BIODIVERSITY IN FRAGMENTED KEY RESOURCE AREAS

PERSISTENCE OF PLANT DIVERSITY AND PRODUCTIVITY IN AN INTENSELY GRAZED KEY RESOURCE AREA

Francis Kamau Muthoni

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DISSERTATION

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List of abbreviations

ASTER	Advanced space-borne thermal emission and reflection radiometer
a.s.l.	Above sea level
ABM	Agent based models
ANOSIM	Analysis of similarities
ANOVA	Analysis of variance
ATCOR-2	Atmospheric Correction Algorithm-2
C.V.	Coefficient of Variation
CAP	Canonical analysis of principle coordinates
CCA	Canonical analysis of variance
DBMs	Distance based methods
db-RDA	Distance-based redundancy analysis
DEM	Digital elevation model
Ecodist	Ecological distance package
EOIA	Earth Observation and Integrated assessment of Lake Naivasha
FBC	Fractional bare-soil cover
FoI	Frequency of inundation
GLM	Generalized linear models
ISODATA	Iterative self-organizing data
J-M	Jeffries-Matusita class separability test
K	Potassium
KARI	Kenya Agricultural Research Institute
KHCDA	Kenya Horticultural Crops Development Authority
KNBS	Kenya National Bureau of Statistics
KRAs	Key resource areas
KWS	Kenya Wildlife Service
Landsat	Land observation satellite
LR	Log-likelihood statistic
LULC	Land use/land cover
LV	latent variables
MANOVA	Multivariate analysis of variance
ManyGLM	Multivariate generalized linear model
MODIS	Moderate resolution imaging spectro-radiometer
MS	mixed grazing signal species
MVABUND	Multivariate analysis of variance
N	Nitrogen
NDVI	Normalized difference vegetation index

NIR	Near infrared
NS	No signal species
NWC	Nakuru wildlife conservancy
P	Phosphorous
PCA	Principle components analysis
PCoA	Principle coordinates analysis
PERMANOVA	Permutational multivariate analysis of variance
PES	Payment of environmental services
PLSR	Partial least squares regression
ppm	Parts per million
PS	Pure signal species
RAMSAR	Convection on wetlands of international importance
RDA	Redundancy analysis
RMSEP	Root mean square error of prediction
ROIs	Regions of interest
SD	System dynamics
SVH	Spectral variation hypothesis
TM	Thematic mapper
TPI	Topographical position index
WSR	Wet season range

Chapter 1

Introduction

1.1 Role of key resource areas (KRAs) in maintaining diversity in savannas

Savannas are inhabited by diverse and abundant plant and herbivore species (Olff et al. 2002, Eby et al. 2014). The abundance of herbivore species is dependent on the availability and distribution of key resources such as water, forage and minerals (de Leeuw et al. 2001, Grant and Scholes 2006, Veblen 2012, Ogutu et al. 2014). In savannas, these key resources exhibit large spatial and temporal variation (Coughenour 1991, Scoones 1991, 1995, Illius and O'Connor 2000, Tzialla et al. 2006). Restricted patches within savannas with high availability of these key resources are known as Key Resource Areas (KRAs; Scoones 1991, Scoones 1995, Illius and O'Connor 2004, Vetter 2005, Ngugi and Conant 2008). These include swamps, valley bottoms and floodplains (Ngugi and Conant 2008, Dahwa et al. 2013). Wetlands in dry-lands are KRAs to grazing herbivores as high availability of water promote forage productivity throughout the year (Scoones 1991, Hongo and Masikini 2003, Sarkar 2006, Ngugi and Conant 2008). These KRAs act as dry season refugia for herbivores when forage is scarce in the outlying Wet Season Range (WSRs; Homewood and Lewis 1987, Scoones 1991, 1995, Ngugi and Conant 2008, Sitters et al. 2009, Kanga et al. 2013). KRAs maintain herbivore populations in dry seasons that disperse to WSR's in wet seasons, thus maintaining a source-sink mechanism between the two landscapes (Illius and O'Connor 2000).

The availability of key resource(s) in KRAs also attract diverse human activities that accentuate habitat fragmentation (Kimani and Pickard 1998, Boone and Hobbs 2004, Western et al. 2009a, Ogutu et al. 2010, Msoffe et al. 2011, Estes et al. 2012, Dahwa et al. 2013). These activities include intensive agriculture, livestock ranching and (semi)-urban settlements. Anthropogenic fragmentation leads to smaller and isolated patches of KRAs that reduce habitat connectivity (Msoffe et al. 2011). This restricts seasonal movements and may increase resident herbivores density (Ogutu et al. 2012). In-turn this induces continuous intense grazing as opposed to traditional seasonal grazing that allowed rest periods for pastures to recover (Coughenour 1991, Metzger et al. 2005, Mekuria et al. 2007). Moreover, management interventions in rangelands such as provision of water and supplementary feeding provide additional "artificial" key resources (Illius and O'Connor 1999, Fynn and O'Connor 2000, de Leeuw et al. 2001, von Wehrden et al. 2012). These may increase herbivore densities beyond the levels that can be optimally supported by the ecosystem leading to catastrophic shifts in vegetation composition (Rietkerk and Van de Koppel 1997). Reduced grazing areas coupled with continuous intense grazing by resident herbivore lead to overgrazing that in-turn alters herbaceous plant composition (Oba et al. 2001, Metzger et al. 2005, Kanga et al. 2013) and productivity (Milchunas and Lauenroth 1993, Keya 1998, Boone and Hobbs 2004).

The impact of grazing in savannas is higher near water sources and attenuate radially with increasing distance from water sources thereby creating a utilization gradient that is known as piosphere (Lange 1969, Derry 2004, Washington-Allen et al. 2004). Development of piospheres around riparian grazing lawns is partly promoted by the presence of central-place foragers that leave and return to water source after each grazing bout (Orians and Pearson 1979, Lewison and Carter 2004). These include the hippopotamus (*Hippopotamus amphibious*) that concentrate its grazing within a limited distance from the water source (Grey and Harper 2002, Lewison and Carter 2004, Kanga et al. 2013).

KRAs on wetlands that border lakes and rivers experience further natural fragmentation from the water-ward side due to fluctuating water levels that cause floods. Frequent floods act as a pulsed resource (Anderson et al. 2008) that add soil organic matter and nutrients embedded on sediments (Gaudet 1977b, Tockner et al. 2000, Kitaka et al. 2002, Nahlik and Mitsch 2008). Flooding is also a disturbance that inhibit growth of plant species that are not adapted to growing in inundated conditions (Gaudet 1977a, Lachavanne and Juge 1997, Tzialla et al. 2006, Onywere 2013). This makes these land-water ecotones to be inherently unstable that increase habitat heterogeneity (Lachavanne and Juge 1997, Nahlik and Mitsch 2008). This causes high temporal turnover in plant community composition and productivity (Sarkar 2006, Tzialla et al. 2006, Ogutu et al. 2012, Viers et al. 2012).

The competing biodiversity conservation and economic development goals in KRAs is a major challenge to conservation managers (Fischer et al. 2008). Economic development in KRAs is inevitable (Msoffe et al. 2011); therefore the challenge remains on how to sustainably conserve biodiversity without hindering economic development (Roberts 1988, Fischer et al. 2008, Mundia and Murayama 2009, Msoffe et al. 2011). This would require detailed understanding of what drives the habitat fragmentation and its effect on the biotic species and their interactions. This is particularly critical for KRAs located in non-protected wildlife areas where exploitation of resources is unregulated (Hongo and Masikini 2003, Morrison and Harper 2009). Over-exploitation of resources in KRAs such as intensive habitat clearing for agriculture and overgrazing could threaten persistence and co-existence of plant and herbivore species and the ecosystem services they provide. However there are limited empirical studies on plant-herbivore interactions in KRAs outside protected areas in East African dry-lands.

1.2 The role of plant and ungulate diversity in regulating ecosystem services in the KRAs

Ungulates grazing alter key ecosystem services in the KRAs (Tanentzap and Coomes 2011, Wright et al. 2012). Overgrazing degrades riparian vegetation that buffer wetlands against nutrient and sediment inflows thus accelerating eutrophication of fresh water bodies (Hongo and Masikini 2003, Harper and Mavuti 2004, Morrison and Harper 2009). Ungulate grazing regulates carbon sequestration rate by stimulating plant productivity (Ekaya et al. 2001, Lohmann et al. 2012). The grazing intensity also determines the standing herbaceous biomass and therefore the carbon stocks in the KRAs (Tanentzap and Coomes 2011, Young et al. 2013). Ungulates disperse plant seeds that are attached to their fur or in their dug (Anderson et al. 2014).

Ungulates modify the nutrient cycle in the landscape by adding and redistributing soil nutrients after defecation (Berliner and Kioko 1999, Augustine and Frank 2001, Augustine 2003a, Augustine and McNaughton 2006). Though their digestion ungulates enhance mineralization of nutrients thus facilitating fast release to the ecosystem compared to slow natural decomposition (Augustine 2003a, Augustine and McNaughton 2006). Moreover, ungulates modify their habitats that in-turn regulates population dynamics of other organisms and their ecosystem functions. Recently Young et al. (2014) demonstrated that high density of ungulates in East-African rangelands reduce the abundance of rodents that are host to fleas that spread zoonotic diseases. Trampling compacts soils layers thus reducing soil infiltration that increase surface runoff and soils erosion (Hongo and Masikini 2003, Cech et al. 2008, Kioko et al. 2012, Dahwa et al. 2013).

Plants provide habitats for other organisms (Bennett et al. 2014), improve soil fertility by adding organic matter after decomposition (Ekaya and Kinyamario 2001) and control soil erosion (Kioko et al. 2012). Diverse plant and ungulate species support economic activities such as eco-tourism that provide income (Homewood et al. 2012).

Therefore habitat fragmentation that alters the diversity of plant and herbivore species in the KRAs affects provision of these ecosystem services (O'Connor and Crowe 2005, Hu et al. 2008). Understanding the changes in plant-herbivore species diversity and interactions in fragmented KRAs would guide formulation of adaptive measures to promote their persistence and co-existence in these landscapes.

1.3 Plant-ungulate interactions on KRAs in savannas

Authors do not agree on whether grazing by large herbivores has a significant effect on plant community composition and productivity in savannas. Three contrasting hypotheses on plant-herbivore coupling in savannas have been proposed; the equilibrium, disequilibrium and non-equilibrium (Illius and O'Connor 1999, 2000, 2004). First, the equilibrium hypothesis suggested that plant-herbivore dynamics in savannas are regulated in a density dependent manner (Sinclair and Fryxell 1985, DeAngelis and Waterhouse 1987, Briske et al. 2003). Proponents of this hypothesis argue that the large populations of herbivores cause overgrazing and eventual collapse of pastoral grazing lands (Coughenour 1991, Behnke 2000, Oba et al. 2000b, Vetter 2005).

Second, the disequilibrium hypothesis posits that plant composition and productivity in African savannas are regulated entirely by variability in rainfall and therefore herbivores have no significant effect (Ellis and Swift 1988, Westoby et al. 1989, Behnke et al. 1993, Briske et al. 2003). This occurs in rangelands experiencing high variability in rainfall (>33% C.V.) because frequent droughts keep herbivores at low densities that allow vegetation to recover (Illius and O'Connor 1999, von Wehrden et al. 2012).

Third, the non-equilibrium hypothesis posits that both equilibrium and dis-equilibrium dynamics occur alternately in both the spatial and temporal dimensions (Illius and O'Connor 1999, 2000, 2004). This is facilitated by the presence of KRAs in savanna landscapes. The KRAs act as dry season refugia where herbivores from surrounding wet season ranges aggregate. It is hypothesized that herbivore populations are in equilibrium with available key resources that ensures their survival during the dry seasons (Illius and O'Connor 1999). The ratio of key to non-key resources regulates the herbivore population and therefore the magnitude of their impact on plant community composition and productivity in the outlying wet season ranges (Illius and O'Connor 1999, 2000). Therefore during the dry seasons the herbivore population in the KRAs are regulated in a density dependent manner hence the equilibrial dynamics (Illius and O'Connor 1999, 2000). However, the surrounding wet season ranges that are driven by dis-equilibrium forces and may experience higher grazing pressure in the wet seasons due to the larger herbivore density that has been maintained in the KRAs during scarcity (Illius and O'Connor 1999, 2000). These herbivores may exert significant effects on plant productivity and composition in the wet season ranges (Fernandez-Gimenez and Allen-Diaz 1999, Illius and O'Connor 1999, Fynn and O'Connor 2000).

The coupling between plant-herbivore dynamics predicted by non-equilibrium hypotheses imply that ungulates in the KRAs depend on plants for survival but also exert significant direct or indirect effects on plant productivity and composition (Augustine and McNaughton 1998). The magnitude of this effect depends on the balance between factors controlling herbivores selective grazing and the plants tolerance to herbivory (Augustine and McNaughton 1998). These factors include the herbivore species assemblage (McNaughton 1985, Young et al. 2013, Eby et al. 2014), density (Coughenour 1991, Young et al. 2013), local abiotic environment (McNaughton 1983, Olff and Ritchie 1998, Augustine and Frank 2001, Augustine 2003a, Augustine 2003b, Augustine and McNaughton 2006, Anderson et al. 2007, Young et al. 2013), body size (McNaughton and Georgiadis 1986, Bakker et al. 2006), spatial-temporal distribution of herbivory (Adler et al. 2001, De Knegt et al. 2008) and evolutionary history of grazing (Milchunas et al. 1988, Cingolani et al. 2005).

Grazing by large herbivores (Augustine and Frank 2001) alters plant communities through defoliation, trampling, seed dispersal and modifying heterogeneity in soil (nutrients, moisture) and canopy (light) resources (Milchunas et al. 1988, Augustine and Frank 2001, Pykala 2005, Golodets et al. 2011). Although the mechanisms through which ungulates impact on the plant community composition and productivity are relatively well known, studies differ on the direction and magnitude of the effect.

Studies based on herbivore exclosures have reported positive impacts (e.g. McNaughton 1983, Anderson et al. 2007, Eby et al. 2014), neutral impacts (e.g. Stohlgren et al. 1999, Dorji et al. 2010, Silcock and Fensham 2013) and mixed impacts (Belsky 1992, Bakker et al. 2006) of grazing on plant richness, diversity or composition. Generally, plant species richness and diversity peaks at intermediate level of grazing (Milchunas et al. 1988, Oba et al. 2001). Low grazing intensities promote competitive dominance by fast growing and canopy dominating species thus lowering diversity of short stature plants (Milchunas et al. 1988, Golodets et al. 2011, Eby et al. 2014). However intense grazing can suppress competitive dominance by reducing competition for nutrients and opening-up canopy spaces to lower stature and inferior competitors' thus increasing richness and diversity (Milchunas et al. 1988, Stohlgren et al. 1999, Borer et al. 2014). The mixed effect of grazing occur when the direction of grazing effect on plant diversity differ depending on the environmental resources or the scales of observation (grain). For instance grazing has been observed to increase diversity on fertile soils but lower diversity on poor or saline soils (Olff and Ritchie 1998, Bakker et al. 2006, Borer et al. 2014). Negative impacts of grazing on plant community composition may arise from selective foraging that suppress the abundance of palatable species in favor of non-palatable species or from overgrazing that reduces abundance of perennial species to less productive annuals (reviewed in; Augustine and McNaughton 1998, Sullivan and Rohde 2002, Vetter 2005).

Grazing by ungulates can increase or decrease herbaceous plant productivity (Milchunas and Lauenroth 1993). Intermediate grazing intensities in resource rich soils (nutrients and moisture) stimulate compensatory growth in plants after defoliation that increases plant productivity (over-compensation; McNaughton 1985, Pandey and Singh 1992, Milchunas and Lauenroth 1993, Oba et al. 2000a, Augustine and McNaughton 2006). Overcompensation occurs as a result of plants responding to defoliation by allocating proportionally more regrowth (compensatory growth) to vegetative biomass to replace the lost tissue (McNaughton 1985, Oba et al. 2000a, Anderson and Frank 2003, Oba et al. 2006). The saliva hormones and growth factors secreted on defoliated plants during grazing bouts stimulate compensatory growth and therefore herbaceous productivity (Dyer 1980, Pandey and Singh 1992). However, intense grazing can lower herbaceous productivity as it reduces survival fitness of the plants due to injury to their apical meristems, stolons and rhizomes where new tillers sprout (Anderson and Frank 2003, Kioko et al. 2012). Intense grazing also reduces the residual aboveground biomass (AGB) that is essential for plant regrowth (Varnamkhasti et al. 1995, Oba et al. 2000a). Low grazing intensity can reduce herbaceous productivity by enhancing accumulation of high biomass that comprise old and moribund stems (Belsky 1992).

Disentangling the magnitude of herbivore effect on plant productivity and composition in different landscapes savanna has remained an active area of research since it guide design of grazing management tools (Hayes and Holl 2003, O'Connor et al. 2010).

1.4 Measuring the impact of ungulate grazing on plant community composition

Range management plans are formulated based on which of the three hypotheses on plant-herbivore coupling is assumed to hold in a particular ecosystem (Coughenour 1991, Oba et al. 2000b). Therefore range ecologists are interested in disentangling which of the three hypotheses holds in different ecosystems (Fernandez-Gimenez and Allen-Diaz 1999, Dorji et al. 2010). Most studies investigating existence of non-equilibrium dynamics in savannas rely on simulation models (Illius and O'Connor 2000, Boone and Wang 2007, Derry and Boone 2010, Richardson et al. 2010, Okayasu et al. 2012). Empirical evidence on non-equilibrium hypothesis on plant-herbivore coupling is limited (e.g. Fynn and O'Connor 2000, Ngugi and Conant 2008, Muthoni et al. 2014). Empirical methods use herbivore exclosures to enable comparison of species community composition and productivity between grazed and ungrazed plots (O'Connor and Roux 1995, Young et al. 1997).

Analyzing plant composition data obtained from grazed and ungrazed treatments enable detection of the multivariate effect of grazing and identification of the species that are most responsive to grazing (Warton et al. 2012). However, typical species abundance data is characterized by high dimensionality with many parameters (species) but limited observations (samples) (O'Hara and Kotze 2010). It also contains many zero's due to a high number of rare species making it over-dispersed (have higher variances than mean) (McArdle and Anderson 2001, ver Hoef and Boveng 2007, Sileshi 2008). These properties makes it difficult to achieve multivariate normality and therefore inappropriate to analyze this data with standard parametric statistical tests that assume multivariate normality such as multivariate analysis of variance (MANOVA; Quinn and Keough 2002).

Detection of the overall multivariate effect of grazing on plant species as well as identification of the species that are most responsive to environmental stress and disturbances such as grazing require robust multivariate statistical methods that are able to handle the above properties of typical species abundance data (Sileshi 2008, Poos and Jackson 2012, Warton et al. 2012). This would avert incorrect conclusions due to methodological artifacts that can misinform range management plans. For example, concluding that grazers have no effect on community composition when there is an effect may result in adoption of policies that increase stocking rates and therefore accelerate range degradation (Oba et al. 2001, Vetter 2005).

1.5 Determinants of spatial turnover in plant composition (beta-diversity) in fragmented KRAs

Sustainable management of KRAs in savannas requires long-term monitoring of range condition to understand how they respond to changing environment and disturbance regimes. Plant community composition is one of the essential biodiversity variables (Skidmore 2013) used as an indicator of range condition (Fernandez-Gimenez and Allen-Diaz 1999, Fynn and O'Connor 2000, Saayman et al. 2013). Most studies analyze plant composition at plot scales (alpha diversity; Belsky 1992, Hayes and Holl 2003, Aarrestad et al. 2011) although conservation plans are formulated at landscape scale (Oindo et al. 2003, Fischer et al. 2008, von Wehrden et al. 2014). Understanding the spatial turnover in plant composition (beta-diversity) in the landscape is more intuitive as it matches the scale at which conservation plans are formulated (Oindo et al. 2003, von Wehrden et al. 2014). Understanding plant beta-diversity aids in identifying locations in the landscape with unique plant composition (Chust et al. 2006). This information is useful for reserve selection and identification of sites that should be prioritized for future floristic surveys (Palmer et al. 2002, Chust et al. 2006).

Information on factors that drive plant beta-diversity in a landscape is equally important for conservation plans (Li et al. 2011). However, there are contrasting views on what drives plant beta-diversity in fragmented landscapes. The niche theory stipulates that the patterns in plant beta-diversity are determined by environmental heterogeneity and related ecological-niches (Hutchinson 1957, Li et al. 2011, Burrascano et al. 2013). In contrast, the unified neutral theory of biodiversity (Hubbell 2001) stipulates that species are distributed randomly but in a spatially auto-correlated dispersal. The species dispersal limits makes geographically near sites to be similar in species composition. However, in reality both niche and the neutral processes can determine plant beta-diversity patterns concurrently (Li et al. 2011, Burrascano et al. 2013).

Disentangling the relative contribution of the environmental heterogeneity and species dispersal limitation is hampered by lack of long-term data in most ecosystems. Traditionally range ecologists rely on floristic field surveys that are laborious, cover relatively small extents (plots) and short temporal periods (Palmer et al. 2002). Effective monitoring changes in plant community composition in rangelands requires methods that are able to cover extensive area and with a higher temporal frequency (repeatability; Palmer et al. 2002). Remote sensing data offers these qualities.

The spectral variation hypothesis (SVH) proposes that the variability in satellite remote sensing reflectance is a surrogate for environmental heterogeneity (Oindo and Skidmore 2002, Palmer et al. 2002, Rocchini 2007, Gillespie et al. 2008, Rocchini et al. 2010). Since species diversity increases with environmental heterogeneity (Li et al. 2011), spectral variation derived from historical satellite images can be used as a surrogate for species diversity. This can aid in reconstructing historical spatial patterns of beta-diversity in extensive landscapes to analyze how plant communities responded to environmental stress or disturbances (Sensu; Washington-Allen et al. 2006, Washington-Allen et al. 2008, von Wehrden et al. 2012). This is critical for data limited and remote KRAs in rangelands (von Wehrden et al. 2012). This would be facilitated by freely available historical archive of satellite data such as Landsat legacy with over four decades (Wulder et al. 2012). Application of SVH for estimating or monitoring plant diversity is still at development stage and techniques of optimizing or improving its accuracy is still an active area of research.

1.6 Research objectives

This thesis aims at understanding the direct or indirect impacts of Lake Naivasha on the biodiversity of its terrestrial fringe zone. This zone is a KRA for wild and domestic ungulates and therefore subject to spatially and temporally varied grazing intensity. The plant and large ungulate species are used as examples of biodiversity since their population dynamics are coupled. The plant-herbivore interactions in this KRA are analyzed to understand how they can persist and co-exist in a KRA that is experiencing natural and anthropogenic fragmentation. The availability of fresh lake water has attracted horticultural development and related economic activities resulting to habitat fragmentation. Specifically we examine; (1) the trend and drivers of large ungulates biomass in the KRA; (2) the impact of large ungulate grazing and rainfall on productivity and aboveground biomass of herbaceous plants; (3) the impact of large ungulate grazing on herbaceous plant community composition and diversity; and (4) the relative contribution of environmental heterogeneity and species dispersal limits (spatial distances) on plant beta-diversity patterns in the KRA.

1.7 Study area

The study was undertaken on the terrestrial fringe zone of Lake Naivasha (Figure 1.1). This is a RAMSAR site (Ramsar 1996) located outside the protected area but adjacent to two protected areas; Hell's Gate and Mt. Longonot National Parks, and a series of private wildlife conservancies. It is located on the floor of the Great Rift-Valley at an elevation of approximately 1890 m. Rainfall occurs in two main seasons (March-May, October-December). Mean annual rainfall is approximately 600mm but characterized by high inter-annual variability (CV ~30%; Becht and Harper 2002). The lake experience frequent lake level changes due to increased discharge from its two main tributaries; Rivers Malewa and Gilgil (Harper et al. 1995). This is linked to land use/land cover (LULC) changes in the upper catchment of the basin (Odongo et al. *In Press*). The lake experienced a 58% (62 Km^2) increase in surface area between January 2010 and October 2013 (Onywere 2013). This flooding inundate of the riparian grasslands even during the dry seasons when they are expected to supplement the scarce forage for herbivores (Harper et al. 1995, Onywere 2013, Muthoni et al. 2014).

Vegetation zonation varies radially with increasing distance from the lake. It ranges from aquatic macropytes (mainly *Eichhornia crassipies* and *Cyperus papyrus*) to grassland then to shrubland and finally to *Acacia xanthophloea* woodland (Gaudet 1977a). Common grasses include *Cynodon dacytlon, Cynodon nlemfuensis and Penisetum clandestinum*. More than 25 native and introduced large ungulate species inhabit the area (Becht et al. 2006, Muthoni et al. 2014, Odongo et al. *In Press*). The common native grazers and mixed feeders include the hippopotamus (*Hippopotamus amphibious*), buffalo (*Syncerus caffer*), common zebra (*Equus burchelli*), eland (*Taurotragus oryx*), impala (*Aepyceros melampus*), Defassa waterbuck (*Kobus ellipsiprymnus*), Thompson's gazelle (*Gazella thomsonii*), common warthog (*Phacochoerus africanus*) and Grant's gazelle (*Gazelle grantii*). This is in addition to livestock (mainly cattle; *Bos indicus*) in private ranches and communal areas. Despite the decreasing grazing area, the ungulate density in the KRA is increasing partly due clearing of two forests; Eburru and Mau Escarpment that acted as their refuge (Harper and Mavuti 2004, Odongo et al. *In Press*). The construction of wildlife fences reduces habitat connectivity thus hindering free movement of herbivores between adjacent ranches. It also restricts communal livestock herding to a few accessible patches that are intensely grazed (Morrison and Harper 2009).

Historically, the area was a communal grazing range for wildlife and nomadic livestock (Harper et al. 2011). Currently, land is sub-divided into privately owned parcels of varying sizes with contrasting land-uses (Figure 1.1). Most land-owners practice wildlife conservation (eco-tourism), livestock ranching and horticultural farming at the same time. Lake Naivasha is the main source of cut flower in Kenya mainly for export (Becht et al. 2006). Extensive agriculture started since the beginning of the 19th century by European settlers and is driven mainly by the availability of water, available fertile and well drained volcanic soils, cheap labour and easy access to markets (Gaudet 1977a, Becht et al. 2006, Justus and Yu 2014). Other economic activities include commercial fishery and geothermal power production (Abiya 1996, Becht et al. 2006, Onywere et al. 2012).

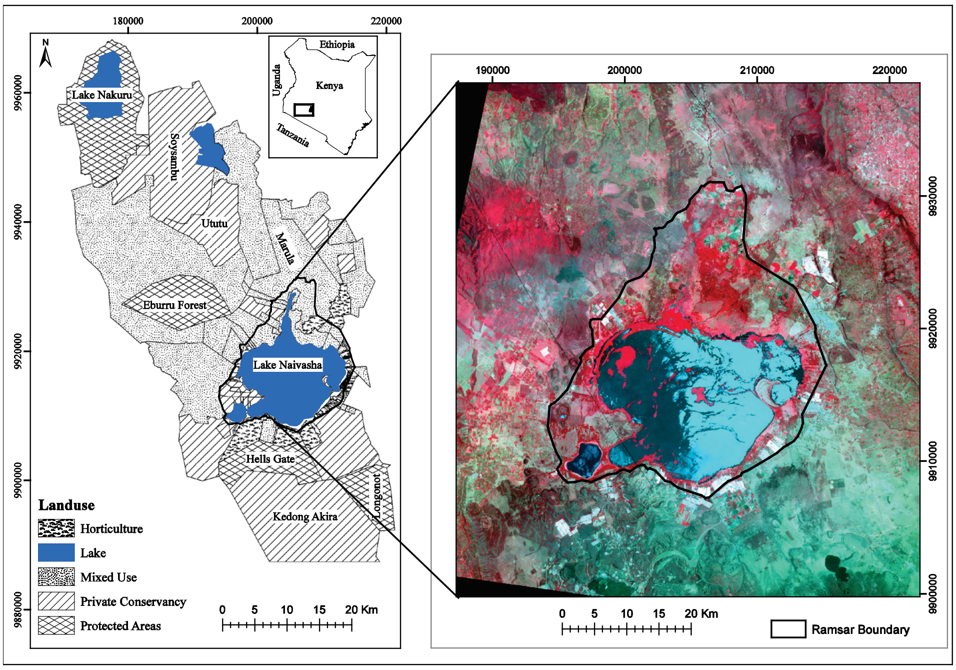

Figure 1.1. The location of Lake Naivasha RAMSAR site superimposed on an ASTER satellite image captured on September 2011 (right) and the main land-use for ranches within the Nakuru Wildlife Conservancy (left). The mixed land-use class represents ranches that practice farming (crop and livestock) and wildlife conservation

1.8 Integrated assessment of Lake Naivasha basin

This thesis is part of an "Earth Observation and Integrated Assessment of Lake Naivasha basin (EOIA)" project that investigated the hydrology, ecology, limnology and socio-economic processes within the basin. The project monitored the key indicators of sustainability that has been identified through stakeholder's analysis (figure 2; van Oel et al. In press). This thesis addresses the flora and fauna richness and abundance as the indicator for sustainability in the ecological subsystem (Figure 1.2).

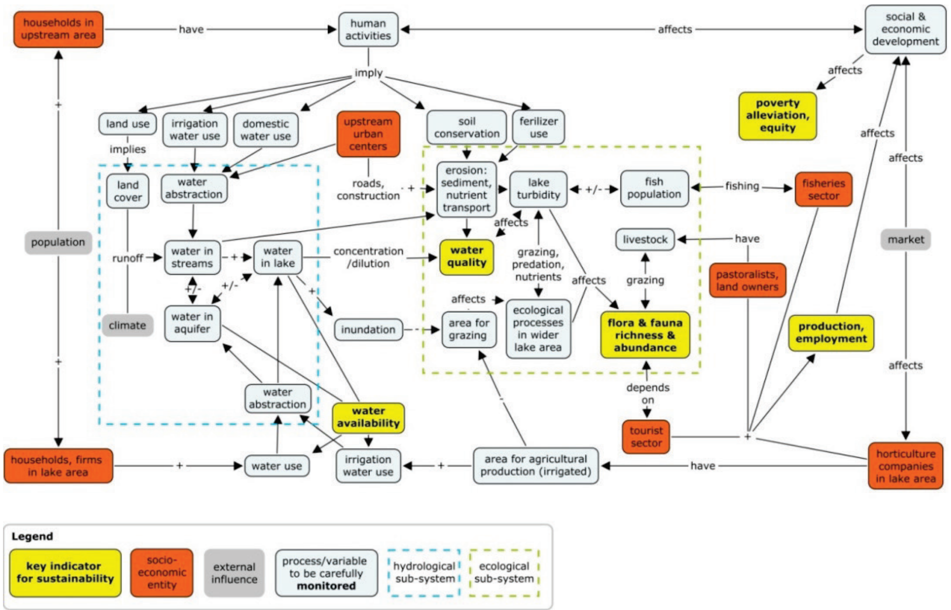

Figure 1.2. The key indicators for sustainability assessed in the earth observation and integrated assessment of Lake Naivasha (EOIA) project (van Oel et al. In press). This thesis addresses the flora and fauna richness and abundance in the ecological sub-system

1.9 Conceptual framework

The availability of key resources mainly the fresh lake water attracts high biodiversity and economic activities on the fringe zone of Lake Naivasha. The anthropogenic fragmentation emanating from economic activities together with frequent floods as a natural disturbance alters the biotic interactions within the KRA. This triggers a cascade of impacts through the ecosystem that change the large ungulate density and consequently their impact on plant community composition and diversity (Figure 1.3). This thesis assesses the drivers and magnitude of this change and evaluates novel methods for long-term monitoring. The thesis focus on the flora and faunal species richness and abundance, which is one indicator of sustainability identified for Lake Naivasha basin (Figure 1.2; van Oel et al. In press). The knowledge obtained from this monitoring and assessment in the KRA can be integrated with results from the other four subsystems in the integrated assessment project (Figure 1.2). Integration of these results is aimed at formulating holistic adaptive management strategies (Savory 1999) that promote persistence and co-existence of plant and ungulate species in this landscape and maintain provision of related ecosystem services.

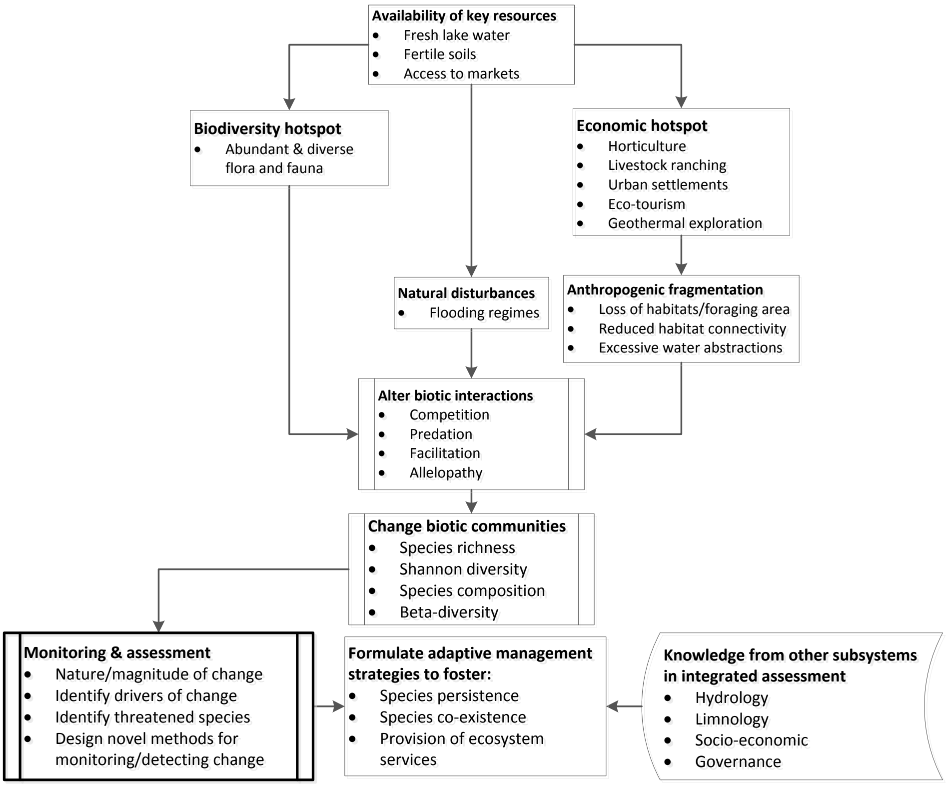

Figure 1.3. The conceptual framework. This thesis focuses on monitoring and assessment section (bold)

1.10 Thesis outline

Chapter one outlines the research problem, objectives, conceptual framework and the study area. It outlines the role of KRAs in regulating plant and herbivore diversity in savannas.

