs are in unprotected lands e.g. buffer, therefore, LULC changes in these areas have substantial impacts inside. This necessitated an inclusion of a 30 km buffer (23,487 km^2) to accommodate edge effects as this area is heavily settled and putting pressure in the ecosystem through livestock transgression, illegal killing of wildlife and deforestation (Gaston *et al.* 2008).

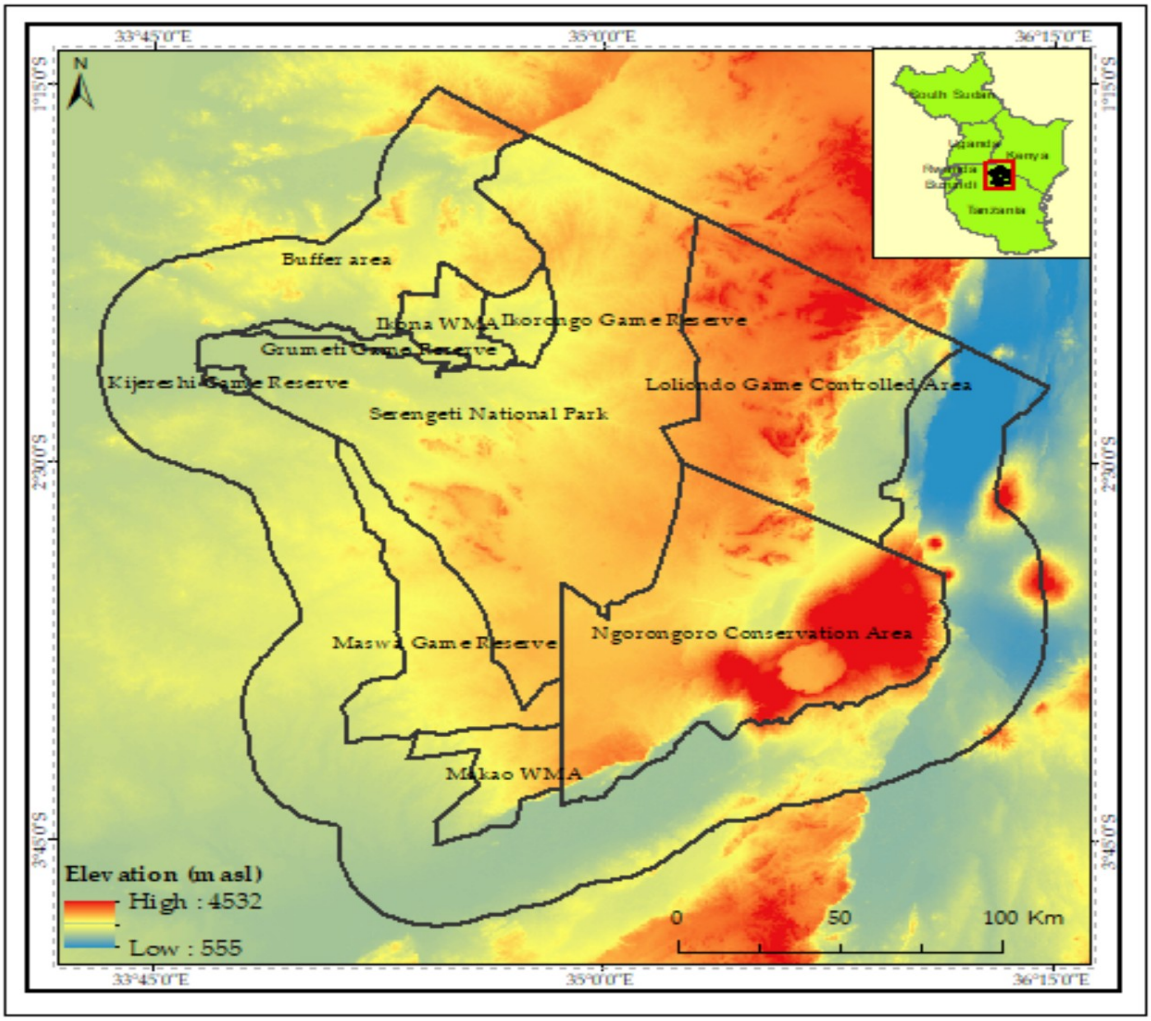

Figure 3.1: Study area showing the PAs network in the SE and the 30-km buffer

2.2 Data types and Sources

2.2.1 Land use and cover change maps

LULC change maps for the years 1995 and 2015 were obtained from the *AfricanBioServices Project*, a European Union Funded Project in the Serengeti-Mara ecosystem. These maps were generated based on three-time series Landsat images using Random Classification Algorithm. The maps had an overall class accuracy of 75%, and classification accuracies of > 85% suggesting an acceptable classification standard. To obtain the spatio-temporal changes between time slices, i.e., 1995 and 2015 a post-detection change analysis was performed in Quantum GIS (QGIS) to obtain the "*change to, "change from" and unchanged classes.* Pre-processing, processing and post processing are provided in our published work (Kija *et al.* 2020).

2.2.2 Population dataset

Human population density (inhabitants per km^2) and rate of increase were calculated following the formula by Puyravaud (2003). The first national population census was done in 1967 and recently in 2012. To obtain the estimated population size for the years (inter-census periods, i.e., 1995 and 2015) that correspond to LULC maps, we used the population projections methods (Weeks 2011).

$$P_{o+t} = P_o(1 + G_r \times t) \quad (1)$$

$$G_r = [(R_b - R_d) + (I_m - O_m)] \quad (2)$$

Where P_{o+t} is the total population estimated from the previous census year to the t next year, P_o is the total population at the census year, G_r is the growth rate, R_b and R_d are the birth and death rates at the census date, respectively, I_m and O_m are the immigration and out-migration rates and t is the number of years after the census date. Population data (birth, death, immigration, out-migration and growth rate) were extracted from the Tanzania National Bureau of Statistics (TNBS).

2.2.3 Precipitation dataset

Precipitation strongly influences vegetation growth and land cover change. The total annual precipitation was extracted from the Climate Hazards Center InfraRed Precipitation with Station (CHIRPS) data (1990-2015) at a spatial scale of 4 × 4 km. We also calculated 2 to 5-year moving averages of the annual precipitation to account for past cumulative effects of precipitation on vegetation structure. Precipitation, among

other drivers, has been reported to influence grassland and woodland cover in the savannah and dryland ecosystems (Govender *et al.* 2006).

2.2.4 Proximity dataset (Distance from rivers and roads)

Roads dataset corresponding to LULC years were used. The 1995 layer (roads and rivers) was obtained from the Africover Database, produced by the Food and Agriculture Organization of the United Nations (Di Gregorio 2005). These layers were extracted from visual interpretation of digitally enhanced Landsat TM images (Bands 4, 3, 2) acquired in 1997 (hence served for the year 1995) and supplemented by 2015 roads data from the TNBS database.

Distance maps were calculated in ArcGIS for distances to both paved and unpaved roads. We assumed that main roads (paved) that connect the area to the rest parts of the country would have more impact compared to minor (unpaved) roads, and for this reason, we arbitrarily assigned a weight of half for minor roads relative to the main road. Proximity data (including distance to agriculture and settlement) were calculated using the Euclidean distance tool in ArcGIS 10.5 (ESRI 2014).

2.2.5 Soil moisture

Soil moisture data were obtained from the Terra Climate website at a spatial resolution of 4 × 4 km. Soil moisture content influences LULC through its effects on agriculture. It influences plant richness, especially the growth of grassland vegetation distribution and vegetation growth (Spehn *et al.* 2000).

2.2.6 Burnt area

Burnt and unburnt areas have a remarkable influence on vegetation structure (Archibald *et al.* 2005, Langner *et al.* 2007). We extracted fire

data from the MODIS (MCD45A1 and MCD64A1) and NOAA-AVHRR websites obtained during 1995-2015.

2.2.7 Topographical derivatives (Elevation and Slope)

Topographical derivatives such as slope and elevation were obtained from the Digital Elevation Model (DEM), downloaded from the Shuttle Radar Topographic Mission (SRTM). These derivatives are known to influence vegetation change (Reed *et al.* 2009). The derivatives were calculated using the *Spatial Analysis* tool in ArcGIS 10.5. The slope function in the *Spatial Analysis* tool calculates the maximum rate of change from every cell to its neighbors. The two derivatives were considered important variables as are always stable, not affected by spatio-temporal situations. In this study, the slope was reclassified into three classes, gentle slope (0.00-4.8^{o}), moderate (4.9-12.00^{o}) and steep slope (13-23^{o}). Elevation was also reclassified to three classes (Low: 562-1159, Medium: 1160-1511 and High 1512-2009 m.a.s.l). Both slope and elevation were reclassified by the natural break classification algorithm.

2.2.8 Elephant density

Elephant density and distribution (1995 and 2015) data were provided by Tanzania Wildlife Research Institute (TAWIRI). These data are collected using the Systematic Reconnaissance Flights (SRF) following methods described in Norton-Griffiths (1978). We opted to use elephants as they have notable effects on woody vegetation structure, at moderate to high population densities (Guldemond and Van Aarde 2008). We reclassified elephant density into three density classes (Low: 0.04-0.56, Medium: 0.57-1.76 and High: 1.77-3.68 elephant/km^{2}).

2.3 Data analysis

2.3.1 Multicollinearity and Spatial autocorrelation

In order to determine correlation, we discriminate the related and unrelated variables by performing a correlation test between independent variables (Menard 2002). We aimed to obtain the best regression model based on criteria of adjusted R square value (Adj-Rsq) among the nine predictors (Table 1) variables using the Variance Inflation Factor (VIF) using the R package “Car” in R version 3.5.1. We retained and used all predictor variables to run the 8 models as they had low VIF (<4).

For detecting the direction of the linear association between the variables, i.e., spatial autocorrelation among observational units (statistically independent and spatial distributed in an identical manner), we plotted values of the residuals of the regression model against distance classes using the Moran’s I statistic in R statistical software (R Development Core Team 2016). The choice of correlogram, over other structure functions (e.g. the variograms and periodograms) was based on its advantages (De Koning *et al.* 1998, Dubé and Legros 2014).

2.3.2 Binomial logistic regression

Two sets of explanatory variables, namely biophysical and socio-economic variables were used in analysing LULC change. We considered nine variables (X_1-X_9) to test their influence on LULC cover changes (Table 1). The response (changes in LULC for the eight classes in 1995 and 2015: both directional changes, i.e., changes from decreasing LULC and changes to the increasing LULC) and explanatory variables were overlaid and corresponding values extracted using the spatial join tool in ArcGIS. However, prior to this, all vector data were rasterized and converted to ASCII format. Different datasets and their sources are shown below (Figure 3.1 and Table 3.1).

To analyse the influence of driving forces (explanatory variables) to LULC change, we employed binomial logistic regression (BLR). BLR is an explanatory approach for testing relations between LULC change and the possible driving factors. We ran sets of models analyzing: (i) the eight LULC changes; (ii) the 2-time windows (1995 and 2015), through study period (1995-2015).

Regression analysis was performed separately for each LULC with an individual set of the possible explanatory drivers (Table 3.1). We evaluated the performance of the eight yielded models (in each study period) using the Receiver Operating Characteristic (ROC) and Area Under Curve (AUC) (Pontius and Schneider 2001). The above metrics are better in predicting model accuracies (Braimoh and Vlek 2005) and sensitivity in modelling the relationship in LULC change (Rutherford *et al.* 2008, Pérez-Vega *et al.* 2012, Rossiter and Loza 2012).

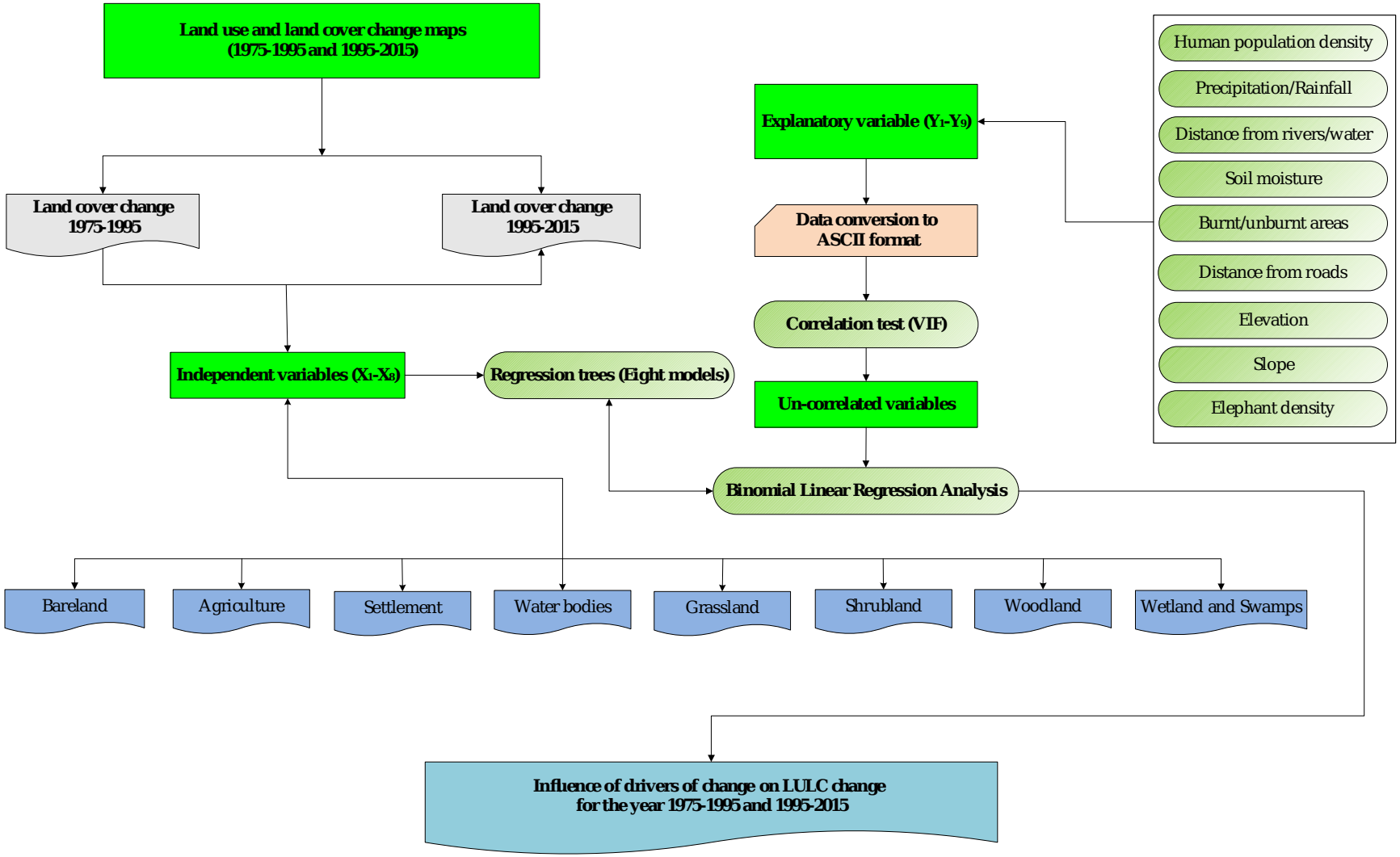

Figure 3.2: Methodological flow chart for LULC modelling

Table 3.1: Response and explanatory variables for the year 1975-1995 and 1995-2015

Variable name	Variable description	Data source
Y_1_Dependent	Bareland change	(Kija *et al.* 2020)
Y_2_Dependent	Agriculture change	(Kija *et al.* 2020)
Y_3_Dependent	Settlement change	(Kija *et al.* 2020)
Y_4_Dependent	Water bodies change	(Kija *et al.* 2020)
Y_5_Dependent	Grassland change	(Kija *et al.* 2020)
Y_6_Dependent	Shrubland change	(Kija *et al.* 2020)
Y_7_Dependent	Woodland change	(Kija *et al.* 2020)
Y_8_Dependent	Wetland and Swamps change	(Kija *et al.* 2020)
X_1_Popn	Human density	National Bureau of Statistics (NBS), 2012
X_2_Precp	Annual precipitation	WorldClim
X_3_Dist_Rivers	Distance to rivers	National Bureau of Statistics (NBS), 2012
X_4_Sm	Soil moisture	WorldClim
X_5_Fire	Fire frequency (Burnt and unburnt areas)	MODIS and NOOA AVHRR
X_6_Dist_Roads	Distance from roads	TANROADS
X_7_Elevation	Elevation in meters	Digital Elevation Model
X_8_Slope	Slope in degrees	Digital Elevation Model
X_9_El popn	Elephant density	TAWIRI (1975-2015)

Dependent variable data refers to change from/to that is calculated based on decreasing (change from/loss) and increasing (change to/gain) state of a particular LULC. Response variables refers to data that are for the first (1975-1995) and second slices (1995-2015).

3. RESULTS

3.1 Model performance

Model results ranged from 0.58 to 1, where > 0.5 implies no better than randomly expected and 1 denoting a perfectly assigned probability model (Pontius and Schneider 2001, Eastman *et al.* 2005). For the year 1995, we obtained three models with AUC < 0.6 and five models with AUC > 0.6 whereas for the year 2015, all eight models had AUCs > 0.6. The obtained AUCs (Table 3.2 and Appendix I and II) are within the acceptable limits, implying that our models are good enough to explain the relationship between the response and predictor variables (Bansal *et al.* 2016). Several authors, have reported that AUCs of > 0.5 - 0.59 implies good, 0.6 - 0.69 better, 0.7 - 0.79 considered as an acceptable, 0.8 - 0.9 as excellent and close to 1 means a perfectly modeled relationship (Hein *et al.* 2007, Baldwin 2009). The accuracy values are presented in percentage (%).

Table 3.2: Model performance based on Area Under the Curve

Land use and cover type	1975-1995		1995-2015	
	AUC	Accuracy	AUC	Accuracy
Bareland	0.93	0.98	0.91	0.98
Agriculture	0.71	0.96	0.72	0.89
Settlement	0.73	0.97	0.79	0.94
Water bodies	0.89	0.99	0.76	0.99
Grassland	0.58	0.79	0.61	0.83
Shrubland	0.59	0.58	0.61	0.57
Woodland	0.58	0.75	0.70	0.80
Wetland and Swamps	0.96	0.99	0.96	0.99

AUC refers to the model results that indicates changes in model performance, while the accuracy refers to the LULC accuracies based on 1975-1995 and 1995-2015 thematic maps (Kija *et al.* 2020).

3.2 Factors influencing land use and land cover change

3.2.1 Human population

Reports shows increased human population trend around the ecosystem and the country at large (Estes *et al.* 2012, URT 2012). The first study slice (1975-1995) indicates negative effects on bareland, water bodies and shrubland. On the other hand, it has positively affected agriculture, grassland, woodland, and wetland and swamps (Table 3.3 and Appendix III). In the second study slice (1995-2015), grassland, shrubland and woodland were negatively affected. Significant positive effects were recorded on bareland, agriculture and settlement (Table 3.4 and Appendix IV).

3.2.2 Precipitation

Changes in annual precipitation negatively affected bareland, water bodies and shrubland (In 1995) and a positive effects on agriculture, grassland and woodland (Table 3.3 and Appendix III). In the year 2015, negative effects were recorded for bareland, water bodies and shrubland cover, whereas, agriculture, grassland and woodland revealed a positive effect (Table 3.4 and Appendix IV).

3.2.3 Distance from rivers

Significant negative effect of distance from rivers in relation to bareland and settlement was observed in the first study period. There was no positive significant effect recorded (Table 3.3 and Appendix III). In the second study period, bareland, wetland and swamps were negatively affected except woodland only which was positively affected (Table 3.4 and Appendix IV).

3.2.4 Soil moisture

Table 3.3 and Appendix III show a significant negative influence of soil moisture on agriculture and water body cover types during the first study period. In the same study window, we recorded a positive effect on bareland and woodland. During the second study period, we

recorded a negative effect on agriculture and shrubland. On the other hand, it positively affected bareland and woodland (Table 3.4 and appendix IV).

3.2.5 Burnt areas

Fire registered a significant negative effect on settlement and shrubland whereas only grassland and woodland were positively affected respectively during the first study slice (Table 3.3 and Appendix III). In the second study slice, agriculture and settlement were both negatively influenced (Table 3.4 and Appendix IV).

3.2.6 Distance from roads

During the study first slice only shrubland was negatively affected. Positive effects were recorded for bareland, water bodies and grassland (Table 3.3 and Appendix III). Shrubland showed a consistent negative effect during the second slice whereas only woodland registered a significant positive effect (Table 3.4 and Appendix IV).

3.2.7 Elevation

Low elevation category negatively affected only shrubland cover type whereas the medium class significantly affected both grassland and shrubland during the first study slice. The high elevation category negatively affected only the grassland. On the other hand, a significant positive effect of low elevation was revealed for bareland and grassland. The medium class affected agriculture and woodland. Only woodland recorded a positive significant effect of the high elevation (Table 3.3 and Appendix III).

In the second slice, no significant effects of the low and medium elevation were recorded to all LULC cover types. The high elevation significantly affected grassland and wetland and swamps. On the other hand, positive influence was recorded for agriculture and settlement in the low-level areas, whereas in the medium elevated areas agriculture,

settlement, shrubland and wetlands and swamps were positively affected. At highly elevated areas, only shrubland and woodland were positively affected (Table 3.4 and Appendix IV).

3.2.8 Slope

Gentle, moderate and steep slopes had a mixed influence on LULC change. In the first slice, we recorded a significant negative effect of gentle slope on grassland cover type. Other slope categories showed no significant negative and positive effects (Table 3.3 and Appendix III). Interestingly, during the second slice, only woodland recorded a significant negative effect of all the three slope categories (Table 3.4 and Appendix IV).

3.2.9 Elephant density

Low elephant density had a significant negative influence on agriculture and settlement in the first slice. Interestingly, in the same slice, positive significant effects of low and medium elephant density were only recorded for shrubland (Table 3.3 and Appendix III). In the second slice, low density exerted a negative significant effect on agriculture, settlement and grassland. The same types showed a consistent significant negative effect of medium elephant density on agriculture and settlement as well as grassland whereas the negative effect of high elephant density was only observed for agriculture. Significant positive effects of low elephant density were recorded for shrubland and wetland and swamps whereas for the medium and high densities effects were observed for shrubland only (Table 3.4 and Appendix IV).