Chapter two investigates the drivers of large ungulate biomass density in the KRA along Lake Naivasha. It analyze how the socio-economic and hydrological processes cascade through different pathways in the ecosystem to alter its biodiversity pattern.

Chapter three investigates the impact of large ungulates grazing and rainfall on productivity (regrowth) and residual aboveground biomass of herbaceous plants.

Chapter four compares a novel method (ManyGLM) against the distance-based redundancy analysis (db-RDA) in detecting the multivariate effect of ungulate grazing on plant community composition and identification of the species that are most responsive to grazing. This chapter is a step toward chapter 5 where the novel method is applied to evaluate impact of ungulate grazing on herbaceous plant community composition in the study area.

Chapter five analyzes the impacts of continuous intense grazing by large herbivore on herbaceous plant diversity and composition in the fragmented KRA.

Chapter six evaluates the relative contribution of environmental heterogeneity and species dispersal limitation (spatial distances) on variation in plant beta-diversity in a highly fragmented KRA. It explores the utility of spectral variation in Landsat satellite imagery as a surrogate for environmental heterogeneity that can be used for monitoring long-term spatial patterns in plant beta-diversity in data limited and remote rangelands that are experiencing varying levels of environmental stress and disturbances. It partitions the variance explained by spectral variation as a surrogate for environmental heterogeneity and the spatial distances (surrogate for species dispersal limits) in explaining variation in plant beta-diversity.

Chapter seven synthesizes the knowledge from all chapters in this thesis particularly how: (1) the impacts of socio-economic activities cascades through different pathways in the ecosystem to affect ungulate biomass on ranches in the lower catchment of Lake Naivasha (chapter 2); (2) the ungulate grazing and rainfall regulate herbaceous residual biomass and regrowth in the KRA (chapter 3); (3) a new method (Manyglm) improves detection of grazing signal on plant community composition in savannas (chapter 4); (4) intense grazing reduces the competitive dominance of perennial grasses and increases the species richness and abundance of annual forbs (chapter 5); and (5) the spectral variation of Landsat imagery as a surrogate for environmental heterogeneity explains higher variance on plant beta-diversity patterns than species dispersal limitation (spatial distances) (chapter 6).

Chapter 2

The drivers of wild ungulate species biomass on the downstream catchment of Lake Naivasha[*]

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[*] Partly based on:

Odongo, V. O., Mulatu, D. W., Muthoni, F. K., van Oel, P. R., Meins, F. M., van der Tol, C., Skidmore, A. K., Groen, T. A., Becht, R., Onyando, J. O. & van der Veen, A.. Coupling socio-economic factors and eco-hydrological processes using a cascade-modeling approach. Journal of Hydrology. DOI: http://dx.doi.org/10.1016/j.jhydrol.2014.01.012 ***(In press)***

van Oel, P. R., Odongo, V.O., Mulatu, D. W., Muthoni, F. K., Ndungu, J. N., van der Veen, A. Supporting IWRM through Spatial Integrated Assessment for the Lake Naivasha basin, Kenya. International Journal of Water Resources Development. DOI:http://dx.doi.org/10.1080/07900627.2014.920248 ***(In press)***

van Oel, P.R., Odongo, V.O., Mulatu, D.W., Ndungu, J., Muthoni, F.K., Ogada, J., et al., 2012. An earth observation and integrated assessment (EOIA) approach for the sustainable governance of a socio-ecological system: the case of the Lake Naivasha basin, Kenya. In: Proceedings of Water Management Issues in Africa: Scientific conference of the NASAC-KNAW collaboration initiative with MAST and Leopoldina on 28-31 March 2012, Réduit, Mauritius.

Abstract

Socio-economic developments in African savannas have resulted to drastic land use/land cover (LULC) conversions with consequent impacts on diverse ecosystem properties. These conversions are more pronounced on agro-pastoral landscapes surrounding wetlands in the dry lands as availability of water attracts agricultural developments. This study uses a cascade modelling approach to investigate how the socio-economic drivers of LULC change cascade through the ecosystem to affect its hydrology and biodiversity. The ungulate biomass in the downstream catchment of Lake Naivasha basin is used as an example. Results revealed a steady increase in ungulate biomass during the study period. It also revealed a sequential high correlation between flower export volume, downstream population and LULC change. The LULC change was significantly correlated with the ungulate biomass. Increased LULC conversions led to aggregation of high ungulate biomass in wildlife friendly ranches along the riparian zone that offer active protection against poaching. This study demonstrates that a cascade modelling approach can improve understanding of how a series of interlinked processes affect biodiversity pattern in an ecosystem.

Key words: Socio-economic; Land use and land cover change; eco-hydrology; cascade modeling; path analysis

2.1 Introduction

Wetlands in African savannas are experiencing rapid rate of socio-economic developments that accentuate anthropogenic fragmentation (Scoones 1991, 1995). This has caused widespread land use/land cover (LULC) changes driven largely by agricultural expansion in former pastoral communal areas (Ottichilo et al. 2000, Western et al. 2009a, Msoffe et al. 2011, Ogutu et al. 2014). These landscapes have traditionally supported abundant and diverse wild ungulate species. The wild herbivores in Kenyan rangelands (except for ostrich) have declined by over half in the last three decades (Ottichilo et al. 2000, Western et al. 2006, Norton-Griffiths 2007, Western et al. 2009b). The decline is largely attributed to LULC changes that reduce the size, quality and connectivity of their habitats (Mundia and Murayama 2009, Western et al. 2009a).

Habitat fragmentation is more severe in wildlife areas located outside the protected areas where development is largely unregulated (Western et al. 2009a, Msoffe et al. 2011). However these landscapes holds about 70% of total wildlife population in Kenya (Western et al. 2006, Norton-Griffiths 2007). The persistence of wildlife inside the protected areas partly depends on these human dominated landscapes as they are migration corridors

(Msoffe et al. 2011) or key resource areas (KRAs) that maintain herbivore populations during the dry seasons (Ngugi and Conant 2008).

The fringe zone of Lake Naivasha is a KRA that was traditionally used for dry season grazing by wild ungulates and nomadic Maasai herdsmen (Harper and Mavuti 2004). However availability of fresh lake water has attracted growth of horticulture industry and socio-economic activities that support or depends on this industry. This has increased the employment opportunities leading to almost ten-fold increase in human population from 44,000 in 1969 to 376,000 in 2009 (Onywere et al. 2012). The expansion of horticulture and settlements reduce the grazing area and alter the migration corridors. Despite the increased socio-economic activities and LULC changes experienced in the lower catchment of Lake Naivasha basin, there is limited knowledge on the impacts of these changes on the biomass of ungulate species. No attempt has been made to analyze the direct and indirect socio-economic processes that drivers the LULC changes and the pathways through which their impact is propagated through the ecosystems to affect the ungulate biomass. Such analysis can identify the most significant drivers of LULC that should be prioritized by conservation initiatives that promote persistence of ungulates in this agro-pastoral landscape. However, identifying these driving factors and processes is confounded by multiple causalities and time-frames at which the processes take effect (Mundia and Murayama 2009).

This study identifies the trend in wild ungulates biomass in the lower catchment of Lake Naivasha basin and the socio-economic and hydrological factors that drive this trend. The study also examines the relative strength of the direct and indirect pathways through which the socio-economic and hydrologic impacts are propagated through the ecosystem to influence the ungulates biomass. The pathways define the propagation of influences from the trigger mechanism and how it is perpetuated through intermediate entities to a response variable that experience the final consequences (Reiners and Driese 2001). The organization of such links is described as a cascade where a series of connected links originate from a trigger that is translated through chains of interdependent elements terminating in a response variable (Burcher et al. 2007).

A cascade modelling approach using path analysis (Shipley 2000) is used to analyze the strength of correlations between entities or responses in the hypothesized pathways. The cascade modeling approach using path analysis as adopted in this study enhances understanding of a complex system with knowledge cross-cutting the socio-economy and eco-hydrology disciplines. This approach is less data demanding and therefore suitable in this relatively data poor environment. It certainly is not the most robust method to apply in a study that involves feedback mechanisms; however, it is a better method to apply in a data scarce environment. Alternatives to cascade modeling would be process-based models (e.g. agent-based models (ABM) or system-dynamics (SD)) that account for relevant feedback mechanisms, explore impacts of future scenarios or compare effects of alternative measures. However, these alternatives are data intensive and complex compared to path analysis. The advantage of using path analysis, however, is that it mirrors theories of causation and inform on which hypothesized causal models best fits the observed pattern of correlations among datasets (Burcher et al. 2007). Also the approach allows one to decompose various factors affecting an outcome into direct and indirect components. This way the method is a first step in developing clear and logical theories about processes influencing a particular response in a system (Lleras 2005).

This chapter is part of a wider study that aimed at quantifying the impacts of socio-economic factors on eco-hydrological regime of Lake Naivasha Basin using a conceptual framework based on cascade modeling. In this chapter only the cascade of the socio-economic and hydrological processes on ecological response (ungulate species biomass) in the downstream catchment of Lake Naivasha is presented. The hypothesized pathways and the direction of effect are shown in Figure 2.3. It was hypothesized that the increased LULC change would cause decline in ungulates biomass since expansions in horticultural farms and human settlements reduce the grazing lawns.

2.2 Methods

2.2.1 Study area

The Lake Naivasha basin is situated in the Great Rift-Valley at a latitude of 0^o 09′ to 0^o 55′S and longitude of 36^o 09′ to 36^o 24′E (Figure 2.1). The daily mean temperature ranges from 8^oC to 30^oC (Figure 2.2). The Lake Naivasha basin experiences an average annual rainfall of ~600 mm that occurs in two rainy seasons; the long rains occur between March - May and the short rains are experienced between October and November (Figure 2.2). The major soils in the study area are of volcanic origin.

Lake Naivasha experience frequent fluctuations of water levels over time and has almost dried in the past years (Gaudet 1977a, Abiya 1996, Verschuren et al. 2000, Onywere 2013). This natural fluctuation, combined with increasing water abstractions have led to occasionally strong decreases of the lake water levels (Becht and Harper 2002, Ondimu and Murase 2007, Otiang'a-Owiti and Oswe 2007, Olaka et al. 2010, Trauth et al. 2010). The frequent fluctuation in lake levels induces vegetation succession along the floodplain thus increasing habitat heterogeneity (Gaudet 1977a). The decline in lake levels increases the grazing area for herbivores. The lake is a RAMSAR wetland (Ramsar 1996). It supports economic activities that include fishing, agriculture, power generation, domestic water supply and eco-tourism (Becht et al., 2005).

Moreover, the basin has experienced increasing pressures on its land and water resources due to an increase in population that is mainly attracted by a flourishing horticultural industry since early 1980s (van Oel et al. 2013). The industry has supported and sustained the economy of the basin through production and export of flowers. The agriculture has encroached on previously communal grazing with significant effects on large herbivore species (Harper and Mavuti 2004).

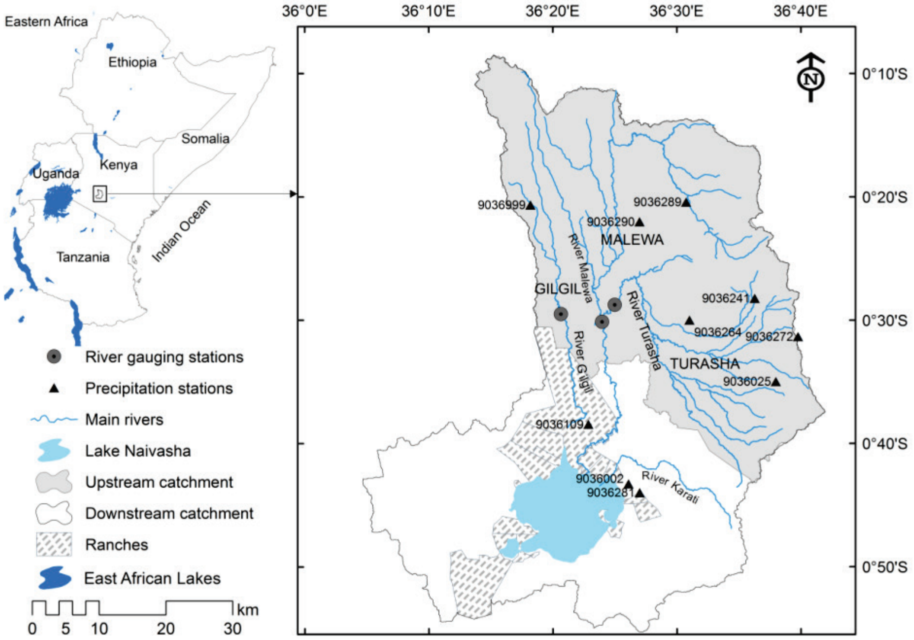

Figure 2.1: Lake Naivasha Basin showing its main rivers and tributaries. The sample ranches in the downstream catchment are highlighted

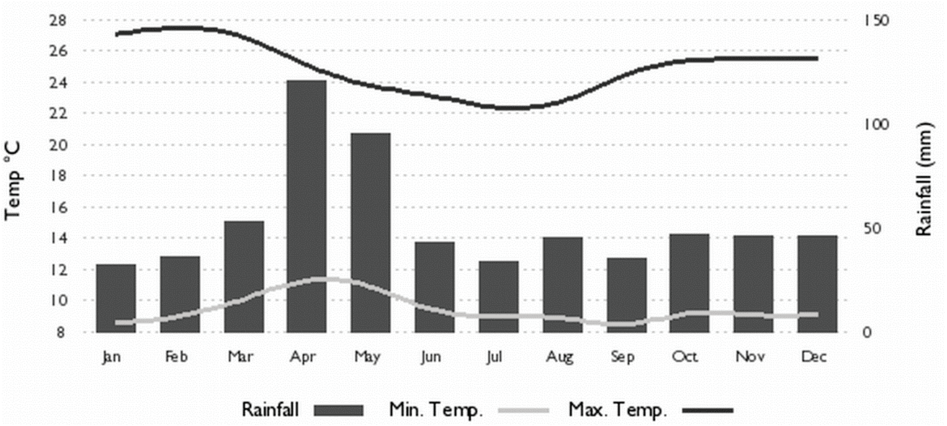

Figure 2.2. Monthly average climatic conditions of temperature and rainfall for Lake Naivasha

2.2.2 Ungulates population data

Downstream LULC and hydrological regimes can impact on biomass density of large herbivore mammals. The trend in large herbivore mammal’s population was obtained from biennial (April and October) wildlife census conducted by Nakuru Wildlife Conservancy (NWC) from 1999 to 2010. The data was collected using a total count of large mammal species on all ranches between Lake Naivasha and Lake Nakuru (Figure 2.1). During the census, the ranches were divided into fixed counting blocks in each ranch delineated by physical barriers such as hills, escarpments and the lake. Each block was assigned a counting team consisting of experienced Kenya Wildlife Service scientists, ranch staff and trained volunteer scouts. Counting was carried out between 0600 to 1000 hrs when most of species are active. This was done using vehicles or walking in some inaccessible sections. Detailed information on the survey method is outlined in Ogutu et al. (2012).

For this study, we selected data for the 11 most common grazers or mixed feeders (Table 2.1) in 16 sampling blocks that are immediately adjacent to Lake Naivasha (Table 2.2). The herbivore numbers were converted to biomass density (kg km^{-2}) using units weights in Coe et al. (1976) and the total area of sampling blocks (275 km^{2}).

2.2.3 Hydrological variables

The rainfall and lake levels are the hydrological variables included the cascade model. Previous studies have demonstrated that the ungulates biomass is correlated with annual rainfall since the later increase forage productivity (Coe et al. 1976, East 1984). The amount of rain that fall on the Lake and its immediate precincts (lake precipitation) was derived as the annual averages for rainfall recorded in three gauging stations (9036109, 9036002 and 9036281; Figure 2.1). Change in lake levels determine the frequency of inundation in the riparian floodplain that in-turn affect forage productivity (Ogutu et al. 2012). Annual averages for the lake levels were computed by averaging daily lake level measurements recorded from a gauging staff located at the Yacht Club on the Eastern shore of Lake Naivasha.

Table 2.1. The unit weights for surveyed wild ungulate species. * represent the mixed feeders while the rest are exclusive grazers

Common name	**Scientific name**	**Unit weight (Kgs)**
Common Zebra	*Equus burchelli*	200
Thomsons Gazelle*	*Gazella thomsonii*	15
Impala*	*Aepyceros melampus*	40
Eland*	*Taurotragus oryx*	340
Buffalo	*Syncerus caffer*	450
Grants Gazelle*	*Gazella granti*	40
Coke's Hartebeest (Kongoni)*	*Alcelaphus lichtensteinii*	125
Defassa Waterbuck	*Kobus ellipsiprymnus*	160
Wildebeest	*Connochaetes taurinus*	123
Common warthog	*Phacochoerus africanus*	45
Hippo	*Hippopotamus amphibius*	1160

Table 2.2. The mammals census blocks

Sampling block	Area (Acres)
Crater Lake/ Indu / Lentolia	1000
Mundui	1145
Hippo Point/ Nderit	500
Olerai	500
Oserian Wildlife Sanctuary	18000
Oserian Game Corridor	3000
Crescent Island	190
Bushy Island/Flay/Yatch club/D'Olier/Higgins/Sanctuary	100
Marula	25000
KARI/Morendat/Ol Magogo	10000
Loldia	6000
Manera	1600
DDD Rocco Farm	200
KWSTI Institute/Annex/Mirera	200
Green Park/Brixia Ltd	1500

2.2.4 Land use/cover variables

Land use/cover was extracted from time series satellite imagery (Table 2.3) using remote sensing techniques. A stratified random sample of 302 ground reference points in major LULC spaced at a minimum distance of 1 km were collected using a GPS. Ground photos taken with a handheld camera and aerial photos of August 2010 acquired from Department of Remote Sensing and Resource Survey (DRSRS) of Kenya were also used to support interpretation and extraction of extra ground reference data.

Table 2.3. Characteristics of satellite images used for LULC classification

Sensor	Spatial resolution (m)	Date	Cloud cover (%)
Landsat TM	30	01-01-86	5
Landsat TM	30	01-02-87	9
Landsat TM	30	14-01-11	13
Landsat TM	30	17-01-11	10

Unsupervised classification was conducted on all the images using the ISODATA algorithm with an initial set of 50 classes. The 50 unsupervised classes allowed for identification of contiguous homogenous classes. Overlaying ground reference points on the contiguous homogenous classes enabled defining of regions of interest (ROIs) for use in supervised classification. A ROI was extracted at locations of each ground reference point. The Jeffries-Matusita (J-M) class separability test was also performed to distinguish different classes based on their spectral profiles (Thomas et al. 1987).

Ground reference points collected during the study (January to March 2012) and aerial photos captured in August 2010 were used to distinguish classes resulting from supervised classification of the 2011 images. Half of the ROIs (n = 151 ROIs) were used for training the maximum likelihood classifier to develop 12 main land use/cover classes of Lake Naivasha Basin for the year 2011. The other half of the reference data (n= 151) were used to conduct the accuracy assessment of the classified LULC map for 2011. Since there was no ground truth data collected in 1986, the LULC map for this year was produced using unsupervised classification in combination with known spectral signatures derived from the 2011 LULC map.

Single LULC change dynamic degree (Puyravaud 2003; Eq. 1) was employed to quantify the rate of LULC change between 1986 and 2011.

$$K_i = \left[\frac{LU_{bi} - LU_{ai}}{LU_{ai}} \right] \times \frac{1}{T} \times 100\% \qquad (1)$$

where K is the annual rate of change of a specific LULC type i, in a fixed time period. LU_{ai} and LU_{bi} is the area of the LULC type i at the beginning and the end of the time period, respectively; and T is the time period. Therefore the rate of LULC change between 1986 and 2011 was used to extrapolate the LULC for each cover class for years that did not have a classified map. A principle components analysis (PCA; Legendre and Legendre 2012) was carried-out on the LULC data (area in Km^2 for each cover type per year) to obtain an orthogonal linear combination of land cover values for each year. The first PCA axis that explained 99% of variance LULC data was used in the subsequent analysis to represent the LULC for each year.

2.2.5 Socio Economic variables

The flower export volume is an indicator for the level of economic activities in the downstream catchment that attracts human population as labourers in horticulture and related industries (Mulatu et al. 2013). Annual flower export volume from 1994 to 2010 was provided by the Kenya Horticultural Crops Development Authority (KHCDA). Decadal human population census data from 1969 to 2009 was provided by the Kenya National Bureau of Statistics (KNBS).

2.2.6 Development of the cascade model

Possible causal paths that linked socio-economic indicators to LULC, hydrological and ecological indicators in the Lake Naivasha basin were established. This chapter presents the results of the cascade model of the downstream catchment only (Figure 2.3). The model explores how the impacts of the economic activity (flower export volume) cascade through the ecosystem to affect the downstream LULC conversions and hydrological regime (lake levels and precipitation) that ultimately impact on the biomass of large wild ungulates (the response).

In this cascade model, the flower export volume as an indicator of economic activity is the stimuli which its impacts are propagated through water abstracted for irrigation and domestic use by the increased human population to affect the lake levels. The developments associated with the horticultural farms have seen an increase in flower export volumes (Otiang'a-Owiti and Oswe 2007). This has led to increased downstream population that is attracted by employment opportunities in the horticultural farms (Mulatu et al. 2013). Increased horticultural farming and human population has consequently increased water abstraction from the lake leading to decrease in lake levels (Becht and Harper 2002). Decline in lake levels increases the grazing area for ungulates (Ogutu et al. 2012). The precipitation falling on the Lake area increases the water levels. It can also increase the ungulate biomass indirectly by promoting forage productivity (Coe et al. 1976, East

1984). Moreover the increased human population accentuates LULC conversions to create more horticultural farms and settlements. This was hypothesized to reduce the ungulates habitats and biomass.

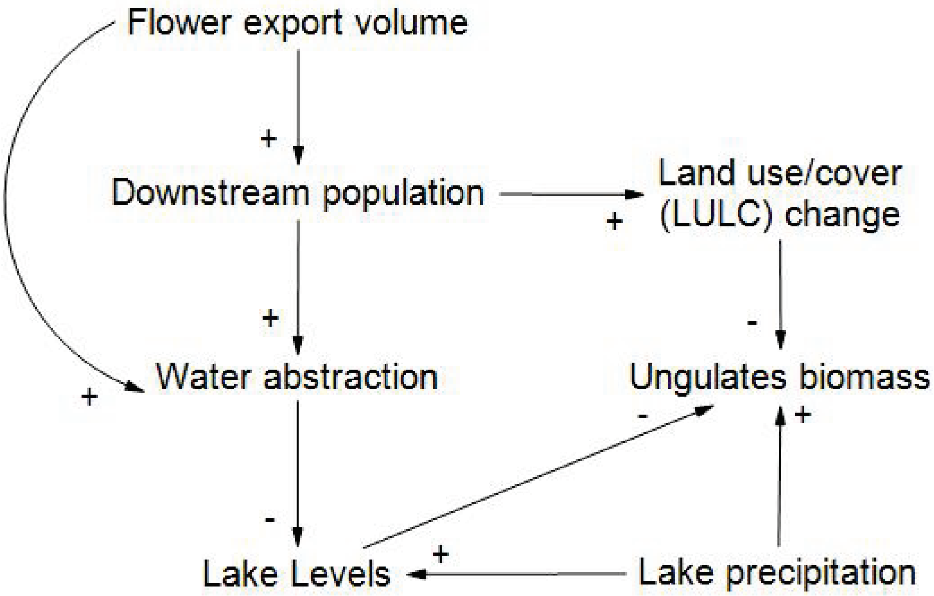

Figure 2.3: The hypothesized cascade model for the downstream catchment that is triggered by flower export with impacts propagating through downstream population, LULC change and hydrological variables to affect the ungulate biomass which is the response variable. The lake levels are reduced by water abstraction and increased lake precipitation. +/- indicates the hypothesized direction of change of the effect

Path analysis (Shipley 2000) was used to quantify the strength of direct and indirect effects of downstream human population, LULC changes, annual precipitation and lake levels changes on the total ungulate biomass density ($Kg^{-1}Km^{2}$). Path analysis use relationships which are defined *a priori* and follow a specific causal hypothesis guided by a conceptual framework to estimate the magnitude and strength of effects (Maloney and Weller 2011). The conceptual framework is normally represented using graphical path diagrams that infer causality as predetermined by a researcher's knowledge of the system. The requirement of *a priori* hypothesis in path analysis makes it an appropriate tool to predict important interactions in a system. The paths are then evaluated either by path coefficients or multiple regression coefficients. Multiple regression coefficients provide information about the correlation between pairs of variables, predicting how much the dependent variable changes with a given change in causal variable (Wootton 1994). Path coefficients indicate the strengths of association, providing a relative measure of the amount of variance explained by different causal variables and the sign of the interaction or effect from the causal variable (Wootton 1994, Grace et al. 2010).

Path analysis was undertaken using Amos version 5.0 (Arbuckle 2006). The estimated path coefficients and multiple regression coefficients were standardized by the ratio of the standard deviations of the independent and dependent variables to allow relative comparison of magnitudes of effects on the different dependent and response variables (Lleras 2005). Detailed description of formulation and procedure in path analysis are given in Shipley (2000).

The standardized partial regression coefficients were used to quantify the amount of variance in dependent and response variables as depicted over an entire pathway or section explained by the preceding cascade model.

2.3 Results

The cascade model revealed that the flower export volume had a 93% correlation with downstream population that in-turn had a strong significant positive effect (99%) on LULC changes (Figure 2.4). The total herbivore biomass density on the fringe zone had almost tripled over the study period (Figure 2.5). This was related to a 93% positive direct correlation with LULC changes. Lake levels had a 4% direct correlation with ungulate biomass while precipitation over the lake had a 4% negative direct correlation. The four variables in the ungulate biomass cascade explained 78% multivariate effect of total ungulate density.

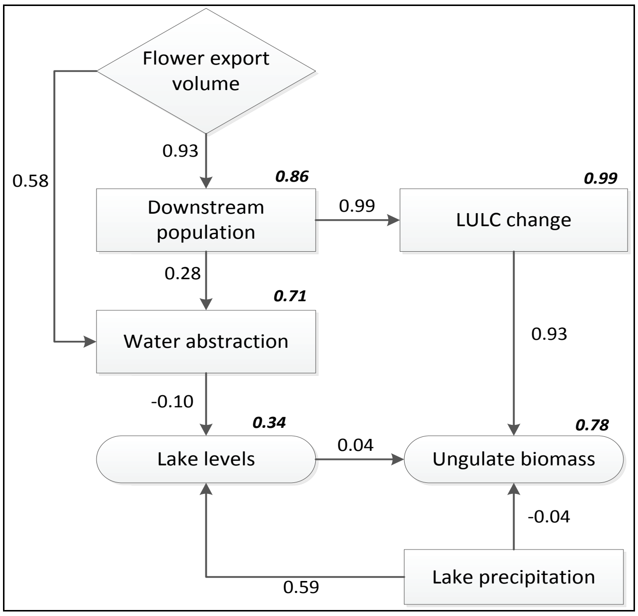

Figure 2.4: Results of the cascade model. Numbers along the arrows are standardized path correlation coefficients and represent the direct bivariate effect of the two linked variables. Bold and italicized numbers on the edges of effect or response variables represent the multiple correlation coefficients that describe the multivariate strength of the preceding model.

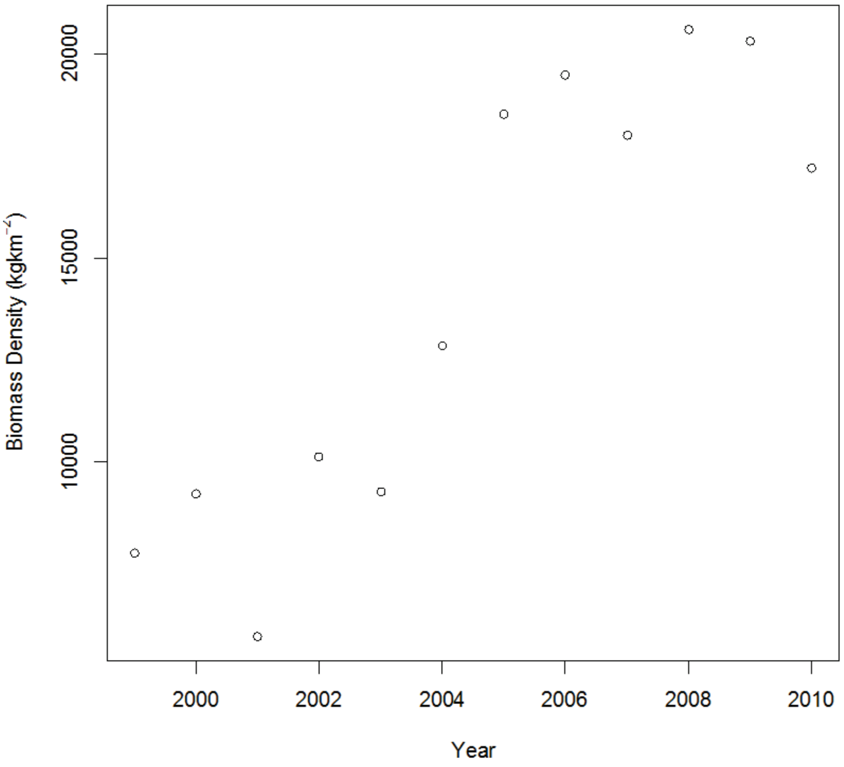

Figure 2.5: Total herbivore biomass density for 12 years on ranches adjacent to Lake Naivasha

2.4 Discussion

Results reveal that increased economic development in the downstream catchment of Lake Naivasha attract population growth that in-turn accentuate the LULC changes. The LULC change was highly correlated with ungulate biomass in the ranches adjacent to Lake Naivasha. The ungulate biomass increased steadily during the period of the study. This was contrary to our hypothesis that LULC changes would reduce the ungulate biomass due to loss of habitats and grazing land. The results also contrast with studies that observed that increased LULC conversion triggered a decline in herbivore biomass density in rangelands within or outside the protected areas (Worden 2008, Mundia and Murayama 2009, Western et al. 2009a). However our results concur with (Harper and Mavuti 2004), who observed that the ungulates biomass especially the buffaloes (*Syncerus cafer*) in the riparian zone had tripled compared to mid-1990’s. They attributed this increase to deforestation of Eburru forest, to the west of the Lake, that previously acted as a refuge of ungulates (Harper and Mavuti 2004). The LULC conversion reduced habitats for the wild ungulates and increased human-wildlife conflicts such as crop raiding and poaching (Mailu et al. 2010). The combination of above factors could have triggered aggregation of the ungulates in the wildlife tolerant ranches on the riparian edge that have lower risk to poaching. These ranches are engaged in eco-tourism and therefore actively protect their wildlife from poaching by providing armed patrol guards and construction of wildlife fences (Muthoni et al. 2014). Active protection in fragmented landscapes can increase resident wildlife biomass as the habitat fragments provide last refuge for certain species (Worden 2008). Nevertheless, the impact of active protection on ungulate biomass in the wildlife friendly ranches in this landscape needs further investigation.

Results also agrees with Western et al. (2006) who observed a non-significant increase in wild ungulate biomass in privately protected wildlife sanctuaries within the Nakuru Wildlife Conservancy (NWC) between 1996-2003. However long-term data on ungulate populations in this landscape is lacking since the earliest systematic monitoring started after 1996 when establishment of private wildlife conservancies became popular (Western et al. 2006).

The low variance explained by the annual precipitation on the herbivores biomass contradicts earlier observations that ungulates density is dependent on annual precipitation (Coe et al. 1976, East 1984, Georgiadis et al. 2003, Ogutu and Owen-Smith 2003). The changes in lake levels was also expected to have significant impact on ungulate biomass since decline in levels increase the area of the highly productive riparian grazing land (Muthoni et al. 2014). However this riparian grassland experience frequent and prolonged flooding even during the dry seasons (Onywere 2013). This reduces the grazing area even during the dry seasons when it is expected to have higher forage compared to non-inundated upland grasslands. Prolonged flooding due to increased lake levels has been observed to reduce herbivores population in the nearby Lake Nakuru as it reduces the foraging area (Ogutu et al. 2012).

2.5 Conclusions

This study investigated the cascading impacts of socio-economic drivers of LULC changes on wild ungulates population in the lower catchment of Lake Naivasha. Horticultural expansion has triggered increase in human population that in-turn accentuates LULC changes in this landscape. The downstream LULC change was highly correlated with increase ungulates biomass in the privately protected ranches along the riparian zone. This study demonstrates that the cascade modelling approach can improve understanding of how a series of interlinked processes affect biodiversity pattern in an ecosystem.