Table 3.3: Regression coefficients for responsible factors determining changes in LULC (1975-1995)

SN	Variable	Model estimate (β) and P-values for each LULC type (1995)													
		Bareland		Agriculture		Settlement		Water bodies		Grassland		Shrubland		Woodland		Wetland and Swamps	
1	Human popn density	-5.840	***	1.361	**	-1.190	NS	-3.454	*	0.684	*	-0.612	*	0.718	**	5.560	***
2	Precipitation	-6.463	***	3.314	***	-0.104	NS	-5.860	***	1.784	***	-2.362	***	1.703	***	9.163	NS
3	Distance from water	-1.209	*	0.246	NS	-0.859	*	-0.388	NS	0.151	NS	0.145	NS	0.131	NS	-7.625	NS
4	Soil moisture	6.150	***	-7.084	***	1.748	NS	-2.892	*	-0.754	NS	0.163	NS	1.017	**	-11.301	NS
5	Fire frequency	-0.672	NS	-0.378	**	-1.488	***	-0.149	NS	0.201	***	-0.123	*	0.178	**	0.152	NS
6	Distance from roads	3.148	*	1.890	NS	-0.294	NS	5.542	***	1.983	***	-1.904	***	-0.574	NS	-2.041	NS
7	**Elevation category (masl)**																
	Low (562 - 1159)	2.975	***	0.902	NS	15.979	NS	2.021	NS	0.597	***	-0.432	***	0.085	NS	16.022	NS
	Medium (1160 - 1511)	-0.887	NS	1.601	**	15.551	NS	0.376	NS	-0.459	***	-0.457	*	0.386	**	13.666	NS
	High (1512 - 2009)	-0.476	NS	0.851	NS	14.595	NS	-0.278	NS	-0.692	***	0.138	NS	0.332	**	-2.211	NS
8	**Slope category**																
	Gentle (0.00 - 4.80)	0.780	NS	-0.355	NS	-0.053	NS	0.338	NS	-0.270	*	0.178	NS	-0.037	NS	16.660	NS
	Moderate (4.90 - 12.00)	1.009	NS	-0.406	NS	-0.052	NS	0.017	NS	-0.191	NS	0.129	NS	0.005	NS	15.499	NS
	Steep (13.00 - 23.00)	0.518	NS	-0.532	NS	-0.272	NS	0.424	NS	-0.12	NS	0.046	NS	0.062	NS	-0.686	NS

										7							
9	**Elephant density**																
	Low (0.04 - 0.56)	-0.534	NS	-0.234	*	-0.727	***	-0.765	NS	-0.039	NS	0.229	***	-0.075	NS	1.316	NS
	Medium (0.57 - 1.76)	-11.223	NS	-12.942	NS	-14.128	NS	-11.559	NS	0.269	NS	0.409	*	-0.459	NS	-14.416	NS
	High (1.77 - 3.68)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

The table refers to the regression coefficient/estimates of each driver of change. Significant *P-values* are summarized and interpreted in three levels, i.e., $P<0.001$ (***), $P<0.01$ (**), and $P<0.05$ (*) and non-significant values denoted by NS.

Table 3.4: Factors determining changes in LULC (1995-2015)

SN	Variable	Model estimate (β) and P-values for each LULC cover type (2015)															
		Bareland		Agriculture		Settlement		Water bodies		Grassland		Shrubland		Woodland		Wetland and Swamps	
1	Human popn density	10.314	***	11.018	***	3.901	*	4.192	NS	-5.914	**	-5.644	***	-7.080	***	1.575	NS
2	Precipitation	-7.208	***	0.991	*	-0.032	NS	-3.451	*	0.512	NS	-0.462	NS	1.871	***	20.382	*
3	Distance from rivers	-1.636	*	-0.187	NS	0.395	NS	-0.813	NS	0.151	NS	0.147	NS	0.441	**	-13.345	*
4	Soil moisture	7.137	***	-3.920	***	1.010	NS	0.606	NS	0.402	NS	-0.845	***	1.705	***	-9.715	NS
5	Fire frequency	-1.776	NS	-0.456	***	-1.831	***	-0.084	NS	-0.032	NS	0.102	NS	0.144	NS	0.098	NS
6	Distance from roads	-2.077	NS	-6.470	***	-0.025	NS	1.874	NS	3.688	***	-1.983	***	2.872	***	-0.431	NS
7	**Elevation category (masl)**																
	Low (562 - 1159)	16.934	NS	0.635	*	3.973	***	1.147	NS	0.315	NS	-0.111	NS	0.085	NS	1.540	NS
	Medium (1160 - 1511)	14.243	NS	1.092	***	2.842	***	0.077	NS	0.069	NS	0.457	***	0.386	**	-1.871	NS
	High (1512 - 2009)	12.720	N	0.247	N	1.357	N	-0.296	N	-	**	0.703	**	0.332	**	-3.158	*

		S		S		S		S	0.491	*		*				
	Slope category															
8	Gentle (0.00 - 4.80)	0.297	NS	-0.355	NS	0.351	NS	15.184	NS	-0.277	NS	0.125	NS	-0.342	*	16.485	NS
	Moderate (4.90 - 12.00)	-0.460	NS	-0.406	NS	0.249	NS	15.636	NS	-0.158	NS	0.166	NS	-0.367	**	15.086	NS
	Steep (13.00 - 23.00)	-0.055	NS	-0.532	NS	0.115	NS	15.418	NS	-0.048	NS	0.126	NS	-0.289	*	-0.310	NS
	Elephant density															
9	Low (0.04 - 0.56)	0.051	NS	-0.396	***	-0.716	***	-0.632	NS	-0.239	**	0.270	***	0.028	NS	1.975	**
	Medium (0.57 - 1.76)	-0.521	NS	-0.652	***	-1.590	***	-0.168	NS	-0.274	*	0.323	***	0.004	NS	-14.815	NS
	High (1.77 - 3.68)	-12.706	NS	-1.416	***	-0.970	NS	-14.846	NS	-0.325	NS	0.388	***	0.183	NS	-15.493	NS

The table refers to the regression coefficient/estimates of each driver of change. Significant *P-values* are summarized and interpreted in three levels, i.e., $P<0.001$ (***), $P<0.01$ (**), and $P<0.05$ (*) and non-significant values denoted by NS.

4. DISCUSSION

4.1 Possible factors influencing land use and cover changes

4.1.1 Human population

The observed consistent negative effect on shrubland in the two study slices could be associated with opening of land for settlement and agriculture (Nzunda 2008, Estes *et al.* 2012, Nzunda and Midtgaard 2017) or negative effect on shrubland as well as grassland cover due to increased livestock on the edges of the ecosystem (Veldhuis *et al.* 2019). The overall effect on the shrubland cover can have cascading effects from woodland or shrubland to other cover types such as bareland (Kija *et al.* 2020). Furthermore, it should be noted that, effects of increased human population density are always not constant across space and time (Chi and Ventura 2011) and its consequences are common phenomena in the world, in particular, African countries (Masek *et al.* 2000, Lambin *et al.* 2001, Geist and Lambin 2002).

The high birth rate (3.5% per year) and continued settlement of pastoralists, agropastoralists, and other socio-economic ventures (from tourism) between 1995 and 2015 in the ecosystem (Estes *et al.* 2012) has increased number of newly emerging population and raised demand for food, fuel and settlement, thus accentuated LULC changes. This circumstance forced people to clear additional land for agriculture and settlement (building poles and timber) thus decline in certain land cover types in the ecosystem. Our findings are similar to a study in Kenya, whereby illegal activities such as charcoal production as a livelihood living strategy is responsible for woodland degradation (Kiruki *et al.* 2017).

4.1.2 Precipitation

Variation in precipitation can trigger changes in grassland cover in terrestrial ecosystems (Bond *et al.* 2003) and could be a key determinant in annual grassland cover change. It is well known that the management regime in the SNP favours grassland over bushland, a situation previously reported in the same or other similar landscapes (Norton-Griffiths *et al.* 1975, Coe *et al.* 1976, Wolanski and Gereta 2001, Ogutu *et al.* 2008, Bartzke *et al.* 2018). It is also possible that precipitation exerted effects on woodland loss, this is similar to findings by Mtui *et al.* (2017) in the Tarangire National Park.

4.1.3 Distance from rivers

The negative effect of rivers on bareland entails the possible trampling effects of animals around the water sources especially during the dry season. Areas around water sources are prone to encroachment by agricultural fields and possible flooding that could lead to bareland (Poyatos *et al.* 2003, Zope *et al.* 2016). Farmers tend to cultivate in fertile areas with good soil moisture, most of which are in areas around water sources including rivers and valleys (Shaxson and Barber 2003, Ogban and Babalola 2009). It has been reported that distance from water sources influence human settlement and hence a strong impact on human population density with a possible effect on land cover types (Kummu *et al.* 2011).

4.1.4 Soil moisture

Soil moisture is the key edaphic factors that influence occurrence and distribution patterns of different land cover types and anthropogenic activities. Farmers tend to cultivate in areas with soils with required soil moisture in addition to other related soil characteristics including types, texture and fertility, hence reduced soil moisture (Corbeels *et al.* 2000, Seneviratne *et al.* 2010). Agriculture in the villages surrounding the ecosystem is partly influenced by variations of soil moisture which is also determined by rainfall and topography (Bogena *et al.* 2012, Rosenbaum *et al.* 2012).

The positive effect of low soil moisture on bareland is possibly accelerated by loss of soil cover biomass, particularly perennial plants in grassland and shrubland (D'Odorico *et al.* 2007, Guo *et al.* 2020). Low soil moisture evokes high surface temperature that affects vegetation cover, leading to an increase of bareland (Wang *et al.* 2017). Additionally, overgrazing and frequent wildfires in low moisture soil also

accelerate the negative changes to bareland cover due to reduced rate of soil cover regrowth (Nunes *et al.* 2011, Kairis *et al.* 2015). The ecosystem is highly characterized by livestock overgrazing, wildlife and frequent wildfires that reduce soil vegetation cover (Archibald *et al.* 2005, Nkwabi *et al.* 2011).

Variations in soil moisture and types affect grass cover which in turn increase bareland (Skarpe 1992, Anderson *et al.* 2007). Generally, bareland have low soil moisture (Collow *et al.* 2014). For woodland, it has been reported that soil moisture in addition to other factors such as rainfall and air temperature influences phenology of woody vegetation (Seghieri *et al.* 2012, Barrett and Brown 2021). Soil moisture at a depth of more than 30 cm, positively correlate with phenology of woody vegetation due to their deep root system. The opposite scenario is true for grasses with shallow root system, hence easily affected by reduced soil moisture at the depth of 30 cm from the surface. Furthermore, we noted soil moisture has a positive impact on woodland cover, a similar observation reported elsewhere (D'Odorico *et al.* 2007, Seghieri *et al.* 2009).

4.1.5 Burnt areas

Wildfire is a common phenomenon in and around the ecosystem. These fires are either due to intentional burning to improve pasture for livestock or as a conservation tool in improving forage quality and quantity. Escape fires are detrimental to crops, hence discouraging human settlement. Fire has an enormous effect on vegetation, predominantly determining the structure, function and dynamics of savanna ecosystems (Amoako and Gambiza 2020).

We observed a significant effect on shrubland cover type, similar to reported cases elsewhere (Dublin *et al.* 1990, Dublin 1995, Rutina *et al.*

2005, Nzunda 2008). Fire has been favouring vegetation sprouting especially shrubland (Nzunda 2008), and frequent wildfires has a cascading negative effects on shrubland to grassland and bareland (Shiferaw *et al.* 2019, Kayombo *et al.* 2020, Bhattarai and Conway 2021). Furthermore, significant positive effects on woodland is probably due to its less damaging effects in savanna ecosystems (Van Langevelde *et al.* 2003). The combination of grazing and browsing pressure in woodland cover reduces fuel loads, hence less burnable materials (Strauss and Packer 2015, Zyambo 2016).

4.1.6 Distance from roads

Locations near roads (edge effects) are prone to changes in LULC (Coffin 2007, Nzunda and Midtgaard 2017) and anthropogenic activities near roadsides have great impacts on cover types (Findlay and Houlahan 1997). Roads construction removes vegetation cover, thus exposing vegetation cover to bare soils (Geist and Lambin 2002). However, its effect is not of the same magnitude, for example, shrubland in favor of other cover types is more affected by distance from roads factor (Schulz *et al.* 2011).

Evidence suggests that roads promote development (Taylor and Goldingay 2010, Van Dijck 2013) and access to areas with shortage of arable land. The same has been reported in the Maasai-Steppe in Tanzania (Msoffe *et al.* 2011). Areas close to PAs are increasingly avoided due to human-wildlife conflict mainly crop-raiding and livestock depredation (Thirgood *et al.* 2005, Matseketsa *et al.* 2019). The negative influence of roads on settlement could be because some numerous tracks and roads were not mapped, therefore could have compromised its influence pattern of settlement, the same had been reported in the Zambezi region in Namibia (Kamwi *et al.* 2018).

4.1.7 Elevation

Significant negative effect of low elevation on shrubland was recorded. Elevation influences soil moisture, hence spatio-temporal distribution of LULC types. Topographically, the ecosystem is characterized by low to moderate elevations forming the well-known grassland plains and savannah (Byrom *et al.* 2015).

Our findings confirm that lowland positively affected grassland and bareland while high elevation negatively affected these cover types and favored shrubland and woodland. Agricultural and human settlement have been positively favored due to soil moisture retaining capacity, high fertility and low soil erosion (Birhanu *et al.* 2019).

4.1.8 Slope

Different slope degrees (gentle, moderate and steep) influences soil moisture and vegetation cover (Gong *et al.* 2008, Birhanu *et al.* 2019). Our observed significant negative effect of the gentle slopes on grassland cover is contrary to Birhanu *et al.* (2019) study in Ethiopia, which reported a positive effect of all slope categories. Inline, they reported a negative effect of all slope categories on shrubland cover, whereas ours recorded a positive influence. The differences could possibly be attributed to differences of slope gradient in the ecosystem, ranging from 500 m in Natron area to 4500 m in the Ngorongoro Crater to (Banyikwa *et al.* 1990, Holdo *et al.* 2020).

For agriculture land cover type, a negative effect of all slope categories was detected. Similar effects had been reported in Ethiopia (Gala *et al.* 2011, Wondie *et al.* 2012). Most agricultural practices are not favored in moderate and steep slopes partly due to inaccessibility, land fragility and nutrients loss (Gebresamuel *et al.* 2010, Birhanu *et al.* 2019).

Agricultural activities are practiced in areas with gentle slopes, due to soil moisture and low loss of soil fertility through surface runoff.

4.1.9 Elephant density

The consistently negative effects to agriculture and settlement could be attributed to human-elephant effects that influence humans avoidance of these areas for agriculture and settlement. Human-elephant conflict areas are prone to crop-raiding, property damage and human injuries or death (Mollel 2017, Koech 2018). We recorded a consistent negative effect on grassland,which is associated with herbivores' grazing and browsing effects (Dublin *et al.* 1990, Dublin 1995, Rutina *et al.* 2005, Kija *et al.* 2020). Inline, we noted a negative effect on woodland in 1995, and shrubland in both study periods, which has a cascading effect on grassland.

Elephant have been reported in savannah and miombo ecosystems as a driver of LULC change (Dublin *et al.* 1990, Morrison *et al.* 2016). Likewise, woodland loss from elephant grazing and browsing effects has been reported in other Tanzanians' ecosystems (Ruess and Halter 1990, Prins and van der Jeugd 1993, Nzunda and Midtgaard 2019) and elsewhere (Guldemond and Van Aarde 2008, Scholtz *et al.* 2014).

5. CONCLUSIONS AND RECOMMENDATIONS

Dynamics of LULC types in the SE is influenced by multiple factors; human population density through its associated socio-economic activities, precipitation, distance from water sources including rivers, soil moisture, fire incidences, distance from roads, topographic features (elevation and slope), and elephant density.

The effect of human population in space and time was not constant. We recorded its negative effect especially in 2015 through: (i) increased bareland, agriculture and settlement areas, of which all reduce or damage wildlife habitats; and (ii) reduced grassland, shrubland and woodlands, each with mixed effect to browsers and grazers. For precipitation, the mean annual variations affected grassland, shrubland

and woodland in an alternating decrease-increase pattern. The observed negative effect of precipitation on bareland reflects the overall increasing trends of rainfall in the ecosystem which support grassland growth, hence reduced bareland cover.

The observed negative effect of distances from water on bareland reflects trampling effects of wild and domesticated animals and farming near or around water sources. Soil moisture, agriculture, water bodies and shrubland were significantly affected negatively, partly due to human pressure. The observed positive effect of soil moisture on bareland could be accelerated by the resultant loss of perennial plants due to overgrazing and wildfires. Wildfires had a mixed effects on different LULC types, negative effects to bareland, agriculture, settlement, grassland and woodland, due to cascading effects from woodland and shrubland to grassland and bareland.

We recorded negative effect of the distance from roads, shrubland being the most affected cover due to anthropogenic activities near roadsides. For topographical variables (elevation and slope), lowland positively affected grassland and bareland, in turn negatively affected by high elevation that favored shrubland and woodland. Further, low and moderate elevations favored most agriculture and human settlement due to the capacity of retaining soil moisture, soil fertility, and low soil erosion rates.

Slope exerted a negative effect on grassland and agriculture, the latter being practiced in areas with gentle slopes, due to soil moisture and surface runoff. Elephant density exerted a consistent negative effects on agriculture and settlement, implying avoidance of human wildlife conflict areas. It had a negative and positive effect on grassland and shrubland respectively, and a change from negative to positive effect on woodland, though not statistically significant. These reflect promising trends in vegetation improvement from grassland to shrubland. The above support previous work in the ecosystem which

reported an increasing shrubland trend in the past 40 years, partly due to transformations from other cover types (Kija *et al.* 2020). Generally, human population density is central to the observed LULC changes.

We, therefore, recommend for: (i) PAs Managers avoid roads construction in shrubland, (ii) Integrated efforts to ensure appropriate anthropogenic activities inside and adjacent PAs in order to reduce its unpreferred effects, (iii) Effective management of prescribed wildfires, (iv) Assess availability and distribution of key resources for elephant, ultimately reducing negative effects of its density, (v) Effective use of PAs management plans, which could ameliorate negative impacts of practices beyond acceptable level.

Author contributions

HHK conceived and designed the study, HKK, JBK and LJM analysed the data. JOO, JRK, MYS and EFN reviewed the drafts of the paper. The *AfricanBioservice* also contributed to this paper as they wrote the funded proposal, which resulted into my PhD programme.

Declaration of competing interest

The authors have no interest or relationship, financial or otherwise that might be perceived as influencing the author's objectivity with this work and thus have no conflicts of interest to declare.

Funding

We thank the *AfricanBioservices* Project, Friedkin Conservation Fund (FCF) and the Rungwa Game Safaris Tanzania for supporting this study.

Acknowledgment

We thank the Tanzania Wildlife Research Institute (TAWIRI) and Tanzania Commission for Science and Technology (COSTECH) for granting us research permit for this work. We are grateful to individuals who have contributed to the success of this study. We thank the Sokoine University of Agriculture for organizing research clearance for

this study. The authors thank the Ministry of Natural Resources and Tourism for granting access to protected areas during data collection.

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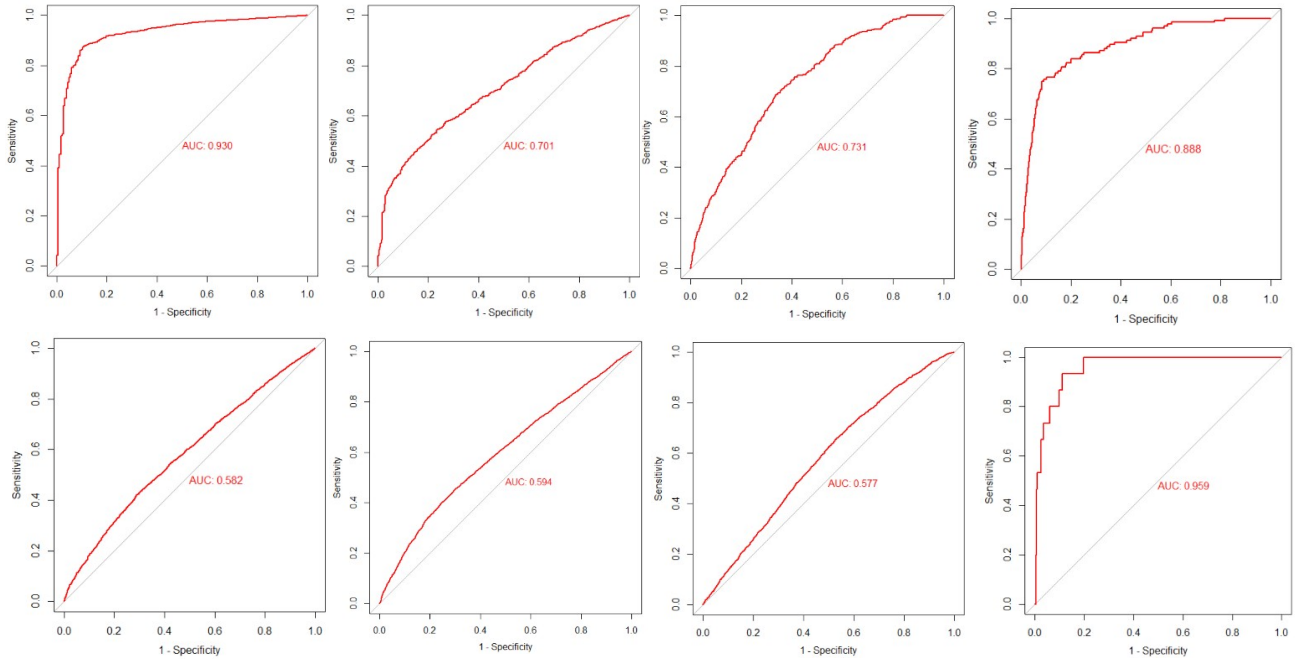
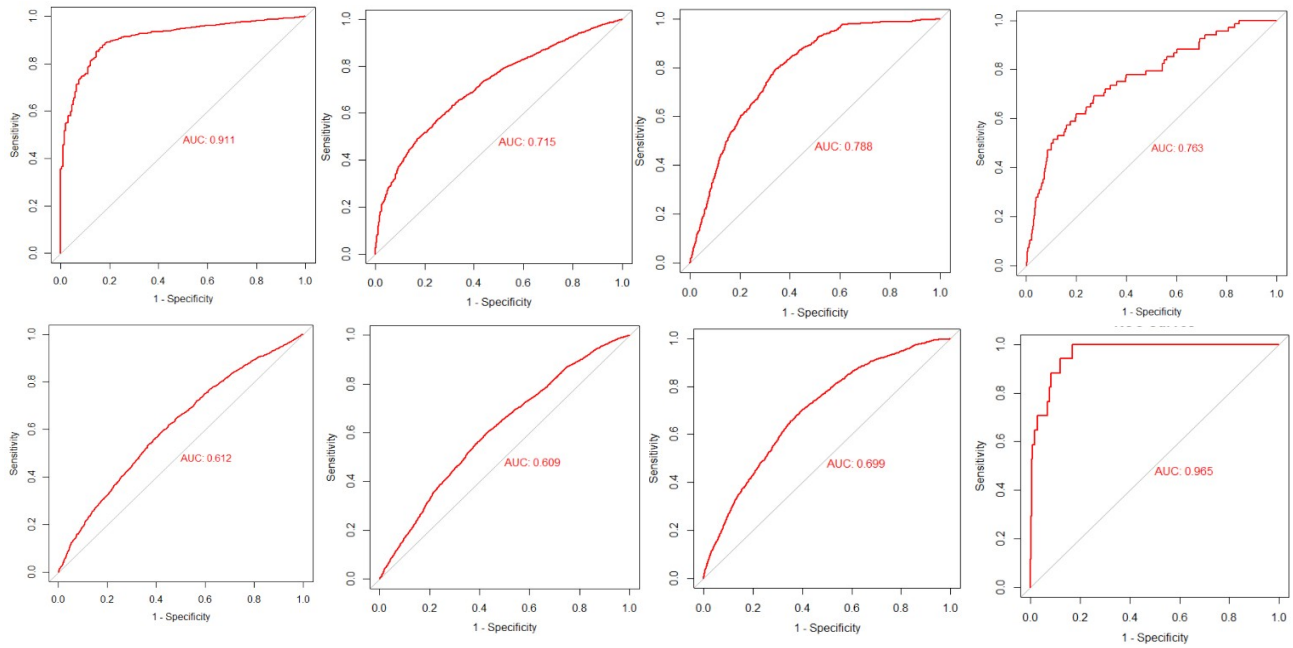
Zyambo, P. (2016). Woodland Conversion by Elephants in Africa: The Search for Causal Factors, Processes, Mechanisms and Management Strategies. Open Journal of Ecology **06**(02): 93-101.