Acknowledgements

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Chapter 3

Ungulate herbivory overrides rainfall impacts on herbaceous regrowth and residual biomass [*]

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[*] This chapter is based on:
Muthoni F.K., Groen T.A., Skidmore A.K. & van Oel P. (2014). Ungulate herbivory overrides rainfall impacts on herbaceous regrowth and residual biomass in a key resource area. Journal of Arid Environments, 100–101, 9-17. http://dx.doi.org/10.1016/j.jaridenv.2013.09.007

Abstract

Key grazing lands that provide dry season forage to both resident and migrating ungulates may experience heavy grazing impacts during the dry season, thereby jeopardizing future forage productivity. In this study a herbivore exclosure experiment was used to quantify the effects of grazing by large ungulates on herbaceous regrowth and residual aboveground biomass in a fragmented key resource area; the fringe zone around Lake Naivasha, Kenya. Top-down control mechanisms were prevalent in both the dry and wet seasons suggesting the existence of a high resident herbivore density. Intense grazing significantly reduced residual biomass that in turn reduced plant regrowth. An increased frequency of defoliation reduced regrowth during the dry season demonstrating the negative effect resulting from high herbivore densities during the dry season. This study indicates that grazing exerts a higher control on regrowth than rainfall as heavily grazed residual biomass did not recover during the following wet season.

Key Words: Top-down control, grazing intensity, herbivore exclosure, Lake Naivasha.

3.1 Introduction

Savanna grasslands are abundantly inhabited by a diverse mix of wild and domesticated herbivores. Grassland productivity is key in providing forage for animals and contributes significantly to global carbon sequestration and stocks (Tanentzap and Coomes 2011) and local nutrient cycling (Augustine and Frank 2001). Despite benefiting from the available forage, herbivores have both positive and negative impacts on herbaceous productivity (e.g. McNaughton 1985, Pandey and Singh 1992, Chase et al. 2000). Positive impacts include stimulation of growth after grazing (compensatory growth) (McNaughton et al. 1996), nutrient cycling (Augustine and McNaughton 2006) and enhancing species diversity (McNaughton 1985). However they may negatively influence herbaceous productivity through reduction of photosynthetic area, loss of nutrients for growth stored in shoots or removal of apical meristems that produce new shoots (Noy-Meir 1993). Herbivore grazing may also reduce survival fitness of the plant due to injury on the stolons or rhizomes (Keya 1997, Anderson and Frank 2003) and physical damage by trampling (Belsky 1992). Moreover, overgrazing may promote bush encroachment (Coetzee et al. 2007, De Knegt et al. 2008) and favour growth of less productive annual grasses and forbs over perennial grasses (Keya 1997).

The magnitude of herbivore effects on vegetation productivity in climatically variable ecosystems remains unresolved. There are no unifying hypotheses about herbivore impacts in African savannas, although several contradicting alternative hypotheses have been developed. The equilibrium hypothesis (DeAngelis and Waterhouse 1987) postulates a density-dependent relationship between herbivores and vegetation productivity, where herbivore density increases with increasing forage productivity until a threshold is reached where competition for forage among herbivores suppresses vegetation productivity. Alternatively, the disequilibrium hypothesis (Ellis and Swift 1988) posits that herbivores have no effect on vegetation productivity in ecosystems experiencing an approximately 30% variation in rainfall. Arguably, frequent droughts maintain herbivore densities at low levels beyond which density they can exert significant top-down control on plant productivity (Vetter 2005, Derry and Boone 2010).

The non-equilibrium hypothesis (Illius and O’Connor 1999, and 2000) argues that both equilibrium and dis-equilibrium processes occur alternately in both the spatial and temporal dimensions. This is facilitated by the presence of key resource areas such as lakes, waterholes, marshes and salt licks in savanna landscapes. Particularly, key resource areas act as dry season refugia where herbivores from surrounding wet season ranges aggregate. It’s argued therefore that during dry seasons key resource areas experience higher top-down control due to aggregation of herbivores that potentially cause further decline in productivity (Illius and O’Connor 1999, and 2000). In contrast, the surrounding wet season ranges are driven by non-equilibrium forces but they experience higher grazing pressure in the wet season due to the larger herbivore density that has been maintained in the key resource areas during scarcity (Illius and O’Connor 1999, and 2000). Therefore, monitoring herbivore impacts in key resource areas is not only important for their sustainable management, but also for the maintenance of diversity in the overlying rangelands.

In savanna landscapes, grazing lands fringing freshwater wetlands are key resource areas. Besides being critical watering points, their shorelines are abundant in high-quality forage. These resources attract high herbivore densities especially during the dry season. Nonetheless, some of these ecotones are prone to fragmentation from two directions (both landward side and lakeside) (Lachavanne and Juge 1997). These include both natural and human perturbations from the landward side, as well as fluctuations in water and nutrient-levels on the lakeside that have direct impact on vegetation productivity. The fringe zone of Lake Naivasha, Kenya, is a typical example. Though the fringe zone was historically a nomadic pastoral area (Abiya 1996), it now constitutes a unique and complex landscape mosaic centered around the Lake, comprising intensive horticulture, urban centres, ranches(wildlife and livestock), a national park and geothermal electricity generation.

Besides the prevalent natural and human induced fragmentation on the fringe zone itself (Onywere et al. 2012), the herbivores utilization of the fringe zone has increased due to a combination of (1) relatively high resident herbivore density (Smart et al. 2001, Harper and Mavuti 2004); Douglas-Hamilton, unpublished) (2) land cover conversions in the surrounding rangelands that trigger immigration of wildlife and livestock (Morrison and Harper 2009); (3) erection of electric fences on wildlife conservancies that lower habitat connectivity and concentrate high grazers densities in some zones and (4) the termination of a wildlife cropping programme since 2003. The combination of all the above has led to increased grazers densities, reduced grazing area, loss of habitat connectivity and probably deteriorated range conditions.

Despite all these documented changes, little is known about the herbivores' impacts on herbaceous vegetation productivity and aboveground biomass (AGB) accumulation in and around the fringe zone. Many studies have focused on productivity of a narrow band of the fringing *Cyperus papyrus* swamp (Muthuri et al. 1989, Jones and Muthuri 1997). It has been shown that the papyrus stands are more degraded at sites that are more accessible to large ungulates, especially buffaloes (Harper and Mavuti 2004, Morrison and Harper 2009). Moreover, in the nearby Hell's Gate national Park, overgrazing was reported to promote encroachment by *Tarchonanthus camphoratus* bushes (Coetzee et al. 2007) that hinders herbaceous productivity as a result of competition for moisture, nutrients and light.

Information on herbaceous productivity and consumption levels by large herbivores on the fringe zone is required for monitoring the ecosystem health (Tappan et al. 2004) and designing appropriate management plans such as wildlife cropping quotas. This can promote sustainable grazing intensities (i.e. managing the proportion of the forage that is consumed relative to available aboveground biomass). Following the predictions of the non-equilibrium hypothesis (Illius and O'Connor 1999, and 2000), it has been hypothesized that top-down control mechanisms are prevalent only during the dry season when grazers aggregate in the key resource area. Therefore, significant impacts of grazing on regrowth and residual aboveground biomass (forage availability) would only be experienced during the dry season. Moreover, regrowth is hypothesized to significantly decline in areas where grazing has been persistently strong, because with increased grazing, the survival fitness of the herbaceous vegetation is lowered due to resulting injury to their meristems, stolons and rhizomes where new tillers sprouts (Keya 1997). To test the above hypotheses, herbaceous biomass regrowth, the consumption by large ungulates and the resultant grazing intensities were estimated for different sites and seasons around Lake Naivasha. Inferences were drawn on the relative effects of both grazing and rainfall on herbaceous regrowth and residual aboveground biomass.

3.2 Methods

3.2.1 Study area

This study was undertaken on the fringe zone of Lake Naivasha (00 45'S and 36° 20'E) in an area covering approximately 500 Km^2 (Figure 3.1). Lake Naivasha is located at the floor of the Great Rift Valley at an altitude of 1890m a.s.l. Annual rainfall is approximately 600mm and is largely bimodal with two rainy seasons; the long rain (March to May) and short rains (October to December). The rainfall is characterized by high inter and intra - annual variability (CV ~ 30%) as witnessed in 2011 when the long rains were below average but the short rains were above normal rainfall (Figure 3.2). The mean temperature ranges from 20 - 26 C°. Soils range mainly from silt loam to clay soils with a humic topsoil that is relatively well drained (Hickley et al. 2004).

The land use on the fringe zone of the Lake has gradually evolved from pure nomadic pastoralism to sedentary farming and ranching (Becht and Harper 2002). As described by (Gaudet 1977a), the vegetation composition changes gradually with increasing distance from the Lake. Vegetation ranges from aquatic macrophytes (*Cyperus papyrus* and *Eichhornia crassipes*) to grasslands and shrublands dominated by *Tarchonanthus camphoratus* and climax into *Acacia xanthophloea* woodlands. Grasses are dominated by *Cynodon dactylon* (increaser II species) and *Pennisetum clandestinum*. Increaser II species are grass species that increase in overgrazed lawns (Danckwerts and Stuart-Hill 1987). Herbaceous species in the woodlands are dominated by *Hypoestes forskahlii and Achyranthes aspera* which are invasive, unpalatable and shade tolerant. These characteristics enhances their ability to spread fast, eventually competitively excluding the palatable perennial grasses (Ng'weno et al. 2010). Bush encroachment, mainly by *Tarchonanthus camphoratus (Coetzee et al. 2007), and Psiadia punctulata*, poses a threat to the distribution and productivity of grasslands (Ng'weno et al. 2010). Common forbs include *Tribulus terrestris, Euphorbia inaequilatera* and *Euphorbia prostrata*. The abundance of these forbs is considered as a bio-indicator of overgrazing (Keya 1998).

Common native grazers and mixed feeders include the hippo (*Hippopotamus amphibius*), buffalo (*Syncerus caffer*), common zebra (*Equus burchelli*), eland (*Taurotragus oryx*), impala (Aepyceros melampus) and Defassa waterbuck (*Kobus ellipsiprymnus*).

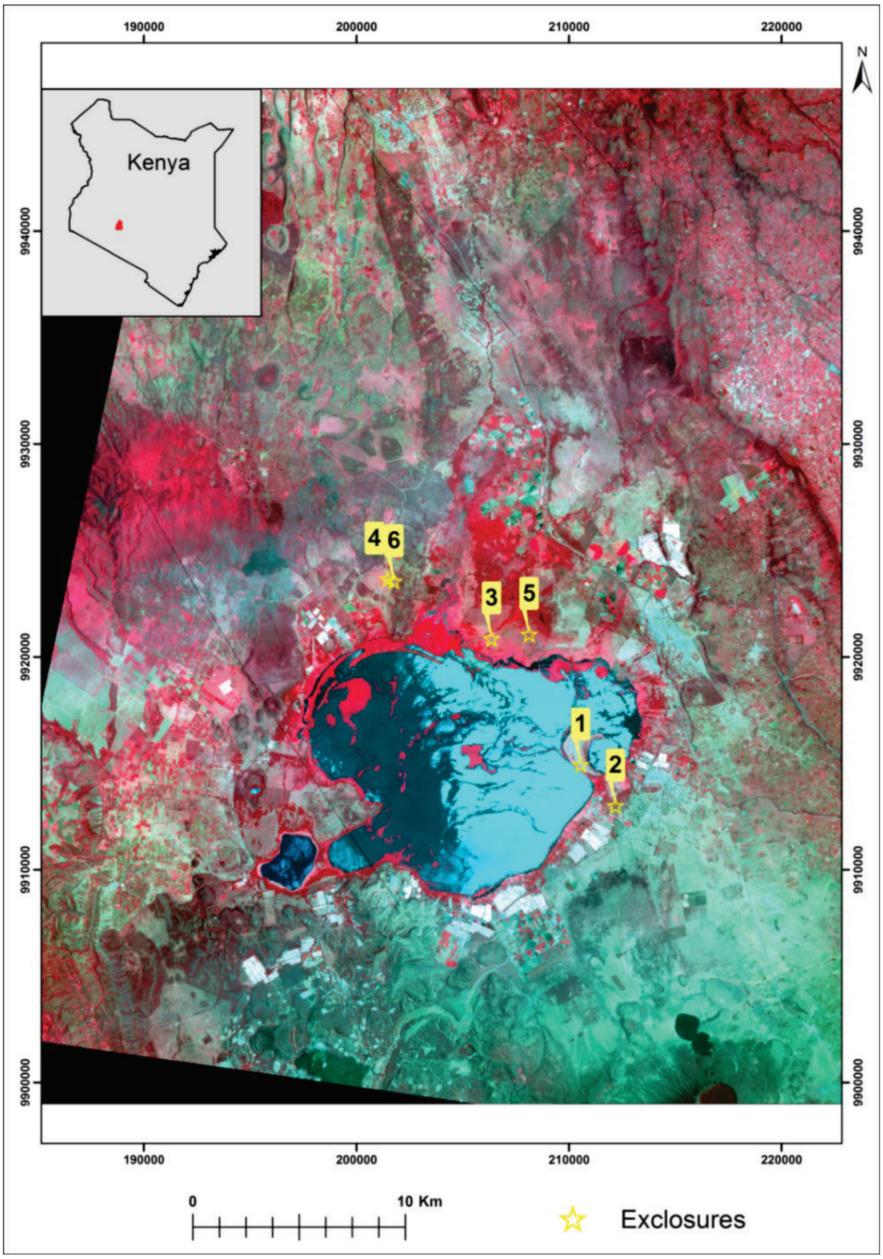

Figure 3.1. The locations of the exclosure experiments superimposed on ASTER satellite imagery taken on 22nd September 2011.

Table 3.1. The characteristic of the exclosure sites. Biomass of individual ungulate species was derived as product of their average live weights (Coe et al. 1976) and species population as per May 2011 census (NWC, Unpublished). The total ungulates biomass was derived by summing the biomass of all ungulate species in each farm. The ungulates densities are underestimated because they are distributed over a limited area in the farms due to other land uses but they can freely move between sites. The population of hippo's that reside in the Lake and can access multiple farms has not been fully incorporated

Site	**Area (Km^{-2})**	**Ungulates**		**Farm**	**Land cover**	**Dominant Grass species**
		Biomass (t)	**Density ($t^{-1}km^{-2}$)**			
1	1.6	167	104.9	Crescent Island	Open grassland	Cynodon nlemfluensis
2	3.3	182	54.8	Sanctuary	Wooded grassland	Cynodon nlemfluensis
3	6.7	55	8.2	Morendat	Open grassland	Cynodon dactylon
4	23.1	343	14.9	Loldia	Open grassland	Cynodon dactylon
5	13.0	172	13.2	KARI	Open grassland	Cynodon dactylon
6	23.1	343	14.9	Loldia	Bushed grassland	Cynodon dactylon

3.2.2 Experimental setup

Herbivore exclosure experiments were utilized to measure the effect of large herbivores on herbaceous vegetation productivity. Six herbivore exclosures were erected on four ranches surrounding Lake Naivasha (Table 3.1, Figure 3.1). Selection of the exclosure locations was based on vegetation type, ease of accessibility and security. The exclosures were 1.5m tall and ringed with barbed wire with a spacing of 15cm. Each exclosure measured 100 m^2 with two adjacent control plots of the same dimensions on either side. The exclosures and their control plots were subdivided into 25 lattice squares each measuring $4m^2$ (2x2m). This size was selected to adequately capture the spatial variability in herbaceous aboveground biomass within the quadrants. Two random quadrants inside each exclosure and in the two adjacent control plots were clipped at ground level approximately every 3 months for one year (June 2011 - June 2012).

The clipped materials were separated into live and total dead (moribund and litter) biomass and weighed separately. The samples were oven dried at $70C^0$ to constant weight before being reweighed to obtain their dry weight (g). In each subsequent clipping, two lattice squares were added to the ones that had already been clipped in the preceding period (Table 3.2). The phytomass clipped from each newly added lattice square at each time period was used to estimate the aboveground biomass. The biomass harvested from previously clipped lattice squares was used to estimate the regrowth under simulated 100% grazing intensity. Thus at the end of the experiment the quadrants that were initially clipped in June 2011 were clipped a total of 5 times while those initialized in June 2012 were clipped only once (Table 3.2).

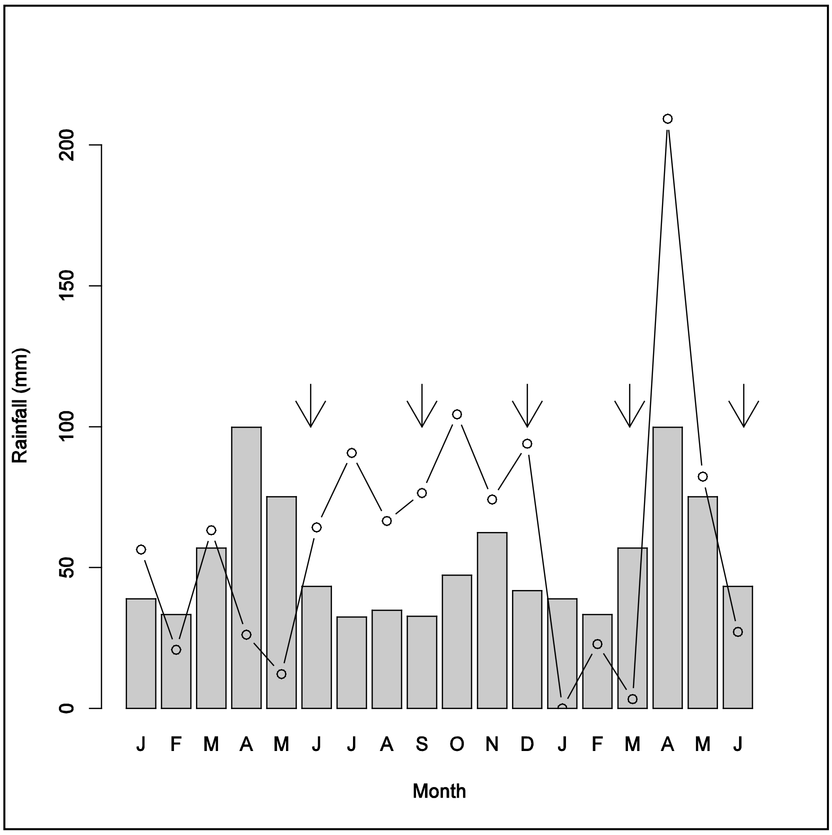

Figure 3.2. Long-term monthly mean rainfall (bars) and total monthly rainfall (solid line) from January 2011 - June 2012 recorded at Crescent Island; East of Lake Naivasha (site 1). The long-term mean was computed using 34 year (1978-2011) monthly rainfall recorded at Crescent Island and the KARI farm (near site 3). The arrows indicate the months when clipping was done.

Table 3.2. The experimental setup for grazed and ungrazed treatments. * and † indicates the lattice squares that were used to estimate the aboveground biomass and regrowth respectively. The numbers in the codes indicate the number of regrowth's that were subsequently clipped after the initiation clipping moment

	Total no. of Clippings				
Period	**5**	**4**	**3**	**2**	**1**
June 2011	*J0				
September	†S1	*S0			
December	D2	†D1	*D0		
March	M3	M2	†M1	*M0	
June 2012	JJ4	JJ3	JJ2	†JJ1	*JJ0

3.2.3 Estimating state variables

Two approaches were used to quantify the effect of grazing. First, the cumulative change in standing aboveground biomass between the grazed and ungrazed treatments was assessed (Mbatha and Ward 2010) and secondly the change in regrowth biomass (hereinafter referred to as regrowth) after simulated severe grazing intensity whereby all the standing crop in the previous season was totally clipped was assessed. The cumulative ungrazed regrowth biomass in each site reflected the potential total productivity (Milchunas and Lauenroth 1993). An approximate estimate of offtake by herbivores (*H*) was derived as the difference between the aboveground biomass of ungrazed and grazed treatments (Keya 1997). Following McNaughton (1985), grazing intensity (*G*) was derived as *1 - (g/ug)* where *g* and *ug* are grazed and ungrazed aboveground biomass at the end of each period. This resulted in a unitless metric ranging from 0 - 1 that reflected the magnitude of pressure exerted by the herbivores on the herbaceous aboveground biomass. The derived grazing intensities and observed grazed (residual) biomass were used to infer the impact of grazers on regrowth of herbaceous vegetation (Varnamkhasti et al. 1995, Keya 1997, Oba et al. 2000a).

3.2.4 Statistical analysis

The aboveground biomass and regrowth data were tested for normality using the Shapiro Wilk test$(\propto \leq 0.05)$ and Log-transformed to reduce heteroscedasticity. Following Augustine and McNaughton (2006), a split plot ANOVA with repeated measures was implemented to test for statistical differences between the grazing treatments at different sites and moments. The data were tested for sphericity using the Mauchley test and if the data did not pass the test, the resulting degree of freedom values were adjusted using the Greenhouse-Geisser correction to correct for type 1 errors (Quinn and Keough 2002).

For the split plot ANOVA models, the grazing treatment and sites represented the between subject factors while time was ‘within subject’ factor. Once significant$(\propto \leq 0.05)$ interaction effects for Grazing*Site and Grazing*Time were detected in the ANOVA model, Bonferonni post-hoc tests that limit type I error were applied to identify the sites or moments when grazing had a significant effect. Planned contrasts $(\propto \leq 0.05)$ were undertaken to test whether the aboveground biomass or regrowth of particular seasons differed significantly with that of previous season. This enabled trend analysis of the changes in the aboveground biomass or regrowth between seasons in relation to rainfall. The planned contrasts were undertaken using a 2-sided t-test using mean squared error from the overall split plot ANOVA for each treatment. The inter-seasonal comparison was related to monthly rainfall recorded at the long-term gauging station located at Crescent Island (site 1).

To disentangle the effect of the frequency of clipping on regrowth, the Kruskal-Wallis rank sum test was used to test whether the differences in the regrowth clipped at different frequencies were significant. This test was used because the data was not normally distributed even after log transformation. For this analysis only the regrowth in ungrazed treatments was utilized to avoid the uncontrolled interaction between natural grazing and clipping that might occur in grazed treatments (McNaughton et al. 1996). Moreover comparisons were made between regrowth from lattice-squares that were clipped in the same season but with differing number of clippings as per experimental design (Table 3.2). Once significant differences were detected following the Kruskal-Wallis test, multiple comparison tests ($p < 0.05$) were run using the Kruskalmc algorithm in pgirmess package (Giraudoux 2012) in R (R Development Core Team 2014).

3.3 Results

3.3.1 Grazing impacts on residual aboveground biomass

Results of the split plot ANOVA model for aboveground biomass revealed a significant main effect of grazing (F1, 24 = 66.15, p = 0.0001) and site (F5, 24 = 39.58, p = <0.0001). Similarly the interaction between Site*Grazing was significant (F5, 24 = 3.26, p = 0.022) revealing grazing impact was not consistent across sites. The ungrazed mean aboveground biomass weights were consistently and significantly higher than those of the grazed treatment, except for sites 5 and 6 ($p > 0.05$; Table 3.3). Moreover, the overall model also showed a significant interaction between Time*Site*Grazing (F10, 49 = 2.11, p = 0.04) revealing that the grazing did not have an equal impact on each moment at each site. The insignificant grazing impacts on site 5 (Table 3.3) may be due to prevalent tall, abundant and highly lignified grasses that are often avoided by grazers (Belsky 1992). The insignificant grazing impacts on site 6 may be due to high variability in aboveground biomass measurements as grasses were partly shaded by shrubs, thus creating patches of low and high aboveground biomass.

The interaction between Time*Grazing was highly significant (F2, 60= 11.29, $p < 0.0001$). The Bonferroni post-hoc test revealed that except for the pretreatment period (June 2011), the mean ungrazed aboveground biomass was significantly higher than that in the grazed treatment (Table 3.4). Planned contrasts showed that the grazed aboveground biomass was significantly different for all comparison periods except between June vs. September 2011 (Table 3.5). However, planned contrasts revealed that the ungrazed aboveground biomass was significantly different in two seasons: between June and September ($t = 3.012$, $P< 0.01$) and March and June 2012 ($t = 2.71$, $P< 0.01$) due to the effect of herbivore exclusion and increased rainfall respectively (Table 3.5). Though the mean ungrazed aboveground biomass was higher in December compared to September (Table 3.3) it was not significantly different ($t = 0.80$, $P< 0.43$) despite the prolonged wet spell.

3.3.2 Grazing intensity and offtake

High grazing intensities ranging from 0.59 to 0.75 were recorded at sites 1-4 (Table 3.3) that were dominated by short-medium height grasses. However, sites 5 and 6 had low intensities (Table 3.3). Considering the temporal dimension, the highest grazing intensities and off take were experienced during the dry spell in March 2012 (Table 3.4).

3.3.3 Grazing effect on regrowth

The results revealed significant main effects from Grazing ($F_{1, 24} = 43.09$, $p < 0.0001$) and Site ($F_{5, 24} = 39.03$, $p < 0.0001$) on levels of regrowth. The interaction effect between Site*Grazing was also significant ($F_{5, 24} = 3.86$, $p = 0.01$) and the ungrazed regrowth was higher compared to that in the grazed treatment, except in site 5 (Table 3.3). The Bonferroni post-hoc test showed that the difference between the grazed and ungrazed regrowth was only significant ($p < 0.01$) in Site 4. Similarly, the interaction effect between Time*Grazing was marginally significant ($F_{2, 48} = 2.78$, $p<0.047$) though a Bonferoni post-hoc test (Table 3.3) showed significant differences between grazed and ungrazed treatments in December ($p < 0.01$) and March ($p < 0.01$). The planned comparison for the different in grazed and ungrazed regrowth was significant between two sequential seasons (December vs. March and March vs. June 2012) due to the effect of moisture stress during a dry spells and increased rainfall in the ensuing wet season respectively (Table 3.5).

The driest season (end March 2012) had the lowest regrowth in both treatments revealing the importance of rainfall on regrowth (Table 3.4), even in areas directly near the lake. The cumulative annual regrowth (Table 3.4) in the ungrazed treatment was assumed to be the minimum potential productivity of the whole landscape considering that all regrowth was sequentially clipped at the end of each season.

Table 3.3. Mean annual aboveground biomass and regrowth (g m^{-2} yr^{-1}) for each site and treatments aggregated for post-treatment periods with the resulting off-take and grazing intensities. P values represent Bonferroni post-hoc results for Site*Grazing effect in overall split-plot ANOVA. Means are ± 1 SE

Site	**Ungrazed**	**Grazed**	**Off-take**	**Grazing Intensity**	**p**
		Aboveground biomass			
1	256 ± 48	68 ± 11	188.01	0.74	0.0128
2	285 ± 65	85 ± 22	200.04	0.70	0.0364
3	634 ± 65	259 ± 78	375.26	0.59	0.0252
4	825 ± 142	210 ± 56	615	0.75	0.0014
5	948 ± 118	717 ± 39	230.13	0.24	>0.05
6	244 ± 74	215 ± 29	28.65	0.12	>0.05
Overall Mean	532 ± 51	259 ± 28	273	0.51	
		Regrowth			
1	119 ± 16	61 ± 6	-	-	> 0.05
2	161 ± 33	91 ± 10	-	-	> 0.05
3	257 ± 45	170 ± 27	-	-	> 0.05
4	327 ± 46	165 ± 25	-	-	0.009
5	170 ± 32	193 ± 23	-	-	> 0.05
6	100 ± 27	71 ± 15	-	-	>0.05
Overall Mean	189 ± 18	125 ± 9	-	-	

Table 3.4. Annual mean aboveground biomass and cumulative regrowth (g m^{-2} yr^{-1}) for two the treatments in each season with their respective offtake and grazing intensities. The p values are results of the Bonferroni post-hoc test for the interaction between the grazing treatments and time (Grazing*Time). *The overall mean aboveground biomass is aggregated for post-treatment period after excluding the initial aboveground biomass in June 2011. **The cumulative annual regrowth is derived by summing mean regrowth for all four seasons. Means are ± 1 SE.

Month	**Season**	**Ungrazed**	**Grazed**	**Off-take**	**Grazing Intensity**	**p**
Aboveground biomass						
June	Wet	300 ± 66	266 ± 39	33.5	-	-
September	Wet	487 ± 88	287 ± 56	200	0.41	< 0.01
December	Wet	580 ± 115	320 ± 49	260	0.45	0.01
March	Dry	475 ± 99	165 ± 47	311	0.65	< 0.01
June	Wet	585 ± 113	265 ± 69	321	0.55	< 0.01
Overall Mean*		532 ± 37	259 ± 26	273	0.51	
Regrowth						
September	Wet	192 ± 33	167 ± 22		-	- >0.05
December	Wet	251 ± 36	125 ± 12		-	- 0.01
March	Dry	81 ± 14	44 ± 7		-	- < 0.01
June	Wet	232 ± 34	166 ± 18		-	- >0.05
Cumulative Mean**		756 ± 38	502 ± 29		-	-

Table 3.5. Planned contrasts of aboveground biomass and regrowth between seasons and grazing treatments.

	Estimate	Std. Error	t	P	-95% Cnf. Lmt	+95% Cnf. Lmt
Grazed aboveground biomass						
June vs. Sept.	-0.0043	0.0741	0.0576	0.9545	-0.1486	0.1571
Sept. vs. Dec.	-0.0999	0.0425	2.3517	0.0272	0.0122	0.1877
Dec. vs. Mar.	0.4278	0.0469	-9.1222	0.0000	-0.5246	-0.3310
Mar. vs. June-2	-0.2810	0.0349	8.0562	0.0000	0.2090	0.3529
Ungrazed aboveground biomass						
June vs. Sept.	-0.3163	0.1047	3.0199	0.0059	0.1001	0.5325
Sept. vs. Dec.	-0.0480	0.0601	0.7988	0.4323	-0.0760	0.1720
Dec. vs. Mar.	0.1104	0.0663	-1.6641	0.1091	-0.2473	0.0265
Mar. vs. June-2	-0.1338	0.0493	2.7124	0.0122	0.0320	0.2356
Grazed Regrowth						
Sept. vs. Dec.	0.0808	0.0591	-1.3666	0.1844	-0.2028	0.0412
Dec. vs. Mar.	0.6323	0.0686	-9.2194	0.0000	-0.7738	-0.4907
Mar. vs. June	-0.7391	0.0596	12.4109	0.0000	0.6162	0.8620
Ungrazed Regrowth						
Sept. vs. Dec.	-0.1548	0.0836	1.8523	0.0763	-0.0177	0.3274
Dec. vs. Mar.	0.5764	0.0970	-5.9427	0.0000	-0.7765	-0.3762
Mar. vs. June	-0.5305	0.0842	6.2992	0.0000	0.3567	0.7044

3.3.4 Regrowth and the frequency of clipping

The frequency of clipping significantly affected regrowth only during the dry season ending March 2012 ($H_2 = 8.95$, $P = 0.011$). The multiple comparison tests following the Kruskal-Wallis test ($P < 0.05$) showed that the lattice-squares that were clipped once in March had significantly higher regrowth compared to those clipped 2 and 3 times (Figure 3.3). Although regrowth was higher on lattice-squares clipped 2 times than those clipped 3 times the difference was not significant. During the wet season ending December 2011, the squares clipped twice had less regrowth than those clipped once though not significant. No consistent trend was observed in wet season ensuing June 2012.

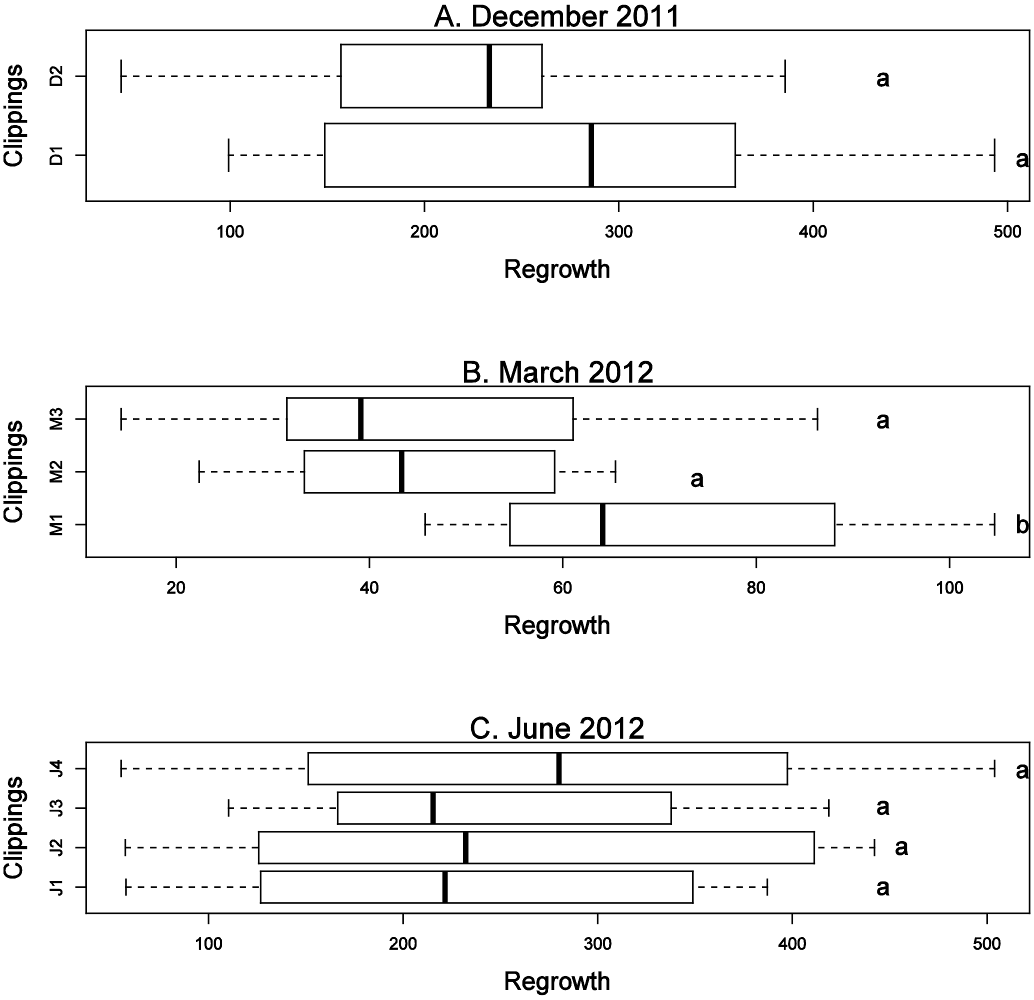

Figure 3.3. Box-plot showing the regrowth (g m^{-2} yr-^{1}) in ungrazed treatments with differing number of clipping for (A) December (B) March and (C) June, aggregated for all the 6 sites. The labels on the y-axis are shown on Table 3.2 and represent the month and the number of regrowth's clipped respectively. The bars with the same labels are not significant while those with differing letters are significantly different. The clipping frequency was only significant during the dry season in March 2012.

3.4 Discussion

3.4.1 Grazing intensity impact on herbaceous residual aboveground biomass

Grazing impacts on residual aboveground biomass were significant in both wet and dry seasons although much more pronounced in the dry seasons. Therefore the hypothesis that grazing impacts would be significant only in the dry season was not supported. The top-down control mechanisms seem to be prevalent even in wet seasons, suggesting that the resident herbivores density is high. This is in agreement with (Harper and Mavuti 2004) who reported a threefold increase in resident buffalo (*Syncerus cafer*) numbers at the former North swamp, from a few hundreds in early 1990s to 1500 individuals in 2004. The hippo population also increased from 218 to 1260 (in 1987 and 2005 respectively (Smart et al. 2001, Douglas-Hamilton et al., Unpublished). Coincident with these population increases, a wildlife cropping programme aimed at controlling ungulate density was terminated in 2003 and the fringe zone surrounding Lake Naivasha has increasingly been converted into a closed system by the erection of electric fences along most of the wildlife conservancies to curb poaching. The latter reduces habitat connectivity and restricts the herbivore movements by closing the migratory corridors.

The increased grazer density was accompanied by a reduced grazing area as a result of increased horticultural expansion and recent frequent flooding that inundates several kilometers of the most productive riparian grassland (Mavuti and Harper 2006). It is hypothesized that the frequent flooding enhances productivity and forage availability in temporarily flooded grasslands, consequently increasing the grazing capacity. The temporarily flooded grasslands were continuously flooded from September 2011 up to August 2012 as witnessed by the flooding of three exclosures that were erected near the lake (not included in analysis). Such prolonged flooding will reduce the grazing area, increasing grazing pressure on the non-inundated grazing lawns, a fact that could have contributed to the significant grazing impacts even in the wet seasons.

The high density of resident herbivores could be linked to the intense grazing observed in four of the six sites that maintained the residual biomass relatively low (short to medium grasses). Grazing intensities influence the amount of residual aboveground biomass (Varnamkhasti et al. 1995, Keya 1997, Oba et al. 2000a). Low residual aboveground biomass translates to fewer meristems from which new tillers can sprout, while extremely high residual aboveground biomass enhances accumulation of dead or moribund stems with little or no regrowth potential. Thus the observed high to severe grazing intensities significantly lowered the residual aboveground biomass, and impacted negatively on plant regrowth. Maintaining a 50% residual biomass after grazing has been recommended for sustainable productivity of rangelands (Keya 1998). However, the grazing intensities in the four sites surpassed this suggested limit.

The intense grazing intensities amid decreasing grazing area may diminish the value of the fringe zone as a key resource area with consequent impacts on biodiversity in both the key resource area itself and the surrounding wet season rangelands. The high grazing intensity may generate a self-reinforcing loop that leads to further degradation by promoting bush encroachment (Coetzee et al. 2007) and proliferation of less productive annual grasses over perennial of grasses in the key resource area (Keya 1997). Despite the detrimental impacts on the key resource area, the reduced productivity may positively impact the surrounding wet season ranges as a result of a decrease in the herbivore population that can be maintained within the key resource area during the dry season. This can reduce the grazing pressure on the surrounding wet season ranges that experience non-equilibrium dynamics (Illius and O'Connor 1999, and 2000). Such a scenario has been reported in Lake Baringo (near Lake Naivasha), where large herbivore densities, maintained by highly productive riparian swamps, increased soil erosion in the surrounding wet season range (Homewood 1994).

3.4.2 Grazing impacts on herbaceous regrowth

The hypothesis that regrowth significantly declines with increasing frequency of clippings was supported but only for the dry season when the plants had low potential for compensatory growth due to moisture stress. Intense defoliation lowers the survival fitness of the herbaceous vegetation (Kioko et al. 2012) through injury to their meristems, stolons and rhizomes where new tillers sprouts (Anderson and Frank 2003). The results demonstrate the potential negative effects of high herbivore densities on a key resource area during the dry season. This concurs with Illius and O'Connor (1999) who noted that prolonged dry spells can induce intense and localized defoliation that may reduce the productivity potential.

Nevertheless, the grazing impact as measured from the regrowth was generally less pronounced. This might be attributable to the extreme clipping intensity that left no residual biomass in the preceding season. As demonstrated by Varnamkhasti et al. (1995) and Oba et al., (2000a), the resulting regrowth could have been higher if moderate grazing was simulated by clipping the grasses inside the exclosure at the same height as outside the exclosures. However, as pointed-out by McNaughton et al. (1996) this would require a subjective visual comparison biased by the species mix. This is especially the case after a prolonged exclosure period when the vegetation composition inside the exclosure is expected to be changing. The low regrowth may have also resulted from reduced N mineralization (Berliner and Kioko 1999, Augustine and McNaughton 2006) in the clipped quadrants since complete removal of all the phytomass left no decomposing litter. In addition, intense defoliation may have slowed regrowth by enhancing evaporation on exposed soils that consequently reduced soil moisture (Cech et al. 2008). Complete defoliation of grass canopy may also reduce infiltration while the accompanying decrease in litter can potentially reduce interception of low intensity rainfall further altering soil moisture dynamics.

The cumulative annual regrowth aggregated for the entire landscape under the simulated severe grazing intensity was 756 ± 38 g m^{-2} yr^{-1}. Since natural grazing rarely defoliates all the available forage, the observed cumulative annual regrowth represents the minimum herbaceous productivity potential of the fringe zone. The estimated regrowth was within the range (439 – 945 g m^{-2}) reported in the nearby Njemps flats within the Kenyan section of Great Rift valley (Ekaya et al. 2001). However regrowth on the sites experiencing light to moderate grazing intensities could have been underestimated because grazing can stimulate regrowth (McNaughton 1985). In support of this, experimental setups that involve moveable exclosures have shown that productivity outside the exclosures may be higher than the permanently enclosed setup in lightly and moderately grazed lawns due to stimulation of growth by grazing (McNaughton 1985, Pandey and Singh 1992). This is in addition to the general underestimation of productivity using any method since productivity, decomposition and turnover are continuous processes while the measurements are discrete in time (Sala and Austin 2000). Lastly, the effect of insects and small herbivores was not quantified though they might exert considerable grazing impact (Okullo and Moe 2012).

Results showed that the grazing pattern was spatially heterogeneous as depicted by significant differences in aboveground biomass between sites and varying grazing intensities among sites. The site differences in grazing intensities reflect grazers' preferences and avoidance and plant specific characteristics that boost their attractiveness or defense from grazing. In agreement with Belsky (1992), grazers preferred sites with short grasses (sites 1 - 4) that are more nutritious, less lignified and have higher digestibility. Herbivores maintain their grazing lawns by repeatedly foraging on the same patches thus maintaining short grasses while avoiding patches with tall and lignified grasses. Such vegetation patterns compromise the recommended 50% use of grazing lawns, which constitute a mosaic of highly used and underutilized patches.

3.4.3 Interaction between rainfall and herbivory

The lowest aboveground biomass and regrowth together with the highest grazing intensities occurred during the dry season. The high grazing intensities during the dry season coincided with the period when plants had low regeneration potential due to moisture stress. This suggests that herbaceous productivity is limited by grazing and seasonality (rainfall). However, the residual aboveground biomass in the grazed treatments remained significantly lower than that in ungrazed treatments even during the wet seasons, revealing that rainfall did not decouple herbaceous productivity from herbivore control. This suggests that the grazers have greater impact than rainfall. This concurs with (McNaughton 1985) who reported that grazers had significantly higher impact on productivity than rainfall in the Serengeti ecosystem. The view that herbivores have no significant impact on herbaceous productivity in climatically variable ecosystems (Ellis and Swift 1988) is challenged.

3.5 Conclusions

Both grazing and rainfall limit herbaceous productivity on the fringe zone of Lake Naivasha. Results suggested that grazing impacts overrode rainfall since herbaceous productivity was not decoupled from herbivore control even in wet seasons. Thus density-dependent mechanisms, although much pronounced in dry season, were also prevalent during wet seasons, when herbivores are expected to disperse into the greener surroundings. Moreover, high grazing intensities in four out of six sites significantly reduced the residual biomass that in turn determines the herbaceous regrowth after defoliation. These results suggest the existence of a high density of resident herbivores within the key resource area that can be partly attributed to decreasing grazing area and limited connectivity between grazing areas due to fencing. An increased frequency of defoliation was demonstrated to lead to lower herbaceous regrowth during the dry season, thus signifying the potential negative effects that may result from aggregation of high herbivore densities in a key resource area during the dry season. The short-term potential of large herbivores exclusion in boosting the recovery of over-utilized pastures was demonstrated. However, long-term effects should be explored by running the experiment over a longer period. The role of flooding in enhancing grazing capacity needs to be evaluated critically as the prolonged flooding may increase grazing intensities in non-flooded grazing lawns rather than subsidizing the limited forage during the dry seasons.

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Chapter 4

Evaluating a new tool (ManyGLM) to improve detection of grazing signal on plant community composition*

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Abstract

There is no agreement on whether grazing exerts significant impacts on plant communities in savannas. A series of empirical studies have investigated which of the competing hypotheses hold in different savannas by analyzing multivariate species abundance data using distance based methods (DBMs). A recent study highlighted major weaknesses in DBMs that may lead to inaccurate conclusions and proposed a novel method, the ManyGLM, to address these limitations. We evaluate the robustness of this novel method using herbaceous plant species data recorded inside and outside herbivore exclosures along Lake Naivasha, Kenya. We compared the significance of grazing treatment on the species composition and abundance indicated by this model against the results from a DBM, the distance-based redundancy analysis (db-RDA). We hypothesized that the pure signal species (occurring in only one treatment) will be most responsive to grazing compared to mixed signal species (occurring in both treatments in differing abundance) and no signal species (equally abundant in both treatments). We compare the species that are identified by both methods as being the most responsive to grazing treatment against this *a-priori* hypothesis. ManyGLM identified the pure signal species to be most responsive to grazing. ManyGLM was able to detect changes in plant composition even when expressed in rare species that are most sensitive to environmental stress. The db-RDA models did not show a consistent pattern in ranking the response of the three types of species to grazing treatment.

Key words: db-RDA; dispersion weighting; distance-based methods; dissimilarity indices; effect species; herbivore exclosure; mean-variance relationship; model comparison

4.1 Introduction

Grazing by large herbivores disturbs plant communities in savannas (Milchunas et al. 1988, Fynn and O'Connor 2000). However, there is no agreement on whether grazing exerts significant impacts on plant communities in savannas. Three main schools of thought have evolved: the equilibrium (DeAngelis and Waterhouse 1987), the disequilibrium (Ellis and Swift 1988) and the non-equilibrium hypotheses (Illius and O’Connor 1999, 2000, 2004). Range ecologists have dedicated considerable attention to disentangling which of the three hypotheses holds in different savannas. This has resulted to a series of empirical studies that investigated the existence of the three mechanisms by analyzing community composition data using distance-based methods (DBMs) (e.g. O'Connor and Roux 1995, Fynn and O'Connor 2000, Sasaki et al. 2008, Dorji et al. 2010, Scogings et al. 2012, Silcock and Fensham 2013). The DBMs (Table 4.1) first summarize the differences in species composition by calculating the ecological distances or dissimilarities (here referred to as dissimilarities) between all pairs of sample sites (Kindt and Coe 2005). The resulting dissimilarity matrix is then used to compare the differences in species abundance between *a priori* defined groups or treatments. This masks the actual species identities. The Euclidean, Chi-square and Bray-Curtis dissimilarities (Table 4.2) are the most widely used in the DBMs.

Different dissimilarity indices used in the DBMs emphasize different aspects of multivariate species data i.e. the differences in species composition, abundances or both (Kindt and Coe 2005, Anderson et al. 2006). Therefore ecologists are faced with difficult task of selecting the appropriate dissimilarity index that fit their data. Often, the multivariate species abundance data depict large proportions of rare species with lower variances in abundance compared to a few but highly variable common species (Warton 2005). Typically, multivariate species abundance data consists of many zero's therefore it is over-dispersed i.e. they have a higher variance than mean (O'Hara and Kotze 2010). Mostly such data exhibit a quadratic mean-variance relationship whereby variances in species abundance increase with increasing mean abundance (Warton 2005, ver Hoef and Boveng 2007).

A recent study in marine ecology has demonstrated that most dissimilarity indices assume mean-variance relationships that are different from that inherent in the multivariate species abundance data, thereby leading to confusion of central location (mean abundances) and dispersion effects (differences in variances) (table 4.1; Warton et al. 2012). This confusion lowers the ability of DBMs to detect multivariate effect, unless it is expressed in species with high variance. The confusion may also lead to erroneous identification of species that are responsible for multivariate effect (Warton et al. 2012). This can ultimately lead to incorrect inference if a significant difference in mean species abundances (locational effects) is detected when only variances are different (dispersion effects; Warton et al. 2012). Transforming the multivariate abundance data rarely rectifies the mean-variance trend in multivariate abundance data, especially where the abundance data contains many zeroes and rare species (O'Hara and Kotze 2010).

To resolve the limitations of DBMs, Wang et al. (2012) proposed a novel multivariate generalized linear models method; ManyGLM which (Warton et al. 2012) demonstrated offers four qualities that are lacking in distance-based methods:(1) it fits models on actual species abundances rather than dissimilarities (2) it allows specification of the actual mean-variance trend in species data before analysis; (3) it has a high power to detect between-treatment effects even when expressed in low variance species, and (4) it has a high power to identify the species that are most responsive to treatment effect. Approximately a year after the new method was proposed, it has received considerable application in plant ecology (e.g. Dossa et al. 2013, Gibb and Cunningham 2013, Bennett et al. 2014). However this method has not been subjected to rigorous testing over a large variety of species data to evaluate its performance compared to the widely used DBMs. Studies comparing results from different methods using the same species dataset (e.g. Skidmore et al. 1996, Guisan et al. 1999, Gilbert and Bennett 2010) are limited despite their potential to highlight strengths and weaknesses of existing techniques, and identify areas that need further improvement or research.

We therefore compare the results of this novel method; the ManyGLM, with a non-parametric DBM; the distance-based redundancy analysis (db-RDA; Legendre and Anderson 1999) using species data recorded from a herbivore exclosure experiment. We compare the ability of the two methods to detect whether large herbivore grazing has a significant impact on plant community (both composition and abundances) as well as their accuracy to identify plant species responding to grazing. We hypothesize that the order of species ranking in term of their contribution to the grazing treatment effect would be; first the species recorded in one treatment only (pure signal species; PS), second the species occurring in both treatments with differing frequencies or abundances (mixed grazing signal species; MS) and finally the species that are equally prevalent or abundant in both treatments (no signal species; NS). The method that ranks the species contribution according to the above ecological expectation is regarded as the most accurate in identifying the species that respond to treatment. Therefore if we find the grazing treatment to have significant impact on the species composition or abundances in the multivariate test, we expect this significance to be matched with above hypothesized ranking of species contribution to the treatment effect.

Our main aim was to deduce whether the resulting explained variances or significance, from the two methods agree with the above *a priori* hypothesis about which species are expected to have the highest response to grazing. This is in recognition of the widely ignored fact that, even if the multivariate species models explain high and significant variances, most of these variances are contributed by generalists or disturbance tolerant species that are prevalent or abundant in all treatments. This leads to conclusions that are contrary to expected ecological responses and therefore indicating a statistical artefact.

We fitted compositional and abundance-based models using the ManyGLM and db-RDA, whereby for the latter we used three ecological dissimilarities that emphasize different aspects of species data i.e. compositional or abundances (Anderson et al. 2006) and also differ in their assumptions on the mean-variance relationship in multivariate data (table 4.1; Warton et al. 2012). We compared the ranking of species response to grazing treatment resulting from the two methods. Ideally simulated data with known effect size should be used for comparing the accuracy of different models (Faith et al. 1987). However we evaluate the two models with actual community composition data (species composition and abundance) recorded in the field since our main aim is to identify the method that ranks the species response to grazing according to *a priori* hypothesis on which species are expected to portray the highest response to treatment.

Table 4.1**:** Description of common distance based methods (DBMs) and the dissimilarity indices

Distance based methods

Method	**Reference**	**Dissimilarity**	**Particulars and application**
Redundancy Analysis (RDA)	(Legendre & Anderson 1999)	Euclidean	Eigen-vector method suitable for constraining variances when species-environment relationship follows a linear gradient.
Canonical Correspondence Analysis (CCA)	(ter Braak 1987)	Chi-square	Eigen-vector method suitable for testing differences in species samples with a uni-modal response to environment.
Distance-based redundancy analysis (db-RDA)	(Legendre & Anderson 1999)	Any	A constrained ordination that factors correlation structure among response variables (species).
Analysis of similarity (ANOSIM)	(Clarke 1993)	Any	Test for significant differences in community data with one grouping factor with two or more levels.
Permutational multivariate analysis of variance (PERMANOVA)	(Anderson 2005)	Any	Nonparametric method that handles multiple grouping factor and their interactions.

Dissimilarity matrices

Index	**Reference**	**Particulars and application**
Jaccard	(Jaccard 1912)	The index is used in the presence-absence species matrix to derive the proportion of unshared species out of the total number of species recorded in the two sample plots.
Euclidean	(Sokal & Sneath 1963)	Metric index used for ordination methods that assume linear gradient (RDA, PCA), no upper bound and assumes a constant mean-variance trend. Emphasize on compositional differences and account for joint absences.
Chi-square	(Chardy et al. 1976)	Used in CCA and emphasizes rare species. No upper bounds. Assumes a proportional mean-variance trend with a slope of 1.
Bray-Curtis	(Bray & Curtis 1957)	Semi-metric index that ranges from 0 to 1. It emphasizes on differences in species abundances. Assumes a quadratic mean variance trend with slope of 2 and equal variances in species abundances within sample groups. Ignores joint absences.

4.2 Methods

4.2.1 Study area

The plant species data were collected on the fringe zone of Lake Naivasha, Kenya. The area is a RAMSAR site (Ramsar 1996) located at the floor of the Great Rift-Valley at an altitude of 1890m a.s.l. Annual average rainfall is approximately 680mm but highly variable (CV ~30%) and occurs in two main seasons (Odongo et al. *in Press*). The vegetation changes gradually with increasing distance from the lake ranging from aquatic macropytes to grasslands to shrublands and *Acacia xanthophloea* woodland (Gaudet 1977b). The area is inhabited by over 25 large wild herbivores such as hippopotamus (*Hippopotamus amphibius*), buffalo (*Syncerus caffer*), common zebra (*Equus burchelli*). These co-exist with livestock in private ranches and nomadic herds in communal areas.

4.2.2 Sampling and data collection

Six herbivore exclosures measuring 10x10m were erected in June 2011 on 5 ranches surrounding Lake Naivasha. Each exclosure had two controls on either side with similar dimensions. The exclosures were located within permanent plots (30x30m) along line transects that has been established for monitoring biomass on (semi)-natural vegetation patches (Muthoni et al. 2014). Herbaceous species were inventoried at the initiation of the exclosure experiment on June 2011 and after one year (July 2012) during the flowering period to facilitate sighting of rare species. All herbaceous species occurring in 5 randomly placed quadrants measuring $1m^2$ in the exclosure and the two controls respectively were identified to species level. Therefore for each exclosure we had 15 quadrants with species data, 10 from the two grazed controls and five from the ungrazed treatment. This yielded 90 quadrants for all six exclosures. The samples for the few species that were not immediately identified were taken to the East-Africa Herbarium in Nairobi, Kenya for identification. Their percentage ground cover was visually estimated. A modified Braun-Blanquet 6 point scale was used to score the species ground cover 1 (<1%), 2 (1-5%), 3 (6-25%), 4 (25-50%), 5 (51-75%) and 6 (76-100%) (Mueller-Dombois and Ellenberg 1974). The species taxonomic keys follows Ibrahim and Kabuye (1987), Agnew and Agnew (1994), and Beentje (1994).

During the initiation of the exclosures in June 2011, three categories of site-specific explanatory variables were collected: 1) soil resources: pH, N, P, K; (2) soil moisture resources: a topographical position index (TPI) as a surrogate for soil moisture availability (with respect to runoff and run-on gradients) (3) disturbances: the fractional bare-soil cover (FBC) as proxy for susceptibility of soils to erosion (Kioko et al. 2012) and frequency of inundation (FoI). For each site four soil cores distributed in a zigzag pattern in each plot and at 10-15cm deep were collected. The four cores for each plot were evenly mixed before being analyzed for pH, N, P and K content in the National Agricultural Research Laboratories, Kenya. The pH was determined with a pH meter, total N (%) through the Kjeldahl method, extractable P (ppm) and K (me %) were determined by the Mehlich double acid method (Mehlich 1984) while the extractable P for soils with pH 7.0 and above were determined using the Olsen method (Olsen et al. 1954).

To derive the TPI, a 30m resolution hydrologically correct digital elevation model (DEM) was generated from contours (20 m interval) and spot heights (both from 1:50000 topographical maps; isolines (from 1957 bathymetry of the lake (Ase et al. 1986) and vector lines representing the rivers. The TPI was derived from the DEM using an algorithm developed by Jenness (2005). The algorithm compares the altitude of a particular cell to that of neighboring cells with a circular moving window with a specified radius. Positive, negative and zero TPI values represent ridges; valleys and flat land respectively. Since the resulting TPI values depend on the specified radius, four distances were used (250, 500, 750 and 1000 m) to evaluate the most appropriate radius in the species models (Guisan et al. 1999). All these distances were included in the PCA analysis for site characteristics (see below).

To derive the FoI, the centroid of each exclosure was used to extract the elevation of each plot from the corrected DEM. The daily lake level measurements for the last 15 years (1997 to 2012) were obtained from a gauging staff located at the Yacht Club on the Eastern shore of Lake Naivasha with a reference elevation level of 1885.26m. The FoI was derived as fractional number of times the lake levels were higher than the elevation of each sampling site.

4.3 *Statistical Analysis*

4.3.1 The response and predictor variables

We evaluated the species response to grazing treatment with two response data sets; the compositional differences with species presence-absence data and the species abundances data. For the compositional differences model, the community matrix was coded 0 and 1 signifying the species presence or absence. In the species abundance-based models the response was a matrix for species abundances (quantified as the average Braun-Blanquet 6 point scale). This has a similar distribution to count data. We derived a subset comprising only the pure signal species from the two community matrices (compositional and abundance data). In the pure signal species matrix we added one dummy species (Addspp) to ensure each row in the data has at least one species to enable calculation of Euclidean dissimilarity. The pure signal only subset was used to fit the pure signal only models using both methods.

The abundance data for fitting the db-RDA was dispersion weighted (Clarke et al. 2006a) to reduce the relative contribution of ubiquitous species with highly variable abundances to the dissimilarity matrix. Dispersion weighting was based on the species mean to variance ratio within each treatment group and was implemented using Vegan package in R (Oksanen et al. 2014). This should ideally make the mean-variance trend for each species per *a priori* group to approximate Poisson's distribution (Clarke et al. 2006a) that is also assumed by Euclidean distance. This would then enable evaluation of the effect of misspecification of mean-variance trend in the data on the results by comparing results of Euclidean with chi-square and Bray-Curtis dissimilarities.

To account for site differences, principal component analysis (PCA) was conducted with environmental variables recorded in the sample sites as input i.e. pH, N, P, K, TPI, FBC and FoI. We utilized the first principle component that explained 79% of variance in environmental conditions. Therefore in all models the species matrix was the response and predictors were the grazing treatment, first principle component of the site characteristics and their interaction.

4.3.2 Description of ManyGLM and db-RDA approaches

The ManyGLM approach allows beforehand specification of the actual mean-variance trend in the species data by selecting an appropriate family of distributions, either negative binomial distribution (for count data) or a binomial for presence/absence data (Wang et al. 2012). The ManyGLM fits a separate GLM model on each species in a given species abundance matrix. It also undertakes separate univariate tests for each species. The test statistic from these univariate tests (either a log-likelihood ratio, Wald and Score) quantifies the strength of species response to treatment effect.

We used the distance-based redundancy analysis (db-RDA; Legendre and Anderson 1999, Legendre and Legendre 2012) approach implemented in "capscale" function within the BiodiversityR package (Kindt and Coe 2005). The db-RDA uses the principle coordinates analysis (PCoA; Gower 1966) to convert the (semi)-metric dissimilarity matrices such as Bray-Curtis into Euclidean space. This allow a linear ANOVA model to be implemented using RDA. The db-RDA has an added advantage than other ordination methods such as RDA and CCA as it allow the use of any suitable dissimilarity index (Table 4.1).

4.3.3 Model fitting and ranking the species contribution to grazing treatment effect

All statistical analyses are executed in R (R Development Core Team 2014). Two different community matrices were constructed to fit two models for both db-RDA and ManyGLM methods. Species compositional model was fitted using the presence-absence (0 or 1) community matrix, while abundance-based models were fitted using a species abundance matrix. In each case we fitted two models using for all species and the pure signal species only subsets. Results from these models enabled comparison of the deviance explained and identity of effect species from the two methods when the community comprised only the species that are known a-priori to be responsive to grazing treatment.

Before fitting the ManyGLM abundance-based model, a mean-variance plot was derived to explore the mean-variance trend in the data (Figure 4.1). We fitted a linear regression line using the means and variances of our data and plotted this regression line on the mean-variance plot. We also plotted regression lines with slope of 1 and 2 similar to that assumed in chi-square and Bray-Curtis dissimilarities respectively. The ManyGLM was fitted with a negative binomial and binomial distribution for the abundance and compositional models respectively using the MVABUND package (Wang et al. 2012) in R. Since a negative binomial model can only be fitted on integer data, the average Braun-Blanquet values were converted from floating point values to integers.

For each ManyGLM model, an ANOVA using the likelihood ratio statistic (Warton 2011) was used to evaluate the significance of the variables and their interactions. The over-dispersion parameter (phi), was estimated using the maximum likelihood estimator (Lawless 1987). This phi parameter is used to describe the over-dispersion in the negative binomial model formula; $Y = \mu + phi * \mu^2$, where Y is the variance and μ is mean species abundance (ver Hoef and Boveng 2007).

We assumed the response variables (species) were not correlated for computational efficiency. The analysis still yielded valid inferences as p-values were calculated using resampling of data rows that cater for correlation in testing (Wang et al. 2012). The p-values for abundance models were derived from an ANOVA like procedure using pit-trap resampling (Warton 2011) of data rows with 1000 iterations to account for correlation between species in the tests (Wang et al. 2012). We used Monte Carlo resampling for compositional models. The resampling returned univariate tests that quantified the response and significance of each species to explanatory variables. The univariate tests are summed to yield the multivariate test statistic (i.e. log-likelihood ratio; Wang et al. 2012).

The p-values for these univariate tests were adjusted for multiple testing using a step-down resampling procedure (Wang et al. 2012). The species response to the treatment effect was ranked based on log-likelihood statistic values from the univariate tests. The fit of the overall ManyGLM model was evaluated by proportion of deviance explained (D^2).

The db-RDA models were fitted using the dispersion weighted response data and the same explanatory variables as used in the ManyGLM models with the “capscale” function in the BiodiversityR package in R (Kindt and Coe 2005). We used the Jaccard dissimilarity to fit the species compositional model while the db-RDA species abundance models were based on three different dissimilarities that assume different mean-variance relationships (Table 4.1). These dissimilarities are: Euclidean (Sokal and Sneath 1963), Chi-square (Chardy et al. 1976) and the Bray-Curtis (Bray and Curtis 1957). To obtain the Chi-square distance the species abundance matrix was Chi-square transformed and analyzed further with Euclidean distance. This procedure produces a Chi-square distance similar to that implemented in Correspondence Analysis (CA) (Legendre and Gallagher 2001).

P-values for the significance of predictors in all db-RDA models were derived using permutation tests with 1000 iterations using the pseudo-F test (Legendre and Anderson 1999). The fit of the overall models was evaluated by the proportion of constrained variance and the significance returned after permutation test of all constrained eigenvalues. The fit of the predictors in db-RDA models was gauged by the percentage of variance explained (R^2) and its significance. The correlation of each species with the db-RDA axis that expressed the grazing treatment was used as indirect post-hoc tests to rank the species response to the multivariate effect (Anderson and Willis 2003).

4.4 Results

4.4.1 The diagnostic tests

The abundance data was over-dispersed since variance was higher than mean (Figure 4.1). The mean-variance trend in the data violated the assumption of equal mean and variances in Euclidean distance and had steeper slopes than that assumed in chi-square and Bray-Curtis dissimilarities (Figure 4.1). To fit the db-RDA models the data was dispersion weighted. This reduced the over-dispersion in the data by half; from slope of 2.2 (Figure 4.1) to slope of 1.1 (Appendix A).

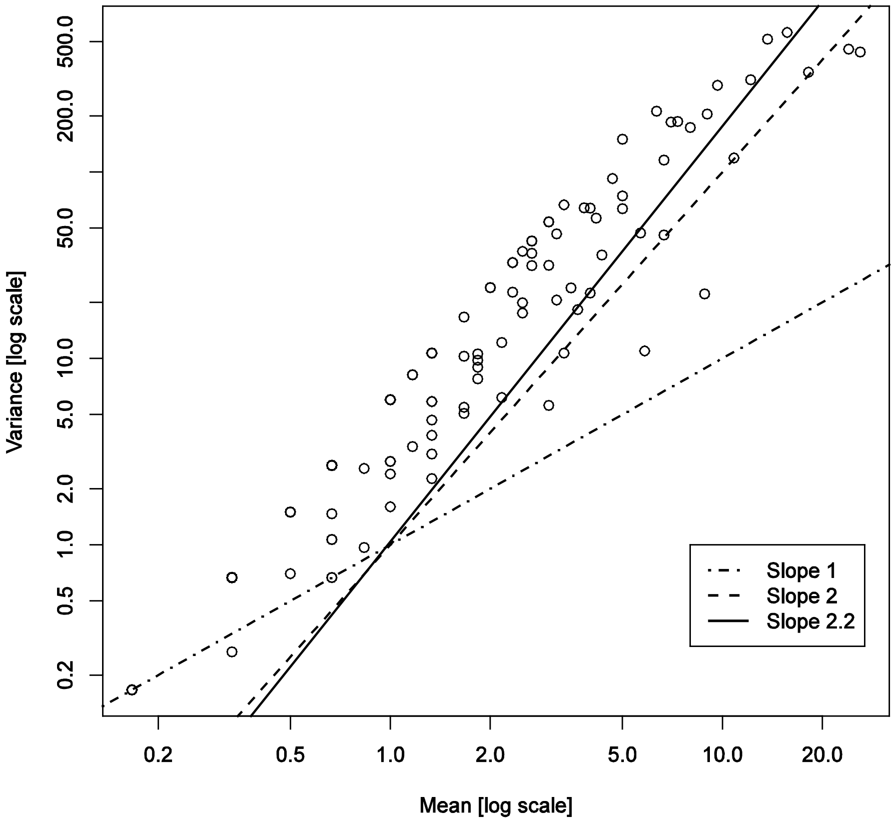

Figure 4.1 The mean-variance relationship in abundance data used to fit the negative binomial ManyGLM model. The data is highly over-dispersed since variance is higher than mean. The regression of mean and variances had a slope of 2.2). The mean-variance trend in the data violated the assumption of equal mean and variances in Euclidean distance and was much steeper than that assumed in chi-square (slope = 1) and Bray-Curtis (slope = 2) dissimilarities

4.4.2 Explained variances and ranking of species responses

For both the compositional and abundance models ManyGLM explained higher overall deviance than equivalent db-RDA models for both all species and pure signal species only models (Table 4.2). The grazing treatment was highly significant ($p <= 0.003$) in all pure species only models. In compositional models for all species, the grazing treatment was significant in the ManyGLM model ($Dev_{3,8}$ =156, $p = 0.002$; Table 4.2) but not for the db-RDA model ($F_{3,8} = 1.19$, $p = 0.25$; Table 4.2).