APPENDICES

Appendix 1: Area Under the Curve for LULC change (1975-1995)



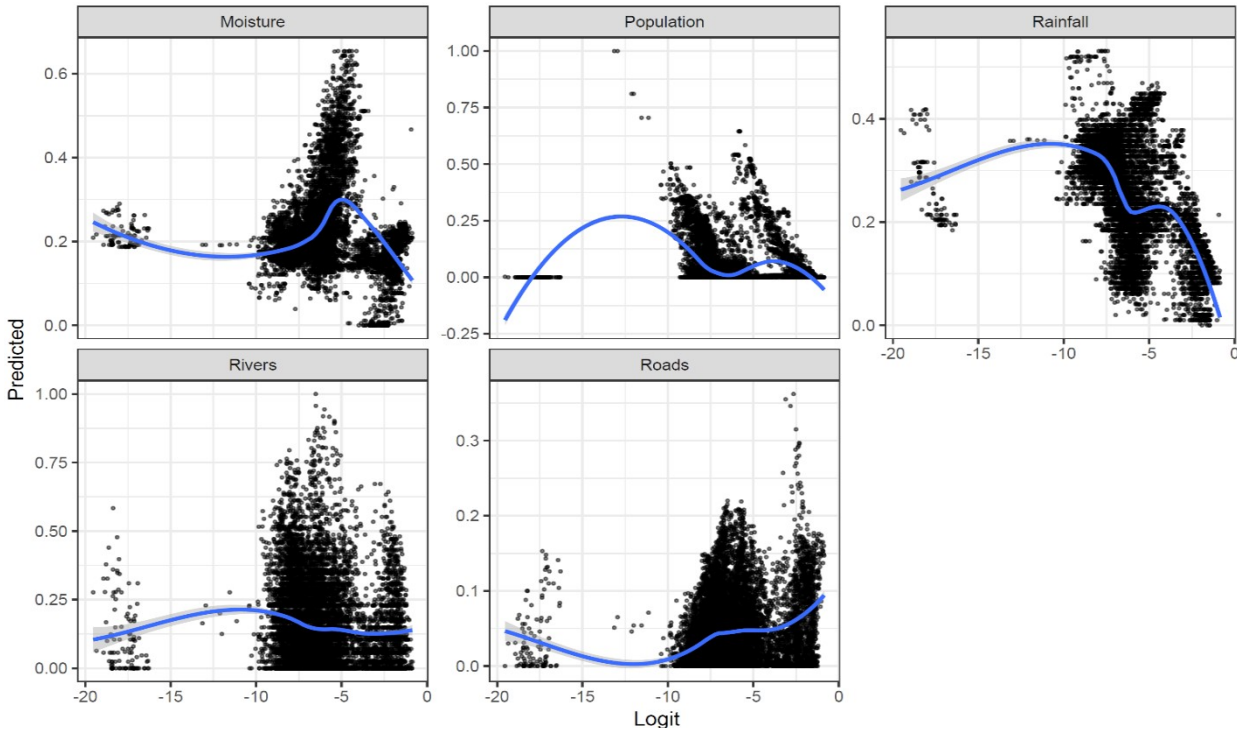
Appendix II: Area Under the Curve for LULC change (1995-2015)



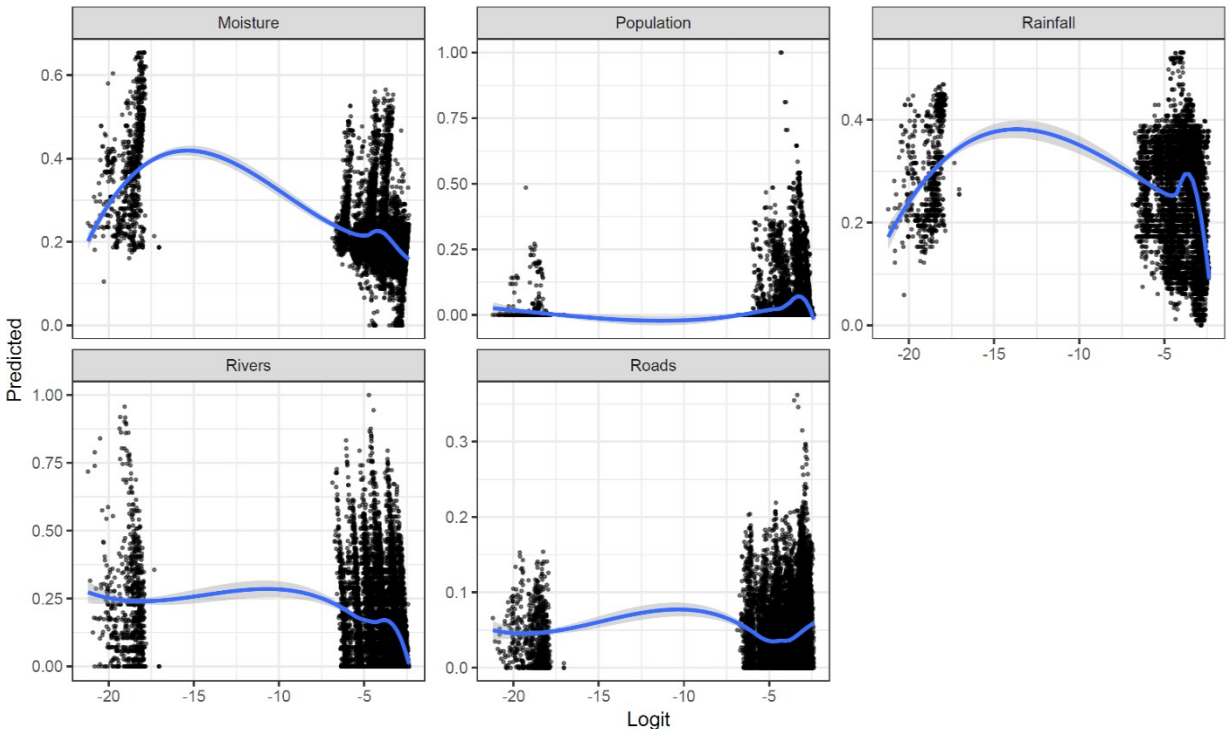
Note: The upper panel of each graph (Left to right): Bareland, Settlement, Agriculture and Water bodies and the lower panel of each graph (Left to right): Grassland, Shrubland, Woodland and Wetland and Swamps.

Appendix III: Probability graphs of LULC change (1975-1995)

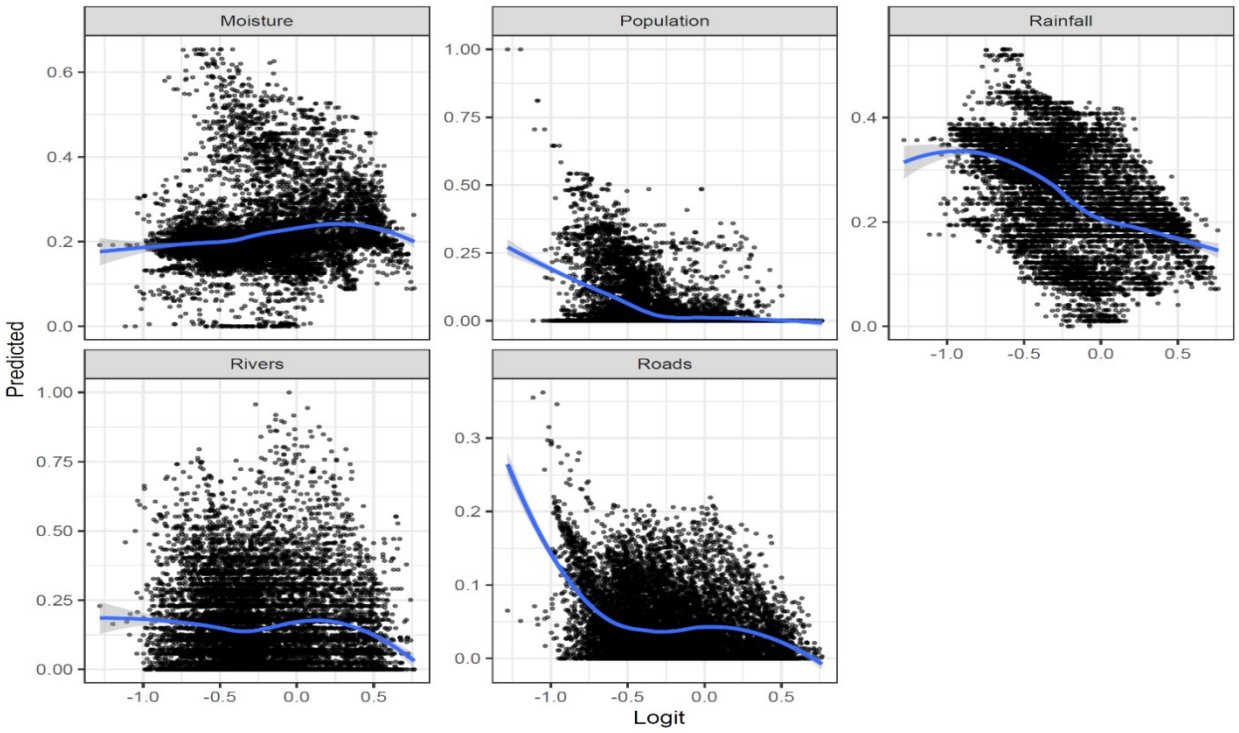
Bareland



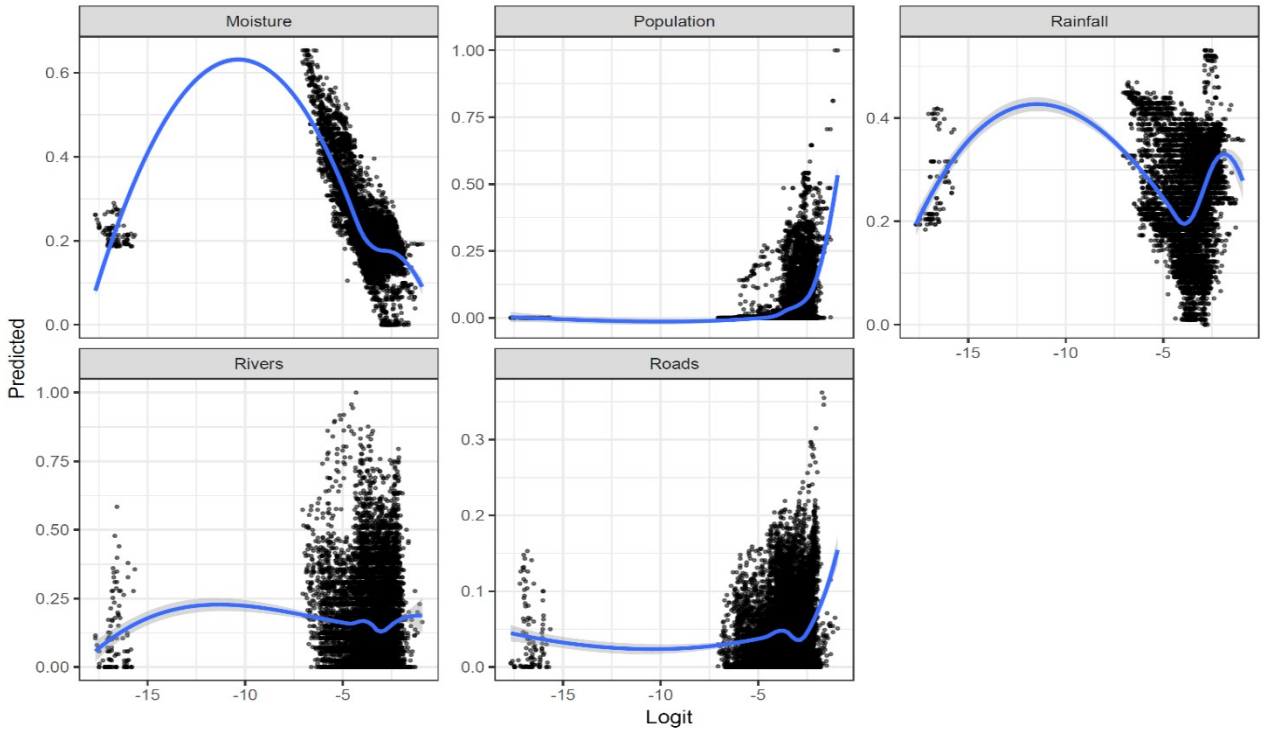
Agriculture



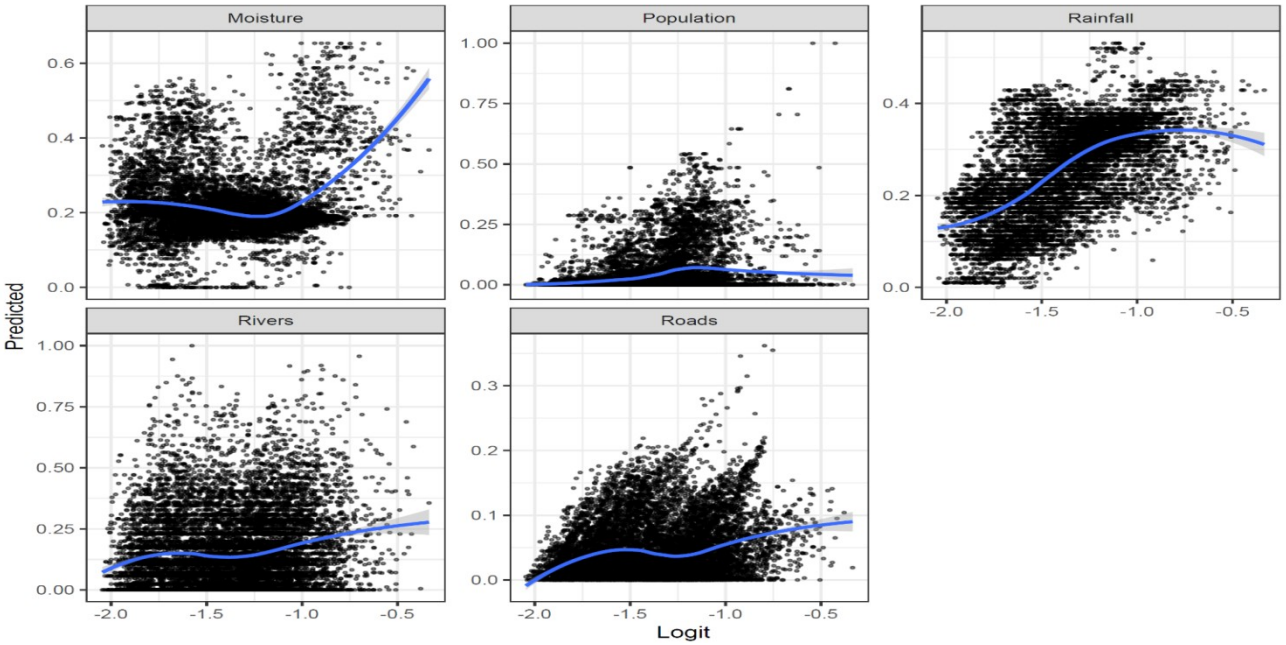
Settlement



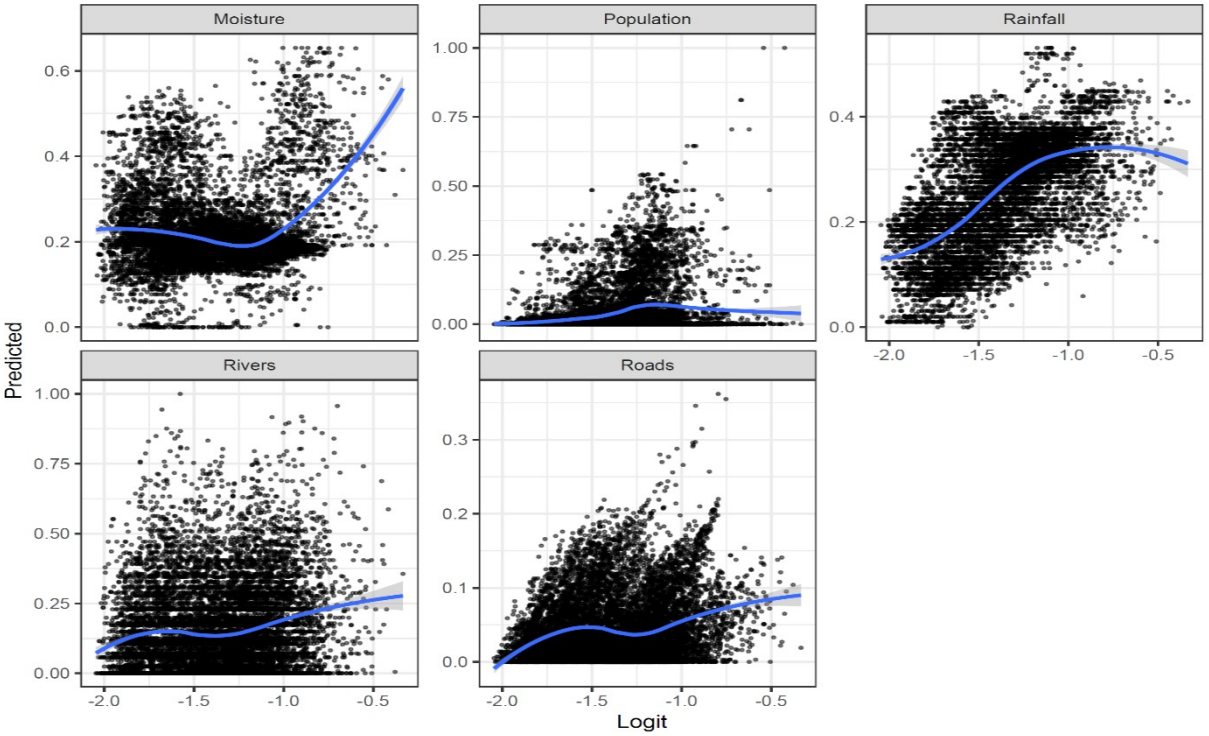
Water bodies



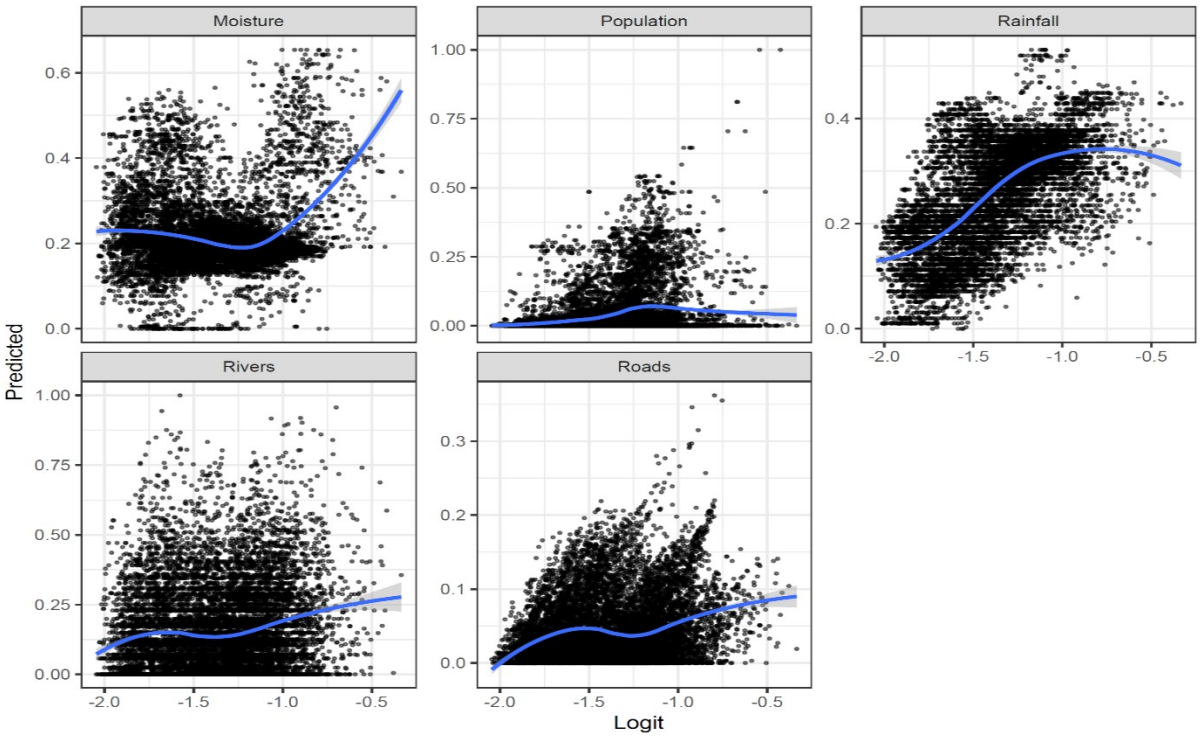
Grassland



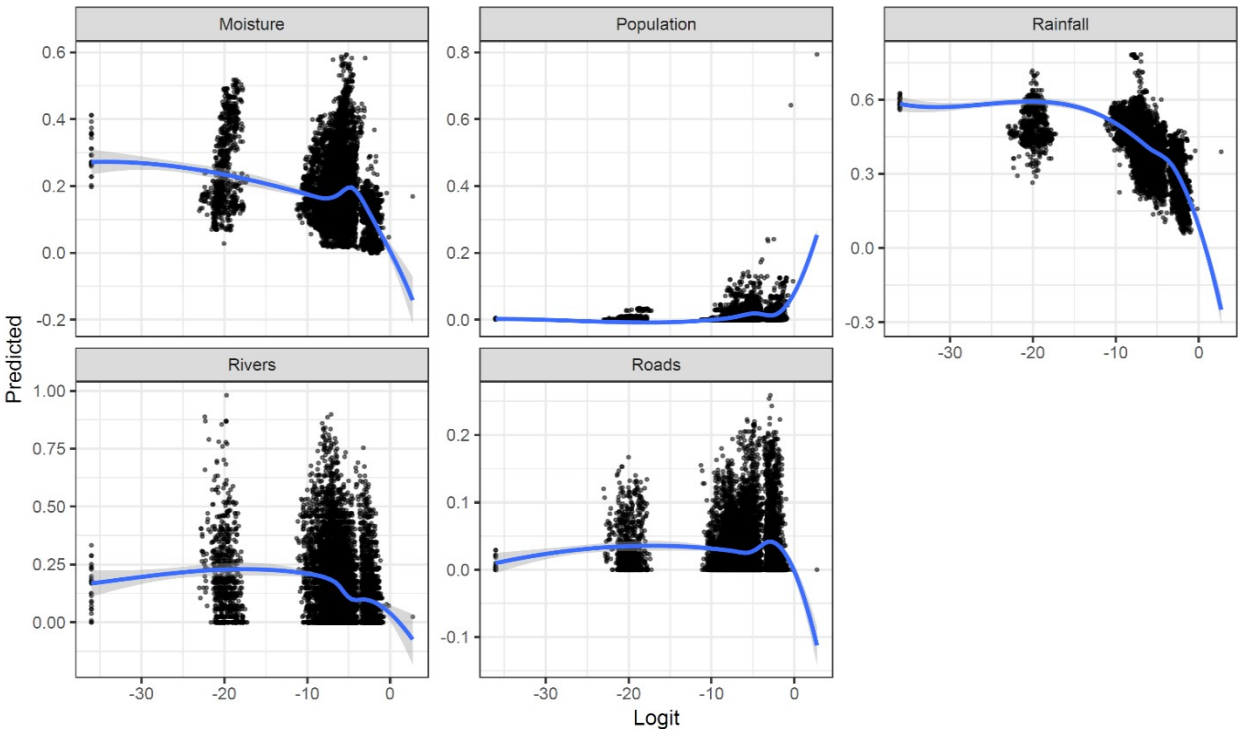
Shrubland



Woodland

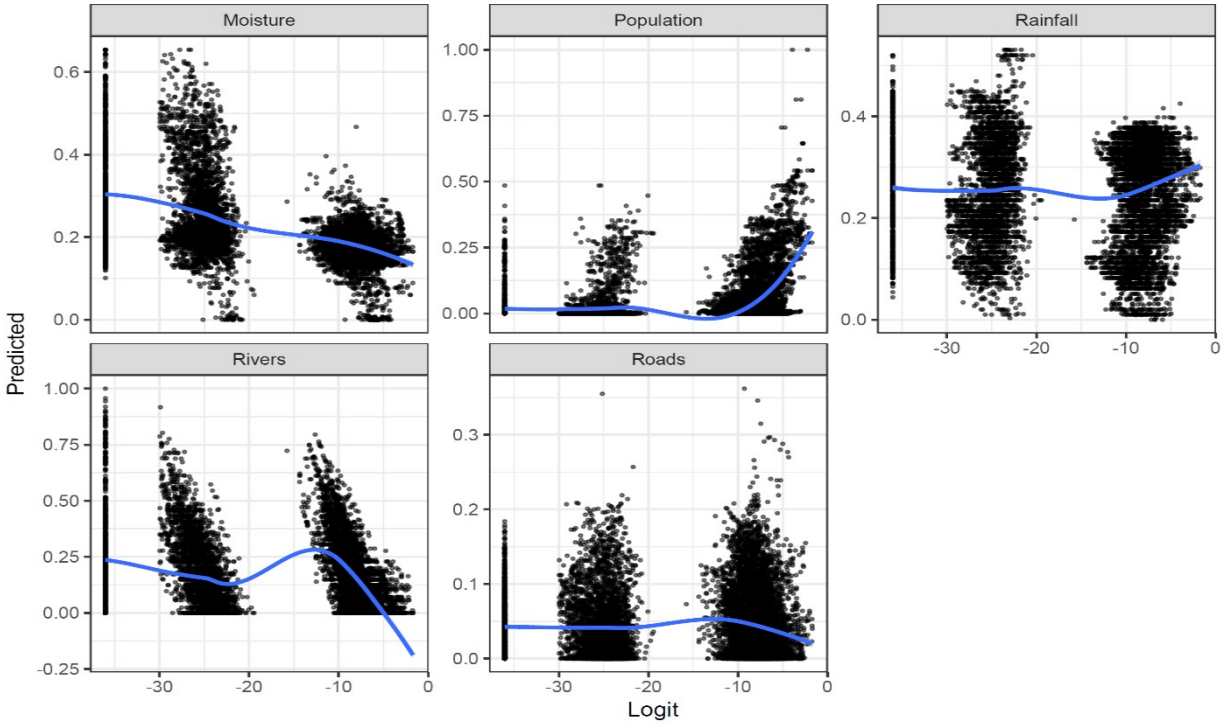


Wetland and Swamps

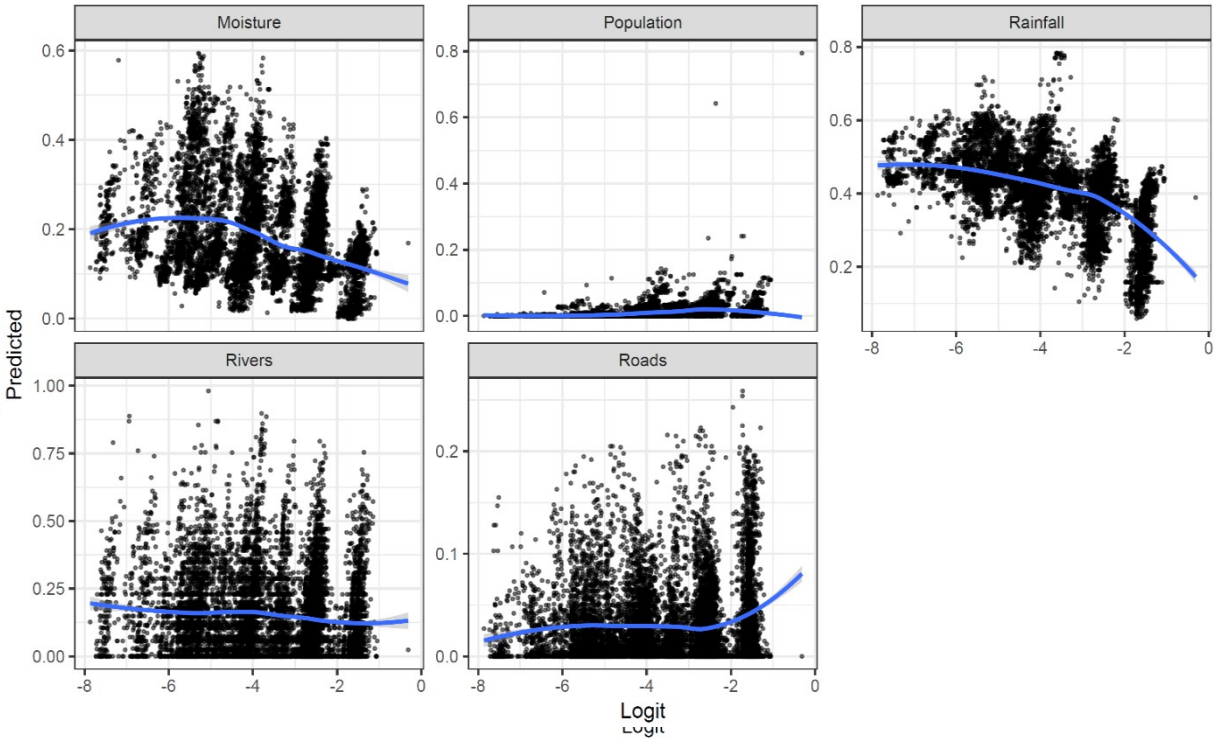


Appendix IV: Probability graphs of LULC change (1995-2015)

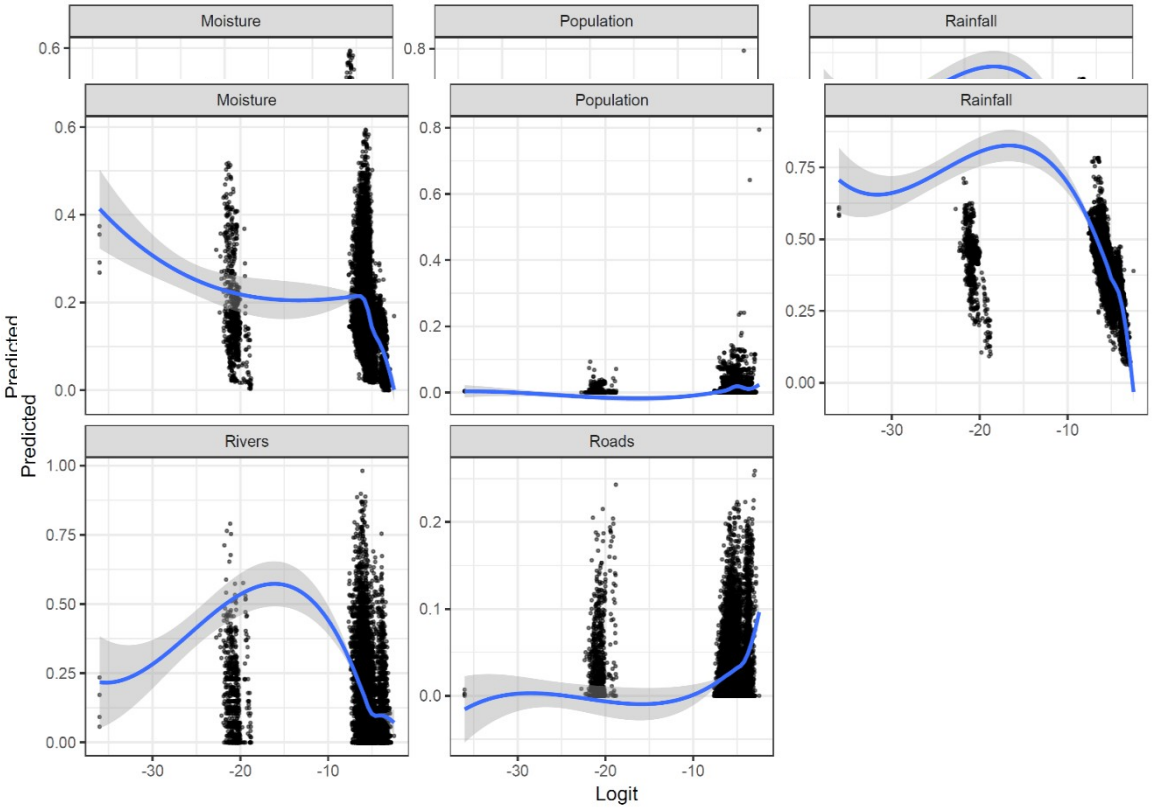
Bareland



Agriculture

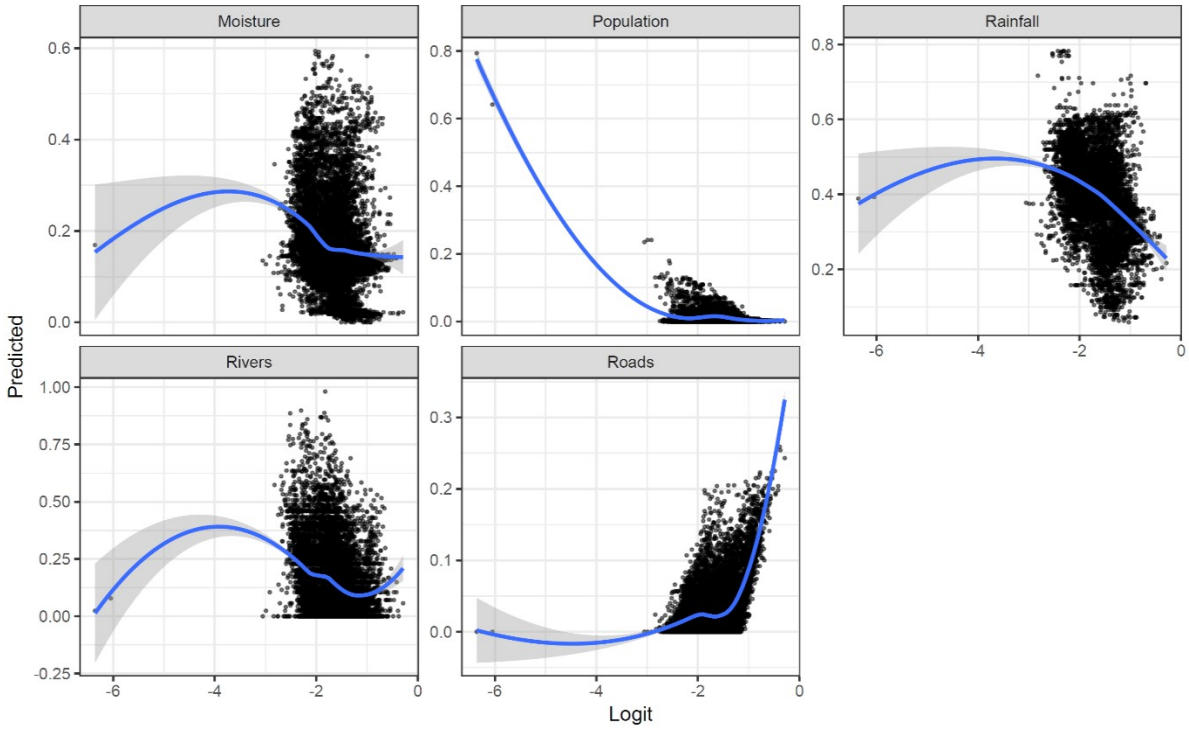


Settlement

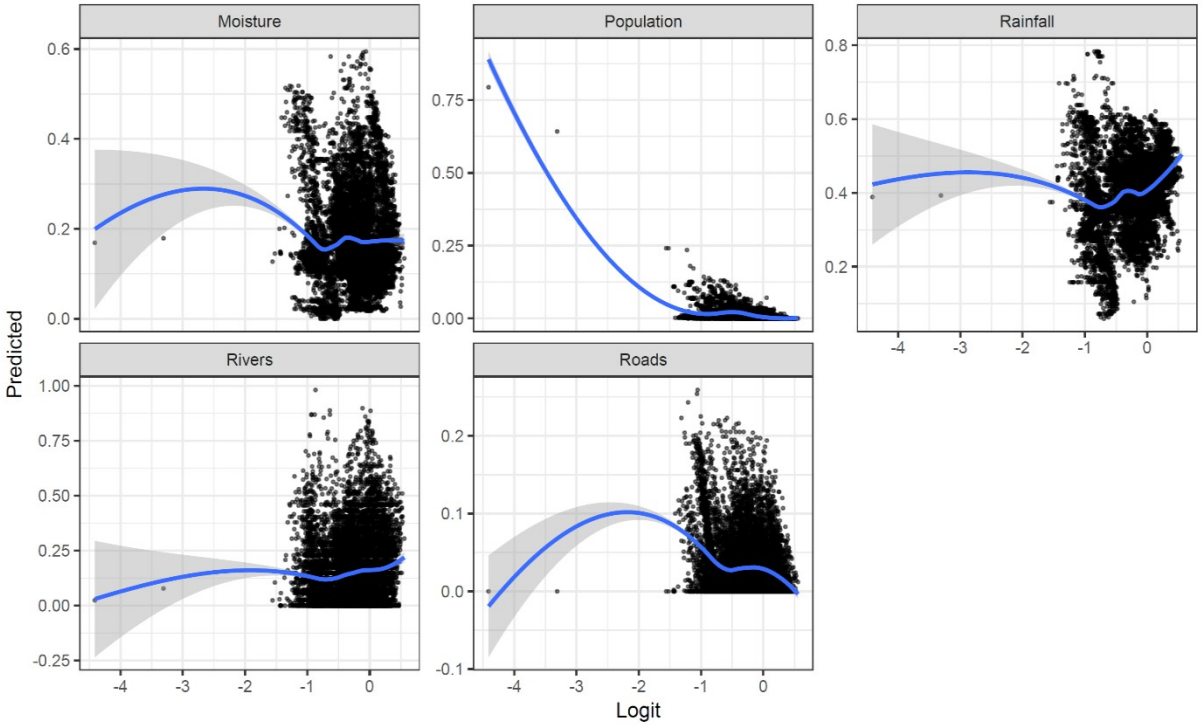


Water bodies

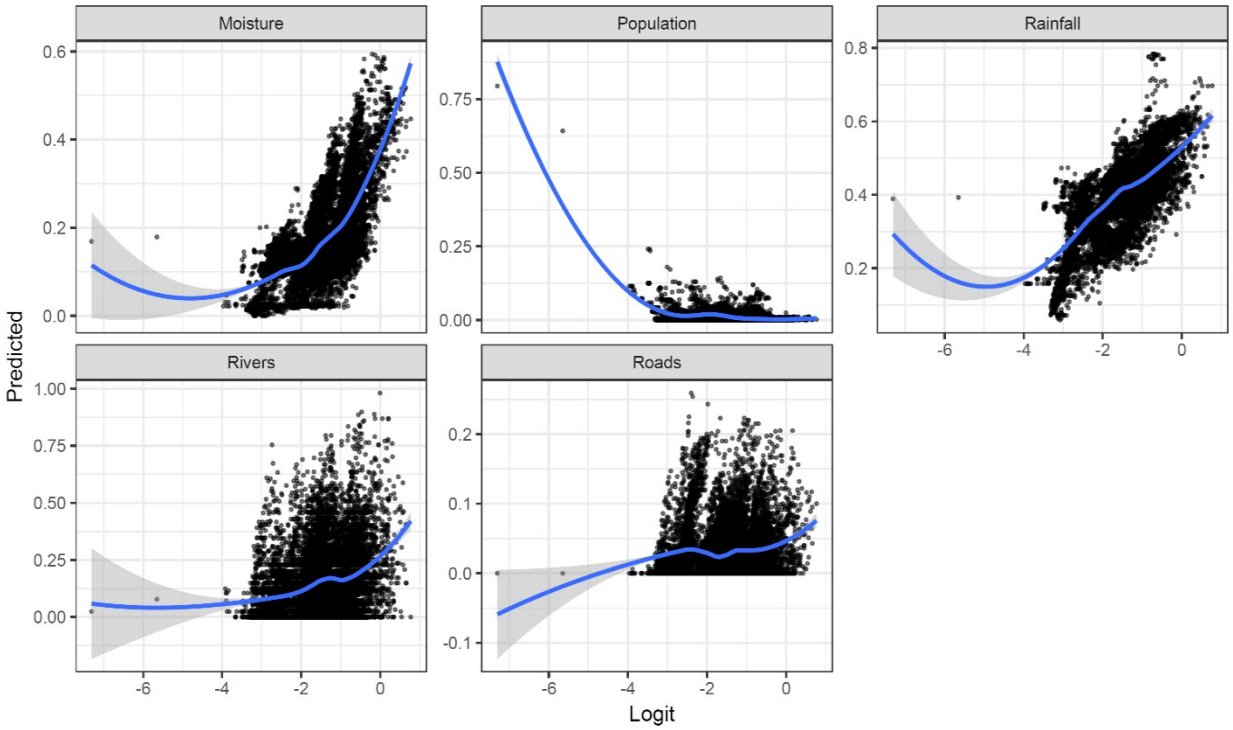
Grassland



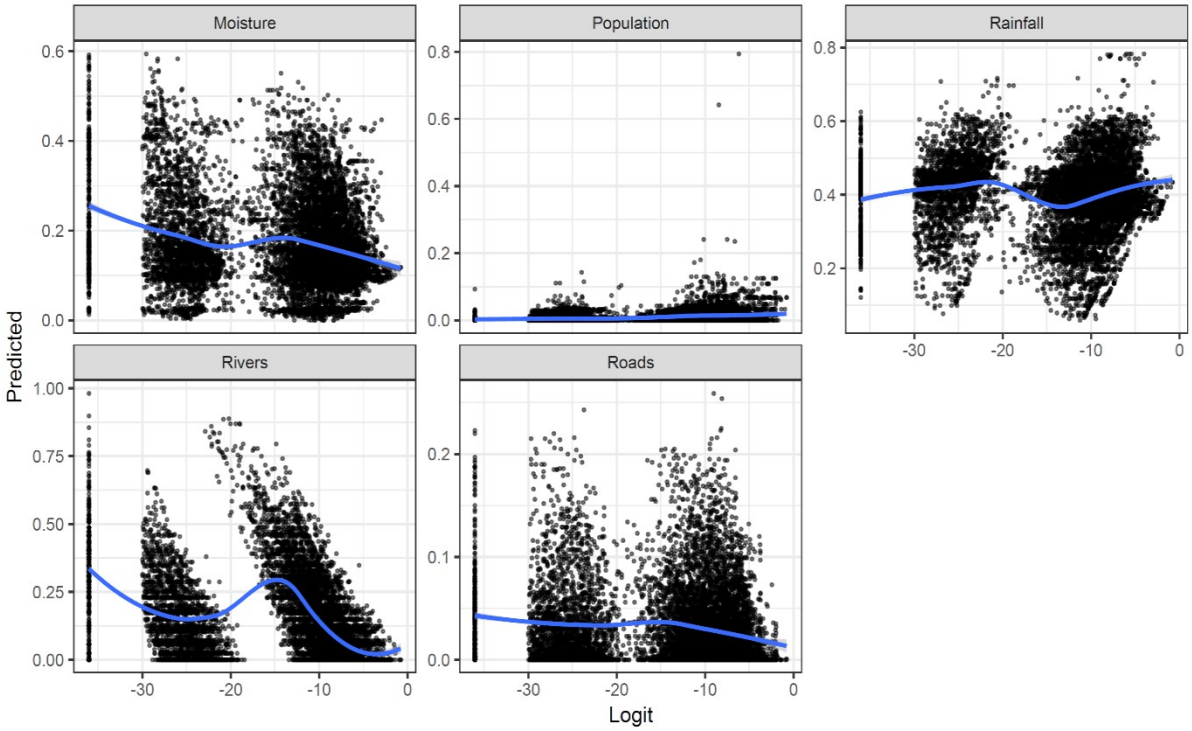
Shrubland



Woodland



Wetland and Swamps


Moisture
Population
Rainfall
Rivers
Roads
Predicted
Logit
0.6
0.4
0.2
0.0
0.8
0.6
0.4
0.2
0.0
0.8
0.6
0.4
0.2
1.00
0.75
0.50
0.25
0.00
0.2
0.1
0.0
-30
-20
-10
0

CHAPTER FOUR

Spatio-temporal changes in wildlife habitat quality in the Greater Serengeti Ecosystem

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Article

Spatio-Temporal Changes in Wildlife Habitat Quality in the Greater Serengeti Ecosystem

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Received: 12 February 2020; Accepted: 17 March 2020; Published: 20 March 2020

Abstract: Understanding habitat quality and its dynamics is imperative for maintaining healthy wildlife populations and ecosystems. We mapped and evaluated changes in habitat quality (1975–2015) in the Greater Serengeti Ecosystem of northern Tanzania using the Integrated Valuation of Environmental Services and Tradeoffs (InVEST) model. This is the first habitat quality assessment of its kind for this ecosystem. We characterized changes in habitat quality in the ecosystem and in a 30 kilometer buffer area. Four habitat quality classes (poor, low, medium and high) were identified and their coverage quantified. Overall (1975–2015), habitat quality declined over time but at rates that were higher for habitats with lower protection level or lower initial quality. As a result, habitat quality deteriorated the most in the unprotected and human-dominated buffer area surrounding the ecosystem, at intermediate rates in the less heavily protected Wildlife Management Areas, Game Controlled Areas, Game Reserves and the Ngorongoro Conservation Area and the least in the most heavily protected Serengeti National Park. The deterioration in habitat quality over time was attributed primarily to anthropogenic activities and major land use policy changes. Effective implementation of land use plans, robust and far-sighted institutional arrangements, adaptive legal and policy instruments are essential to sustaining high habitat quality in contexts of rapid human population growth.