Table 4.2: The significance of the grazing treatment in ManyGLM and db-RDA models based on three different dissimilarity indices using all species and pure signal only species. All models are based on 3 and 8 degrees of freedom for model and residuals

Model	**Compositional Model**						**Abundance models**											
	ManyGLM			**db-RDA**			**ManyGLM**			**db-RDA**								
Dissimilarity Index				**Jaccard**						**Euclidean**			**Chi-square**			**Bray-Curtis**		
Predictors	**Dev**	**D^2**	**p**	**F**	**R^2**	**P**	**Dev**	**D^2**	**p**	**F**	**R^2**	**P**	**F**	**R^2**	**P**	**F**	**R^2**	**p**
Pure signal species only models																		
Treatment	131.67	0.3	0.001	2.63	0.2	0.001	140.89	0.4	0.003	2.24	0.2	0.003	2.7	0.2	0.002	2.43	0.2	0.002
PC1	113.62	0.3	0.004	1.10	0.1	0.25	109.19	0.3	0.036	1	0.1	0.47	0.9	0.1	0.46	1.04	0.1	0.37
Treatment:PC1	0.94	0.0	0.97	1.10	0.1	0.35	0.13	0.0	0.955	1	0.1	0.52	0.93	0.1	0.52	1.04	0.1	0.48
Overall model	246.23	0.6	0.002	1.6	0.4	0.001	250.21	0.6	0.001	1.41	0.3	0.17	1.52	0.4	0.13	1.5	0.4	0.002
All species Models																		
Treatment	155.6	0.2	0.002	1.19	0.1	0.25	160.7	0.2	0.09	0.96	0.1	0.48	0.88	0.1	0.59	0.88	0.1	0.55
PC1	278.35	0.3	0.001	1.4	0.1	0.08	271.3	0.3	0.02	1.64	0.1	0.1	1.34	0.1	0.14	1.28	0.1	0.2
Treatment:PC1	57.75	0.1	0.06	0.62	0.1	0.93	77.6	0.1	0.3	0.93	0.1	0.53	0.62	0.1	0.92	0.55	0.1	0.9
Overall model	491.7	0.5	0.004	1.07	0.3	0.3	509.6	0.5	0.001	1.17	0.3	0.34	0.94	0.3	0.59	0.91	0.3	0.63

We classified the species into three categories based on their response to grazing (Tab le 4.3) and ranked them based on the log-likelihood statistic for the ManyGLM models and the species correlation with the second db-RDA ordination axis (CAP 2) that expressed the grazing treatment (Figure 4.2). For both the compositional and abundance based models the order of species ranking in term of their response to grazing treatment (first to last) in ManyGLM was; the pure signal, mixed signal and no signal (Figure 4.3). Even for abundance-based models, ManyGLM showed higher sensitivity to between treatment differences in species prevalence compared to abundances (compare the higher scatter in ManyGLM models in Figure 4.4 with Figure 4.5). For all models, ManyGLM ranked the species with the highest between treatment differences in species prevalence as the most responsive to grazing treatment. In cases where the pure and mixed species signal species had equal difference in prevalence, ManyGLM ranked the pure signal species higher than mixed signal species (Figure 4.4). The ranking of species response to grazing in db-RDA models did not reveal any consistent pattern since the ranks of the three categories of species overlapped (Figure 4.3). The db-RDA models based on Euclidean and chi-square dissimilarities ranked some no signal species as being more responsive to grazing than the pure signal species (Figure 4.3). We did not detect significant difference in ranking of species response to grazing treatment between the abundance-based db-RDA models based on the three dissimilarities.

Table 4.3: Classification of species based on their compositional (presence/absence) and abundance response to grazing treatments

Species Type	**Class Name**	**Class description**	**No. of Species** **Composition**	 **Abundance**
1	Pure signal (PS)	Occur in only one treatment	43	43
2	Mixed signal (MS)	Occur in both treatments in differing frequency/abundance	27	43
3	No signal (NS)	Equal prevalence/abundance in both treatments	20	4
		Total	90	90

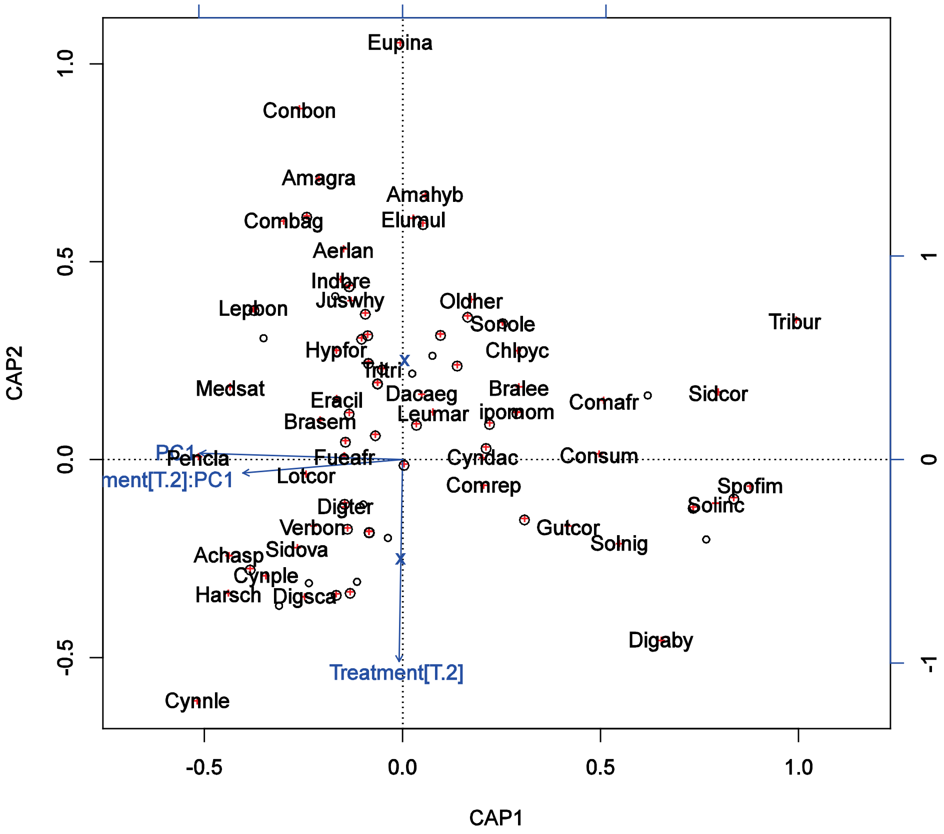

Figure 4.2 The ordination plot for db-RDA model based on chi-square dissimilarity. The grazing treatment was expressed by the second axis (CAP 2). Only a subset of species is shown to avoid overlapping. The species codes are shown in Appendix B, the black circles and red crosses represent the site and species centroids. Blue crosses are centroids for the two treatments

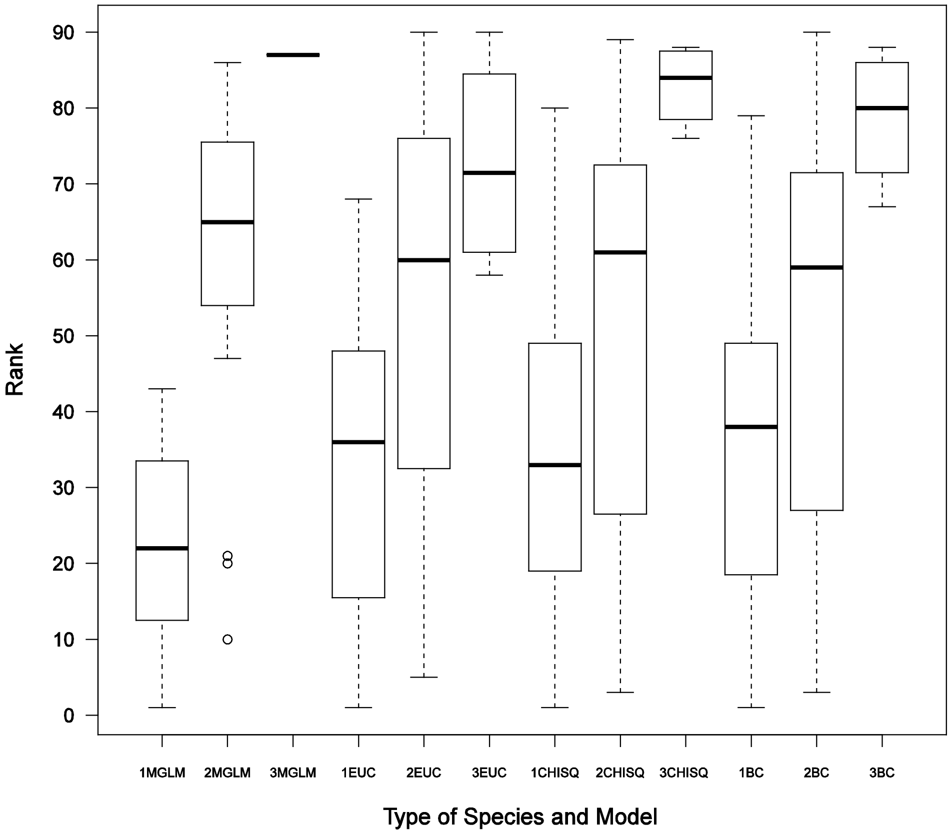

Figure 4.3 Ranking the species response to grazing treatments in ManyGLM and db-RDA abundance-based models. The x-axis labels MGLM represent the ManyGLM while EUC, CHISQ and BC represent the db-RDA models based on Euclidean, Chi-square and Bray-Curtis dissimilarities respectively and the suffixes 1, 2 and 3 in these x-axis labels signify the pure signal, mixed signal and no signal species respectively. Low rank signify higher response to grazing

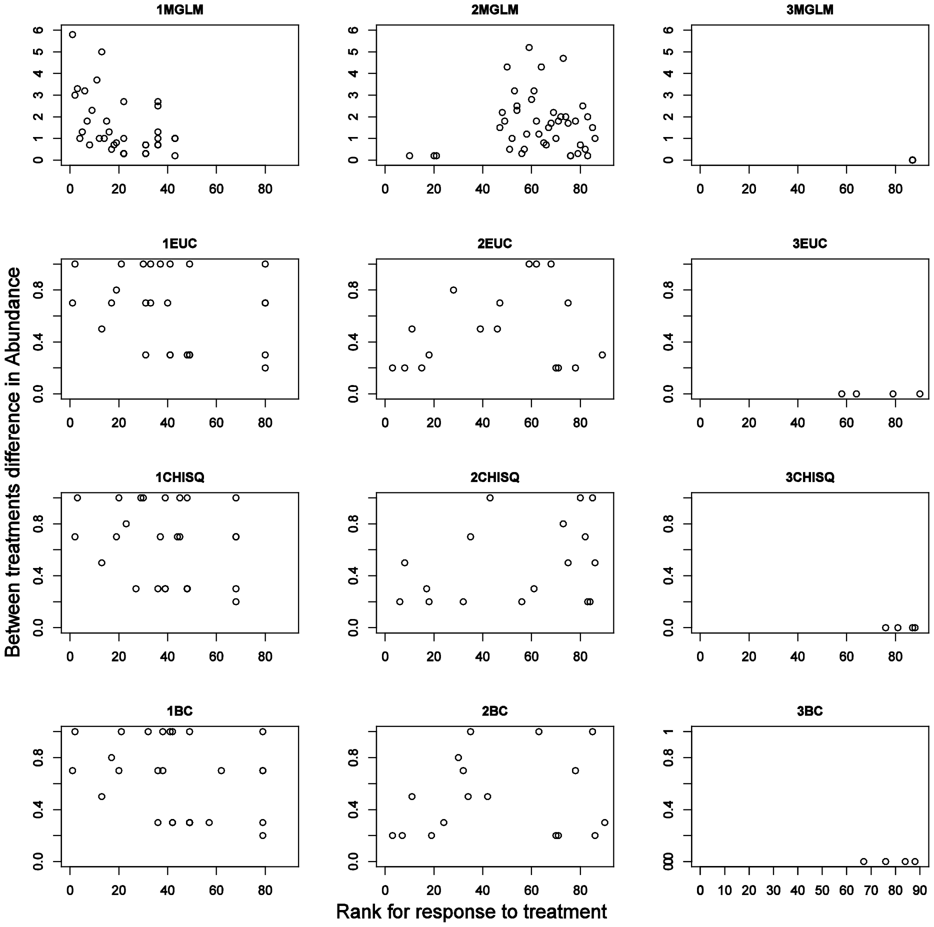

Figure 4.4 Ranking of species response to between treatment difference in species prevalence (frequency of occurrence) for the ManyGLM and the three db-RDA models based on different dissimilarity. The labels are as in Figure 4.3

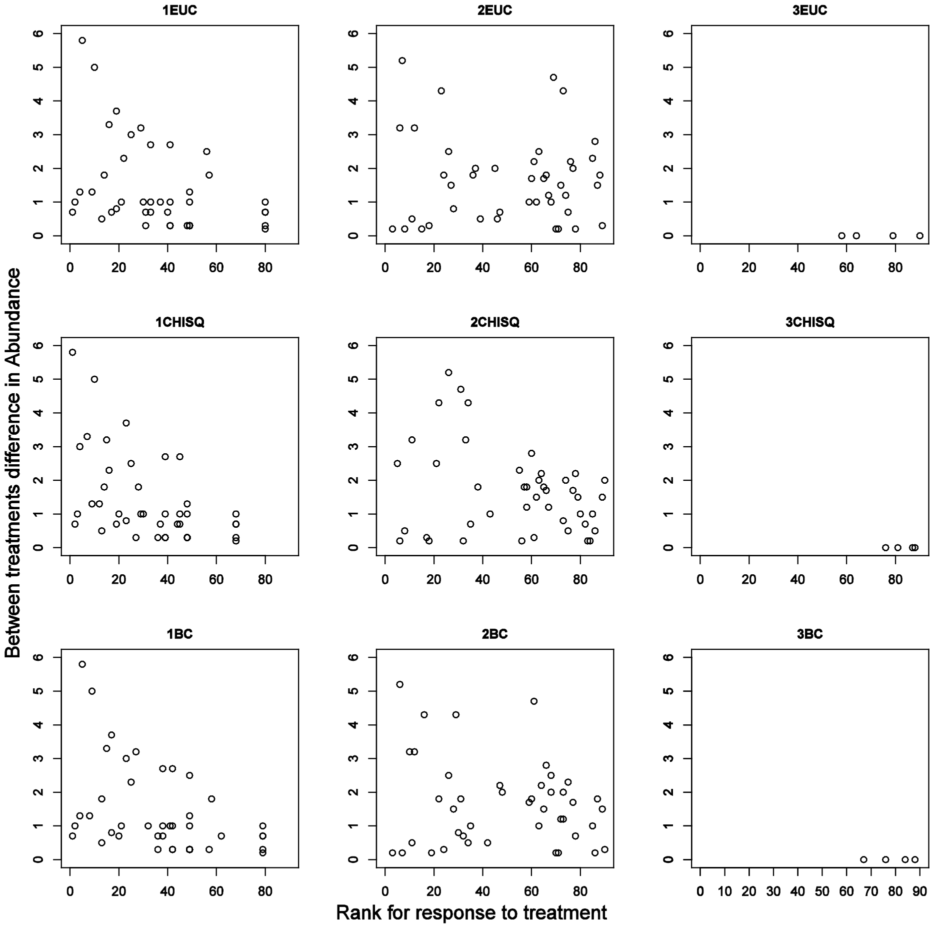

Figure 4.5 Ranking of species response to between treatment difference in abundances for the ManyGLM and the db-RDA models based on three dissimilarities. The labels are similar to Figure 4.3

4.5 Discussion

The ManyGLM explained higher deviance and showed more significant effects from grazing compared with db-RDA, for both species composition and abundance models. The two methods revealed distinct differences when identifying the species that respond to grazing treatment. In agreement with our hypothesis, ManyGLM ranked the pure signal species as the most responsive to grazing treatment. These pure signal species were rare annual species that caused the highest compositional effects as they were excluded in the ungrazed treatment. This resulted to ManyGLM to be more sensitive to between treatment differences in species prevalence compared to differences in abundances (Figure 4.4 and Figure 4.5). Its sensitivity to compositional differences was higher than db-RDA models based on the Euclidean and chi-square dissimilarities which emphasize the rare species (Kindt and Coe 2005). The db-RDA models did not show a consistent pattern in ranking of species response to treatment as the three categories of species overlapped in the ranks (Figure 4.3). In some instances, db-RDA models based on Euclidean and Bray-Curtis dissimilarities ranked the no signal species as being more responsive to grazing than the pure signal species (Figure 4.3). This suggests that earlier studies to discern grazing impacts on community composition that used the DBMs may have incorrectly identified the no signal (non-responsive) species as being the most responsive to grazing.

The higher sensitivity to differences in species prevalence than abundances in ManyGLM abundance-based models is attributed to negative binomial distribution that gives more weight to rare species (ver Hoef and Boveng 2007). These rare species contribute the largest compositional effect due to their high sensitivity to disturbances or environmental stress compared to common species that have broader tolerances (Poos and Jackson 2012). Higher sensitivity to these rare pure signal species is an important attribute of the ManyGLM as it demonstrates the ability to detect the slightest of change in community composition as opposed to DBMs that detect changes when expressed in most abundant and also variable species. Higher sensitivity to rare species (compositional effects) observed in ManyGLM suggests that this method would be the most applicable for testing grazing effects in communities characterized by high species turnover. These include rangelands experiencing high compositional changes due to intense grazing that enhance invasion of rare annual herbs or forbs (Metzger et al. 2005, Anderson et al. 2007). The results of ManyGLM contrast with the db-RDA method, which was sensitive to ubiquitous (also most variable) species. These species are largely generalists and therefore poor indicators of changing range condition.

The flexibility of DBMs, like db-RDA, in the use of different suitable dissimilarity indices is viewed as an advantage as it highlights different aspects of data (Anderson et al. 2006). However use of dissimilarities that mis-specify the mean-variance relationship in multivariate data could cause confusion of locational (mean abundance) and dispersion (variability) effects in the models, leading to inappropriate conclusions (Warton et al. 2012). The dissimilarities with flexibility of selecting the appropriate mean-variance trend in the data before-hand are yet to be developed (Anderson et al. 2006). Thus when using the DBMs, like db-RDA, data transformations and/or standardizations are recommended to achieve the correct mean-variance trend assumed by the selected dissimilarity (Legendre and Gallagher 2001). However, global transformations that are applied uniformly to all species (e.g. log transformation) are unlikely to rectify the mean-variance trend in multivariate abundance data that consists of many zeroes and rare species

(McArdle and Anderson 2004, O’Hara and Kotze 2010). Therefore the mean-variance trend in the data would limit the number of appropriate dissimilarities that can be applied. Moreover, interpretation of results from transformed data (e.g. log-abundances) is challenging compared to their original absolute abundances like the ones maintained in the ManyGLM. Besides, the use of dissimilarities in the DBMs masks the actual species identity.

In our case, the data was dispersion weighted to differentially down-weight the influence of ubiquitous species with variable abundances. This was expected to result in a mean variance trend approximately similar to a Poisson distribution that is assumed by Euclidean dissimilarity. Therefore we expected results based on Euclidean dissimilarity to be more significant compared to the other two dissimilarities. However, dispersion weighting reduced over-dispersion by half (from slope of 2.2 to 1.1) but did not remove it (Appendix A). This is similar to results of Clarke et al. (2006a) who observed small and subtle effect of dispersion weighting on abundance data. The resulting mean-variance trend after dispersion weighting was closer to that assumed by chi-square dissimilarity (Appendix A). We did not detect significant difference in variances explained or in ranking of the species responses to treatment between the models based on the three dissimilarities. Therefore no conclusions could be made on the effect of misspecification of the mean-variance between the three dissimilarities. The three dissimilarities differ in their emphasis on either species composition and abundances and how they treat the species data. For example, the Euclidean dissimilarity factors the joint absences that are not accounted for in Bray-Curtis dissimilarity (Clarke et al. 2006b). Therefore the effect of mis-specification of the mean variance trend may have been confounded by the varying emphasis on different aspects of the data in the three dissimilarities. This demonstrates the intricate complexity in selection and use of dissimilarities.

The ManyGLM approach has an advantage of avoiding the rigors of selecting a suitable dissimilarity index or applying data transformations to match the mean-variance relationship in the data to that assumed by these dissimilarities. However, in the ManyGLM approach an appropriate distribution that corresponds with the mean-variance trend in the data has to be selected e.g. a Poisson, negative binomial or binomial distribution. Misspecification of this distribution in ManyGLM is equally problematic as that of mean-variance trend in DBMs (Warton et al. 2012). This emphasizes the need for diagnostic tests to examine the properties of species data to determine the appropriate distributions.

4.6 Conclusions

The ManyGLM explained higher deviance than db-RDA models in species composition and abundances. This was attributed to the distinct difference between the two methods in identifying the species that are responsive to grazing. The ManyGLM ranked highly the pure signal species that comprised rare species that are highly sensitivity to disturbances or environmental stress. The db-RDA models did not show a consistent pattern in ranking of species response to treatment. In some instances, the db-RDA models based on Euclidean and Bray-Curtis dissimilarities ranked the no signal species as being more responsive to grazing than the pure signal species. This suggests that conclusions drawn by earlier studies to support or oppose the equilibrium, disequilibrium and non-equilibrium hypotheses in savannas using the DBMs may have incorrectly identified the no signal species as being responsive to grazing. Incorrect inferences due to statistical artifacts may have mis-informed conservation plans, for example, reducing stocking rates in disequilibrium communal rangelands where herbivore grazing has limited or no impact on plant community composition (Oba et al. 2000b, Western et al. 2009a).

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Chapter 5

Grazers degrade range condition by increasing richness of annual forbs along Lake Naivasha[*]

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[*] This chapter is based on:
Muthoni, F. K., T. A. Groen, A. K. Skidmore, and A. G. Toxopeus. Grazers degrade range condition by increasing richness of annual forbs along Lake Naivasha, Kenya. Afr. J. Ecol. **(Under review after revision)**

Abstract

Habitat fragmentation in pastoral landscapes concentrates plant and herbivore species into small isolated patches. This reduces the environmental niche and alters plant-herbivore interactions that in-turn change plant community composition. We evaluated the effect of grazing on herbaceous plant diversity in a fragmented RAMSAR site (Lake Naivasha) using data recorded from herbivore exclosures. GLMs were fitted to test the significance of grazing treatment on plant diversity. The Wilcoxon signed-rank test was used to test the significance of differences between treatments in abundance of herbaceous species with varying growth forms and cycle. Excluding grazers significantly reduced the species richness but had marginal effects on Shannon diversity and abundances. The reduced species richness was due to competitive exclusion of annual herbs from the ungrazed treatment largely by three dominant perennial grasses. High richness of annual forbs in the grazed treatment and dominance by perennial increaser-II grasses suggest that this landscape is over-grazed. We identified species that are most responsive to grazing and therefore useful indicator species during bio-assessment of range condition. Results suggests that range monitoring programs should consider both richness and the traits of the species that increase.

Key words: competitive exclusion; grazing intensity; habitat fragmentation; herbivore exclosure; species diversity; species composition

5.1 Introduction

Wetlands in savannas are key resource habitats due to a high availability of resources such as forage and water (Scoones 1995, Tzialla et al. 2006). Some wetland habitats provide dry season grazing lawns for large herbivores. However, the accumulation of key resources in these wetlands attracts diverse economic activities such as agriculture leading to intense anthropogenic fragmentation that reduces grazing areas and connectivity between wet and dry season grazing lawns. This has resulted in isolated (semi)-natural habitat patches surrounding the wetlands that are inhabited by pockets of resident herbivore populations (Odongo et al. *in Press*). The reduced habitat connectivity concentrates high herbivore densities in these isolated patches and alters the grazing cycle from seasonal to continuous grazing (Metzger et al. 2005). This may cause intense grazing that change the plant community composition.

Patches dominated by humans are located outside the protected areas but they hold high densities of herbivores. In Kenya, 70% of the total wildlife population resides in human dominated landscapes (Norton-Griffiths 2007). The persistence of wildlife inside the protected areas also depends on these human dominated landscapes as they are important migration corridors or dispersal areas during the dry seasons (Caro and Scholte 2007, Estes et al. 2012). Therefore understanding the ecological integrity of human dominated grazing areas is vital for overall wildlife management. However, little information is available on their range condition as most studies are biased toward the existing protected areas.

The rangeland surrounding Lake Naivasha is a typical example of such a human dominated landscape facing an imminent tragedy of commons (Hardin 1968). This is due to competing economic development and conservation goals. Historically, the area was a communal grazing range for wildlife and nomadic livestock (Harper et al. 2011). However, the grazing area has reduced due to horticultural expansion, increased settlement and geothermal electricity generation (Onywere et al. 2012, Muthoni et al. 2014, Odongo et al. *in Press*). The grazing area is further reduced by frequent floods along the riparian zone that occur for prolonged periods even during the dry seasons (Muthoni et al. 2014). The combination of these anthropogenic and natural disturbances has resulted to a unique landscape mosaic characterized by; (1) contrasting land-use regimes within ranches (2) decreasing grazing land (3) decreasing habitat connectivity and (4) increasing herbivore densities (Harper and Mavuti 2004, Muthoni et al. 2014, Odongo et al. *in Press*).

Currently, land is sub-divided into privately owned parcels of varying sizes with contrasting land-uses (Figure 5.1). Most land-owners practice wildlife conservation (eco-tourism), livestock ranching and horticultural farming at the same time. Habitat connectivity is further reduced by construction of wildlife fences that hinder free movement of herbivores between adjacent ranches. It also restricts communal livestock herding to a few patches that are intensely grazed (Morrison and Harper 2009). The grazing lands on the outlying wet season range have been reduced mainly due to increased settlements and clearing of two forests; Eburru and Mau Escarpment (Onywere et al. 2012, Were et al. 2013, Odongo et al. *in Press*). These forests acted as wildlife refuges and their clearing promoted herbivores to migrate to wildlife friendly ranches that are adjacent to the lake (Harper and Mavuti 2004).

The increased large herbivore density accompanied by a decreasing extent of grazing lands could result in intense grazing that change the plant species diversity and composition. Information on herbivore impacts on plant species diversity and composition in the terrestrial zone adjacent to Lake Naivasha is scanty. To the best of our knowledge only one study investigated the impact of large herbivores on plant community composition on a narrow *Cyprus papyrus* band along the edge of the lake (Morrison and Harper 2009). This paper presents a first study to extend this to the larger terrestrial zone that is utilized by an increasingly dense population of resident herbivores in all seasons compared to the narrow aquatic zone that is periodically flooded. This information is vital for formulating adaptive management policies to promote a sustainable co-existence of diverse and abundant plant and herbivore species within this landscape.

An exclosure experiment was set up to investigate the grazing impacts of large herbivores on herbaceous plant diversity and composition. Considering the long grazing history in this landscape we expect the herbaceous species to be adapted to high grazing pressure. Therefore excluding grazers would reduce the abundance of grazing tolerant species (often annuals and inferior competitors), leading to an initial reduction in species richness, Shannon diversity and abundance of annual species. We also hypothesized that grazing exclusion would increase competitive exclusion by dominant perennials resulting to significant increase in the abundance of dominant perennials. We examined the change in species richness and Shannon-D diversity together with the shift in composition (species abundances) to infer the validity of the above assumption. We also investigated how the abundance of four growth forms responded to grazing exclusion.

5.2 Methods

5.2.1 Study area

The study was undertaken on the fringe zone of Lake Naivasha (Figure 5.1). This is a RAMSAR site (Ramsar 1996) located outside the protected area but adjacent to two protected areas; Hell's Gate and Mt. Longonot National Parks, and a series of private wildlife conservancies. It is located on the floor of the Great Rift-Valley at an elevation of approximately 1890 m. Rainfall occurs in two main seasons (March-May, October-December). Mean annual rainfall is approximately 680mm but characterized by high inter-annual variability (CV~30%; Becht and Harper 2002). There is a distinct vegetation zonation moving away from the lake. It ranges from aquatic macropytes (mainly *Eichhornia crassipies* and *Cyperus papyrus*) to grasslands then to shrublands and finally to *Acacia xanthophloea* woodland (Gaudet 1977a). Common grasses include *Cynodon dacytlon, Cynodon nlemfuensis* and *Penisetum clandestinum*. More than 25 native and introduced large ungulate species inhabit the area (Odongo et al. *in Press*). The common native grazers and mixed feeders include the hippopotamus (*Hippopotamus amphibius*), buffalo (*Syncerus caffer*), common zebra (*Equus burchelli*), eland (*Taurotragus oryx*), impala (*Aepyceros melampus*), Defassa waterbuck (*Kobus ellipsiprymnus*), Thompson's gazelle (*Gazella thomsonii*), common warthog (*Phacochoerus africanus*) and grant gazelle (*Gazelle grantii*). This is in addition to livestock (mainly cattle; *Bos indicus*) in private ranches and communal areas.

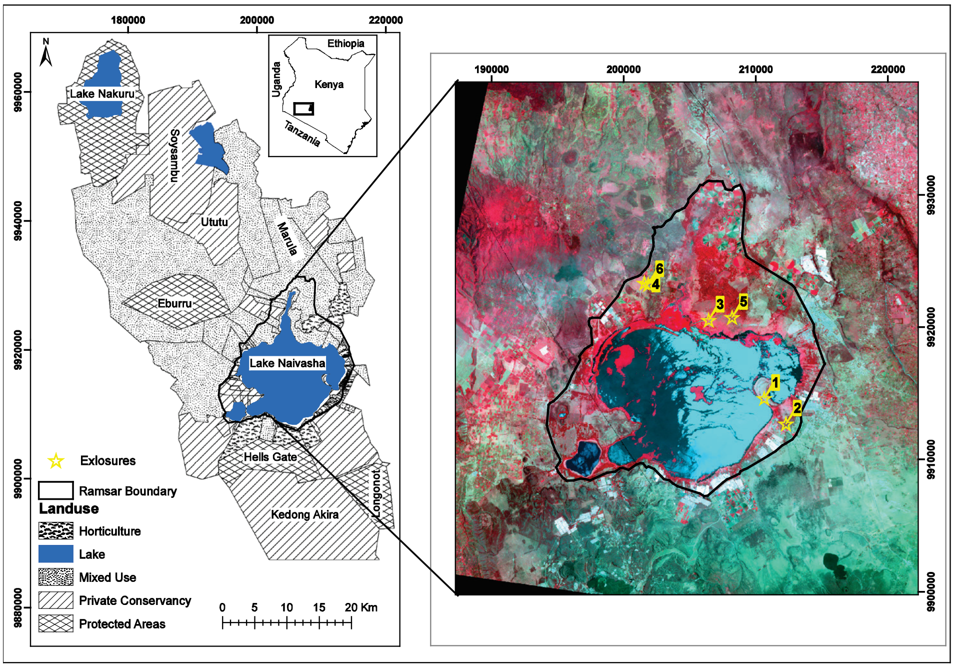

Figure 5.1 Location of the exclosures and land-uses for ranches within the Nakuru Wildlife Conservancy. The map of Lake Naivasha RAMSAR site is superimposed on an ASTER satellite image captured on September 2011

5.2.2 Plant species sampling

We sampled 5 ranches adjoining Lake Naivasha (Figure 5.1). In June 2011, we constructed six herbivore exclosures of 10m x 10m with two adjacent unfenced controls (Figure 5.2). These were located within permanent plots that have been marked for monitoring vegetation (Muthoni et al. 2014). The exclosures were located on (semi)-natural grasslands and effectively excluded medium to large ungulates. We surveyed the herbaceous plant species after one year of excluding grazers (July 2012) during peak biomass to capture rare species. The herbaceous plants were defined as all vascular plants with height below 50cm. We identified herbaceous species within five random quadrants (1x1 m) in each exclosure and controls together with a visual estimate of their percentage ground cover. A total of 90 quadrants were sampled in all six exclosures. We used a modified Braun-Blanquet six point scale to score the species ground cover 1(<1%), 2 (1-5%), 3 (6-25%), 4 (25-50%), 5 (51-75%) and 6 (76-100%) (Mueller-Dombois and Ellenberg 1974). The species taxonomy follows Ibrahim and Kabuye (1987), Agnew and Agnew (1994) and Beentje (1994).

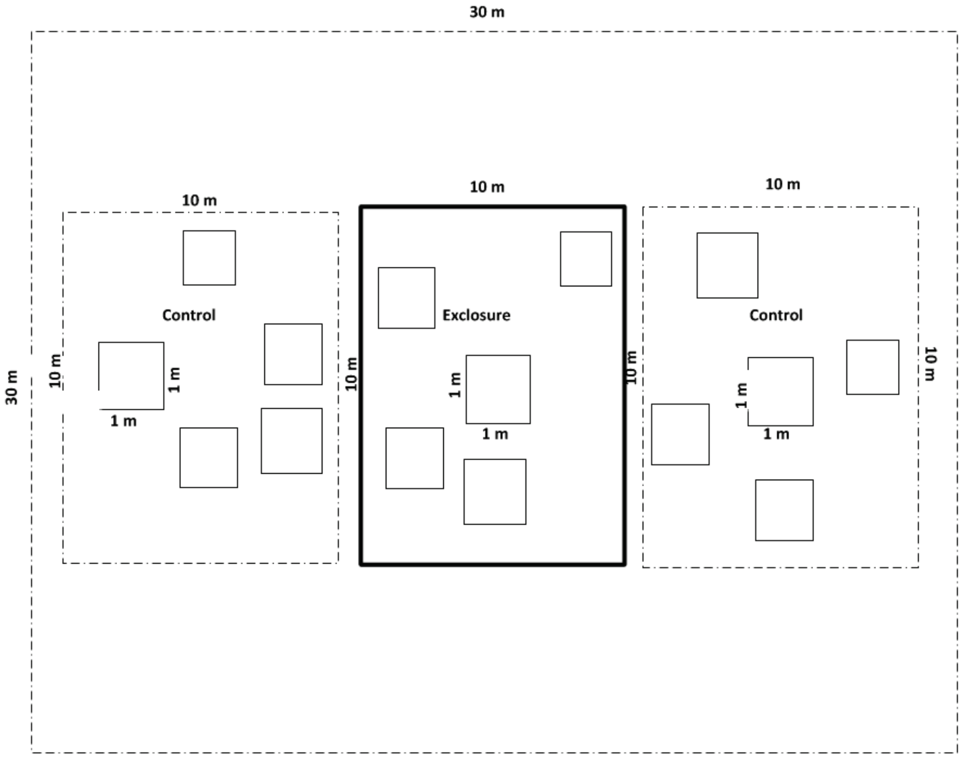

Figure 5.2 The design of the exclosure experiment. The five random quadrants in each treatment measured 1m^2

During initiation of the exclosure experiment (June 2011), we collected four classes of environmental variables at each site. First, we derived the topographical index (TPI) as proxy for soil moisture resources. A 30x30m resolution hydrologically correct digital elevation model (DEM) was interpolated from contours with 20 m interval, spot heights from 1:50000 topographical maps and isolines from 1957 bathymetry of the lake (Ase et al. 1986) as well as rivers as vector lines. We generated TPI from this DEM using the algorithm developed by (Jenness 2005).

Secondly, we generated frequency of inundation (FoI) and fractional bare soil (FBC) as indicators of flooding disturbance and vulnerability to erosion respectively. To derive the FoI, we extracted the elevation of the centroid of each exclosure from the DEM. The daily Lake level measurements for 15 years (1997 to 2012) were obtained from a gauging staff located at the Yacht Club (near site 1) with a reference elevation level of 1885m. We calculated FoI as fraction of times the lake levels were higher than elevation of the centroid.