Keywords: Serengeti ecosystem; threats; InVEST model; protected areas; savannah; quality; buffer

1. Introduction

Quality wildlife habitats, the areas that provide shelter and forage and support survival of wildlife species, are declining worldwide [1]. Habitat quality is the ability of the land to provide essential habitat components for a particular species, and is among the key ecological attributes that determine wildlife population status in landscape [2]. The quality of a habitat influences wildlife

The aim of this study was to map and quantify changes in wildlife habitat quality in space and time in the Greater Serengeti Ecosystem (GSE) using the Integrated Valuation of Environmental Services and Tradeoffs (InVEST) model. Understanding spatial and temporal dynamics of habitat quality is fundamental to effective management of ecosystems experiencing changing land use and cover. More precisely, we evaluated changes in habitat quality at three points in time (1975, 1995, and 2015) to provide a quantitative basis for improving wildlife habitat management and enhancing natural ecological processes in the GSE and possibly elsewhere.

2. Materials and Methods

2.1. Study Area

The Greater Serengeti Ecosystem (GSE) is located in northern Tanzania, within the Greater Serengeti-Mara Ecosystem (GMSE) that is defined by movements of migratory wildebeest (*Connochaetes taurinus*) and the common zebra (*Equus quagga buchellii*) between the Serengeti National Park in Tanzania and the Maasai Mara National Reserve in Kenya. The Serengeti ecosystem (1° 24' 57.16" S to 3° 45' 35.31" S and 33° 52' 0.15" E to 35° 59' 41.53" E) covers 33,106 km^2. It is world-famous for its wildebeest, zebra and Thomson's gazelle (*Eudorcas thomsonii*) migration, the largest terrestrial migration of large herbivores remaining on Earth [36–38]. This migration involves about 1.3 million wildebeest, 0.2 million zebra and 0.4 million Thomson's gazelle [39]. The migration is mostly confined within protected areas, notably the Serengeti National Park, Ngorongoro Conservation Area, Maswa, Grumeti and Ikorongo Game Reserves and Ikoma Wildlife Management Area in Tanzania and the Masai Mara National Reserve in Kenya (Figure 1).

The ecosystem has diverse vegetation cover, land cover, uses, and management types, including protected areas, traditional pastoral, agro-pastoral or cultivated areas (large and small-scale farms), forests, and wildlife conservation areas [39]. Anthropogenic activities strongly influence ecological processes and ecosystem structure within the protected areas. As a result, land use and cover changes in the buffer area exert substantial impacts on the flora and fauna inside the protected areas [23]. We defined a 30 km buffer (23,487 km^2) around the protected area to analyze edge effects linked to surrounding anthropogenic activities. The whole study area therefore covers about 56,593 km^2 (Figure 1).

Broadly, the study area has nine administrative units with different management regimes, ranging from total exclusion of human activities in National Parks and Game Reserves (IUCN category II), multiple land use with nationally controlled human activities, such as in the Ngorongoro Conservation Area where livestock grazing and human settlement are allowed (IUCN category V and VI) and locally controlled use of resources (Wildlife Management Areas) and free use zones (the 30 km buffer area) in which livestock grazing, agriculture, human settlements, and other land uses are not restricted (Figure 1). The Ngorongoro Conservation Area was declared a UNESCO Man and Biosphere Reserve in 1971 and a World Heritage Site in 1979 whereas the Serengeti National Park was declared a UNESCO World Heritage Site in 1981.

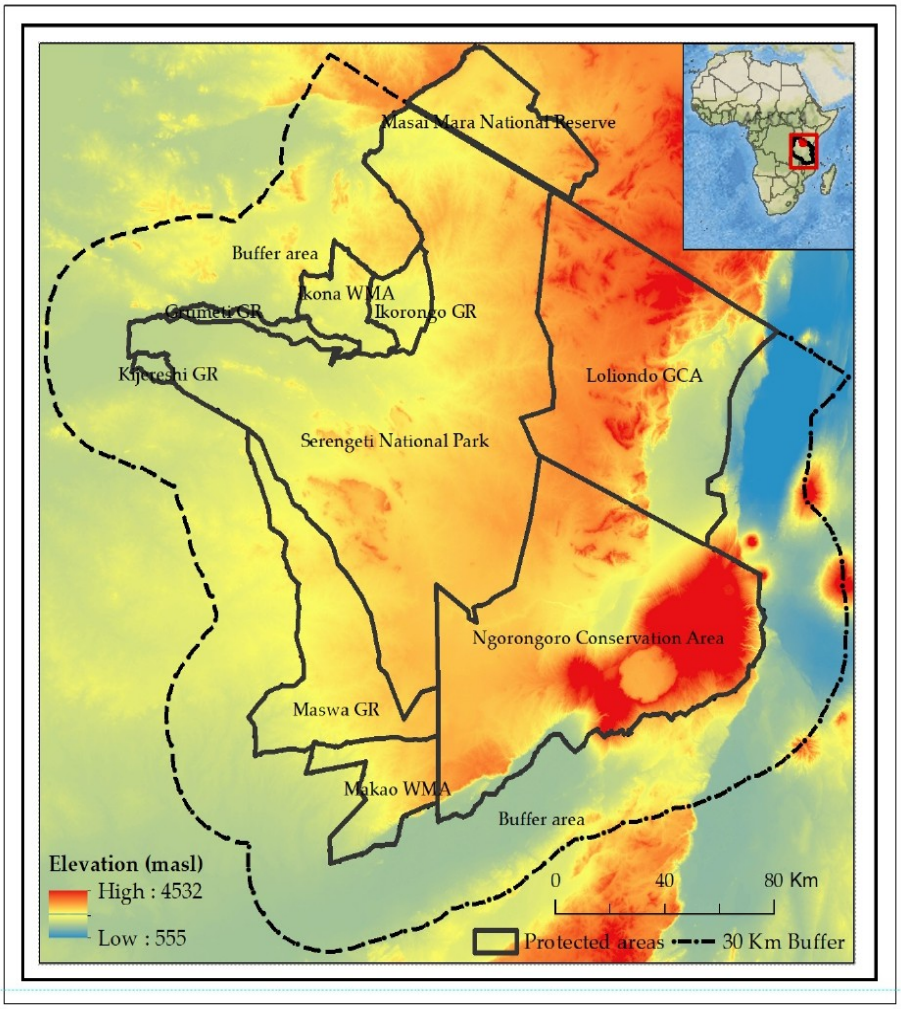

Figure 1. Map of the study area (the red dot in the small inset shows the location of the study area in East Africa). The red box shows the location of Tanzania and southern Kenya in Africa.

2.2. Modelling Habitat Quality Using the InVEST Model

We used the Integrated Valuation of Environmental Services and Tradeoffs (InVEST) model to evaluate changes in habitat quality in the ecosystem. InVEST is a spatially-explicit geographic information system (GIS) based tool for evaluating habitat condition in terrestrial or aquatic ecosystems based on data from land use and land cover (LULC) maps and biophysical factors. The InVEST model assumes that high-quality habitat supports high biodiversity as opposed to areas with low or poor-quality habitats [40–42]. The InVEST model evaluates habitat condition based on (i) relative impacts of each threat, (ii) habitat sensitivity to the threat, (iii) the distance between the threat and the habitat, and (iv) the degree to which the land is legally protected [43].

2.3. Data Requirements and Sources

The InVEST model uses maps as information sources and produces maps as outputs. Table 1 shows the model's data requirements. These are described in detail in Sections 2.3.1 to 2.3.5 below.

Table 1. Input data for the Integrated Valuation of Environmental Services and Tradeoffs (InVEST) habitat quality model.

Data type	Data description
1. Land use and cover map (LULC)	Land use and cover map for the study ecosystem.
2. Threat data	Raster data with the distribution and intensity of each habitat threat.
3. Legal accessibility	Data showing the legally recognized level of protection for each habitat.
4. The sensitivity of habitat types to each habitat threat	LULC table with habitat types and their sensitivities on a scale from 0-1, with 1 denoting the highest possible level of habitat sensitivity [44,45].
5. Half saturation constant	Determined half-saturation value at 0.5 [4].

2.3.1. Land Use and Land Cover (LULC) Data

Landsat Multispectral Scanner (MSS), Thematic Mapper (TM) and Landsat-8 (Operational Land Imagery) time series images for the years 1975, 1995 and 2015 corresponding to paths 168, 169 and 170 and rows 61, 62 and 63 of the Landsat Worldwide Reference System (WRS) were downloaded from the Earth Explorer (https://earthexplorer.usgs.gov/) web platform. The potential effects on the images of seasonal differences in vegetation phenology between the three periods were minimized by downloading image scenes captured on similar satellite overpass times or seasons, particularly dry periods spanning January-February, July-August and October-November. Dry season images are preferable to wet season images because they have relatively lower cloud cover.

Approximately 1918 training and validation samples were collected at randomly selected sampling points in the GSE between 2015 and 2016. For historical images, the Herlocker (1976) and Reed et al. [46] were used to obtain the training and testing sets for the 1975 and 1995 imageries, respectively. The images were pre-processed and classified using the collected samples through the random forest (RF) classification algorithm [47]. Eight land cover classes, including woodland, shrubland, grassland, wetland and swamps, water bodies, settlement, agriculture, and bareland, were distinguished. The classifier achieved accuracies of 88.4%, 90.6%, and 93.4% with Kappa Indices of Agreement of 0.86, 0.87, and 0.91 for 1975, 1995, and 2015 thematic maps, respectively, which are adequate for most practical applications. Most of the natural vegetation constitutes key wildlife habitats [48]. Furthermore, the mapped LULC are known to support a wide array of wildlife species. Woodland and mosaic (shrubland, grassland and riverine) habitats were considered key habitats for various wildlife species [49], and thus were assigned the highest suitability index. For aquatic habitats, such as wetlands and swamps, suitability increases with increasing size. Anthropogenic land cover types such as bareland, settlements and agricultural areas, roads, and other features were considered unsuitable for wildlife. We assigned either 0 or 1 (binary index) to each LULC class, with 0 indicating unsuitable and 1 denoting highly suitable habitats.

2.3.2. Habitat Threat Data

We identified and selected seven anthropogenic threats to habitats (Table 2) in the protected area and human-dominated buffer in the study ecosystem. The selected four threat factors are roads, rivers, major urban centers [2,50], and cultivated plus built-up areas. Roads (paved and unpaved) can threaten habitat integrity by restricting wildlife movements between habitat patches [51–53], enhancing accessibility of protected areas (e.g., for poachers), providing pathways for invasive species [54], and accelerating habitat loss and fragmentation and hence biodiversity loss [55]. Highly utilized rivers and other water sources can threaten habitats in the ecosystem by attracting human activities, which, in turn, depress habitat quality and threaten wildlife species [50] and rank among the leading causes of contemporary global biodiversity loss [3,56]. The habitat threat data were

obtained from various sources. Data on roads and rivers for 1975, 1995, and 2015 were obtained from the Tanzania National Bureau of Statistics (TNBS) database (https://www.nbs.go.tz/), DIVA-GIS (http://www.diva-gis.org/), Africover, AfricanBioServices project (https://africanbioservices.eu/), digitization of standard topo sheets (1:50,000), especially for 1975, and fieldwork (2016-2018). Major urban centers, cultivated and built-up areas were also considered as habitat threats as they degrade natural habitats [57]. Data on cultivated and built-up areas were extracted from LULC maps for 1975, 1995, and 2015.

The threat factors summarized in Table 2 show habitat-specific threats, impact distance (at which each threat would affect the habitat) and scale (ranging from 0 to 1), which quantifies the impact of each threat factor on habitat quality relative to other threats in our strata which comprises wildlife management areas, game controlled areas, game reserves, conservation areas, and national parks.

Table 2. Ecological habitat threat factors.

Threat factor	Maximum Distance (Km)	Weight	Decay
Population	25	1	Exponential
Agriculture	15	0.8	Exponential
Paved road	20	0.5	Linear
Unpaved road	27	0.6	Linear
Permanent river	15	0.5	Exponential
Seasonal river	10	0.3	Exponential
Livestock distribution	8	0.4	Exponential

Note: The maximum distances are based on values modified from [5], [52,53], [58-60].

2.3.3. Legal Accessibility

Legal accessibility is the degree to which land is legally protected against anthropogenic activities. Legal accessibility is important in assessing habitat quality of a landscape [59]. The InVEST model assumes that the legal accessibility of land is important in minimizing threats as it is typically accompanied with administrative policies or management plans and that protected areas are less impacted than non-legally protected areas [44]. We obtained spatial data on protected areas from the Tanzania Wildlife Research Institute (TAWIRI) and TNBS [27]. Based on the status of their protection, we determined the value of protection status as indicated in Table 3. Wildlife management areas (WMAs) were excluded from the 1975 and 1995 analyses because they came into existence in 2007. Kijereshi was a WMA in 1994 before it was upgraded to a game reserve in 1996.

Table 3. Weights assigned to legal accessibility.

Category	Weight
Buffer	1
Game Controlled Area	0.50
Wildlife Management Area	0.40
Conservation Area	0.35
Game Reserve	0.25
National Park	0.15

2.3.4. Habitat Sensitivity

Each habitat type is assumed to be sensitive to a particular threat and not all habitat threats have equal impacts on all habitat types. We converted the threats data (Section 2.3.2) from a vector to a raster data format using ArcGIS 10.5 (ESRI 2019). We normalized and ranked threat maps on a threat intensity scale ranging from 0 to 1, where 0 represents the least and 1 the highest threat level. For example, a given habitat or LULC would score 0 if it is not and 1 if it is sensitive to a specific threat factor, respectively [44].

Information on how habitats in the study area respond to threat factors was either unavailable or only partially available. Therefore, we sought expert knowledge of likely habitat responses to the threat factors from ecologists who had worked in the ecosystem. Based on this, we generated a sensitivity table (Table 4) showing the sensitivity of each LULC class to specific habitat (Section 2.3.1) threat factors. The impact of a threat factor on a given habitat was determined by several factors, including the distance from the habitat type to the threat; the closer a threat is to a habitat, the higher its expected impact [2,44].

Table 4. Habitat suitability and sensitivity of each land-use type to ecological threat factors.

Land use type	Habitat	Sensitivity to						
		Agric	Pvdrd	Unpvrd	Prvs	Srvs	Popn	Lvst
Bareland	0	0	0	0	0	0	0	0
Agriculture	0	0	0.1	0.2	0.7	0.4	0.5	0.2
Settlement	0	0.8	0.2	0.5	0.6	0.3	0.6	0.3
Water bodies	1	0.5	0.2	0.2	0	0	0.8	0.2
Grassland	1	0.9	0.5	0.7	0.6	0.4	0.7	0.8
Shrubland	0.6	0.5	0.2	0.3	0.3	0.2	0.6	0.3
Woodland	0.8	0.8	0.4	0.6	0.5	0.3	0.7	0.2
Wetland and Swamps	0.6	0.6	0.5	0.5	0.4	0.2	0.7	0.6

Agric = agriculture, Pvdrd = paved road, Unpvrd = unpaved road, Prvs = permanent river, Srvs = seasonal river, Popn = population, and Lvst = livestock.

We resampled the LULC and other data layers to 500 m × 500 m resolution. We chose this resolution based on compound analysis of the study area size and computational feasibility. The study area size of 56,600 km^2 yielded approximately 5.05 billion cells at a 30 m × 30 m resolution, which was computationally too expensive to process. We reduced computational complexity by resampling the pixels to 2.02 billion cells at a 500 m × 500 m resolution for further analyses.

The resampled datasets were projected to the Universe Transverse Mercator (UTM) Zone 36 South using the World Geodetic System (WGS) 1984. In addition, all raster datasets were re-sampled to a common 500 m grid for ease of processing.

2.3.5. Half-Saturation Constant

Half or semi-saturation constant k is used by the InVEST model to convert the habitat degradation score into habitat quality score. The value of k is normally set equal to half (0.5) of the grid cell size [42,48].

2.4. Data Analysis

2.4.1. Modelling Habitat Quality Using the InVEST Model

Habitat quality is the ability of the environment to provide essential conditions required for sustenance or persistence of an individual organism [61] and hence is a major determinant of landscape biodiversity. Larger habitats support more biodiversity and vice-versa. Furthermore, the more degraded an area is, the lower is the biodiversity value it can hold [2]. Habitat quality is assumed to depend upon the relative impact of threats, the sensitivity of habitats to the threats, the distance between a habitat and sources of the threats, and location of protected areas. The model uses an exponential decay function to describe the impact i_{rxy} of threat r from a grid cell y on a habitat in grid cell x, located at a linear distance d_{xy} from a threat source [48]:

$$i_{rxy} = \exp\left[-\left(\frac{2.99}{d_{rmax}}\right)d_{xy}\right] \quad (1)$$

The total threat level D_{xj} in a grid cell x with LULC j is then calculated as:

$$D_{xj} = \sum_{1}^{R} \sum_{1}^{Y} \left(\frac{W_r}{\sum_{1}^{R} W_r} \right) r_y \, i_{rxy} \beta_x S_{jr} \quad (2)$$

where R is the number of all the ecological threat factors, D_{xj} is the set of all grid cells on raster map r, W_r is the threat weight that relates the destructiveness of a degradation source to all habitats, r_y indexes all grid cells in raster map r, i_{rxy} is a function describing the exponential decay in habitat quality as a function of distance from ecological threat factors, β_x is the level of accessibility to grid cell x, with 1 indicating complete accessibility and 0 complete inaccessibility, and S_{jr} is the sensitivity of land use type j (habitat type) to the ecological threat factor r.

Finally, the habitat quality Q_{xj} of LULC j is calculated based on the habitat suitability of LULC j using [48,62]:

$$Q_{xj} = H_j \times \left[1 - \left(\frac{D_{xj}^z}{D_{xj}^z + k^z} \right) \right] \quad (3)$$

where $H_j$is a habitat quality score ranging from 0 to 1, with non-habitat land use and cover types given a score of 0 and perfect habitat classes a score of 1, D_{xj} is the total threat level in grid cell x with land use and cover type j, k is the half-saturation constant, and z is a constant.

Using the natural breaks (Jenks) classification method, we sliced the resultant habitat quality score map into four habitat class categories: poor, low, medium, and high. Natural breaks is a standard classification method that arranges dataset values into different internally homogenous classes [63].

3. Results

3.1. Habitat Quality (1975–2015)

The ecosystem was dominated by low-quality followed by high-quality habitats in 1975 (Figures 2 and 3). In the subsequent 21 years (1975–1995), the poor-quality habitats increased four-fold, the low-quality habitats reduced by a half, and the medium-quality habitats doubled in size, but the high-quality habitats hardly changed relative to 1975 (Figures 2 and 3). In the 21 years leading to 2015 (1995–2015) the poor-quality habitats doubled, the low-quality habitats reduced to 0.59 times, and the medium-and high-quality habitats reduced to 0.62 times, whereas the high-quality habitat increased 1.3 times relative to 1995 (Figures 2 and 3). Overall, most of the poor-quality habitats in 1975 became either poor- or medium-quality habitats during 1975-1995 but most low-quality habitats in 1995 were reduced to poor-quality habitats during 1995-2015. Over the entire study period (1975–2015), a large part of the low-quality habitats was degraded to poor-quality habitats in the ecosystem and its surrounding buffer zone (Figure 3).

At the stratum level in 1975, the high-quality habitats were the most prevalent in the WMAs and the national park (NP), which also had large coverage of the low-quality habitats, while low-quality habitats dominated the buffer zone (BF), conservation area (CA) and the game reserves (GR) in 1975 (Figure 4). In 1995, poor- and low-quality habitats characterized the buffer zone, medium-quality habitats dominated the GCA, medium- and high-quality habitats dominated the CA, WMAs and the national park, and low- and medium-quality habitats predominated in the GRs (Figure 4). In 2015, poor-quality habitats dominated the buffer zone, medium-quality habitats dominated the GCA and WMAs, high-quality habitats dominated the CA and the national park, and low-quality habitats dominated the GRs (Figure 4). Across 1975–2015, habitat quality declined most markedly in the buffer zone. Generally, areas with greater protection had relatively large proportions of medium and high-quality habitats.

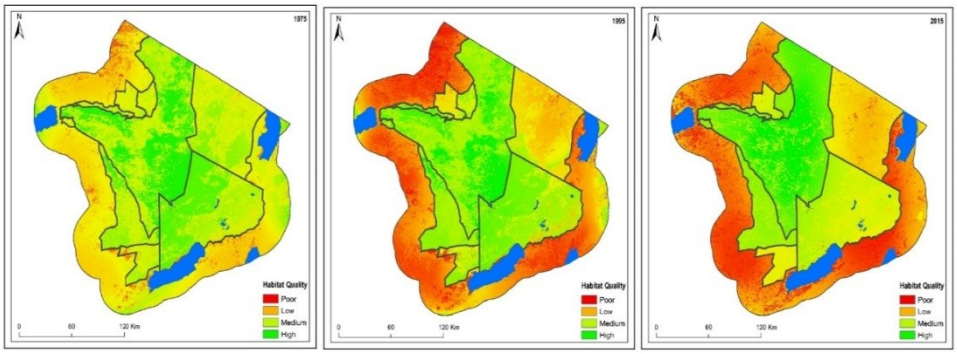

Figure 2. The spatial distribution of the four habitat quality classes in the ecosystem and the surrounding buffer zone in 1975, 1995, and 2015.

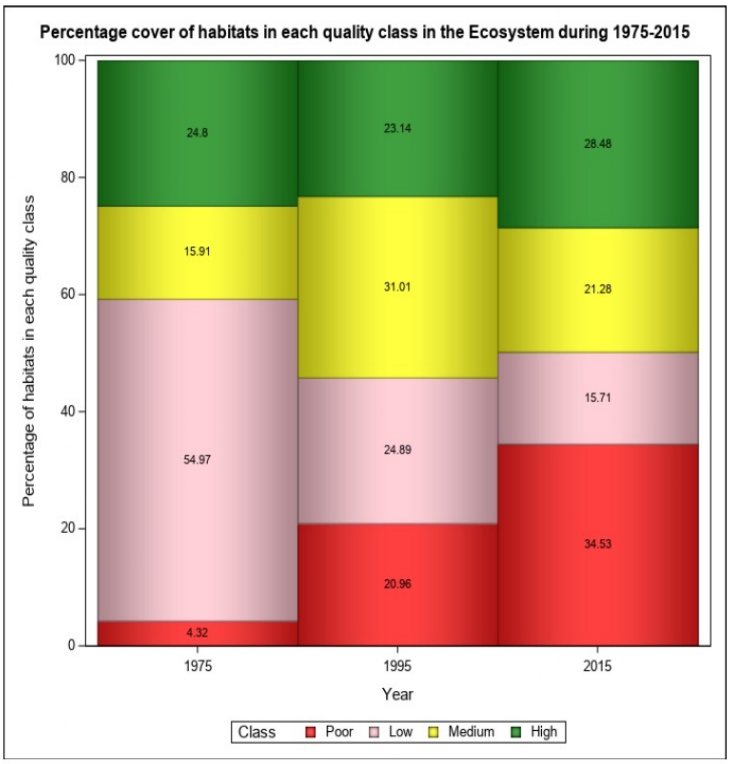

Figure 3. Cumulative percentage cover of habitats in each of the four quality classes in the ecosystem and surrounding 30 km buffer zone in 1975, 1995, and 2015.

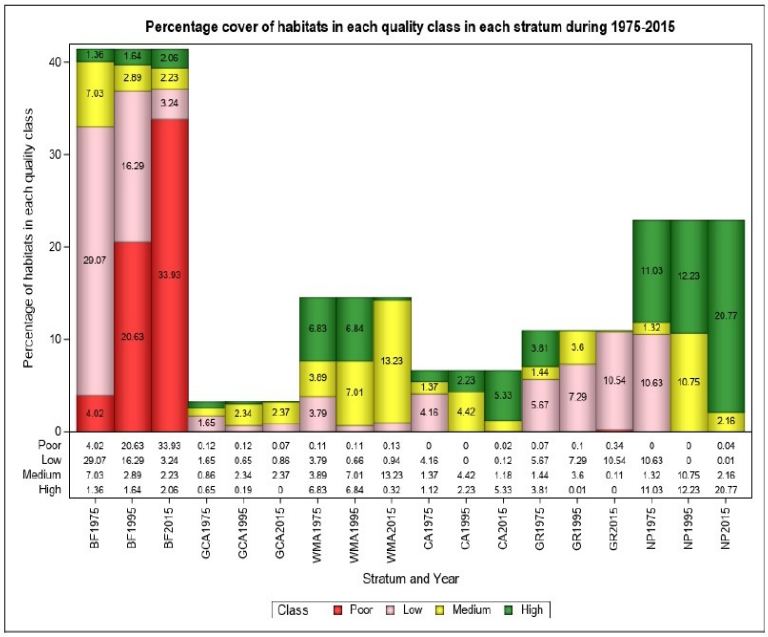

Figure 4. Cumulative percentage cover of habitats in each of the four quality classes for each stratum in the ecosystem and surrounding 30 km buffer zone in 1975, 1995, and 2015. BF = buffer zone, GCA

= game controlled area, WMA = wildlife management areas, CA = conservation area, GR = game reserves, NP = national park.

3.2. Changes in Habitat Quality During 1975–1995, 1995–2015, 1975–2015

At the level of the ecosystem and its surrounding buffer area, poor- and medium-quality habitats increased whereas low- and high-quality habitats decreased during 1975–1995. During 1995–2015, both poor- and high-quality habitats increased whereas low- and medium-quality habitats declined. Across the 41-year study period (1975–2015), poor-quality habitats increased 2.5-fold, medium- and high-quality habitats increased slightly, and low-quality habitats declined markedly in the ecosystem and its adjacent buffer area (Figure 5). Most of the decline in low-quality habitats during 1975–2015 occurred during 1975–1995 (Figure 5).

Across the individual strata, poor-quality habitats increased most remarkably in the buffer area throughout 1975–2015 (Figure 6). In the buffer area, poor-quality habitats increased remarkably during 1975–2015 but declined slightly in 2015 relative to 1995. Low- and medium-quality habitats declined in the buffer area throughout 1975–2015 (Figure 6). In the GCA, only minor changes occurred in habitat quality during 1975–2015. In the WMAs, medium-quality habitats expanded whereas low- and high-quality habitats contracted throughout 1975–2015 (Figure 6).

In the CA, high-quality habitats increased four-fold whereas low- and medium-quality habitats declined during 1975–2015. In the GRs, low-quality habitats increased whereas high-quality habitats declined during 1975–1995. Poor- and low-quality habitats expanded whereas medium- and high-quality habitats reduced during 1975–2015 (Figure 6).

In the Serengeti National Park, the high-quality habitats increased two-fold whereas low- and medium-quality habitats declined markedly during 1975–2015 (Figure 6).

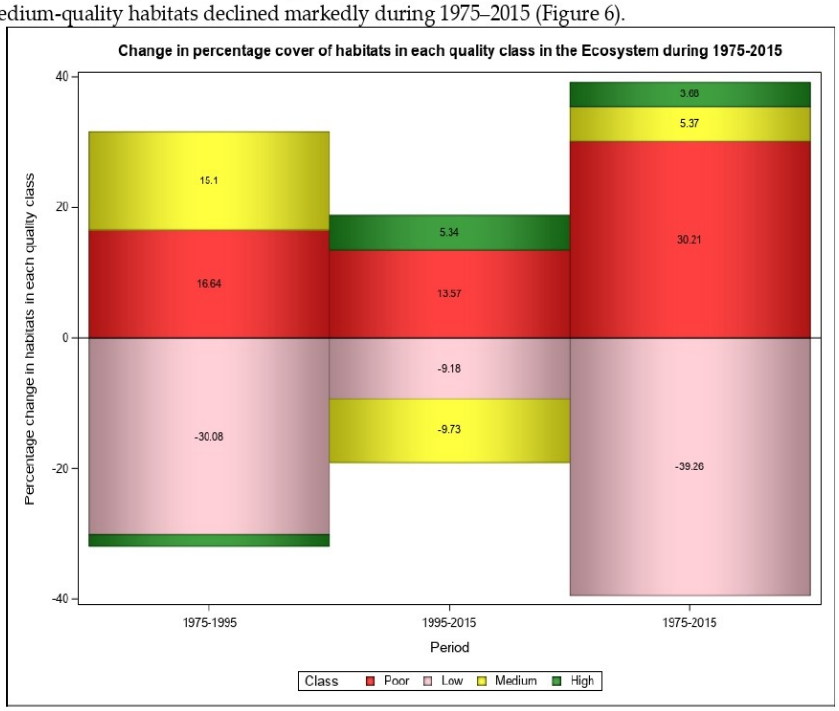

Figure 5. Changes in percentage cover of habitats in each of the four quality classes in the entire ecosystem and surrounding 30 km buffer zone during 1975–1995, 1995–2015, and 1975–2015. BF = buffer zone, GCA = game controlled area, WMA = wildlife management areas, CA = conservation area, GR = game reserves, NP = national park.

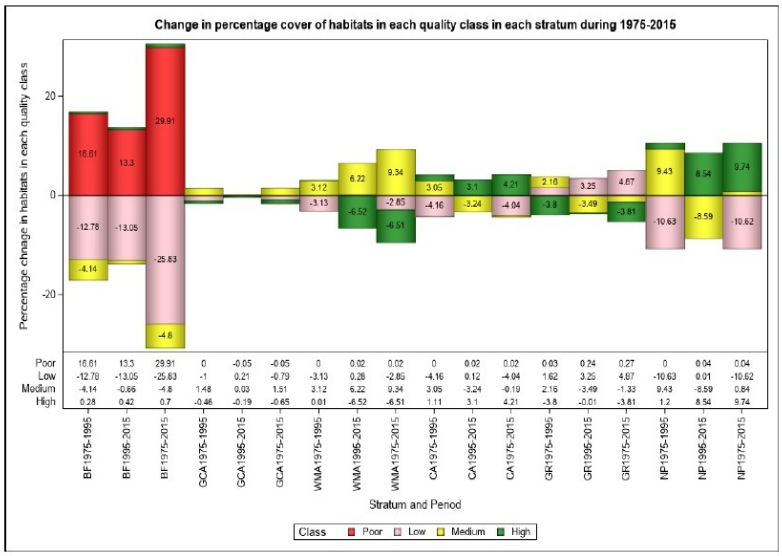

Figure 6. Changes in percentage cover of habitats in each of the four quality classes for each stratum in the ecosystem and surrounding 30 km buffer zone during 1975–1995, 1995–2015, and 1975–2015.

3.3. Transformations of Habitat Quality Classes (1975–1995, 1995–2015 and 1975–2015)

During 1975–1995 the ecosystem and its buffer area experienced high transformation of the low-quality to poor- and medium-quality habitats (Figure 7), whereas the medium-quality habitats were partially transformed to low-quality habitats. The high-quality habitats were partly transformed to the medium class. However, during 1995–2015, more low-quality habitats were transformed to the poor-quality class, and much of the medium-quality to high-quality habitats (Figure 7). Overall (1975–2015), most of the low-quality habitats were transformed to the other quality classes, predominantly the poor-quality class (Figure 7). Generally, the high-quality habitats decreased slightly because of contributions to the other classes.

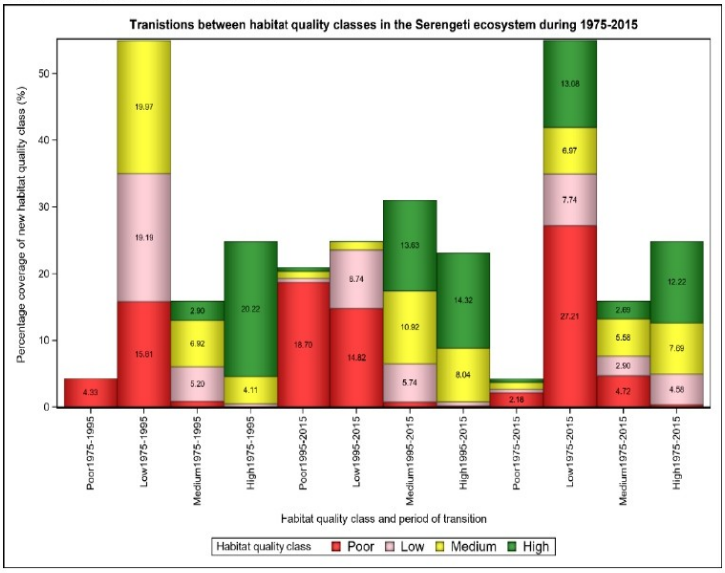

Figure 7. Transitions in habitat quality classes in the Greater Serengeti Ecosystem (GSE) during 1975–2015.

4. Discussion

We found substantial changes in the overall habitat quality in the GSE and its surrounding buffer area during the 41-year study period (1975–2015). This was manifested in an overall eight-fold increase in poor-quality habitats but only 1.2-fold increase in high-quality habitats. Moreover, low-quality habitats declined three-fold whereas the medium-quality habitats first increased two-fold and then declined by a quarter. The greatest overall decline in habitat quality occurred in the buffer area followed by the protected areas with low protection status (GCA, WMA, GRs). The Ngorongoro Conservation Area (CA) with a medium conservation status had an overall three-fold increase in the medium quality habitats whereas the most strictly protected Serengeti National Park had an overall eight-fold increase in the high-quality habitats during the 41-year study period (1975–2015). We summarize the detailed patterns of changes in habitat quality for the GSE and its surrounding buffer area (30m) next.

4.1. Habitat Quality (1975–2015)

The high proportion of low-quality habitats in 1975 can mainly be attributed to the Arusha Declaration of 1967 and Iringa Declaration (*Siasa ni Kilimo*, i.e., Politics is Agriculture) of 1972 both of which promoted agricultural production as the economic backbone of Tanzania [64]. Furthermore, the villagization policy initiated in 1974 encouraged local communities to move and establish new settlements in collective villages, called "Ujamaa Villages", to enhance social services and common use of tools of agricultural production, such as tractors [65–67].

The policy was implemented through a large-scale resettlement program across mainland Tanzania, which had significant environmental implications [65,66]. More lands were opened up for establishment of new farms for various cash crops (cotton, sisal, and coffee), and food crops (paddy rice, wheat, and maize) depending on the local agro-climatic conditions. In consequence, the villagization policy led to significant changes in land use, soil erosion and land degradation in the country [66]. In 2012, changes in land use and land cover around the GSE were probably responsible for changes in habitat quality [5].

The improvements in habitat quality through 1975–1995 can be attributed to various conservation and environmental management measures. For example, farmers were encouraged by the Government of Tanzania to adopt and practice modern agricultural techniques with low environmental impacts [65]. Nevertheless, low agricultural production due largely to challenges associated with implementing the policy, including distance to the initial farms and climatic conditions, resulted in only slight improvements to habitats quality [68–70]. Besides, areas such as Kijereshi, Ikorongo, and Grumeti that were initially open areas (OAs) were upgraded to game controlled areas (GCA) [27]. Despite the relatively high proportion of low-quality habitats by 2015, various conservation efforts plus strengthened legal and institutional frameworks contributed to increased coverage of the medium- and high-quality habitats. These included upgrading of the GCAs to game reserves and establishment of wildlife management areas (Ikona and Makao WMAs). By 1975, the only protected areas in the ecosystem were the Serengeti NP, the Maswa GR, and the Loliondo GCA as the other areas were under a non-protected status.

Between 1975 and 1995, three game reserves (Kijereshi, Ikorongo, and Grumeti) were established leading to restricted access to livestock grazing and agriculture [27]. This is consistent with the increase in habitat quality with upgrading of the conservation status of protected areas in the ecosystem. As a result, buffer areas with the weakest protection status, followed by GCA, were dominated by poor- and low-quality habitats. Strictly protected areas have stronger protection mechanisms against destructive anthropogenic activities within their boundaries [71,72] and serve as cushions against deleterious anthropogenic activities around their borders. As national parks and game reserves exclude most forms of human activities [27], habitat quality and intactness in such protected areas are expected to be high. Yet, our findings and those of previous studies suggest that human activities are adversely impacting wildlife habitats in the ecosystem [8,73], reducing the effective size of the protected areas [74], wildlife habitats, and their ecological productivity [74,75]. These adverse effects are more evident in the Ngorongoro conservation area that allows settlement

Acknowledgments: We thank the Tanzania Wildlife Research Institute (TAWIRI) for granting study leave and permission to HK to undertake research work, and Tanzania National Park (TANAPA), Ngorongoro Conservation Area (NCAA), Tanzania Wildlife Management Authority (TAWA), and Wildlife Management Area Authorities (WMAs) for granting access to the areas under their jurisdiction for data collection. We also thank Itaely Nassary, Noel Alfred and Mawazo Nzunda for safe driving during data collection and Dr. Devolent Mtui for assisting with data collection.

Conflicts of Interest: The authors declare no conflict of interest.

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CHAPTER FIVE

Dynamics of herbivore distribution and habitat selection in the Greater Serengeti Ecosystem, Tanzania

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Submitted to the Journal of *Global Conservation and Ecology*

Dynamics of herbivore distribution and habitat selection in the Greater Serengeti Ecosystem, Tanzania

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Abstract

Understanding herbivore's spatio-temporal distribution and habitat selection is key in ecology and management of species in protected landscapes. This study was conducted in the Great Serengeti Ecosystem, Tanzania, with an overanching objective of determining the dynamics of herbivore's distribution and habitat selection of seven medium to large-sized herbivores (impala, grant's gazelles, wildebeest, zebra, buffalo, giraffe, and elephant). Herbivores aerial survey data and remote-sensing-based habitat quality maps covering two study periods (1995 and 2015) were used to assess habitat selection. Herbivores were aggregated according to their feeding guilds: browsers (grant's gazelles and giraffe), grazers (wildebeest, zebra and buffalo), and mixed feeder (impala and elephant), and habitats characterized into low, medium, and high qualities, derived from quality habitat maps generated from Integrated Valuation of Environmental Services and Tradeoffs (InVEST) model. We utilized the kernel density to map species distribution range. Bonferroni confidence interval and Chi-square goodness-of-fit test were used to assess habitat selection. We observed a significant clustered distribution pattern for all herbivores across space and time. We recorded high mean species observations in Serengeti National Park (NP), followed by Game Reserves (GRs) and least in Wildlife Management Areas (WMAs). The herbivore's mean sightings were higher for 2015 than for 1995. Herbivores distribution ranges contracted for browsers and expanded for grazers and mixed feeders for 2015 in comparison to 1995. Our data suggest that herbivores significantly avoided low-quality habitats and favored high-quality habitats across space and time. Information on specie's distribution, habitat selection and use are useful in determining high priority areas for effective conservation practices. Our study recommends (i) more protection efforts and haltering habitats degradations, (ii) integrated efforts to control habitat degradations towards enhancement of quality habitat conditions, (iii) strengthen conservation and management practices, including protection, in less protected areas (PAs) such as WMAs and GCA where we recorded low mean abundance and declined distribution range of the studied animals, (iv) a temporal study covering both wet and dry seasons to examine species guild's spatio-temporal changes, (v) management and conservation strategy of wild herbivores needs to take into consideration habitat selection by each species.

Keywords: Protected area, ecosystem, habitat quality, InVEST model, Aerial census data

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1.0 INTRODUCTION

Understanding herbivore's spatio-temporal distribution and habitat selection is important in the ecology and management of species in protected landscapes. Herbivores' spatial distribution is synergistically influenced by several biotic and abiotic factors (Lewis *et al.* 2017). These are the welfare factors in wildlife habitats including resources such as food, water, shelter, useable space and cover that are present in an area allowing species occupancy, survival, and reproduction (Hall *et al.* 1997). Abiotic factors such as temperature, precipitation, and soil types and moisture are increasingly known to influence the distribution of wild herbivores in terrestrial landscapes (Guisan and Thuiller 2005, Meier *et al.* 2010, Van der Putten *et al.* 2010).

Wildlife habitats are the ecologically important areas that offer a range of structural features and interspersion that influence overall specie's quality (Morrison 2002, Forbey *et al.* 2017). The herbivore distribution pattern can be described as random, uniform, or clustered. A random distribution pattern occurs when environmental conditions and resources are consistent while an even distribution occurs when the distance between neighboring individuals is maximized (Katili *et al.* 2017). On the other hand, a clustered distribution is when animals exhibit a clumped distribution (Katili *et al.* 2017). The distribution patterns are mainly attributed to either the social behavior of the animals or resources availability (Krausman 1999, Katili *et al.* 2017). However, distribution patterns of herbivores is also a function of habitats selection and use by the animals.

Habitat selection is a specie's behavioral process to choose habitats based on their availability, quality and quantity (Hutto 1985, Krausman 1999, Lele *et al.* 2013) whereas habitat use is the way individuals use biophysical resources across habitat types (Litvaitis *et al.* 1994, Krausman 1999). Wildlife are habitat specific and use the selected habitat with respect to its availability and quality. Habitat quality is defined as the ability of an environment to supply the necessary requirements for specie's reproduction, survival and persistence (Hall *et al.* 1997, Johnson and Arcata 2005, Johnson 2007). Highly selected habitats are those used more than would be expected (Aebischer *et al.* 1993). For example, some species prefer large tracts of similar habitats, i.e. low interspersion, while others require multiple habitat types in proximity to one another, i.e. high interspersion (DeLong and Brittingham 1997). Such variations in species habitat selection are based on the fact that habitats vary in terms of quality and quantity, and some survival risks such as predation and competition (Lin and Batzli 2001), and human-induced causes such as poaching and degradation (Kideghesho *et al.* 2006, Strauss *et al.* 2015, Kija *et al.* 2020).

In our understanding, most of the closely related studies conducted in the ecosystem had been focusing on habitat use, habitats selection or preference, or wildlife-habitats association, had study gaps un-addressed. The studies focused on single species, one habitat of one

feeding guild. For example, Kreulen (1975) studied wildebeest (*Connochaetes taurinus*) habitats selection in relation to mineral salt (calcium). McNaughton (1985) study on ecology of a grazing ecosystem was limited to the northern SNP. Mduma and Sinclair (1994) studied habitats selection of oribi (*Ourebia ourebi*) in northern SNP. The study did not consider habitats dynamics for the oribi. Furthermore, Pettorelli *et al.* (2009) focused on habitat use by cheetah (*Acynonyx jubatus*) in south-eastern plains of SNP. Another study by (Ndibalema 2007) focused on habitat use of migrating wildebeest in the SNP and adjacent PAs. The study considered habitats in terms of vegetation cover types, where the habitats quality component was not considered.

Other researchers used multi species in relation to habitats yet had study gaps remaining. For example, Bukombe *et al.* (2016), studied on resource selection and utilization in the western SNP, using five grazers (Topi, buffalo, impala, wildebeest, and zebra). The study was limited to only four vegetation types (grassland, bushland, bush-grassland, and woodland) and missing the habitat quality component. Anderson *et al.* (2016) studied on species and habitats association considering eight most common herbivores (elephant, buffalo, zebra, wildebeest, hartebeest, topi, impala, and Thomson gazelle) and their most abundant predator, lion. Nonetheless, this study was limited to small area (1125 km^2) in the plains of central part of SNP.

Our study, therefore, attempted to fill the gaps of knowledge by focusing on feeding guilds that partition body size, feeding style (grazers, browsers, and mixed feeders), and foraging style (migratory and resident species) covering the entire ecosystem across 20 years study period (1995-2015). We studied spatio-temporal distribution of herbivores across PAs categories to ascertain how the distribution is influenced by protections levels.