Thirdly, we collected soil resources i.e. pH, N, P and K. In each site we collected four soil cores at a depth of 10-15 cm distributed randomly in a zigzag pattern. We mixed the four cores to form a uniform sample for each site. We analyzed the N, P, and K concentration and pH values for each sample using standard methods at the National Agricultural Research Laboratories-Kenya. Fourthly, we used the percentage tree-shrub cover (FTC) and bush cover (FBC), visually estimated within each 30 x 30 m plot, as a proxy for light resources.

5.2.3 Statistical Analysis

All statistical analyses were executed in R (R Development Core Team 2014). We reduced the site specific environmental variables i.e. pH, N, P, K, TPI, FBC, FoI, FTC and FBC to two orthogonal variables using principal component analysis (PCA; Legendre and Legendre 2012). The site characteristics in the models were substituted with the first PCA axis that explained 79% of the variance. We derived a species cumulative curve to assess the adequacy of the sampling effort. Species rarefication was applied to cater for different sample sizes between the two treatments (Kindt and Coe 2005). A species rank abundance curve was derived to investigate which species were dominating in abundance.

We used Generalized Linear Models (GLM’s) to discern the significance of grazing treatment on species richness (the number of species in a sample plot) and Shannon diversity, measured with Shannon-D, the conversion of the Shannon-Wiener index to effective number of species (Jost 2006). This index is effective in capturing the actual magnitude of difference in diversity between treatments compared to the standard Shannon-Wiener index (Jost 2007). This is because the standard Shannon-Wiener index is non-linear and does not satisfy the doubling property (Hill 1973). When partitioning diversity into alpha and beta components, adding two equally species rich communities with x distinct species should yield 2x species (Jost 2007). The Shannon-D was derived using the Vegetarian R package (Charney and Record 2012) as: $ShannonD = \exp(-\sum_{i=1}^{s} p_i \ \ln p_i)$.

The response variables in the GLM models were species richness and Shannon-D while predictors were grazing treatment and the first PCA axis (PC1) that represented the site characteristics. The species richness and Shannon-D models were fitted with a Poisson and quasi-Poisson distribution respectively and a log-link function (Quinn and Keough 2002). The overall fit of the model was assessed by the deviance explained (D^2) while an ANOVA test was used to test the significance of predictors and their interactions.

To test whether the grazing treatment had significant effect on abundances of individual species we fitted a novel multivariate GLM (ManyGLM) with a negative-binomial response (Wang et al. 2012). The response in these models was the species matrix and predictors were similar to that in the species richness model. The ManyGLM algorithm was implemented in the MVABUND R package (Wang et al. 2012). The algorithm models the actual species abundances directly and accounts for the mean-variance relationship that is inherent in plant abundance data (Warton et al. 2012, Muthoni et al. Under-review). ManyGLM fits multiple GLM models to all species simultaneous while returning univariate tests that identify the species that express the treatment effect. We evaluated the significance of the overall multivariate effect and the predictors using an ANOVA using a resampling procedure with the log-likelihood (LR) test statistic (Wang et al. 2012). This ANOVA test also returned univariate tests showing the significance of each species' response to the grazing treatment. This allowed ranking the species according to their responsiveness to grazing treatment.

We compared the abundances of four growth forms (forbs, grasses, sedges and dwarf shrubs) and growth cycle (annuals and perennials) between the two treatments using the Wilcoxon signed-rank test (Hollander and Wolfe 1973).

5.3 Results

5.3.1 Grazing treatment impact on species diversity and composition

The species richness and Shannon-D in the grazed treatment was two times higher than in the ungrazed treatment (Table 5.1). The GLM model revealed that excluding grazers significantly lowered species richness in all exclosures ($Dev_{3,\ 8}$ = 32, $p<0.001$, D^2 = 0.4, Table 5.2). The species cumulative curve revealed that the sampling effort was exhaustive since the rate of change in richness in both treatments flattened after the third site (Figure 5.3). The ManyGLM revealed a marginally significant effect of grazing treatment on species abundances ($Dev_{3,\ 8}$ = 161, p = 0.09, D^2 = 0.5; Table 5.2). The univarite tests from ManyGLM revealed that the rare annual species were the most responsive to grazing as they were excluded in the ungrazed treatment (see the ranking in Appendix B). Univariate tests revealed that only nine of these annual species showed significant ($p<0.05$) differences in abundance between treatment (Appendix B). Analysis of abundances of species with differences in growth cycle (annuality) and life form revealed that the abundance of annuals and forbs was significantly higher ($p<0.05$) in the grazed treatment (Table 5.3). There was no significant difference in abundance of grasses between the treatments (Table 5.3) since the community was dominated by three generalist perennials grasses that were abundant in both treatments; *Cynadon dactylon (Cyndac), Cynadon nlemfluensis (Cynnle)* and *Pennisetum clandestinum (Pencla)* (Figure 5.3).

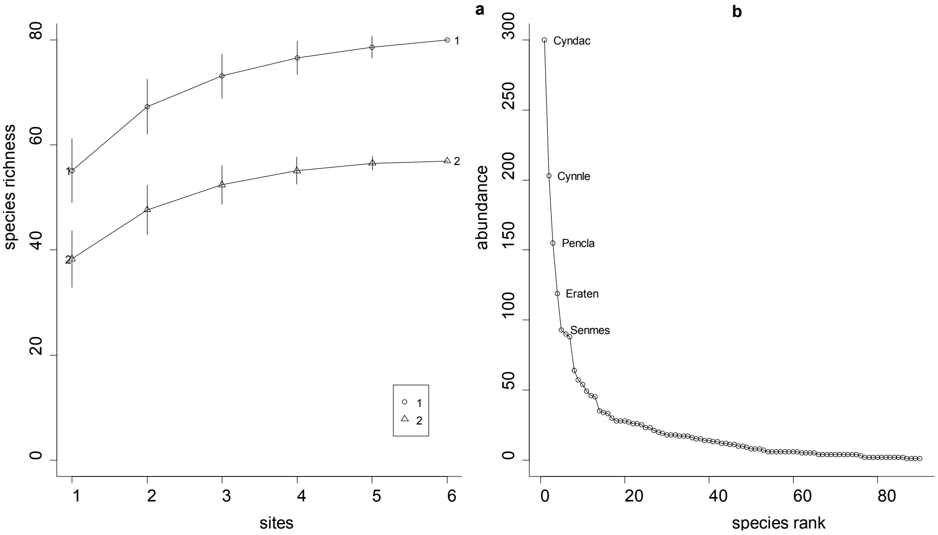

Figure 0.3 The species accumulation curve with rarefaction (a) for the grazed (1) and ungrazed (2) treatments and rank abundance curve (b) for species in all sites. Full species names are shown in Appendix B

Table 5.1: The species richness and Shannon-D between grazing treatments in all exclosures

Sites	**Treatment**	**1**	**2**	**3**	**4**	**5**	**6**	**Mean**
Richness	Grazed	26	33	19	36	12	47	29
	Ungrazed	11	4	9	15	8	36	14
Shannon-D	Grazed	16	18	9	24	5	31	17
	Ungrazed	8	2	6	10	4	24	9

Table 5.2: The significance and deviance explained by grazing treatment on species richness and abundances. All models are based on 3 and 8 degrees of freedom for model and residuals

	Species richness		**Species Shannon-D**		**Species abundance**	
Variable	**Deviance**	**P**	**Deviance**	**P**	**Deviance**	**P**
Treatment	32.33	<0.001	16.84	0.17	160.7	0.09
PC1	1.22	0.27	2.05	0.62	271.3	0.02
Treatment*PC1	0.45	0.50	0.56	0.79	77.6	0.3

Table 5.3: The significance of differences in abundances between treatments for species with varying life forms and growth cycles from a Wilcoxon signed-rank test

		Species Abundances			
Species Type	**N**	**Grazed**	**Ungrazed**	**V**	**p**
Annuality					
Annual	49	1.6	0.6	918	0.037
Perennial	41	3.2	3.3	408	0.984
Life Form					
Forbs	59	1.4	0.7	1196	0.001
Grass	24	4.6	4.5	162	0.742
Sedges	3	1.6	0.3	6	0.250
Dwarf shrub	4	2.8	3.5	1	0.423

5.4 Discussion

Excluding grazers for one year significantly reduced herbaceous species richness but had marginal effect on Shannon-D and abundance (Table 5.1). The lower effect on Shannon-D and species abundances is because the community was dominated by three grazing tolerant perennial grasses that had no significant change in abundance between the two treatments (Appendix B). These included the *Cynodon dactlylon (Cyndon)*, *Cynodon nlemfuensis* (*(Cynnle)*) and *Penisetum clandestinum* (*Pencla*). After excluding grazers; these dominant perennials competitively excluded the grazing tolerant annual forbs in the ungrazed treatment thereby causing a decline in species richness and Shannon-D. This agrees with earlier finding that grazers increase plant species diversity by suppressing the competitive dominance of the dominant perennial species (Olff and Ritchie 1998, Golodets et al. 2011). The results also agree with earlier studies that removal of grazing in semi-arid grasslands with long history of grazing will reduce herbaceous species diversity (Milchunas et al. 1988, Eby et al. 2014). However, continuous intense grazing increased richness and abundance of annual forbs that is of low productivity and grazing value (Metzger et al. 2005, Ng'weno et al. 2010, Young et al. 2013). This suggests that range monitoring programs should consider both richness and the traits of the species that increase. Intense grazing may lead to a species rich range that is dominated by grazing tolerant annual forbs with limited productive potential. This highlights the need for controlling grazing intensity as a management tool for maintaining herbaceous diversity in savannas.

The grazing-tolerant annual species that were most responsive to grazing exclusion (Appendix B) are common in intensely grazed East-African rangelands (Ibrahim and Kabuye 1987, Belsky 1992, Kioko et al. 2012). This includes *Euphorbia inaquilatera* (Eupina), *Amaranthus hybridus* (Amahyb), *Elusine multiflora* (Elumul). The significantly higher abundance of these annuals forbs in the grazed treatment is an indicator of overgrazing and declining range condition in this landscape. This is despite the observed increase in species richness. Our results reveals that range condition monitoring programs should consider both richness and the traits of species that increase (Wesuls et al. 2013). Moreover the annual forbs that were ranked as having the largest contribution to treatment effect could be used as indicators of overgrazing when assessing range condition. The indicator species gives early warning for impending changes in range condition (Saayman et al. 2013). They would be essential in monitoring the efficiency of grazing management practices such as stocking levels on community composition.

The three perennial dominant grasses; *Cynodon dactlylon*, *Cynodon nlemfuensis* and *Penisetum clandestinum* are generalists hence capable of tolerating intense grazing and arid conditions (Ibrahim and Kabuye 1987). This is related to their fast growth and lateral spread through stolons and underground rhizomes (Ibrahim and Kabuye 1987, Belsky 1992). The lateral spread confers competitive advantage in uptake of soil resources (Milchunas et al. 1988).

The two co-geners; *Cynodon dactylon* and *nlemfluensis* are increaser-II species as their abundance increases with grazing pressure (Kioko et al. 2012). However when subjected to intense grazing and trampling they may develop defensive trait by producing high levels of hydrogen cyanide *(cyanogenesis; Georgiadis and McNaughton 1988)*. *High levels of* cyanide cause bloating and death of herbivores *(Georgiadis and McNaughton 1988).* Samples of *Cynodon dactylon* from Lake Naivasha were reported to have high levels of cyanide (Hayward and Hohl 1995). Therefore continuous intense grazing can trigger development of defense traits in these dry season forage grasses, making them un-utilizable by grazers. This could explain why *Cynodon plectostachyus,* that is known to be highly cyanogenic when intensely grazed or tramped, was found only in site 1 that had the highest grazing intensity (Muthoni et al. 2014).

The other dominant grass; *P. clandestinum* is highly productive and nutritious therefore of high grazing value (Ibrahim and Kabuye 1987, van Oudtshoorn 1992). The abundance of this grass is increasing along the periodically flooded edges of Lake Naivasha where it succeeds the drying *Cyperus papyrus* (Morrison and Harper 2009). The drying of papyrus is largely attributed to decline in lake levels. This suggests that the decline of the lake levels is beneficial to large herbivores, at least in the short-term, since it increases the grazing area that is colonized by this high quality forage grass.

However this zone is experiencing prolonged flooding even during the dry seasons when it is expected to supplement the scarce forage (Muthoni et al. 2014). A detailed simulation analysis is needed to unravel the long-term net effect of flooding regime on forage availability in this landscape.

Our results suggest that conservation efforts should prioritize on these three dominant grasses compared to rare annuals because their local extinction would have negative consequences on ecosystem functions such as provision of forage and ground cover to control erosion. This is contrary to common practice of prioritizing conservation of rare species to prevent extinction although this rare species may have limited contribution to ecosystem functioning (Walker 1995, Arponen 2012).

The relatively short duration of our experiment excludes us from making conclusions on the effect of long-term climatic variability that might affect species response (Belsky 1992, Fynn and O'Connor 2000, Angassa and Oba 2010). The compositional changes are normally a gradual process interspersed by static periods (Westoby et al. 1989, Belsky 1992, Fuhlendorf et al. 2001). A 44 year exclosure experiment in savanna (Fuhlendorf et al. 2001) revealed that grazing intensity determines the long-term change in species composition. However, climate variability influenced the short-term rate of compositional turnover and species abundances. Our short-term experiment support the effect of intense grazing on composition turnover. However, there is a possibility that the observed changes may be a transition state in a temporary oscillating system (Fuhlendorf et al. 2001). Some original species may have disappeared before construction of exclosures due to the prolonged exposure to intense grazing or other environmental stress that might limit full recovery even after exclusion (Silcock and Fensham 2013). This can only be verified using longer-term exclusion experiments (Sensu Young et al. 1997, Hejcmanová et al. 2010) but none exist in this landscape to date. Our experiment is an initial step toward a long-term monitoring in this landscape.

Acknowledgements

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Chapter 6

Spectral distances explains higher variance in plant β-diversity than spatial-autocorrelation[*]

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[*] This chapter is based on:
Muthoni, F. K., T. A. Groen, A. K. Skidmore, and A. G. Toxopeus. Spectral distances explains higher variance in plant β-diversity than spatial-autocorrelation. International Journal of Applied Earth Observation and Geoinformation **(Under review after revision)**.

Abstract

Most ecosystems lack long-term extensive data that can support analysis of what determines their inherent biodiversity patterns. The spectral variation hypothesis (SVH) suggests that between-plot differences in remotely sensed signal (spectral variation) is a proxy for environmental heterogeneity that enhance plant beta-diversity; the between sites difference in plant species composition and abundances. Spatial distances also control plant beta-diversity patterns. The relative importance of environmental (spectral) variation and spatial distances in explaining variation in plant beta-diversity remains unclear. We evaluate the potential of spectral variation of Landsat-TM data and spatial autocorrelation in predicting variation in plant beta-diversity in a fragmented landscape. We use Mantel correlograms to investigate the correlation between spectral distances and beta-diversity and the presence of spatial dependency in spectral distances and beta-diversity. We fit a partial least squares regression (PLSR) to predict the variance in the plant beta-diversity explained by spectral and spatial distances and partition the variances due to pure spectral, spatial dependency in spectral distances and purely spatial autocorrelation. Mantel correlograms revealed an exponentially decaying correlation between beta-diversity and spectral distances that was significant between plots with short spectral distances (low spectral dissimilarity) and at the farthest lag distances (high spectral dissimilarities). Therefore dissimilarity in beta-diversity was lower at shorter spectral distances but increased with increasing spectral distances. We detected significant spatial autocorrelation in beta-diversity and spectral distances suggesting that the variation in beta-diversity was influenced by spatial structure directly and indirectly through spatially dependent environment (spectral distances). The PLSR model explained 37% of total variance in beta-diversity. Combination of the proportion of total variance explained purely by spectral distances (30%) and spatially dependent spectral variation (36%) revealed that environmental (spectral) distances explained cumulative higher variance in beta-diversity (66%) than purely spatial autocorrelation (34%). Results revealed that both environmental heterogeneity and dispersal limit contributed significantly to variation in beta-diversity in this landscape. This suggests that conservation initiatives should aim at enhancing habitat diversity and the abundance of individual species to increase propagues for dispersal.

Key Words: Environmental heterogeneity; Lake Naivasha; Mantel correlograms; dispersal limit; spectral variation hypothesis; variance partitioning.

6.1 Introduction

Understanding the factors that determine the variation in plant beta-diversity; the differences in species composition and abundances between the sampling units in a given locality; (Tuomisto and Ruokolainen 2006); is essential for ecosystem management. This is because conservation interventions are prioritized based on understanding or predictions of what drives the ecosystems (Gilbert and Bennett 2010). However, knowledge on what drives beta-diversity in most ecosystems is limited due to lack of long-term data necessary to validate species-environment models. To obtain these data, ecologists rely on costly and labor intensive field measurements of environmental variables and floristic surveys. These surveys are based on their prior knowledge (or bias) of what are important niche variables to be measured in the field and often cover limited spatial and temporal extents (Palmer et al. 2002). Alternative means of overcoming this data limitation are needed to facilitate timely and cost effective monitoring of variations in beta-diversity patterns over extensive spatial and temporal extents.

Recent studies have demonstrated the applicability of spectral variation in remotely sensed imagery for estimating plant beta-diversity (reviewed in Gillespie et al. 2008, Rocchini et al. 2010). These studies are based on the spectral variation hypothesis (SVH) that stipulates that the spectral heterogeneity (variation in reflectance in remotely sensed imagery) is a proxy for habitat heterogeneity (Oindo and Skidmore 2002, Palmer et al. 2002, Tuomisto et al. 2003, Foody 2005). According to niche theory (Hutchinson 1957), species diversity in a particular location is determined by environmental heterogeneity and related ecological-niches. Sites with high variability in remotely sensed reflectance indicate higher environmental heterogeneity that supports higher number of niches that are inhabited by high number of species, thus enhancing beta-diversity (Rocchini et al. 2010). The use of remotely sensed metrics to estimate plant beta-diversity has been suggested to be cost effective especially in data limited regions (Rocchini et al. 2010). This would enable rapid assessment of beta-diversity over large spatial and temporal scales that is essential for formulating robust conservation plans (Rocchini et al. 2010). However, the SVH has been tested on limited ecosystems.

According to Tobler’s law (Tobler 1970) nearby locations are likely to be more similar in species composition than far ones. Therefore the relationship between community data and environment (spectral) distances are expected to be non-stationary (Foody 2005). Despite this, most studies based on SVH do not account for contribution of spatial autocorrelation (reviewed in Rocchini et al. 2010). Moreover, the Hubbel’s neutral theory of biodiversity (Hubbell 2001) predicts that species are distributed randomly irrespective of environmental conditions but in a spatially auto-correlated dispersal that make near sites to be more similar in diversity than far ones (Tuomisto and Ruokolainen 2006). Therefore including spatial distances in beta-diversity models would account for species dispersal limitation (Chust et al. 2006). The relative importance of environmental (spectral) variation and spatial distances in explaining variation in plant beta-diversity remains unclear.

We derive beta-diversity as the between sites Bray-Curtis dissimilarity in plant community composition (comprising both species composition and abundances) in a fragmented and data limited landscape surrounding Lake Naivasha, Kenya. We use the between sites Euclidean distances in reflectance of the Landsat-TM bands 3-5 and 7 and the normalized difference vegetation index (NDVI) to derive the spectral distances that are used as proxy for environmental heterogeneity. The Euclidean distances in geographical coordinates between sampling plots was used as spatial descriptors. We use Mantel correlograms to investigate the correlation between the beta-diversity and the environmental (spectral) heterogeneity and to examine the presence and the structure of spatial dependency in beta-diversity and spectral distances. The structure of spatial dependency detected by mantel correlograms was used to generate spatial lag-distance classes that were used as spatial descriptors in a partial square regression (PLSR) model. The PLSR model partitions the variance in plant beta-diversity explained by environmental (spectral) distances, spatial distances and jointly by both predictor matrices due to spatial dependency of environmental (spectral) distances.

We hypothesize that the beta-diversity and environmental (spectral) distances have significant spatial dependency. We also hypothesize that variation in beta-diversity will be driven largely by environmental heterogeneity hence the spectral variation would explain significantly higher variation in plant beta-diversity than spatial-autocorrelation. This is based on observation by Gaudet (1977a) that vegetation zonation surrounding lake Naivasha varies along an environmental gradient that radiates away from the edge of the lake in relation to changes in soil moisture and soil types.

6.2 Methods

6.2.1 Study Area

The study was undertaken on the fringe zone of Lake Naivasha, Kenya that is a RAMSAR wetland (Ramsar 1996, Map 1). Historically the area was a dry season foraging zone for both wild and domestic ungulates (Harper and Mavuti 2004). However, it has experienced gradual habitat fragmentation due to increased horticultural developments, settlements, fluctuating lake levels and intense grazing (Harper and Mavuti 2004, Muthoni et al. 2014).

Currently (semi)-natural vegetation patches are interspersed between anthropogenic landscape. The vegetation ranges from aquatic species, to open *Tarchonanthus camphoratus* shrubs and *Acacia xanthophloea* woodlands, see (Gaudet 1977a, SPARVS 2008) for detailed description of vegetation types. The range is inhabited by over 25 large ungulate species (Odongo et al. *in Press*) while also holding substantial livestock populations. Land tenure comprises private ranches and communal grazing lands.

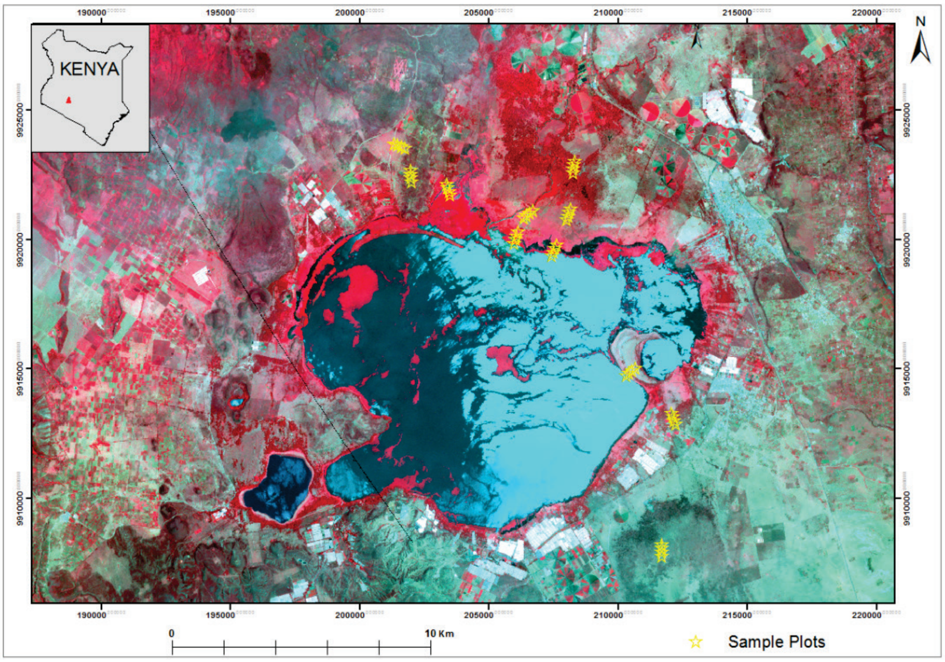

Figure 6.1 The location of sampling plots superimposed on Aster satellite image of September 2011. The plots were located on eleven transects each with four plots

6.2.2 Vegetation sampling

We established permanent plots (n = 44) measuring 30x30 m for monitoring vegetation on five ranches adjacent to lake Naivasha, Kenya (Figure 6.1). The plots were located on a gradient radiating away from the lake. All plant species in each plot were identified together with their percentage ground cover. Herbaceous species were recorded on five replicate 1x1 m quadrants in each plot while the cover of trees and shrubs was estimated for the entire plot.

6.2.3 Deriving distance Matrices

We expressed all variables as pairwise distance matrices following the observation that analyzing the variance in beta-diversity between sample sites explained by spatial-autocorrelation can only be validly tested if the hypotheses are stated in terms of distances (Tuomisto and Ruokolainen 2006). The beta-diversity represented the turnover in species composition and abundances amongst the 44 sample plots. This was derived by calculating the Bray-Curtis dissimilarity (Bray and Curtis 1957) from the abundance of 90 species recorded in the 44 plots. This yielded 946 distance pairs calculated as n*(n-1)/2 where n is the total number of plots.

Spectral data was derived from a medium resolution (30m) Landsat-TM image (path 169/row 060) downloaded from Reverb website (NASA 2013) and was captured at same time of the floristic survey (July 2011). This image was level L1T processed that included geometrical correction with 1629 ground control points (GCP's; RMSE = 2.27 pixels). The geometric reference of the image was transformed to UTM Arc 1960 reference grid. A geo-referenced roads vector data from a 1:50000 topographical map was overlaid on the transformed image to verify the accuracy of the geometric correction. We observed a perfect match between the roads on the vector data and the image, hence no further geometrical correction was done. We used the Atmospheric Correction Algorithm-2 (ATCOR-2; Richter 1996) to remove haze and other atmospheric effects (e.g. scattering and absorption) that attenuate the reflectance of ground targets (Vanonckelen et al. 2013). The algorithm was run using constant atmospheric conditions for the tropical-rural atmosphere, rural aerosol type, visibility of 16 Km and an average elevation of 1900m a.s.l., since the required meteorological data (e.g. aerosol concentration, albedo and optical depth; Kwarteng and Al-Ajmi 1996) for the time of image acquisition were not available. The atmospheric correction generated the apparent ground reflectance values for each pixel.

We extracted the reflectance values of the four Landsat-TM bands (3-5 and 7) and the (NDVI) at the centroid of each plot using a bilinear interpolation that averaged the values for adjacent pixels to avoid edge effect. We calculated Euclidean distance matrices from each of the four spectral bands plus NDVI to avoid important matrices being diluted by non-responsive ones in the model (Lichstein 2007), resulting to five spectral distance matrices. The four Landsat-TM bands (3-red: 0.63-0.69 hm; 4-near-infrared: 0.76-0.90 hm, 5-shortwave infrared: 1.55-1.75 hm and 7-shortwave infrared: 2.08-2.35 hm) has been recommended for discriminating vegetation community composition (e.g. Tuomisto et al. 2003, Hernández-Stefanoni et al. 2012). The normalized difference vegetation index (NDVI) was derived as (B4-B3/B4+B3) where B3 and B4 are the red and NIR bands respectively. NDVI represent the productivity pattern that is a proxy of environmental heterogeneity and its applicability in discriminating plant community composition has been demonstrated (e.g. Oindo and Skidmore 2002, He and Zhang 2009, Dalmayne et al. 2013). To standardize the reflectance units from different bands, the extracted pixel values for each band were normalized to zero mean and unit variance. The spectral distance matrices were calculated as the Euclidean distance of standardized pixel values for each band and NDVI values between sample plots. The spatial distance matrix was derived as the Euclidean distance between geographical coordinates of the centroids of each sample plot.

6.2.4 Statistical analysis

All analysis were carried out in R (R Development Core Team 2014). We investigated the presence and structure of spatial autocorrelation in beta-diversity and spectral distance matrices using the Mantel correlogram (Oden and Sokal 1986) in "ecodist" R package (Goslee and Urban 2007). The mantel correlogram calculates and plots the spatial autocorrelation measured as the Mantel statistic-r_M in a response matrix (e.g. beta-diversity matrix) at different lag-distance classes derived from a given spatial distance matrix (Legendre and Legendre 2012). The number of lag-distance classes was determined using the Sturge's rule by coding all the distance pairs falling within a particular lag-distance class with value 1 while the non-member distance pairs were coded zero (Legendre and Legendre 2012). The Mantel correlogram plots the derived Mantel-r_M (y-axis) against the mean distance in each lag-distance class (x-axis) to illustrate the structure of correlation at different lag-distances. A steep and smooth decay curve in the correlogram indicates that the predictor explains high variance on the response matrix (Nekola and White 1999, Hubbell 2001, Laliberté 2008). A "bumpy" curve reflects low contribution of the predictor matrix.

Mantel correlograms allows a qualitative assessment of spatial dependency in response and predictor variables (Tuomisto and Ruokolainen 2006). This is a reliable guideline on whether to account for spatial-autocorrelation in models that partition variances to avoid biased estimates of type I errors (Legendre and Fortin 1989). We investigated the spatial structure in beta-diversity and spectral distance matrices. The significance of the Mantel-r_M at each lag-distance class was tested using 1000 permutation tests (Legendre and Legendre 2012). The test returned a table listing the mean distance of each lag-distance class, the number of dissimilarity pairs within each lag-distance class, the Mantel-r_M statistic (range from -1 to 1) and the p-values from a two tailed test of the hypothesis that the mean distances or dissimilarity in a lag-distance class is significantly different from the mean of all the other lag-distance classes combined (Goslee and Urban 2007).

We partitioned the variance in beta-diversity explained by the spectral and spatial distance matrices by fitting a PLSR model using the "pls" R package (Mevik and Wehrens 2007). The PLSR is suitable for regressions with many collinear predictors, whereby it reduces the high dimensionality by forming a few uncorrelated latent variables (LV) that are used to fit the models. In the PLSR, beta-diversity was the response matrix and the predictor matrices included the five spectral distances (4 Landsat-TM bands and NDVI) and the spatial autocorrelation represented by the lag-distance classes that exhibited significant spatial autocorrelation with either the beta-diversity or spectral distances in the Mantel correlograms. We included a second order polynomial for the five spectral distance matrices to cater for the non-linear response pattern relationship with the beta-diversity that was observed in the Mantel correlograms. The calculated spectral distances were square root transformed to reduce heteroscedasticity. The optimal number of latent variables used to fit the PLSR models were selected as the ones that minimized the Root Mean Square Error of Prediction (RMSEP) in cross-validation to achieve highest possible prediction accuracy without over-fitting the model. In a leave-one out cross-validation, a jackknifing approach was used to calculate the p-values ($p< 0.1$) for each predictor matrix (Magiera et al. 2013). We sequentially removed the non-significant predictor matrices until only the significant predictors remained that were used to fit the final model with seven spatial lag-distance classes; 1, 2, 3, 4, 5, 8 and 9 (Table 6.1).

The model fit was assessed by the RMSEP and the percentage of the variance in beta-diversity explained. Following (Pineiro et al. 2008) the model fit was further evaluated by regressing the measured and predicted beta-diversity as response and predictor respectively. The independent and joint variance explained by spectral and spatial autocorrelation was quantified using the variance decomposition method procedure (Borcard et al. 1992) to partition variances explained by; (a) spectral variation only, (b) jointly by spectral and spatial auto-correlation and (c) spatial variation only. This involved fitting three models (1) spectral distances only model providing the amount of variance explained by (a+b); (2) the spatial model with only the lag-distance matrices (explaining variances b+c) and (3) a full model with the above two explanatory matrices (explaining variances (a+b+c). The variance explained purely by spectral variation was derived as $a = (a+b+c) – (b+c)$, spatial autocorrelation only was $c = (a+b+c) – (a+b)$ and the variance explained jointly by spectral and spatial variation was $b = (a+b+c) - a - c$. We expressed the independent and joint variance explained by the two categories of predictor matrices as percentage of the total variance explained by the full model (a+b+c).

6.3 Results

The Mantel correlograms revealed that the correlation between beta-diversity and spectral distances exhibited a roughly exponential decay trend (Figure 6.2). This correlation was significant (Mantel-$r_M < 0.05$) between plots with short spectral distances (low spectral dissimilarity) and at the farthest lag distances (high spectral dissimilarities; Figure 6.2). Thus dissimilarity in beta-diversity was lower at shorter spectral distances but increases with increasing spectral distances. However, the Mantel correlograms revealed significant positive autocorrelation in beta-diversity and spectral distances (four Landsat-TM bands and NDVI) in at least the first spatial lag-distance class (mean distance = 0.86 Km; Figure 6.3). Significant negative spatial-autocorrelation in beta-diversity and spectral distances was observed in several spatial lag-distance classes (Figure 6.3). The structure of spatial autocorrelation in beta-diversity and spectral distances exhibited a non-linear pattern.

The overall PLSR model was fitted with three latent variables and had an RMSEP of 0.13 (16% of the overall mean beta-diversity; 0.8). A plot of the measured vs. the predicted values revealed high uncertainty in predictions when the measured beta-diversity was below 0.6 (Figure 6.4). The PLSR explained 37% total variance in beta-diversity in cross-validation out of which 30%, 36% and 34% was contributed purely by environmental (spectral) distances, spatial dependency in environmental (spectral) distances and purely spatial, respectively.