Furthermore, we strived to assess the contraction or expansion of herbivores' distribution ranges in space and time. Finally, our study linked spatio-temporal dynamics of herbivores' distribution in relation to habitat selection. We selected, seven key wildlife species under three feeding guilds; browsers (Grant's gazelle *Gazella granti* and giraffe *Giraffa camelopardalis*), grazers (buffalo *Syncerus caffer,* plain zebra *Equus quagga* and wildebeest *Connochaetes taurinus*) and mixed-feeders (impala *Aepyceros melampus* and elephant *Loxodonta africana*) to test three hypotheses and five predictions; H_1) herbivores differ in distribution patterns across space and time; H_2) quality of habitats at spatio-temporal scale influences the contraction and expansion of herbivores' distribution range; H_3) high-quality habitats attract herbivore species; H_4) high protection status of PA categories attracts herbivores and influences contraction and expansion of their distribution range. P_1) herbivores across PAs categories can be predicted to exhibit a ra

ndom distribution pattern at spatio-temporal scale; P_2) If the distribution ran ge of herbivores in different feeding guilds is determined by quality habitats then we expected to record more contraction in poor quality habitats; P_3) If protection status of habitats such as those in different PA categories influenc e contraction and expansion of herbivores' distribution range then we exp ected to record more contraction in areas with less protection status; P_4) If h erbivores select habitats based on their quality then when high-quality habit ats are available they will use those habitats; P_5) If herbivores select habitats based on protection status, reflected in different PA categories, then we expe cted to sight more herbivores in PA categories with high protection.

2.0 MATERIALS AND METHODS

2.1 Study area

The Serengeti ecosystem (33,106 km^2) encompasses a network of nine PAs in northern Tanzania. The PAs comprise the Serengeti National Park (SNP), Ngorongoro Conservation Area (NCA), Maswa, Kijereshi, Grumeti, and Ikorongo Game Reserves (GRs) and Loliondo Game Controlled Area (GCA) whereas the Wildlife Management Areas (WMAs) are Ikona and Makao, (Figure 5.1). The ecosystem has diverse land uses and land management practices, including traditional pastoralism, agro-pastoralism, cultivation, forest reserves and wildlife conservation (Thirgood *et al.* 2004). The diverse and changing land-use practices and cover types likely have consequences to habitats and distribution of biodiversity inside and outside the PAs (Veldhuis *et al.* 2019, Kija *et al.* 2020).

Both biotic and abiotic factors determine the spatial distribution and heterogeneity of vegetation types in the ecosystem (Whittaker and Levin 1977). The vegetation is shaped, furthermore, by the composite effects of fire and herbivory (Norton-Griffiths 1979, Barnes 1983, Belsky 1984, Archibald *et al.* 2005). The ecosystem is watered and drained by several seasonal rivers, notably the Grumeti, Munge, Bologonja, Orangi, Mbalageti. But only the Mara River flows all year through the Mara Reserve in Kenya and then southeastward through the SNP to Lake Victoria (Sinclair *et al.* 2015).

Rainfall is bimodal, with short rains falling in November-December and long rains spanning March-May. There are also two dry seasons, with the long dry season covering June-October and the short dry season in January-February (Norton-Griffiths *et al.* 1975, Ogutu *et al.* 2008, Bartzke *et al.* 2018). The mean annual precipitation ranges from 500 mm from the southeast to 1200 mm in the northwest of the ecosystem (Norton-Griffiths *et al.* 1975, Ogutu *et al.* 2008).

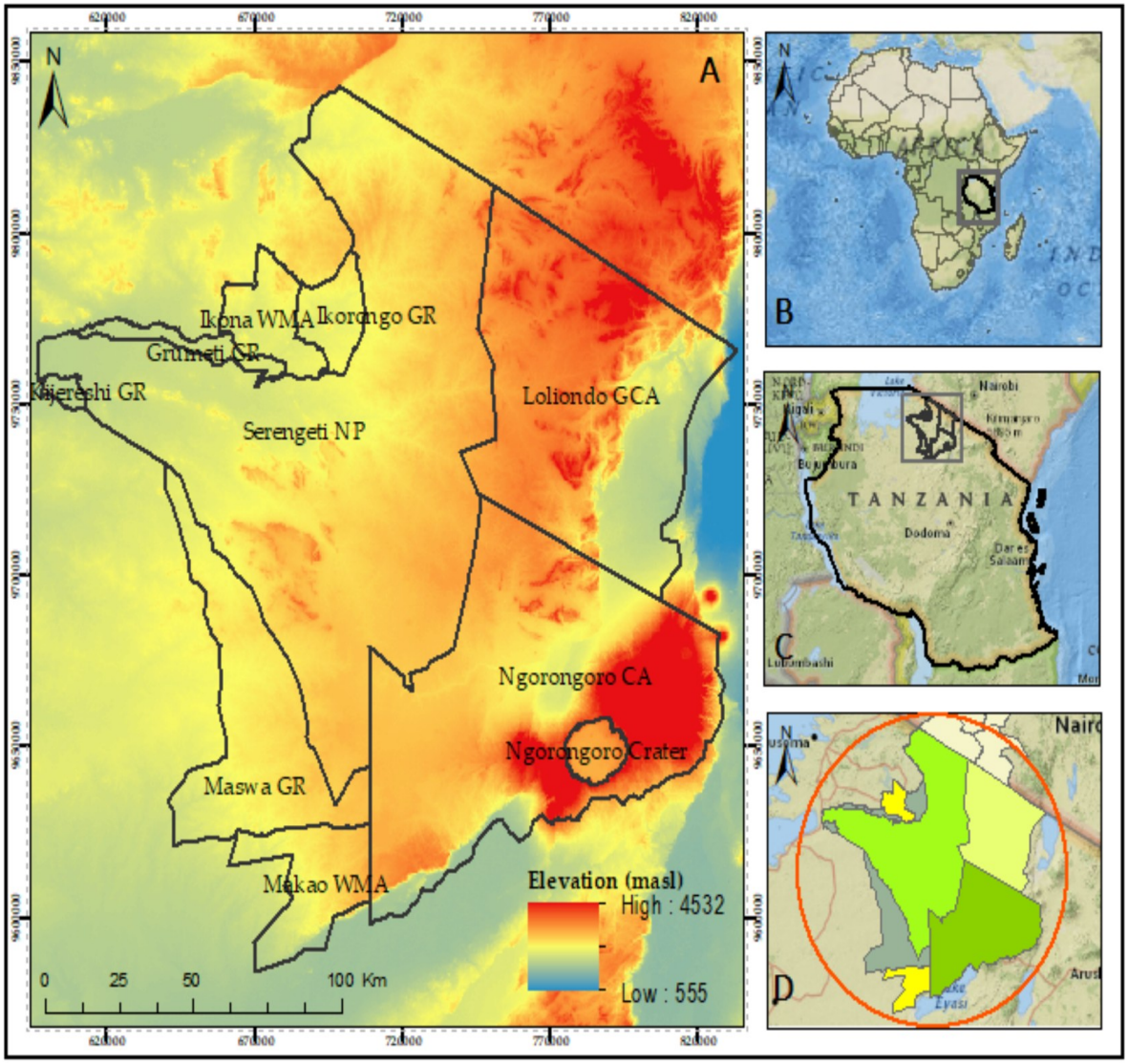

Figure 5.1: Map of the study ecosystem showing the (A) location of the GSE in relation to (B) Africa, (C) Tanzania and (D) Greater Serengeti-Mara Ecosystem (Kenya and Tanzania).

2.2 Data types and Sources

2.2.1 Habitat quality maps

Habitat quality maps were used to evaluate habitat quality (Kija *et al.* 2020) using the Integrated Valuation of Environmental Services and Tradeoffs (InVEST) model. InVEST models habitat quality and rarity as proxies for biodiversity, ultimately estimating the extent of habitat and vegetation types across a landscape, and their state of degradation. Habitat quality and rarity are functions of four factors: the relative impact of each threat, the relative sensitivity of each habitat type to each threat, the distance between habitats and sources of threats, and the degree to which the land is legally protected (Sallustio *et al.* 2017, Sharma *et al.* 2018).

The InVEST model combines information on land use and land cover (LULC) and threats to biodiversity to produce habitat quality maps. Landsat Thematic Mapper (TM) and Landsat-8 (Operational Land Imagery) dry seasons images for 1995 and 2015 were classified to characterize LULC maps using the Random Forest (RF) method (see details in Kija *et al.* 2020). The habitat quality maps integrated LULC with threats maps. The habitat quality maps were re-classified into three equal interval classes: low (0.00-0.33), medium (0.34-0.66) and high (0.67-1.00). The classes considered species' habitat requirements and forage selection, utilization or both, derived from expert knowledge. We assumed these habitats can provide the resources essential for the survival and reproduction of the study species.

2.2.2 Spatio-temporal distribution

The population of herbivores has been surveyed in the Serengeti ecosystem every three years since the 1980s by the Serengeti Research Institute (SRI) and the Conservation Information and Monitoring Unit (CIMU) through Tanzania Wildlife Research Institute (TAWIRI). The aerial censuses are conducted using the systematic reconnaissance flight (SRF) technique (Norton-Griffiths (1978).

Here, we consider only the wet seasons (April and May) censuses conducted between 1991 and 2018 that coincided with the habitat quality maps. For species habitat use analysis, reasonably large sample size is needed to assure a reasonable approximation of the Chi-square distribution. To achieve this, we aggregated the aerial surveys for 1991 and 1996 to capture the conditions around 1995 (referred to as 1995) and for 2014 and 2018 to represent the conditions around 2015 (referred to as 2015).

2.2.3 Selection of study species

We considered the most common medium to large herbivore species (Table 5.1). These species possess contrasting life-history traits (e.g., body size and gut morphology (ruminants versus non-ruminants)), feeding styles (grazers, browsers and mixed feeders) and foraging styles (wide-ranging, migratory and resident) (Guldemond and Van Aarde 2008). These contrasting traits and strategies enable the study species to

play differential roles in shaping the structure and function of savannah ecosystems such as the Serengeti (Anderson *et al.* 2016). For example, impala seasonally switches from predominantly grazing in the wet season to primarily browsing in the dry season, a strategy that facilitates ecological co-existence (Kleynhans *et al.* 2011). Elephant (*Loxodonta africana*) provide vital ecosystem services as bulk feeders able to open up dense woody vegetation, allowing sprouting of herbs, shrubs, and grassland favored by many small to large herbivores (Guldemond *et al.* 2017). Zebra (*Equus quagga*) is well adapted to using forage of low nutritional value, especially old-growth with low-quality plant matter (Mueller 2019). Grant's gazelle (*Gazella granti)* is considered as browsers, their primary feeding habit in the Serengeti plains.

Table 5.1: Studied herbivore species and their common and scientific names, average body size and feeding guilds

Species	**Scientific name**	**Body size (Kg)[a]**	**Feeding guild**
Impala	*Aepycerus melampus*	40	Mixed feeder
Grant's gazelle	*Gazella granti*	50	Browser
Wildebeest	*Connochaetes taurinus*	125	Grazer
Zebra	*Equus quagga*	260	Grazer
African Buffalo	*Syncerus caffer*	700	Grazer
Giraffe	*Giraffa camelopardalis*	1250	Browser
Elephant	*Loxodonta africana*	1725	Mixed feeder

Body sizes are based on Coe *et al.* (1976), Bothma *et al.* (2004) & Skinner and Chimimba (2005).

3.0 DATA ANALYSIS

3.1 Herbivore distribution

The herbivore counts (5 × 5 km grids) were overlaid on the ecosystem boundary, which is covered by 1453 grid cells. To map and visualize the herbivores distribution, we assigned the counts to the grid centroid. We used the spatial join tool (ESRI 2014) to establish whether or not a grid centroid falls within a given PAs category. We mapped species distribution using the kernel density tool (ESRI 2014). To establish herbivore's range contraction or expansion, we compared the number of grid cells occupied by each species in the two periods (1995 and 2015). To test whether the range of a species differed at the ecosystem level, or individual PAs between the two study periods, we used the Kruskal-Wallis test, followed by Pairwise Wilcoxon rank-sum test to identify pairs with statistically significant differences.

3.2 Habitat selection

We estimated herbivore's habitat selection using sightings in three habitat types and calculated expected sightings accounting on the relative area of each habitat type. Herbivore's sightings were overlaid to the habitat quality map, and the corresponding habitat quality value extracted. Our use of wildlife sightings on habitat selection rests on the premise that selection is a functional response, a positive function of the availability and not proportional use of a particular habitat type (Bjørneraas *et al.* 2012, Bukombe *et al.* 2019). We assumed that (1) each herbivore has an equal chance to select any of the habitats available, and (2) herbivore observations were random and unbiased. We used individual groups of animals as the unit of analysis because members of a species in a herd do not behave independently due to social interactions.

The herbivore's habitat selection was determined using a combination of Bonferroni simultaneous confidence intervals (Neu *et al.* 1974) and Chi-square goodness-of-fit test. The expected number of sightings for each habitat type is obtained by multiplying the relative area of the habitat type by the total number of wildlife sightings. The Chi-square goodness-of-fit statistic is calculated as:

$$\chi^2 \geq \sum_{i=1}^{n} \frac{\left(O_i - E_i\right)^2}{E_i}$$

where χ^2 = ¿ Chi-square, O = Observed use and E = Expected use.

The Chi-square goodness-of-fit test helps establish whether the "observed" frequency of use of a particular habitat differs significantly from its "expected" frequency given its availability. The Bonferroni confidence interval ascertains if there are differences in habitat utilization, i.e., whether a particular habitat type is exceptionally preferred by an animal species given its availability.

To determine whether a particular habitat is used less, proportionately, or more than would be expected, the lower and upper

confidence limits are evaluated against the expected utilization proportions. When the expected value is less than the lower bound, the habitat is used more than expected, i.e., preferred, and when the expected value is greater than the upper bound, the habitat is used less than expected. When the expected value is between the lower and upper margins, then habitat use is proportional to its availability.

4.0 RESULTS

4.1 Distribution and habitat selection by browsers

Browsers (n = 709 sightings) constituted 43.1% of herbivores sightings in 1995, with the mean herd size being highest for the NCA, intermediate for GCA and SNP and least for WMAs ($\chi 2 = 87.37$, df = 4, $p < 0.01$, Table 5.2). Spatially, were widely distributed in the eastern, southeastern and western SNP and the northern half of NCA but occurred at relatively lower concentrations in central NCA, Maswa and southwest SNP (Figure 5.2). Herbivores significantly avoided low-quality habitats in the WMAs, GCAs and NCA and medium-quality habitats in SNP and significantly preferred high-quality habitats across PAs and a wider distribution (Table 5.3 and Figure 5.2).

In 2015, (n = 450 sightings) constituted 30.8% of herbivore, with a higher mean number of sightings for NCA and GCA ($\chi 2 = 41.54$, df = 4, $p < 0.01$, Tables 5.4 and 5.5). A high concentration of sightings per cell was in the western, eastern and southeastern plains of SNP, northeast, central to the southwest of NCA, and western to south of Loliondo GCA plains but low concentrations in GRs, WMAs and northern SNP (Figure 5.2). Browsers significantly avoided the low-quality habitats in all the PAs categories and medium-quality habitats in the GCA and NCA but preferred high-quality habitats in the WMAs, GCA, and NCA (Table 5.6).

Both the mean number of sightings per grid ($\chi 2 = 122.62$, df = 4, $p < 0.01$; Tables 5.4) and distributional range (by 12.3%; Figure 5.2) of browsers declined at ecosystem and PAs categories. Moreover, showed significant differences in their selection of the medium versus high and low- versus medium-quality habitats between 1995 and 2015 ($p < 0.01$). Notably, the low-quality habitats selected in 1995 in the SNP and GRs, were completely avoided in 2015. Similarly, habitats selected in the GCA and NCA in 1995 were clearly avoided in 2015 (Tables 5.3 and 5.6).

4.2 Distribution and habitat selection by grazers

Grazers (n = 561 sightings) comprised 34.1% of herbivore sightings and were widely distributed in 1995, with high mean sightings per cell in the SNP and the GRs. Within the PAs category, the mean sightings per cell were significantly higher ($\chi 2 = 75.53$, df = 4, $p < 0.01$) in the NCA than in the WMAs (Tables 5.2).

Western, central, and north SNP, Ngorongoro crater and the northern part of the MGR had more concentration than the western Loliondo, north and south-west Ngorongoro, Maswa south and in the WMAs (Figure 5.2). Grazers significantly avoided low-quality habitats in all

regimes except in the GRs, and significantly preferred medium and high-quality habitats in the WMAs and the GCA, respectively (Table 5.3).

During 2015, grazers (n = 610 sightings) were sighted in all the PAs categories and represented most of the herbivore sightings (41.8%), with the highest mean sightings per cell in the GCA and NCA.

Frequency of sightings also differed significantly across PAs categories ($\chi 2 = 26.50$, df = 4, $p < 0.01$, Tables 5.2). Majority concentrated in western and southern Loliondo GCA, Serengeti-Ngorongoro Plains, southwest NCA, western and eastern SNP but a few occurred in northern SNP and the WMAs (Figure 5.2). Grazers significantly avoided low-quality habitats across PAs, medium quality habitats in the GCA and NCA but preferred high-quality habitats. Grazers also significantly preferred medium habitat quality in GRs, and high-habitat quality in the GCA and NCA (Table 5.6).

Generally, more grazers were sighted per grid cell in 2015 than in 1995 ($\chi 2 = 26.93$, df = 4, $p < 0.01$, Tables 5.2, 5.4 and 5.5), consistent with a concurrent range expansion of 7.7%. The range expansion occurred across the ecosystem except in the GRs and SNP (Table 5.4). The distribution of grazers shifted from the northwest to the plains, resulting in a distributional pattern stretching from western Loliondo, through the central SNP to the plains, south-west NCA and southeast Loliondo GCA (Figure 5.2). Grazers significantly avoided medium-quality habitats (in 2015) that they used proportionately in the GCA and NCA in 1995. They exhibited a little shift between 1995 and 2015 in their selection of the high-quality habitats across the PAs categories except in the NCA (Tables 5.3 and 5.6).

4.3 Distribution and habitat selection by mixed feeders

Mixed feeders (n= 375 sightings) constituted 23% of herbivore sightings in 1995 and were uniformly distributed across the ecosystem (Tables 5.2). Mixed feeders concentrated at high densities in the northern and western Serengeti, Kijereshi and Maswa GRs and in the WMAs but occurred at medium densities in western Loliondo GCA (Figure 5.2). Mixed feeders avoided low-quality habitats in PAs except in the GRs and favoured high-quality habitats especially in the less PAs categories (Table 5.3).

A similar distribution pattern was evident in 2015 (n = 399 sightings), in which mixed feeders comprised 27.4% of herbivore sightings (Tables 5.5). They were also uniformly distributed in the western and central SNP, GRs, and downward the Makao WMA. Mixed feeders had medium to low densities in western NCA (Figure 5.2), avoided poor-quality habitats and selected high-quality habitats in the GCA and NCA (Table 5.6).

Mixed feeders were not only more evenly distributed over the ecosystem, with almost equal mean sightings per cell across all the PAs

but also maintained a comparable distribution patterns between 1995 and 2015. However, their overall range expanded by 4.6% from 1995 to 2015. This expansion occurred in all the PAs categories except in the WMAs and GRs, regardless of the increase in mean sightings per cell (Table 5.2 and Figure 5.2). Generally, mixed feeders exhibited no evident shift in habitat selection, but tended to avoid poor-quality habitats and favor medium and high-quality habitats especially in the less PAs categories (Tables 5.3 and 5.6).

Table 5.2: The total number of 5 × 5 km grid cells with sightings (*N*) of at least one of the study species and the average (Mean ± S.E) number of sightings per grid cell by PA categories and feeding style in the GSE in 1995

Protected area category	Area (km²)	Browsers		Grazers		Mixed feeders	
		N	Mean ± S.E	*N*	Mean ± S.E	*N*	Mean ± S.E
Wildlife Management Areas	1,866	21	1.33 ± 0.16^{a,b,d}	12	1.17 ± 0.11	25	1.20 ± 0.08
Loliondo Game Controlled Area	6,218	90	3.19 ± 0.23	49	1.29 ± 0.08	25	1.28 ± 0.09
Ngorongoro Conservation Area	8,263	183	3.45 ± 0.18	114	1.13 ± 0.04	11	1.00 ± 0.00
Game Reserves	3,757	87	1.72 ± 0.12^{a,b}	96	1.75 ± 0.10^{a,b}	116	1.28 ± 0.05
Serengeti National Park	13,001	328	2.18 ± 0.08^{a,b,c}	290	1.82 ± 0.06^{a,b}	198	1.35 ± 0.04

$^{a, b, c}$, and ^{d} indicate significance difference ($p < 0.05$) relative to GCA, CA, GR and NP, respectively.

Table 5.3: Habitat preference across habitat quality classes and feeding guilds in 1995

Protected area category	Browsers			Grazers			Mixed feeders		
	Low	Medium	High	Low	Medium	High	Low	Medium	High
Wildlife Management Areas	AV*	PU	PR*	AV*	PR*	PU	AV*	PU	PR*
Loliondo Game Controlled Area	AV*	PU	PR*	AV*	PU	PR*	AV*	PU	PR*
Ngorongoro Conservation Area	AV*	PU	PR*	AV*	PU	PU	AV*	PU	PR*
Game Reserves	PU	PU	PR*	PU	PU	PU	PU	PU	PU
Serengeti National Park	PU	AV*	PR*	AV*	PU	PU	AV*	PU	PU

AV = Avoided, PU = Proportional use, PR = Preferred, and * = Significant level i.e., $p < 0.05$

Table 5.4: Grids (5 × 5 km) occupied by wild herbivores in 1995 and 2015 in PAs of different categories in the GSE

Protected area category	TnG	1995			2015		
		BR	GRr	MF	BR	GRr	MF
Wildlife Management Areas	99	21	12	25	10	18	20
Loliondo Game Controlled Area	273	90	49	25	70	86	50
Ngorongoro Conservation Area	387	183	114	11	156	175	22
Game Reserves	225	87	96	116	45	88	90
Serengeti National Park	469	328	290	198	169	243	217

TnG=Total number of grids, BR=Browsers, GRr=Grazers, and MF=Mixed feeders

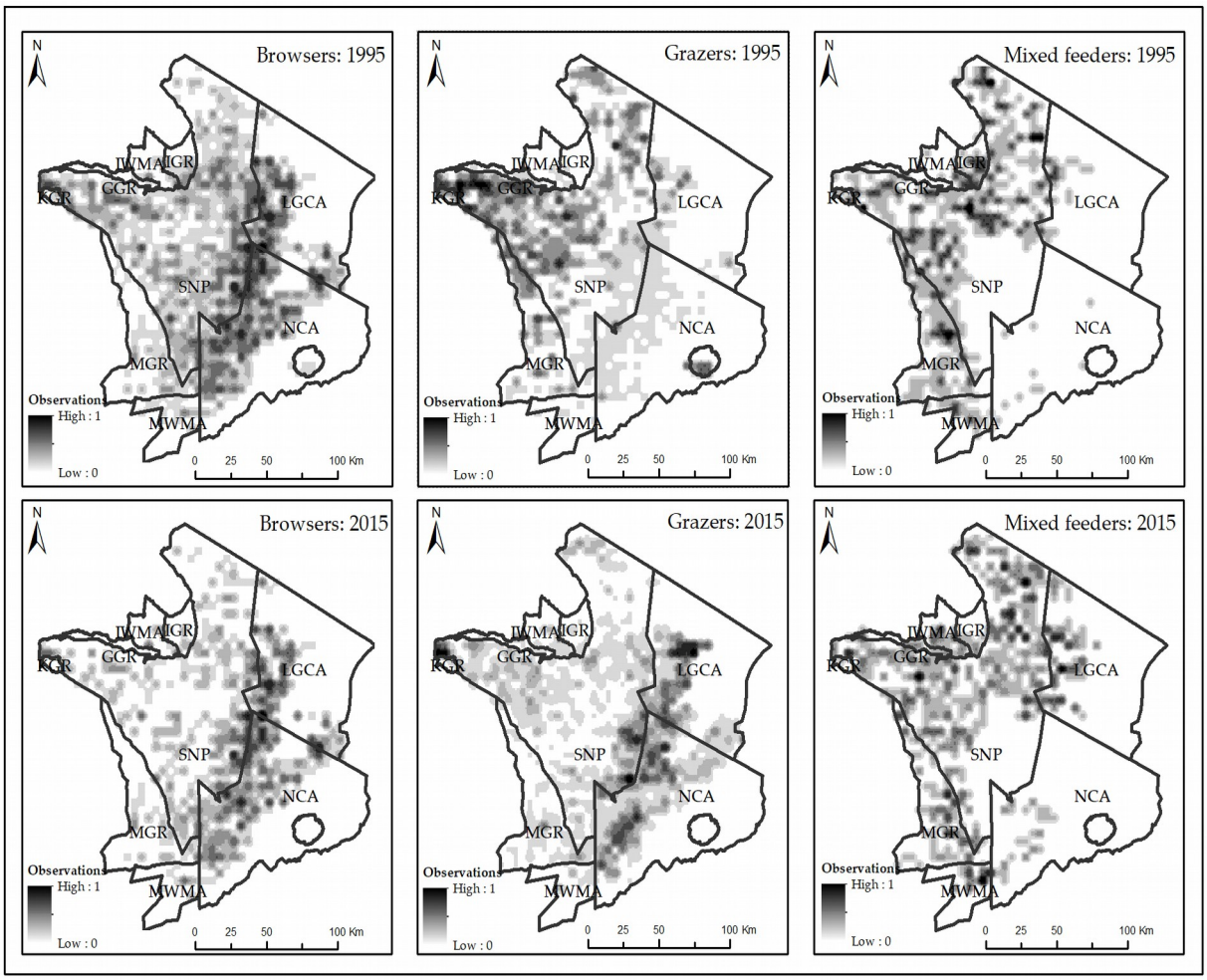

Figure 5.2: Herbivore distribution in the SE in 1995 and 2015

Table 5.5: The total number of 5 × 5 km grid cells with sightings (*N*) of at least one of the study species and the average (Mean ± S.E) number of sightings per grid cell by PAs category and feeding style in the GSE in 2015

Protected area category	Area (km²)	Browsers		Grazers		Mixed feeders	
		N	Mean ± S.E	*N*	Mean ± S.E	*N*	Mean ± S.E
Wildlife Management Areas	1,866	10	1.60 ± 0.31	18	1.67 ± 0.21[a, b]	20	2.40 ± 0.36
Loliondo Game Controlled Area	6,218	70	2.99 ± 0.23	86	4.87 ± 0.53	50	2.14 ± 0.18
Ngorongoro Conservation Area	8,263	156	3.01 ± 0.19	175	4.46 ± 0.33	22	1.32 ± 0.10
Game Reserves	3,757	45	1.78 ± 0.14[a, b]	88	2.09 ± 0.41[a, b]	90	1.74 ± 0.10
Serengeti National Park	13,001	169	1.87 ± 0.08[a, b]	243	2.42 ± 0.14[a, b,c]	217	1.77 ± 0.07

[a, b, c], and [d] indicate significance difference ($p < 0.05$) relative to GCA, CA, GR and NP, respectively

Table 5.6: Habitat preference across habitat quality classes and feeding guilds in 2015

Protected area category	Browsers			Grazers			Mixed feeders		
	Low	Medium	High	Low	Medium	High	Low	Medium	High
Wildlife Management Areas	AV*	PU	PR*	AV*	PU	PU	AV*	PU	PU
Loliondo Game Controlled Area	AV*	AV*	PR*	AV*	AV*	PR*	AV*	AV*	PR*
Ngorongoro Conservation Area	AV*	AV*	PR*	AV*	AV*	PR*	AV*	PR*	PR*
Game Reserves	AV*	PR*	PU	AV*	PR*	PU	AV*	PU	PU
Serengeti National Park	AV*	PU	PU	AV*	PU	PU	AV*	PU	PU

AV = Avoided, PU = Proportional use, PR = Preferred, and * = Significant level i.e., $p < 0.05$

5.0 DISCUSSION

5.1 Distribution and habitat selection by browsers

Our study revealed that distribution pattern and habitats selection varied within and between PAs categories across spatio-temporal scale. The variations in distribution together with the associated contraction of the distribution range were mainly linked with habitats quality and protection levels in PAs categories. However, the influence of other factors such as the presence or absence of predators in determining habitats selection by herbivores remains (Massé and Côté 2009, Burkepile *et al.* 2013).

A higher abundance of browsers in SNP and GRs could be attributed to high protection status and possible availability of browsing forage resources particularly woodland and shrubland (Mlingi 2015). The low mean abundance and declined distribution range in less PAs (WMAs and GCA) and in NCA could be linked to species' sensitivity to human disturbances (Riggio *et al.* 2018) especially the increasing livestock and settlement (Ogutu *et al.* 2011, Schuette *et al.* 2016). Human-related activities can negatively impact LULC and wildlife habitats, thus herbivores abundance and distributions. In this case, fewer browsers are expected in human-modified landscapes (Kideghesho *et al.* 2006, Holdo *et al.* 2011, Kija *et al.* 2020).

Factors such as poaching could partially lead to low abundance, hence population decline. We can partially associate browsers' decline in the GRs and SNP with poaching (Sinclair *et al.* 2008, Strauss *et al.* 2015, Marealle *et al.* 2020). The decline in distribution range is consistent with previous studies in the SNP (East 1998, Strauss *et al.* 2015) and in other ecosystems in Tanzania (Stoner *et al.* 2007, Caro 2008, Mtui 2014, TAWIRI 2015, IUCN 2016, Mtui *et al.* 2017). However, contrary to our results, a stable and increasing population has recently reported in the country-wide population assessment (O'connor *et al.* 2019, TAWIRI 2020).

Interestingly, browsers significantly avoided low-quality habitats in all except in Loliondo GCA and NCA in 1995, which were completely avoided in 2015. They proportionally utilized medium and preferred high-quality habitats across the study periods. This could be attributed to the fact that browsers are sensitive to habitat conditions, and our data suggests avoidance of low-quality habitats in almost categories. This can be partially linked to habitat degradations in the ecosystem (Kija *et al.* 2020) as browsers (e.g., Grants gazelles) have low cellulolytic activities (Gordon and Illius 1996). The observed selection of some low-quality habitats in the SNP and GRs in 1995 that were avoided in the second study period (2015) could be explained by the availability of the high and medium quality habitats, given other factors remain constant.

Selection of medium and high-quality habitats suggests improved habitats quality at spatio-temporal scale (from 1995 to 2015) in the ecosystem and availability of the optimal quality habitats that are essential for providing protection, breeding, roosting, and feeding to enhance survival and reproduction (Kija *et al.* 2020).

Furthermore, preference for medium and high-quality habitats could also be attributed to body sizes and guild's feeding partitioning (Cromsigt *et al.* 2009, Anderson *et al.* 2016, Bukombe *et al.* 2019). For example, in this feeding guild, Giraffe (large body size), is solely a browser whereas Grant's gazelle (medium-sized) tends to switch between browsing and gazing feeding patterns. However, browsing is its primary feeding habit and is limited to lower-level forages (Oindo 2002) such as thorny shrubs, legumes, and forbs (Tieszen *et al.* 1979, Spinage *et al.* 1980).

5.2 Distribution and habitat selection by grazers

We observed an overall higher mean number of grazers in both periods than any other guilds across PAs categories across space and time. This could be due to their abundance and a wider distributed herbivore in savannah ecosystems (Caro 2015, Schuette *et al.* 2016) and probably driven by the availability of medium and high-quality habitats in grassland cover (McNaughton 1983, Schuette *et al.* 2016, Kija *et al.* 2020), rainfall gradient, fire and feeding effects of grazers (Govender *et al.* 2006, Hassan 2007, Holdo *et al.* 2009). High abundance of grazers in the SNP (dominated by grassland) could be attributed to species' visibility against predators and the forage resources (Owen-Smith 2002, Riginos and Grace 2008). These observations support earlier studies e.g. Sinclair (1972) who found grazers were abundant. Recent studies suggest an increasing population in the Serengeti ecosystem (TAWIRI 2010, TAWIRI 2018, Gunda *et al.* 2020), however, we noted a contraction of their distribution range in the GRs and SNP (with mean observations tripled in GCA and NCA). This has been also reported in other ecosystems such as Katavi-Rukwa (Mtui *et al.* 2017).

The observed expansion in distribution range during study periods could be attributed to the species feeding ecology, especially in search of nutritive plant species or quality habitats across PAs categories, thus, shaping the habitat and affecting spatio-temporal distribution of other grazers (Roug *et al.* 2020). Fire could also be an important factor, which affects grazers' distribution through enhancing habitats quality attributes including availability and quality forage resource (Hassan 2007, Veldhuis *et al.* 2019).

We observed clear shifts in habitat use by grazers, which was revealed by an increase in many grazers' sightings in high-quality habitats during both study periods. Their distribution patterns were in line with the spatio-temporal distributions of different quality habitats in the ecosystem (Kija *et al.* 2020). The selection of medium to high-quality habitats is consistent with other studies in Germany and Norway (Heinze

et al. 2011, Bjørneraas *et al.* 2012). However, our study findings are contrary to other studies elsewhere, for instance, Godvik *et al.* (2009) reported red deer's (a grazing herbivore) selection of pastures was inversely proportional to the availability of higher quality habitats.

The observed shift in habitat selection could be attributed to the fact that grazers, always tend to distribute and forage in areas with moderate to high abundant quality foraging resources, e.g., the short grasses (which are among the preferred habitats for the species), especially in the plains and other grassland habitats (Treydte *et al.* 2009). From an ecological perspective, grasses have high-quality forage material making be among the most preferred habitats by grazing species (McNaughton 1983). However, intra-specific differences are unavoidable, for example, in the grazing feeding guild, species such as zebra and buffalo, their habitat selection varies, the former is more adapted to low-and-medium (fibrous) forage, while the latter is adapted to high-quality habitats (Mandinyenya *et al.* 2020). Therefore, we assume that the observed shift in habitat selection by grazers in the GSE is related to quality grassland habitats in the ecosystem (Estes *et al.* 2012, Kija *et al.* 2020).

5.3 Distribution and habitat selection by mixed feeders

We noticed a non-significant difference in mean observations of mixed feeders across the study periods, except an expanded distribution range, a situation that could be associated with the increase in species' population in the ecosystem (Holdo *et al.* 2009, TAWIRI 2014, Morrison *et al.* 2018, TAWIRI 2018). Mixed feeders (e.g., impala) tend to have a small group size or mean observations in human-impacted areas as supported by our findings in WMAs, GCAs and GRs.

On the other hand, small mean size for mixed feeders, especially the impala could be affected by hunting pressure (Setsaas *et al.* 2018), that had been taking place in GRs, GCAs and WMAs. However, variation in mean densities and distribution is a common phenomenon in savannah ecosystems (Gandiwa 2014).

The observed similar distribution range for mixed feeders between 1995 and 2015 could be associated with areas that are shrubland and woodland-dominating in the ecosystem (Kija *et al.* 2020). Mixed feeders tend to prefer shrubland and woodland-dominated areas (Rutina *et al.* 2005, Treydte *et al.* 2009, Gandiwa *et al.* 2011, Pittiglio *et al.* 2013). A similar observation has been reported in savannah ecosystems (Dublin 1995, Zyambo 2016). Consistence (with a little shift) in the distribution of mixed feeders over time inside and outside of core PAs has also been reported in a study by Mtui *et al.* (2017).

Mixed feeders avoided low and selected medium-and-high quality habitats in proportional to their availability. The results corroborate with previous studies that reported the influence of habitat type and dietary on the distribution of large savannah herbivores in the western SNP (Bukombe *et al.* 2018, Bukombe *et al.* 2019) and elsewhere in savannah

ecosystems (Kos *et al.* 2012) and contradicts to the widely known hypothesis that, large herbivores (such as elephant) selects poor habitat quality (Cromsigt *et al.* 2009). Shifts in habitat selection during 1995-2015 could be associated with both changes in land cover and habitat qualities in the ecosystem (Kija *et al.* 2020) as species in this feeding guild have different feeding strategies (Kos *et al.* 2012). The observed habitats selection of various quality classes by mixed feeders entails a functional response in habitat use and selection that have been reported elsewhere (Johnson 2007, Kos *et al.* 2012, Okello *et al.* 2015).

Furthermore, our findings suggest that an increase in the high and medium habitat quality classes between 1995 and 2015 could have contributed to rational habitats selection and use with a proportionally increased population in the ecosystem.

6.0 CONCLUSIONS AND RECOMMENDATIONS

Our study demonstrates that all the studied herbivores in the GSE exhibited a clustered distribution pattern that is probably linked to innate, social behavior, forage resources or strategies against predators. The observed pattern is contrary to the widely known theory that animals are always randomly distributed. For the 20 years study period, browsers demonstrated a declined distribution range, attributed to anthropogenic pressure that led to poor habitat quality. We also noted an expansion of the distribution range of grazers and mixed feeders across the ecosystem being attributed to either general species trend or improved conservation efforts leading to improved habitats quality. The study revealed that a high level of PAs status can contribute to increased mean species observations and distribution range.

Resource selection influenced by habitat quality is the prime determinant of herbivores' distribution in terrestrial protected landscapes. Moreover, herbivores' mean observations within the ecosystem differed across PAs categories. For instance, we observed high mean species observations within the SNP followed by GRs and NCA, indicating either a general trend or habitat conditions and effectiveness of PAs in conserving wildlife habitats. The observed decline of distribution range for species, e.g., browsers, across PAs calls for conservation attention for this feeding guild. Herbivores 'selection and use of medium and high-quality forages could be attributed to the need for maximization of fitness. Always species tend to forage high-quality habitats, with associated environmental variables that are deemed necessary for species survival.

The study findings provide management insights for the key wildlife habitats in the study ecosystem and how herbivore species utilize available habitats and the way they are distributed in the ecosystem. We suggest that modelling herbivores' spatio-temporal distribution in relation to habitat selection at the local and landscape-level is important, as can provide useful information on how animals are distributed and the linkage with habitat quality in space and time. The information is

important for sustainable conservation and management of wildlife, through different ways, including i) providing information on distribution patterns, and ii) information on the proportion of available habitats for use, (iii) generating information for planning purposes. We recommend that; (i) Integrated efforts are needed to control habitat degradations in the ecosystem towards enhancement of quality habitat conditions (as the recorded/observed selection of high and medium quality habitats, and avoidance of low-quality habitats by the animals), (ii) Strengthen conservation and management practices, including protection, in less PAs such as WMAs and GCA where we recorded low mean abundance and declined distribution range of the studied animals, (iii) Management and conservation strategy of wild herbivores needs to take into consideration habitat selection by each species, (iv) A temporal study coverage for wet and dry seasons would be a perfect fit to examine species guild's spatio-temporal changes.

Author contributions

HHK conceived and designed the study, HKK, JBK and LJM analysed the data. JOO, JRK, MYS and EFN reviewed the drafts of the paper.

Declaration of competing interest

The authors have no interest or relationship, financial or otherwise that might be perceived as influencing the author's objectivity with this work and thus have no conflicts of interest to declare.

Funding

The core funding for this research was received from the *African BioServices* (ABS) Project, the European Funded Project, with additional support from the Friedkin Conservation Fund (FCF) and the Rungwa Game Safaris Tanzania.

Acknowledgment

We would first of all like to thank those who assisted in collecting d ata for this study. Special thanks are attributed to the Tanzania Wildlife Research Institute (TAWIRI) for granting research permits for this study, and for granting study leave to the first author.

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CHAPTER SIX

6.0 GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

Spatio-temporal dynamics of LULC change and its implication to wildlife habitats and population requires an understanding of pattern and process involved as well as the driving forces. Habitat conditions and wildlife population in the Greater Serengeti Ecosystem cannot be inferred without a solid understanding of LULC change, its dynamics and consequences. Ecological information on LULC change (driving forces and its impacts), habitats and population will help relevant conservation initiatives and programs that aimed to improve the quality of habitats, thus wildlife sustainability. So far, this research works, it is the first expansive study that covered a wider time span of 40 years to quantify changes in LULC, habitats and species distribution and abundance in the study area.

This chapter discusses the (i) major scientific findings and implications, recognizes the (ii) limitation of the study and future direction of the study. Finally, it set out the conclutions and recommendations to conservation managers, decision and policy-makers.

6.1 Major scientific findings and implications/Key contribution of the study

This study has provided evidence-based information on changes and associated drivers to inform wildlife management practitioners for appropriate improvements to wildlife habitats. The mapped and quantified wildlife habitat quality in space and time at three points in time (1975, 1995, and 2015) provided a quantitative basis for improving wildlife habitat management and enhancing natural ecological processes in the Serengeti ecosystem and possibly elsewhere. The obtained information on species distribution, habitat selection and use are useful in determining high priority areas for effective conservation practices.

An increasing level of LULC and habitats quality negative changes with in PAs with less restrictions of human activities (WMAs, GCA, GRs, NCA and NP). informs the respective PA managers, neighboring authorities, policy makers and supporting stakeholders to review and strengthen their conservation strategies to safeguard land cover and habitat quality for healthy wildlife populations. For NCA the recorded negative changes provide an alert to the management, conservation practitioners policy makers and players to ensure to Multiple Land Use goals are achieved. The findings for the WMAs, gives useful lessons to other areas potential for establishing new WMAs and to those countries that attempts to learn from Tanzania regarding this paradigm shift in conservation that aims to safeguard communities' interests and conservation goals, in this case LULC, wildlife habitats, animals and ecological integrity of the ecosystem or landscape.

6.2 Study limitation

Our research findings are not free of limitation, some gaps exist which needs further work to improve the study. These limitations are as follows:

1. LULC change have implication to both ecological areas and human life, therefore integration of socio-economic data in space and time would is needed. The current study did not include this aspect.

2. The current study did not project (model) LULC change and habitat quality for the next 20 or 40 years to ascertain the future situation

3. The spatio-temporal distribution assessment used only one-season data "wet", a study using both wet and dry seasons integrated with habitat selection and quality

would provide essential information on how animals are distributed in relation to habitat quality.

4. Detailed study is needed to establish the declining trend of browsers as well as the reasons for mixed feeders (e.g., elephant) use of the areas outside the core PAs.

6.3 General Conclusions

The study revealed that the ecosystem and its buffer area experienced substantial LULC changes during the past 40 years (1975-2015) involving transformation from one type cover to another. Generally, more land cover conversions occurred in the buffer area and PAs with low protection status, notably the GCA and WMAs. LULC changes and associated drivers have significant adverse impacts on wildlife habitats quality and species distributions. Human population growth in and around the ecosystem has probably led to increasing pressure on land as a consequence of the growing need to cater for settlement and agricultural. This study has revealed that dynamic of LULC change showed an increase in agricultural and settlement areas, at the expense of woodland and other native vegetation. Therefore, it is important for protected area management authorities and policy makers prioritize on effective management to remedy the observed and likely future impacts to the ecosystem.

Multiple drivers influenced LULC changes in the GSE across space and time. The proximate and underlying drivers factors that significantly involved in the dynamic of LULC and driving factors were human population density through its associated socio-economic activities, precipitation, distance from water sources including rivers, soil moisture, fire incidences, distance from roads, topographic features (elevation and slope), and elephant density. However, human population density was the major driver associated

with the observed change in the ecosystem. Land use planning, resource zone management plan and a conservation hearted community could ameliorate the situation.

For habitat quality, an InVEST model (Integrated Valuation of Environmental Services and Tradeoffs) revealed an overall increase in habitat quality (1975–2015) with conservation status of PAS within the ecosystem and its surrounding buffer area at spatio-temporal scale. Poor-quality habitats increased over time (eight-fold) mostly in the buffer area, whereas PAs, especially the SNP, maintained high-quality habitats throughout (1975–2015). Anthropogenic activities such as livestock keeping, overgrazing, settlements and agriculture in human-dominated areas, unless checked, will continously impact the habitat quality and disrupt natural ecological processes.

Regarding the herbivore population, all the studied species exhibited a clustered distribution pattern. Browsers (grant gazelle and giraffe) demonstrated a declined distribution range, attributed to anthropogenic pressure that led to poor habitat quality especially areas with low conservation status. Grazers (buffalo, wildebeest and zebra) and mixed feeders (elephant and impala) recorded an expanded distribution range. Resource selection influenced by habitat quality is the prime determinant of herbivores distribution in the ecosystem. The contracted herbivores distribution calls for a special attention by conservation managers and decision makers.

To this end, the findings of this research agree that the mounting pressure on LULC changes is expected to have an adverse effect on wildlife habitat quality and species' spatio-temporal distribution pattern. Growing population pressure and its associated attributes have been the major driving forces of LULC in the ecosystem.

6.4 General Recommendations

To address LULC changes (objective one), maintenance of high-quality habitats (objective two) and wildlife populations (objective three), and dynamics of wildlife population (objective four) in the ecosystem, the following key options are crucial;

1. Effective conservation policies and regulation of socio-economic activities in the study ecosystem and its buffer area in order to ameliorate the declining vegetation cover, especially along the PAs boundaries; formulation and effective implementation of sound policies and far-sighted spatial land use plans to safeguard the future integrity of the iconic ecosystem and its surrounding buffer zones.

2. Integrated efforts to ensure appropriate human populations inside and around the GSE so as to reduce its unpreferred effects on the various land cover types in the area; Effective management of both prescribed and wild fires; Study on availability and distribution of key resources for the elephant so as to influence even utilization of different habitats, ultimately reducing the observed negative effects of its density, and Effective use of GMPs, which could ameliorate negative impacts of various practices.

3. Strengthening legal and institutional arrangements, such as establishing new or upgrading low PAs status, which deemed important in improving and maintaining habitat quality. Effective enforcement of the Wildlife Conservation Act (WCA) and WMA regulations and integrate them with other related legislation to safeguard high-quality wildlife habitats in PAs and their buffer zones.

4. Further study is recommended for modelling spatio-temporal distribution using both wet and dry seasons data in relation to habitat selection at local and landscape-level, to provide information on how animals are distributed and the linkage with habitat quality.

5. Further studies are recommended to regularly monitoring changes in LULC cover and their influencing drivers and how these affects both dynamics of population and distribution pattern of wildlife at spatio-temporal scale in the GSE.