Table 6.1: The structure and significance of spatial autocorrelation in beta-diversity. The lag-distance classes were derived using the Sturge's rule in Mantel correlogram

Lag classes	**Mean distance (Km)**	**Lag-distance range (Km)**	**Number of distance pairs**	**Mantel-r_M**	**p**
1	0.86	0 .00- 1.71	168	0.43	0.001
2	2.57	1.72 - 3.42	136	0.04	0.333
3	4.29	3.43 - 5.13	108	-0.12	0.004
4	6.01	5.14 - 6.86	146	-0.08	0.079
5	7.72	6.87 - 8.55	101	-0.10	0.017
6	9.44	8.56 - 10.22	66	0.06	0.18
7	11.15	10.23 - 11.95	30	-0.01	0.728
8	12.87	11.96 - 13.72	80	-0.18	0.001
9	14.58	13.73 - 15.38	60	-0.08	0.053
10	16. 30	15.39 - 17.06	20	-0.13	0.008
11	18.02	17. 07 - 19.03	28	0.00	0.922

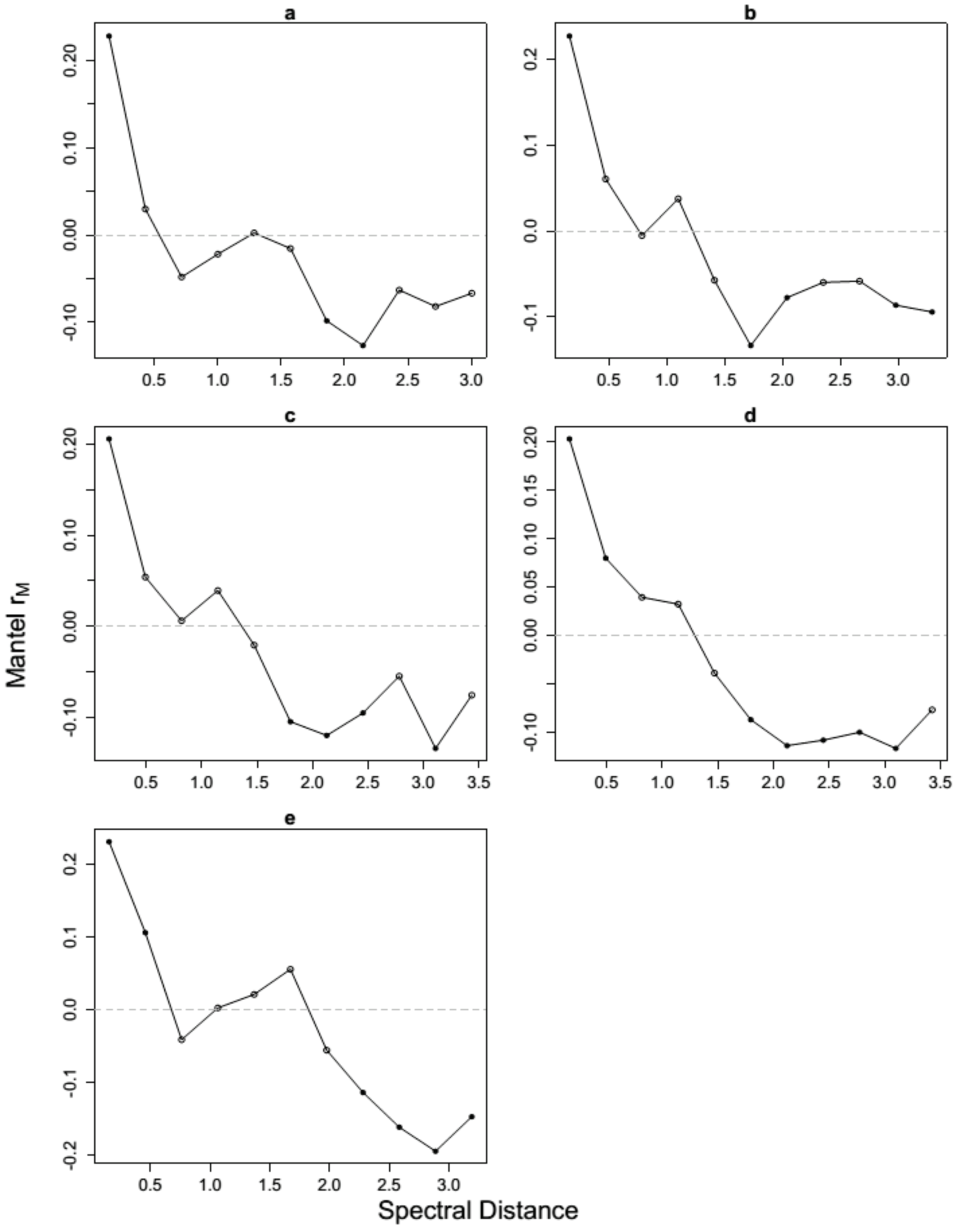

Figure 6.2 Mantel correlograms showing the structure and significance of the correlation between beta-diversity and (a) Landsat-TM bands 3 (b) band 4, (c) band 5 (d) 7 and (e) NDVI index respectively in eleven spectral lag-distance classes. Solid dots represents the lag-distance classes with significant spatial autocorrelation (Mantel-r_M, $\alpha < 0.05$) while the open dots are not significant. The x-axis represents the eleven lag-distance classes derived using Sturge’s rule (Table 6.1). The Mantel-r values above and below zero represent positive and negative autocorrelation respectively. Significant Mantel-r was observed between plots with short spectral distances (similar spectral reflection) and in farthest spectral distances (dissimilar spectral response)

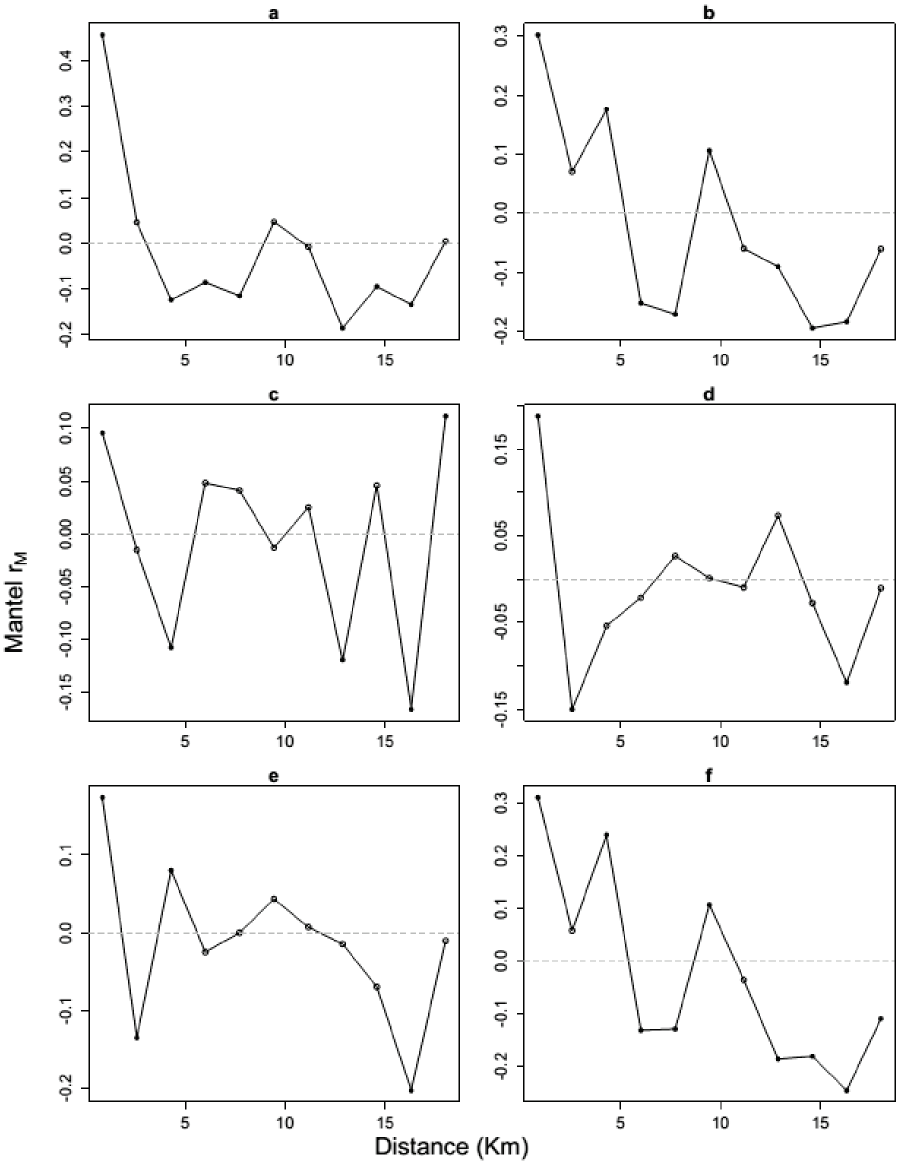

Figure 6.3 Mantel correlograms showing the structure and the significance of spatial autocorrelation (measured as Mantel-r_M) in (a) beta-diversity, (b) spectral distances in bands 3, (c) band 4, (d) band 5, (e) band 7 and (f) NDVI index, respectively. Symbols are similar to Figure 6.2

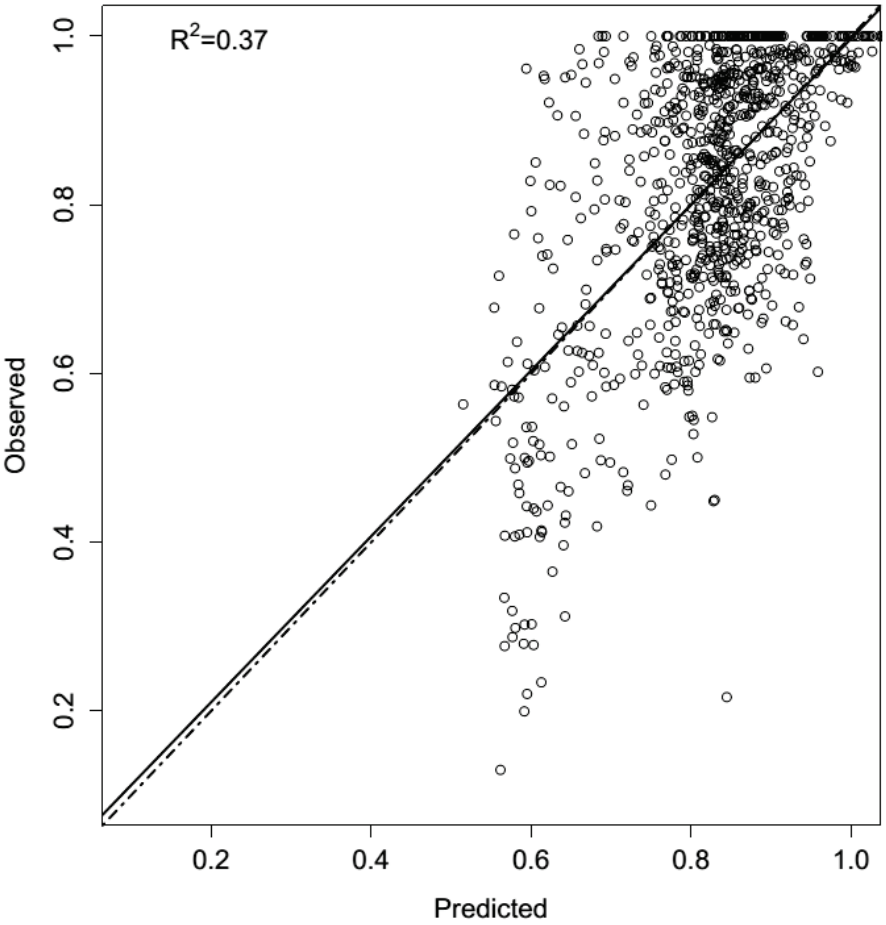

Figure 6.4. The results of the model validation using measured vs. predicted beta-diversity. The model explained 37% of variation in beta-diversity and was fairly accurate when measured beta-diversity was above 0.6 possibly due to high plant compositional heterogeneity in the fragmented landscape

6.4 Discussion

The correlation between beta-diversity and spectral distances exhibited a significant exponential decaying gradient (Figure 6.2). This indicates similar habitats (shorter spectral distances) had similar beta-diversity values and sites with far spectral distances were dissimilar in beta-diversity. This pattern demonstrates the potential of spectral distances in estimating beta-diversity in data limited ecosystems as suggested in previous studies (e.g. Rocchini et al. 2010, Dalmayne et al. 2013). Particularly, the moderate resolution Landsat data used in this study is freely available and have long-term legacy (four decades since 1972; Wulder et al. 2012) that can facilitate extensive spatial and temporal monitoring of beta-diversity patterns. This is in addition to the high temporal resolution remotely sensed global products such as Moderate Resolution Imaging Spectro-radiometer (MODIS; Huete et al. 2002). There is increasing evidence that variability in the reflectance of these remotely sensed products can enhance monitoring the spatial and temporal variation in beta-diversity within or between landscapes that are experiencing perturbations such as flooding (Nogueira et al. 2010), overgrazing (e.g. Dalmayne et al. 2013), bush encroachment (Oldeland et al. 2010), land-cover changes (Cho et al. 2012) and global change (e.g. He and Zhang 2009). Spectral variation could be essential in optimizing reserve selection by facilitating fast identification of locations in the extensive landscapes with high variation in beta-diversity (least overlap in community composition; Chust et al. 2006).

Results revealed that both environmental heterogeneity and dispersal limit contributed significantly to variation in beta-diversity. However, 66% of total variance explained was due to environmental control (variances a+b; 30% purely spectral and 36% spatially structured environment) compared to only 34% that was purely due to spatial processes. Therefore results support our hypothesis that environmental (spectral) variation explains higher variation in beta-diversity than spatial auto-correlation in this fragmented landscape. This agree with studies that observed that environmental (spectral) variation explained higher variance than spatial distances when modeling variation in beta-diversity in fragmented ecosystems as it explains the actual habitat differences (Tuomisto et al. 2003, Rocchini et al. 2010, Hernández-Stefanoni et al. 2012). The lower variance explained by geographical distances in fragmented systems is because two geographically near sites might experience varying magnitude of fragmentation resulting to different species composition (Rocchini et al. 2010).

For the landscape surrounding Lake Naivasha, both the environmental (spectral) and spatial autocorrelation were significant drivers of beta-diversity. This suggests that conservation managers in this landscape should prioritize on enhancing habitat heterogeneity and increasing abundances of each species at all possible locations to increase propagues for random dispersal (Gilbert and Bennett 2010).

The significant spatial autocorrelation in beta-diversity and spectral distances (Figure 6.2) relate to the fact that plant communities and environment variables that underpin their distribution are often spatially structured with near sites likely to be similar in plant composition and/or environmental conditions (Murwira and Skidmore 2005, De Knegt et al. 2008, 2010). This underscores the need to account for spatial dependency in the models estimating beta-diversity. The purely spatial variance (variance c) represents processes unrelated to environment that structure the beta-diversity pattern in the landscape; mainly the dispersal limitation (Borcard et al. 1992, Chang et al. 2013). If we fitted a model with the environmental (spectral) distances alone (sensu Rocchini 2007, Rocchini et al. 2009a, 2009b, Dalmayne et al. 2013), it would have explained only 25% of the variance in beta-diversity. This comprises the variance due to pure spectral variation and spatial dependency of the spectral distances (variance a+b). However after including the spatial autocorrelation the explained variance increased to 37% due to additional 12% variance explained purely by space (variance c). Our results concur with earlier studies that found that accounting for spatial dependency in SVH based models increases the prediction accuracy since the species dispersal limitations are included (e.g. Foody 2005, Hernández-Stefanoni et al. 2012).

The significant variance explained purely by spatial auto-correlation (variance c) suggests that models estimating beta-diversity from environmental (spectral) distances only will have unexplained spatial pattern; referred to as residual spatial-autocorrelation (Legendre and Fortin 1989). This would violate the assumption of independent residual errors. This can inflate the degree of freedoms thus bias estimation of type-1 errors, leading to conclusions that the correlation or regression coefficients are significant when they are not (Legendre and Fortin 1989, De Knegt et al. 2010). This further emphasizes the need for investigating the presence of spatial auto-correlation and accounting for it in models estimating variation in beta-diversity from spectral distances. Despite this, only a few studies based on the SVH has attempted to account for spatial-autocorrelation (Foody 2005, Hernández-Stefanoni et al. 2012).

The PLSR model explained relatively low variance in beta-diversity similar to Dalmayne et al. (2013) who used higher spatial resolution worldview imagery. Our model also had higher uncertainty in predicting beta-diversity when measured beta-diversity was below 0.6. This could be related to samples that were obtained from a highly heterogeneous landscape (mean beta-diversity = 0.8) experiencing high human and naturally induced fragmentation. Our model also had high unexplained (residual) variance (63%). This may arise from; (1) stochastic processes such as random dispersal and mortality (Hubbell 2001); (2) important variables were not included (Chang et al. 2013), for example the management regimes; (3) characteristic noise in the species composition data due to high number of zero observations (Rocchini 2007, Rocchini et al. 2009a, 2009b); (4) the spectral or spatial resolutions of the data (Oindo et al. 2003, Foody 2005, Dalmayne et al. 2013) and (5) sampling design with unequal samples in lag-distance classes (Feilhauer and Schmidtlein 2009).

6.5 Conclusions

Results revealed that environmental (spectral) distances explained higher variance (66%) in plant beta-diversity than spatial-auto-correlation (34%) in the landscape surrounding Lake Naivasha. The Landsat-TM satellite data offers a time and cost effective proxy for environmental heterogeneity that can be useful for rapid assessment of variation in beta-diversity in data limited ecosystems. Results further suggest that accounting for spatial dependency would increase the prediction accuracy of the models based on SVH. Failure to account for spatial autocorrelation might lead to residual autocorrelation (purely spatial variance) that can inflate estimation of model coefficients. Our results support both the environmental heterogeneity and dispersal limit in controls variation in plant beta-diversity in this landscape. This suggests that conservation initiatives in this landscape should balance between enhancing habitat heterogeneity and promoting the abundance of individual plant species to increase propagues for dispersal.

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Chapter 7

Persistence of plant diversity and productivity in a fragmented key resource area: a synthesis

7.1 Introduction

The terrestrial zones that border wetlands in savannas are dry season KRAs for herbivores due to high availability of forage (Scoones 1991, Ngugi and Conant 2008). These KRAs in savannas act as source-sink landscapes where herbivores congregate during the dry seasons when forage is scarce and disperse to their wet season ranges (Scoones 1995, Illius and O'Connor 2000). KRAs enhance survival of herbivores during scarcity (Illius and O’Connor 1999, 2000), so are critical in determining the density of herbivores and magnitude of their impacts on plant composition and productivity in the outlying wet season ranges (Homewood and Lewis 1987, Illius and O’Connor 1999, Vetter 2005). However, availability of water on KRAs adjacent to wetlands attracts a variety of economic activities that cause habitat fragmentation (Kimani and Pickard 1998, Boone and Hobbs 2004, Western et al. 2009a, Ogutu et al. 2010, Msoffe et al. 2011, Estes et al. 2012, Dahwa et al. 2013). This is in addition to natural fragmentation, such as the frequent floods on KRAs (Gaudet 1977a, Lachavanne and Juge 1997, Tzialla et al. 2006, Onywere 2013). The increased natural and anthropogenic fragmentation in KRAs hampers their role in maintaining plant and herbivore diversity and providing related ecosystem services (Scoones 1991, Sarkar 2006).

The terrestrial fringe zone along Lake Naivasha is an example of fragmented KRAs. It was traditionally used as dry season forage for both wild and domestic ungulates (Harper and Mavuti 2004). The availability of fresh water has led to the development of intensive horticulture farming in this zone (Justus and Yu 2014), accentuating land conversions that lead to reduction of grazing area. This may lead to overgrazing that has ramifications on plant productivity, diversity and composition. Despite the increased fragmentation in the KRAs, long-term monitoring of changes in plant-herbivore dynamics is lacking (Vetter 2005, Ngugi and Conant 2008). This is despite the potential usefulness of knowledge generated from such monitoring in guiding biodiversity conservation strategies to promote persistence of these species in the KRAs and indirectly in the outlying wet season ranges.

This thesis investigates the drivers of ungulate biomass (chapter 2) and the impacts of ungulate grazing and rainfall on herbaceous plant regrowth (productivity), residual aboveground biomass (chapter 3) and community composition (chapters 4 and 5) in a KRA along Lake Naivasha Kenya. The thesis further compares the robustness of a novel multivariate GLM (ManyGLM) method with a traditional distance-based method for measuring impacts of ungulate grazing on plant community composition (chapter 4). It applies the novel method (ManyGLM) to quantify the impact of ungulate grazing on plant diversity and composition (chapter 5). The thesis also quantifies the relative contribution of spectral variation in Landsat satellite reflectance as a surrogate for environmental heterogeneity and species dispersal limitation on plant beta-diversity in a fragmented KRA along Lake Naivasha, Kenya (chapter 6). This chapter outlines the major findings, their ecological implications and recommends future research.

7.2 What drives the ungulate biomass in the lower catchment of Lake Naivasha?

Results from chapter 2 revealed that horticultural activities and associated increase in human population were strongly correlated with the LULC change in the downstream catchment of Lake Naivasha. Consequently, the LULC change was highly correlated with ungulate biomass in wildlife-friendly ranches. The ungulate biomass increased steadily over the 12 years period (1999-2010). The increased LULC conversions in the larger landscape in the downstream catchment of Lake Naivasha may have accelerated the loss of habitats for wild ungulates (Harper and Mavuti 2004) and increased human-wildlife conflicts (Mailu et al. 2010). This could have prompted the large aggregation of herbivore biomass in the wildlife-tolerant ranches adjacent to the Lake Naivasha that actively protect their wildlife. These ranches offer security from poaching and have abundant high quality forage along the lacustrine edge. Results agree with hypothesis put forward earlier by Harper and Mavuti (2004) that the resident ungulate biomass in the key resource area along Lake Naivasha has increased due to increased settlement, cultivation and deforestation (especially of the nearby Eburru forest).

The observed increase in ungulate biomass in the private ranches along Lake Naivasha contrasts with an over 60% decline in protected and communal pastoral areas in Kenya since 1977 (Ottichilo et al. 2000, Western et al. 2006, Norton-Griffiths 2007, Western et al. 2009b). Results from chapter 2 suggests that the reported country-wide decline in ungulate biomass is not spatially uniform, as availability of key resources and management regime (active protection) can interact to cause increases in some patches. This demonstrates the importance of incorporating the key resources and management when assessing persistence of ungulates in an ecosystem (Coughenour 1991, Ogutu et al. 2010, Ogutu et al. 2014). The results also demonstrate that the cascade modeling approach can improve understanding of how a series of interlinked processes in the ecosystem affect its biodiversity pattern.

7.3 Do grazing ungulates significantly impact herbaceous plant regrowth, biomass and diversity?

Results from chapter 3 indicated that continuous intense grazing by ungulates significantly reduced herbaceous plant regrowth (productivity) and the residual aboveground biomass which is an essential determinant for regrowth potential. The herbivore impact was significantly stronger during the dry season when large herbivore densities are expected to aggregate in the KRA and plants have lower survival fitness. However, the impact of ungulate grazing was still significant even in wet seasons when rainfall was expected to decouple plant dynamics from herbivore control, a fact that suggests the existence of high density of resident herbivore in the KRA. Moreover the simulated grazing revealed that higher intensity of defoliation significantly reduced herbaceous plant regrowth during the dry seasons. This further emphasizes the detrimental effect of continuous intense grazing on herbaceous regrowth in this landscape.

Results from chapter 5 revealed that exclusion of ungulates grazing significantly reduced richness of annual forbs. Result suggests that ungulate grazing increased richness of annual forbs in the grazed treatment by reducing competitive dominance of three perennial grasses. This agrees with previous studies that observed that continuous intense grazing increases herbaceous diversity but negatively impact plant composition by promoting abundance of annual species at the expense of perennials (Milchunas et al. 1988, Belsky 1992, Stohlgren et al. 1999, Metzger et al. 2005, Golodets et al. 2011, Borer et al. 2014).

The decline in the quality of the KRA observed in chapters 3 and 5 could precipitate a series of ecological changes in the KRA and the outlying wet season range. Systems in which annual species dominate systems are more sensitive to droughts than systems dominated by perennial species (Vetter 2005, Gillson and Hoffman 2007). Therefore the increased abundance of annual forbs and reduced herbaceous productivity in the grazed treatment increase the susceptibility of this KRA to droughts. The quality and size of the KRA determine the population of ungulates that can be maintained in the KRA during the dry season (grazing capacity) and consequently the magnitude of their impact on outlying wet season range if seasonal movements are not hindered (Illius and O’Connor 1999, Okayasu et al. 2012). If the ungulate movements are not restricted, the decline in the range condition in the KRA could decrease the population of ungulates that access the wet season range at the end of the dry spell (Homewood and Lewis 1987, Illius and O’Connor 1999). If the original condition of the wet season range was poor, then the decline in quality of KRA could reduce the grazing intensity thereby promoting vegetation recovery (Okayasu et al. 2012, von Wehrden et al. 2012).

The results from chapters 3 and 5 support the non-equilibrium hypothesis that predicts a density-dependent plant-herbivore interaction in the KRAs that is stronger during the dry seasons when these landscape patches are intensely utilized due to forage scarcity in the wet season ranges (Illius and O’Connor 1999, 2000, 2004). The effect of ungulates was greater than that of rainfall. This contradicts the disequilibrium hypothesis that predicts that ungulates grazing have no significant effect in savannas (Ellis and Swift 1988, Westoby et al. 1989, Behnke et al. 1993, Briske et al. 2003). Though there is ample theoretical evidence in support of the non-equilibrium hypothesis, systematic empirical tests are rare. Therefore results in this thesis are a useful additional empirical evidence to support this hypothesis.

7.4 Are the traditional methods of detecting change in plant composition due to grazing pressure adequate?

The equilibrium, disequilibrium and non-equilibrium hypotheses on plant-herbivore coupling in savannas predict contrasting impact of ungulates on plant composition (Illius and O’Connor 1999, Illius and O'Connor 2000, Illius and O’Connor 2004). Range conservation plans are formulated on the basis of which of the three hypotheses is understood or assumed to drive the plant community composition in a particular landscape (Oba et al. 2000b). Therefore wrong conclusions or predictions on what drives the plant composition in a landscape could lead to inappropriate range conservation plans (Warton et al. 2012). For example, livestock development projects in African savannas in 1980s and 1990s failed as they were based on assumption of equilibrium dynamics that predict that these rangelands were overstocked (Behnke 2000, Oba et al. 2000b, Vetter 2005, Washington-Allen et al. 2008). This led to stock reductions even on rangelands where grazers had no significant effects. It also promoted subdivision of rangelands and sedentarization of nomads that reduced seasonal mobility of livestock (Oba et al. 2000b). Disentangling which of the three hypotheses drives plant composition in different landscapes in savannas requires understanding which methods are more accurate under different situations.

Chapter 4 evaluated a new multivariate GLM approach (ManyGLM) against a distance-based method (DBM): the distance-based redundancy analysis (db-RDA). The evaluation was based on the *a priori* hypothesis that the ranking of plant species response to grazing from the most responsive to the least responsive should be: pure signal species, mixed signal species, no signal species (Table 4.3, chapter 4). Results in chapter 4 indicated that the

ManyGLM ranked the species response to grazing as predicted *a priori,* while the db-RDA models did not show a consistent pattern in ranking the response of the three types of plant species to grazing treatment. The ManyGLM was able to detect grazing signal even when expressed in rare species, while the db-RDA was largely responsive to most abundant (also most variable) species in the community. This aspect of ManyGLM is particularly important when detecting the grazing signal in range-lands, since ungulates largely influence plant community composition by reducing competitive dominance of superior competitors, which in-turn promotes establishment of inferior competitors that are usually rare plant species (chapter 5). These rare species are the first to respond to change in grazing pressure. Therefore higher sensitivity to change in their abundance reflects the strength of the ManyGLM to detect subtle changes in the community composition. The result demonstrates the potential of ManyGLM to give early warning of overgrazing when the abundance of plant rare species (mainly annual forbs) start to increase in communities dominated by perennial species. Early detection of overgrazing could facilitate early implementation of remedial adaptive measures such as culling. This demonstrates how the choice of analytical method can influence the formulation of range management policies.

7.5 What determines the plant beta-diversity in the fragmented KRA along Lake Naivasha?

Most conservation plans are formulated at landscape scale (Oindo et al. 2003, Fischer et al. 2008, von Wehrden et al. 2014). Understanding the spatial turnover in plant composition (beta-diversity) in the landscape is more intuitive than alpha diversity, since it is the scale at which conservation plans are formulated (Oindo et al. 2003, von Wehrden et al. 2014). However, disentangling what drives plant beta-diversity in fragmented landscapes is hampered by lack of long term series of data. Novel data and methods are needed to generate this knowledge. Results in chapter 6 demonstrated the applicability of spectral variation of Landsat images as a surrogate for environmental heterogeneity in monitoring spatial variation in plant composition (beta-diversity). Remote sensing offers a large synoptic cover and high repeatability that allow monitoring over longer spatial-temporal scales (Gillespie et al. 2008, Rocchini et al. 2010) compared to labor-intensive and time-consuming field surveys (Palmer et al. 2002). Therefore predicting the changes in plant beta-diversity due to environmental stress or disturbance regimes in data-limited and/or remote ecosystems would benefit from more freely available satellite data, especially the Landsat archive that span over four decades.

Ungulate grazing is one of the processes that enhance spatial heterogeneity in vegetation directly through defoliation and trampling or indirectly through redistribution of nutrients within the landscape (Augustine and McNaughton 1998, Augustine and Frank 2001, Augustine 2003b, Augustine and McNaughton 2006, Golodets et al. 2011, Dalmayne et al. 2013). The frequency of flooding regime also enhances environmental heterogeneity that shapes temporal patterns in plant composition on the floodplain (Gaudet 1977a, Lachavanne and Juge 1997, Tzialla et al. 2006, Onywere 2013). Results indicate that spectral variation captured from freely available Landsat satellite data capture habitat differences created by these disturbance regimes (Dalmayne et al. 2013).

Chapter 6 also revealed that the spectral variation as a surrogate for environmental heterogeneity explained more variance in plant beta-diversity than dispersal limitation (spatial distances) in this fragmented KRA. Results support both the niche theory and Hubbell's neutral theory of biodiversity in regulating plant beta-diversity in this landscape. The two theories advocate contrasting management interventions. Management interventions based on niche theory aim at the preservation or restoration of species-specific niches (Gilbert and Bennett 2010, Li et al. 2011). However, Hubbell's neutral theory posits that habitat characteristics are unimportant in maintaining diversity. Therefore management measures based on this theory are aim at increasing the abundance of each species at each location in the landscape, to maximize the number of propagules available for random dispersal (Daleo et al. 2009, Gilbert and Bennett 2010). This suggests that to enhance plant beta-diversity in the KRA around Lake Naivasha, conservation initiatives should aim at increasing both habitat diversity and the abundance of individual species.

Another finding presented in chapter 6 is that accounting for spatial dependency in species models based on SVH improves estimation of plant beta-diversity. This is because the plant diversity and environmental data exhibit spatial dependency that makes sites nearby more likely to be similar than sites far away (Murwira and Skidmore 2005, De Knegt et al. 2010). Therefore the relationship between diversity and environment is non-stationary (Foody 2005). Despite this most studies that predict plant beta-diversity from remote sensing data fail to account for spatial dependency in the beta-diversity and the spectral (environmental) distances (reviewed in Gillespie et al. 2008, Rocchini et al. 2010). This may introduce residual spatial auto-correlation in the species-environment models leading to violation of the assumption of independently distributed residual errors (De Knegt et al. 2010). Violating this assumption could lead to biased estimation of type I errors as a result of inflated degrees of freedom (Legendre and Fortin 1989, Dormann et al. 2007, De Knegt et al. 2010).

7.6 Proposed adaptive management strategies to promote plant diversity and productivity in the KRA along Lake Naivasha

Adaptive management measures are needed to mitigate the negative impacts of increased LULC conversion on ungulate biomass (chapter 2) and the continuous intense grazing on plant regrowth, residual aboveground biomass (chapter 3) and community composition (chapter 5). The loss of wildlife habitat can be mitigated by land-use zoning in the KRA to delineate land to be used exclusively for conservation, agriculture or settlement (Fischer et al. 2008, Msoffe et al. 2011, von Wehrden et al. 2014). This would promote intensive cultivation on existing agricultural land without expansion into natural or semi-natural vegetation. The conserved (semi)-natural habitats can act as source of plant propagules for dispersal in the landscape.

Connectivity between the (semi)-natural habitats can be improved by opening the traditional migratory corridors (Toxopeus et al. 1994, Fischer et al. 2006, Msoffe et al. 2011, de Leeuw et al. 2014, Ogutu et al. 2014). This can facilitate seasonal movement of grazers depending on the forage availability. By contrast, continuous grazing (the prevalent practice) does not allow rest periods for vegetation to recover (Coughenour 1991, Msoffe et al. 2011, von Wehrden et al. 2012). The corridors can be created by initiating a payment of ecosystem services (PES) scheme that entails compensating land owners for setting aside some sections of their land exclusively for conservation (Kemeri-Mbote 2005, Wambuguh 2007, de Leeuw et al. 2014). Currently there is a proposal to create the "three lakes wildlife corridor" (http://crisscrossafrica.com/crisscrossafrica.pdf) to connect all ranches within the Nakuru Wildlife Conservancy (NWC): a network of ranches covering an estimated 350,000 acres between Lakes Naivasha, Elementaita and Nakuru (Figure 5.1).

Grazing management is viable tool for the restoration of degraded grazing land (Papanastasis 2009, O'Connor et al. 2010). It would entail managing the type of grazers, their density, distribution, season and the duration of use (Papanastasis 2009). However, the choice of grazing management tool to be applied in a particular landscape depends on conservation management goals (Hayes and Holl 2003). Results in chapters 3 and 5 suggest that increasing the ungulate density would be viable if the conservation goal is to maximize herbaceous diversity. However, reducing ungulate density would be tenable if the goal is to maximize herbaceous productivity. Livestock density can be regulated by adjusting the stocking rate on the basis of acreage, season and range condition (Oba et al. 2000b, O'Connor et al. 2010) or by rotational grazing to stimulate recovery of over-utilized pastures (Coughenour 1991, Mekuria et al. 2007). The wild ungulate biomass can be regulated by sustainable harvesting (Norton-Griffiths 2007, Wambuguh 2007) and translocation (Griffith et al. 1989, Lekolool 2012). Wildlife harvesting could reduce grazer density and generate revenue to offset costs incurred by ranchers for keeping wildlife (Norton-Griffiths 2007, Wambuguh 2007). A wildlife harvesting program that was being trialed in this landscape was terminated due to difficulties in enforcement (Mailu et al. 2010).

7.7 Conclusions and future research

The key conclusions from this thesis are:

1. Socio-ecological development in the lower catchment of Lake Naivasha triggers LULC changes with impacts cascading in the ecosystem through multiple pathways to affect the ungulate biomass. The cascade modeling approach can improve understanding of the strength of interactions between a series of interlinked processes in the landscape (chapter 2).
2. Ungulate grazing pressure had significantly higher impact on herbaceous regrowth and residual aboveground biomass in the KRA along Lake Naivasha than rainfall. The impact of ungulate grazing is significant in both dry and wet seasons, suggesting a high resident herbivore density (chapter 3).
3. The ManyGLM approach is more robust than db-RDA in detecting the between-treatment difference in plant species abundance due to grazing and in identifying the species that are responsive to grazing. This suggests that methodological artifacts can lead to inappropriate conclusions on the significance of grazing on plant composition, thereby misleading the formulation of range conservation plans (chapter 4).
4. Ungulate grazing significantly increased the richness and abundance of annual forbs by reducing competitive dominance of three perennial grasses. Complete exclusion of ungulates in this landscape would reduce plant diversity but further increase in ungulate grazing intensity would accelerate transition from a landscape dominated by more productive perennial species to one dominated by less productive annual species(chapters 3 and 5).
5. Spectral variation in remotely sensed satellite reflectance is a reliable surrogate for environmental heterogeneity. This offers a time and cost-effective method of estimating plant beta-diversity in data-limited ecosystems.
6. Environmental heterogeneity explains more variance in plant beta-diversity in the KRA along Lake Naivasha than species dispersal limitation. To maintain the high plant beta-diversity in this landscape, conservation initiatives should focus on enhancing environmental heterogeneity and increasing the abundance of each species in all sites, so that more propagules will become available for random dispersal (chapter 6).

The current research investigated the persistence of plant species diversity and productivity in a fragmented and intensely grazed KRA along the Lake Naivasha. The non-equilibrium hypothesis proposed by (Illius and O'Connor 1999, 2000, 2004) predicts that KRAs maintain high herbivore numbers during the dry seasons that exert significant impact on plant communities on the wet season ranges. However, the research described in this thesis did not investigate the plant-herbivore dynamics in the surrounding wet season ranges. Therefore this experiment should be expanded by comparing the plant-ungulate interactions in the KRA and the outlying wet season ranges. This could include comparisons of plant-ungulate dynamics in the wet season ranges with and without KRAs, to clearly establish the role of KRAs in regulating plant-herbivore interactions. To test this, long-term exclosure experiments (sensu Young et al. 1997) should be implemented, to capture the seasonal variability that characterizes savanna ecosystems. These experiments can be replicated on ranches with contrasting management regimes i.e. communal grazing land, group ranches and private sanctuaries (Mbatha and Ward 2010). This can disentangle the role of management regimes in modifying plant-herbivore interactions in this landscape.

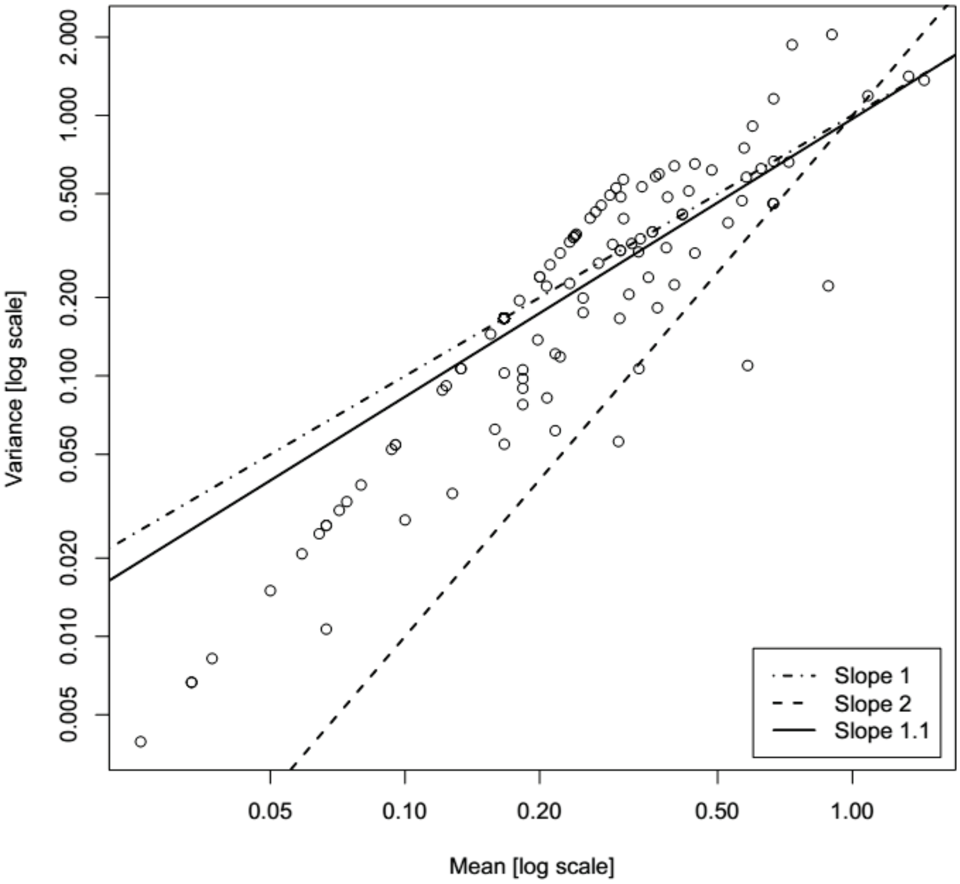
The analysis of spectral variation in historical archives of satellite imagery can be used to reconstruct the spatial patterns of plant beta-diversity in the landscape. This could elucidate how plant communities have responded to varying environmental stress or disturbances.

Different ungulates differ in their foraging behavior depending on their body size and physiology (McNaughton and Georgiadis 1986, Bakker et al. 2006, O'Connor et al. 2010, Kanga et al. 2013). Due to data limitations this thesis did not differentiate the impact of different ungulate guilds in the landscape, for example by comparing the impacts of wild ungulates and livestock or comparing central-place foragers and migratory herds in terms of their impact on plant productivity and composition. Such a study should investigate the role of ungulate species interactions such as facilitation and competition in modifying their impacts on plant composition and diversity (Veblen and Young 2010, Odadi et al. 2011). Research on effect of different guilds would guide implementation of adaptive management options such as determining guild-specific stocking rates and culling quotas.

A population viability analysis of each wild ungulate species in this KRA should be undertaken to predict their future populations in view of declining habitats. This would require the development of new protocols for an annual census incorporating demographic characteristics of the recorded species i.e. sex and age.

An evaluation is needed of the potential of sustainable harvesting of wild ungulates to reduce grazing pressure in this landscape. This would guide managers involved in the re-introduction of the sustainable wildlife harvesting program. The proposed evaluation would entail detailed analysis of the population dynamics and foraging ecology of existing ungulate species and insight into the spatial-temporal dynamics in plant composition and productivity in this landscape. Such information is generally lacking in this landscape. The findings reported in chapters 2-6 represent a first attempt to generate the knowledge required to formulate adaptive management strategies to promote persistence of plant diversity and productivity in a KRA experiencing high ungulate grazing pressure.

Appendix A



The mean variance trend after dispersion weighting of species abundance data used to fit the db-RDA models. Dispersion weighting reduced over-dispersion by half (slope =1.1)

Appendix B

The ranking the response of species to the treatment effect in ManyGLM and db-RDA abundance-based and compositional models for all species. Ranking for ManyGLM is based on the log-likelihood (LR) statistic value while for db-RDA it is based on the correlation with the CAP axis (Cor-X) that expressed the grazing treatment for models based on different dissimilarity indices. For both models ties are given the same rank. The species abundances in each treatment are multiplied by 10 to convert them to integers. The species response types are (1) pure signal, (2) mixed signal and (3) no signal species.

					Abundance models								Compositional Models			
			Between treatments difference in		ManyGLM		Euclidean		Chi-square		Bray-Curtis		ManyGLM		Jaccard	
Species Code	**Species Name**	**Species Type**	**Abundance**	**Prevalence**	**LR Statistic**	**Rank**	**Cor CAP-X**	**Rank**	**Cor CAP-X**	**Rank**	**Cor CAP-X**	**Rank**	**LR statistic**	**Rank**	**Cor CAP-X**	**Rank**
Eupina	*Euphorbia inaquilatera*	1	5.8	6	19.514	1	0.851	5	1.000	1	0.574	5	16.636	1	0.964	1
Amahyb	*Amaranthus hybridus*	1	3.0	4	9.904	2	0.409	25	0.665	4	0.281	23	7.638	3	0.608	3
Elumul	*Eleusine multiflora*	1	3.3	4	9.051	3	0.505	16	0.606	7	0.338	15	7.638	2	0.613	2
Amagra	*Amaranthus graecizans*	1	1.0	3	5.623	4	1.137	2	0.707	3	0.731	2	5.178	4	0.528	5
Tarmin	*Tagetes minuta*	1	1.3	3	5.547	5	0.932	4	0.594	9	0.615	4	5.178	9	0.437	10
Oldher	*Oldenlandia herbacea*	1	3.2	3	5.401	6	0.356	29	0.401	15	0.257	27	5.178	7	0.444	8
Oxysin	*Oxygonum sinuatum*	1	1.8	3	5.368	7	0.250	57	0.314	28	0.172	58	5.178	8	0.437	9
Conbon	*Conyza bonariensis*	1	0.7	3	5.352	8	1.216	1	0.883	2	0.781	1	5.178	6	0.526	7
Juswhy	*Justicia whytei*	1	2.3	3	4.856	9	0.434	22	0.398	16	0.278	25	5.178	5	0.528	6
Indspi	*Indigofera spicata*	2	3.7	3	4.14	10	0.675	8	0.612	6	0.431	7	3.256	10	0.551	4
Setpum	*Setaria pumila*	1	1.0	2	3.48	11	0.447	19	0.344	23	0.328	17	3.175	17	0.265	26
Eruara	*Erucastrum arabicum*	1	5.0	2	3.428	12	0.443	21	0.360	20	0.306	21	3.175	19	0.260	28
Aerlan	*Aerva lanata*	1	1.0	2	3.42	13	0.651	10	0.529	10	0.418	9	3.175	15	0.350	21
Traber	*Tragus berteronianus*	1	1.8	2	3.398	14	0.340	30	0.304	30	0.218	32	3.175	12	0.356	18
Triter	*Tribulus terrestris*	1	1.3	2	3.365	15	0.558	14	0.437	14	0.358	13	3.175	14	0.351	20
Indbre	*Indigofera brevilcalyx*	1	0.5	2	3.339	16	0.665	9	0.452	12	0.425	8	3.175	11	0.356	17
Porole	*Portulaca oleracea*	1	0.7	2	3.26	17	0.558	13	0.437	13	0.358	13	3.175	13	0.351	19
Cyprot	*Cyperus rotundus*	1	0.8	2	3.226	18	0.480	17	0.367	19	0.310	20	3.175	16	0.349	22
Sonole	*Sonchus olearaceus*	1	0.3	2	2.773	19	0.447	19	0.344	23	0.328	17	3.175	18	0.265	27
Cyprig	*Cyperus rigidifolius*	2	2.7	2	1.769	20	0.514	15	0.377	18	0.320	19	1.359	53	0.394	11
Medsat	*Medicago sativa*	2	1.0	2	1.645	21	1.037	3	0.180	56	0.652	3	1.552	20	0.373	13
Witsom	*Withania somnifera*	1	0.3	1	1.54	22	0.301	37	0.313	29	0.194	41	1.477	35	0.175	40
Tritri	*Trianthema triquetra*	1	0.3	1	1.54	22	0.292	41	0.227	39	0.189	42	1.477	28	0.172	42
Crapla	*Craterostigma plantagineum*	1	0.3	1	1.54	22	0.312	31	0.243	36	0.199	36	1.477	30	0.179	35
Croinc	*Crotoraria incana*	1	0.3	1	1.54	22	0.308	33	0.191	45	0.197	38	1.477	34	0.177	39
Cypang	*Cyperus angolensis*	1	0.3	1	1.54	22	0.050	80	0.116	68	0.065	79	1.477	49	0.088	67
Chesch	*Chenopodium schraderianum*	1	0.3	1	1.54	22	0.252	49	0.185	48	0.179	49	1.477	40	0.152	48
Chrspp	*Chrolophytum spp*	1	0.3	1	1.54	22	0.252	49	0.185	48	0.179	49	1.477	42	0.152	50
Melova	*Melhania ovata*	1	0.3	1	1.54	22	0.252	49	0.185	48	0.179	49	1.477	45	0.152	53
Parpat	*Pavonia patens*	1	0.3	1	1.54	22	0.252	49	0.185	48	0.179	49	1.477	46	0.152	54
Schpin	*Schkuhria pinnata*	1	0.7	1	1.535	31	0.292	41	0.227	39	0.189	42	1.477	38	0.172	45
Crakil	*Crambe kilimandscharica*	1	0.7	1	1.535	31	0.050	80	0.116	68	0.065	79	1.477	48	0.088	66
ipomom	*Ipomea mombassana*	1	0.7	1	1.535	31	0.050	80	0.116	68	0.065	79	1.477	52	0.088	70
Hibvit	*Hibiscus vitifolius*	1	0.7	1	1.535	31	0.253	48	0.338	27	0.178	57	1.477	39	0.153	47
Evoals	*Evolvulus alsinoides*	1	0.7	1	1.535	31	0.252	49	0.185	48	0.179	49	1.477	44	0.152	52
Euppro	*Euphorbia prostrata*	1	2.5	1	1.534	36	0.312	31	0.243	37	0.199	36	1.477	31	0.179	36
Chlvir	*Chloris virgata*	1	1.3	1	1.534	36	0.308	33	0.191	45	0.197	38	1.477	33	0.177	38
Jusdic	*Justicia dicliptoroides*	1	1.0	1	1.534	36	0.292	41	0.227	39	0.189	42	1.477	36	0.172	43
Chlgay	*Chloris gayana*	1	2.7	1	1.534	36	0.252	49	0.185	48	0.179	49	1.477	41	0.152	49
Indbog	*Indigofera bogdanii*	1	1.0	1	1.534	36	0.251	56	0.343	25	0.179	49	1.477	47	0.151	55
Solnig	*Solanum nigrum*	1	1.0	1	1.534	36	0.294	40	0.216	44	0.145	62	1.477	29	0.198	33
Eraqua	*Eragrostis quadriagulis*	1	1.0	1	1.534	36	0.252	49	0.185	48	0.179	49	1.477	43	0.152	51
Polcam	*Pollichia campestris*	1	0.2	1	1.386	43	0.292	41	0.227	39	0.189	42	1.477	37	0.172	44
Chamim	*Chamaechrista mimosoides*	1	0.2	1	1.386	43	0.308	33	0.191	45	0.197	38	1.477	32	0.177	37
Digmac	*Digitaria macroblephara*	1	0.2	1	1.386	43	0.050	80	0.116	68	0.065	79	1.477	50	0.088	68
Hirdif	*Hirpicium diffusum*	1	0.2	1	1.386	43	0.050	80	0.116	68	0.065	79	1.477	51	0.088	69
Galpar	*Galinsoga parviflora*	2	1.5	1	1.381	47	0.165	72	0.087	79	0.117	65	0.345	70	0.131	56
Comafr	*Commelina africana*	2	2.2	1	1.269	48	0.119	76	0.146	64	0.121	64	0.451	67	0.067	74
Pricur	*Priva curtisiae*	2	1.8	0	0.991	49	0.417	24	0.176	57	0.300	22	0	88	0.025	88
Chlpyc	*Chloris pycnothrix*	2	4.3	1	0.989	50	0.429	23	0.272	34	0.337	16	0.451	62	0.113	60
Combag	*Commelina bengalensis*	2	0.5	2	0.911	51	0.620	11	0.599	8	0.380	11	1.552	23	0.371	16
Jusuny	*Justicia unyorensis*	2	1.0	1	0.835	52	0.242	59	0.028	85	0.204	35	0.451	65	0.111	63
Hypfor	*Hypoestes forskahlii*	2	3.2	1	0.791	53	0.581	12	0.273	33	0.366	12	0.451	57	0.197	34
Bralee	*Brachiaria leersioides*	2	2.5	1	0.665	54	0.047	85	0.181	55	0.083	75	0.451	66	0.111	65
Digsca	*Digitaria scalarum*	2	2.3	0	0.655	54	0.381	26	0.350	21	0.277	26	0	90	0.021	90
Lepbon	*Lepidium bonariense*	2	0.3	2	0.55	56	0.461	18	0.378	17	0.279	24	1.552	22	0.371	15
Mondeb	*Monechma debile*	2	0.5	0	0.536	57	0.280	46	0.113	75	0.207	34	0	87	0.025	87
Gutcor	*Gutenbergia cordifolia*	2	1.2	1	0.534	58	0.193	67	0.171	58	0.093	72	0.451	58	0.173	41
Harsch	*Harpachne schimperi*	2	5.2	0	0.509	59	0.705	7	0.341	26	0.530	6	0	77	0.053	77
Sidcor	*Sida cordifolia*	2	2.8	2	0.508	60	0.039	86	0.167	60	0.116	66	1.552	26	0.239	32
Digaby	*Digitaria abyssinica*	2	3.2	1	0.395	61	0.716	6	0.461	11	0.398	10	0.345	68	0.241	31
Digter	*Digitaria ternata*	2	1.8	0	0.385	62	0.306	36	0.124	65	0.225	31	0	84	0.025	84
Leumar	*Leucas martinicensis*	2	1.2	1	0.368	63	0.135	74	0.117	67	0.092	73	0.451	63	0.113	61
Tribur	*Trifolium burchellianum*	2	4.3	2	0.366	64	0.139	73	0.349	22	0.237	29	1.552	27	0.242	30
Erabra	*Eragrostis braunii*	2	0.8	0	0.337	65	0.367	28	0.115	73	0.227	30	0	85	0.025	85
Achasp	*Achyranthus aspera*	2	0.7	0	0.331	66	0.278	47	0.246	35	0.218	32	0	78	0.041	78
Hellon	*Heliotropium longiflorum*	2	1.5	0	0.323	67	0.372	27	0.153	62	0.246	28	0	72	0.085	71
Brasem	*Brachiaria semindulata*	2	1.7	2	0.272	68	0.201	65	0.097	77	0.158	59	1.552	21	0.372	14
Senmes	*Senecio mesogrammoides*	2	2.2	1	0.198	69	0.228	61	0.089	78	0.188	47	0.451	60	0.127	58
Sidova	*Sida ovata*	2	1.0	0	0.153	70	0.181	68	0.226	43	0.142	63	0	80	0.027	80
Verbon	*Varbena bonariensis*	2	1.8	0	0.132	71	0.196	66	0.171	58	0.148	60	0	89	0.022	89
Eracil	*Eragrostis cilianensis*	2	2.0	0	0.12	72	0.301	37	0.151	63	0.182	48	0	81	0.027	81
Cynple	*Cynodon plectostachyus*	2	4.7	1	0.085	73	0.174	69	0.297	31	0.147	61	0.451	61	0.124	59
Solinc	*Solanum incanum*	2	2.0	2	0.085	74	0.285	45	0.114	74	0.092	73	1.359	56	0.259	29
Ocigra	*Ocimum gratissimum*	2	1.7	0	0.072	75	0.234	60	0.123	66	0.077	77	0	73	0.085	72
Ariado	*Aristida adoensis*	2	0.2	0	0.051	76	0.168	71	0.044	83	0.094	71	0	83	0.025	83
Lotcor	*Lotus corniculatus*	2	0.2	0	0.051	76	0.173	70	0.040	84	0.096	70	0	79	0.027	79
Eraten	*Eragrostis tenuifolia*	2	1.8	2	0.04	78	0.026	88	0.236	38	0.021	87	1.552	25	0.290	25
Dacaeg	*Dactyloctenium aegyptium*	2	0.3	2	0.027	79	0.007	89	0.162	61	0.003	90	1.552	24	0.292	24
Lipjav	*Lippia javanica*	2	0.7	1	0.021	80	0.128	75	0.060	82	0.068	78	0.451	64	0.113	62
Cynnle	*Cynodon nlemfuensis*	2	2.5	1	0.017	81	0.204	63	0.613	5	0.098	68	0.345	69	0.157	46
medlac	*Medicago lacinata*	2	0.5	2	0.014	82	0.295	39	0.015	86	0.189	42	1.359	55	0.313	23
Cyndac	*Cynodon dactylon*	2	2.0	1	0.01	83	0.087	77	0.001	90	0.098	68	0.451	59	0.127	57
Sidsch	*Sida schimperiana*	2	0.2	0	0.01	83	0.073	78	0.279	32	0.032	86	0	76	0.064	76
Pencla	*Pennisetum clandestinum*	2	1.5	2	0.007	85	0.033	87	0.004	89	0.016	89	1.359	54	0.391	12
Spofim	*Sporobolus fimbriatus*	2	1.0	0	0.006	86	0.217	62	0.071	80	0.041	85	0	74	0.085	73
Asymys	*Asystasia mysorensis*	3	0.0	0	0	87	0.244	58	0.100	76	0.080	76	0	71	0.111	64
Comrep	*Commelina reptans*	3	0.0	0	0	87	0.202	64	0.069	81	0.114	67	0	75	0.064	75
Consum	*Conyza sumatrensis*	3	0.0	0	0	87	0.002	90	0.011	87	0.044	84	0	82	0.026	82
Fueafr	*Fuerstia africana*	3	0.0	0	0	87	0.056	79	0.006	88	0.018	88	0	86	0.025	86

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Summary

Wetlands in dry lands have high concentrations of key resources such as soil moisture and nutrients that promote availability of forage during the dry seasons. The high availability of key resources ensures the survival of ungulates during the dry seasons that migrate to surrounding wet season ranges (WSRs) at the end of dry spell. The key resource areas (KRAs) are therefore important in regulating the ungulate density and their impacts in the surrounding wet season ranges (WSRs). However, high availability of key resources attracts human activities that cause anthropogenic fragmentation in the KRAs. These activities include intensive agriculture, livestock ranching and human settlements. The KRAs in the wetlands also experience natural perturbations due to frequent floods that temporarily inundate part of their landscape. These landscapes are therefore biodiversity and economic hotspots. Conserving biodiversity in these landscapes is critical, as it safeguard important ecosystem services and functions. The challenge remains on how to conserve biodiversity amid economic development in these landscapes.

The main objective of the research presented in this thesis is to investigate the role of terrestrial fringe zone along Lake Naivasha in maintaining plant and ungulates diversity. This fringe zone is a KRA for both wild and domesticated ungulate species. The research focused on plant and ungulate species to represent biodiversity in this landscape because their dynamics are interrelated. The specific objectives were to investigate; (1) the drivers of large ungulate biomass in the KRA (chapter 2); (2) the impact of large ungulate grazing and rainfall on productivity and residual aboveground biomass of herbaceous plants (chapter 3); (3) the impact of large ungulate grazing on herbaceous plant community composition and diversity (chapters 4 and 5); and (4) the relative contribution of environmental heterogeneity and species dispersal limits on plant beta-diversity patterns in the KRA surrounding Lake Naivasha (chapter 6).

Results presented in chapter 2 of this thesis reveals that socio-ecological development in lower catchment of Lake Naivasha triggers LULC changes, the impacts of which cascade in the ecosystem through multiple pathways to affect the ungulate biomass. This study demonstrates that a cascade modeling approach can improve understanding of how a series of interlinked processes shapes the biodiversity pattern in an ecosystem. Results presented in Chapter 3 reveals that ungulate grazing pressure had significantly higher impact on herbaceous regrowth and residual aboveground biomass than rainfall. The impact of ungulate grazing was significant in both dry and wet seasons, suggesting a high resident herbivore density. The notion that herbivores have no significant effect on plant dynamics in savannas is

challenged. Resulted presented in Chapter 4 reveals that the ManyGLM approach is more robust than db-RDA in detecting the between-treatment difference in plant species abundance due to grazing and in identifying the species that are responsive to grazing. This suggests that methodological artifacts can lead to inappropriate conclusions on the significance of grazing on plant composition. Range conservation policies are formulated based on understanding or predictions on what drives plant compositional patterns. Therefore methodological artifacts can mislead formulation of range conservation plans. The results presented in chapter 5 reveals that ungulate grazing significantly increases the richness and abundance of annual forbs by reducing the competitive dominance of three perennial grasses. Complete exclusion of ungulates from this landscape would reduce plant diversity, but further increase in ungulate grazing intensity would accelerate transition from a landscape dominated by more productive perennial species to one dominated by less productive annual species.

Results presented in Chapter 6 reveals that spectral variation in remotely sensed satellite reflectance is a reliable surrogate for habitat heterogeneity, and thus offers a time and cost-effective method of estimating plant beta-diversity in data-limited ecosystems. Results demonstrate the potential of Landsat satellite reflectance in monitoring plant beta-diversity in large areas that would be impractical using the field surveys. Results in Chapter 6 also reveal that environmental heterogeneity explains more variance in plant beta-diversity than species dispersal limitation in the KRA along Lake Naivasha. Therefore to maintain the high plant beta-diversity in this landscape, conservation initiatives should focus on enhancing environmental heterogeneity and increasing the abundance of individual species in all sites, to offer more propagules for random dispersal. Results in Chapter 6 further demonstrate that accounting for spatial dependency improves estimation of plant beta-diversity. Failure to account for spatial dependency introduces residual spatial auto-correlation in the species-environment models that violates the assumption of independently distributed residual errors. This results to biased estimation of type I errors as a result of inflated degrees of freedom.

In conclusion, research presented in this thesis investigates how plant diversity and productivity can be maintained in a fragmented KRA with high ungulate density. Availability of key resources along Lake Naivasha attracts socio-economic developments that accelerate changes in land use/land cover. This reduce the (semi)-natural habitat for large herbivores that in-turn lead to high herbivore biomass in the remaining habitat patches. The high ungulate biomass has negative impact on plant diversity and productivity. Adaptive measures for land use and grazing management are recommended to improve the ability of this KRA to maintain high plant diversity and related ecosystem services.

Samenvatting

Wetlands in droge gebieden hebben hoge concentraties van belangrijke hulpbronnen, zoals bodemvocht en nutriënten, die de aanwezigheid van voedsel voor hoefdieren tijdens het droge seizoen stimuleren. De grote beschikbaarheid van deze hulpbronnen verzekert de overleving van hoefdieren die tijdens het einde van droge seizoen naar deze gebieden trekken. Deze sleutelgebieden (Key Resource Areas; KRA's) reguleren daarom in belangrijke mate de dichtheid van hoefdieren en hun effect op de omliggende gebieden die tijdens de nattere periodes door de dieren worden bezocht. De grote beschikbaarheid van hulpbronnen trekt echter ook menselijke activiteiten aan, die versnippering in KRAs tot gevolg hebben. Activiteiten die ontplooit worden omvatten onder andere intensieve landbouw, extensieve veehouderij en het realiseren van nederzettingen. Naast deze menselijke factoren, vinden er ook natuurlijke verstoringen plaats in KRA's, door bijvoorbeeld frequente overstromingen. KRA's zijn dus zowel economische- als biodiversiteitshotspots. Het beschermen van de biodiversiteit in deze landschappen is belangrijk omdat die belangrijke ecosysteem functies verschaffen. The uitdaging is hoe die biodiversiteitsbescherming te realiseren te midden van economische ontwikkelingen.

Het hoofddoel van het onderzoek beschreven in dit proefschrift is om de rol van de oeverzone rondom het Naivasha meer in het behouden van plant en hoefdieren diversiteit te onderzoeken. Deze oeverzone is zowel voor wilde als gedomesticeerde hoefdieren een sleutelgebied. Dit onderzoek richtte zich voornamelijk op planten- en hoefdieren soorten als indicatoren voor biodiversiteit omdat hun dynamiek aan elkaar gekoppeld is. De specifieke doelstellingen waren om (1) de sturende processen voor grote hoefdieren biomassa in KRA's te onderzoeken (Hoofdstuk 2), (2) het effect van te bepalen van begrazing door grote hoefdieren en neerslag op de productiviteit en uiteindelijke staande bovengrondse biomassa van kruidachtige plantensoorten (Hoofdstuk 3), en (3) het effect hiervan op de samenstelling en diversiteit van de plantengemeenschappen (Hoofdstukken 4 en 5), en, uiteindelijk, (4) de relatieve bijdrage van ruimtelijke heterogeniteit en dispersiebeperkingen van planten op de beta-diversiteit in de KRA's rondom het Naivasha meer vast te stellen (Hoofdstuk 6).

De resultaten in hoofdstuk 2 laten zien dat socio-economische ontwikkelingen in de lager gelegen delen van het stroomgebied rondom het meer veranderingen in landgebruik hebben veroorzaakt die via verschillende routes indirecte gevolgen hadden voor de hoeveelheid hoefdieren. Deze studie laat zien hoe een cascade-benadering om het systeem te modelleren ons begrip vergroot over hoe gekoppelde processen de biodiversiteit kunnen beïnvloeden. Het effect van begrazing was significant in zowel droge als natte seizoenen wat een grote residente populatie hoefdieren in de oeverzone van het meer suggereert. Dit daagt de hypothese dat hoefdieren geen significant effect hebben op de dynamiek van Savannes uit. Resultaten in hoofdstuk 4 laten zien dat de ManyGLM benadering robuuster is dan de db-DRA voor het waarnemen van het effect van begrazing op de vegetatie compositie en voor het identificeren van de meest responsieve soorten.

Dit suggereert dat methodologische ongeregeldheden tot onjuiste conclusies over het effect van begrazing op plantensamenstelling kunnen leiden. Beschermingsmaatregelen in grasland gebieden worden opgesteld aan de hand van kennis, of voorspellingen over wat de plantensamenstelling aanstuurt. Daarom kan het zo zijn dat methodologische ongeregeldheden beschermingsmaatregelen verkeerd kunnen voorlichtten. De resultaten uit hoofdstuk 5 laten zien dat begrazing door grote hoefdieren de plantenrijkdom kan verhogen en dat de abundantie van eenjarige kruidachtige soorten toe neemt ten koste van drie meerjarige grassoorten. Complete uitsluiting van grote hoefdieren zorgt dus voor een afname van de diversiteit, maar een verdere toename in begrazing zorgt voor een transitie van een landschap gedomineerd door productievere neerjarige soorten tot een landschap gedomineerd door minder productieve eenjarige soorten.

De resultaten in hoofdstuk 6 laten zien dat spectrale variatie in satelliet waarnemingen een betrouwbaar surrogaat vormen voor omgevingsheterogeniteit, en dus gebruikt kunnen worden in een tijds- en kosteneffectieve methode voor het schatten van beta-diversiteit in plantengemeenschappen in gebieden waar weinig gegevens zijn. De resultaten laten de mogelijkheden zien van het gebruik van Landsat gegevens om planten beta-diversiteit te monitoren over grote gebieden waar veldwerk onpraktisch zou zijn. Resultaten in hoofdstuk 6 laten ook zien dat omgevingsheterogeniteit meer variatie in planten beta-diversiteit verklaart dan dispersiebeperkingen van planten in de KRA rondom het Naivasha meer. Derhalve lijkt het er op dat om een hoge plantendiversiteit in het gebied te behouden, beheersmaatregelen zich beter kunnen richten op het bevorderen van omgevingsdiversiteit en de abundantie van individuele soorten in alle gebieden om plantmateriaal voor dispersie beschikbaar te maken. De resultaten in dit hoofdstuk laten verder zien dat door rekening te houden met ruimtelijke afhankelijkheid de inschatting van beta-diversiteit verbeterd. Geen rekening houden met ruimtelijke afhankelijkheid introduceert residuele ruimtelijke autocorrelatie in soorts-omgevingsmodellen, die de aanname van onafhankelijk verdeelde rest termen schendt. Dit kan leiden tot inflatie van vrijheidsgraden en een verhoogde kans op type I fouten.

Het onderzoek in dit proefschrift heeft onderzocht hoe planten diversiteit en productiviteit kan worden behouden in een gefragmenteerde KRA met hoge hoefdierdichtheden. Beschikbaarheid van belangrijke hulpbronnen in en om het Naivasha meer trekken socio-economische ontwikkelingen aan die veranderingen in landgebruik versnellen. Dit vermindert het totale (semi) natuurlijke gebied beschikbaar voor grote herbivoren, wat op zijn beurt weer leidt tot hoge dichtheden in de overblijvende delen. De hoge hoefdier dichtheid heeft negatieve gevolgen op planten diversiteit en productiviteit. Maatregelen die deze gevolgen zouden kunnen verzachten worden voorgesteld om de capaciteit van deze KRA om een hoge planten diversiteit en gerelateerde ecosysteem diensten te blijven waarborgen.

List of Publications

Refereed Journal Articles

van Oel P.R., Odongo, V.O., Mulatu, D.W., Muthoni, F.K., Ndungu, J.N., Becht, R., Onyando, J.O., van der Veen, A. *In press*. Supporting IWRM by addressing complexity through spatial Integrated Assessment for the Lake Naivasha basin, Kenya. Accepted, *International Journal of Water Resources Development*. DOI: http://dx.doi.org/10.1080/07900627.2014.920248

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Biography

Francis Kamau Muthoni was born on 29th October 1979 in Murang'a Kenya. He attended Mihuti primary school and obtained the Kenya Certificate of Primary Education (KCPE) in 1993. He joined Weithega High school for his secondary education and acquired the Kenya Certificate of Secondary Education (KCSE) in 1997. In 1999 he enrolled in Moi University, Kenya to pursue a Bachelor of Arts degree in Geography (GIS and remote sensing majors). After graduating in 2003 he worked as a GIS analyst in different conservation projects in East Africa. From 2006-2007 he worked as a GIS analyst in Terra Nuova East-Africa in the European Union funded "Trans-boundary Environmental Project (TEP): improving pastoral livelihoods in East African drylands". After successive implementation of the TEP project he worked as a GIS analyst in the University of Cambridge Laikipia Elephant Project (LEP) until 2008. In 2007 he was awarded a scholarship by ESRI conservation program to study advanced spatial analysis in GIS at ESRI campus at Redwood, California, USA. In 2008 he was awarded the European Union Erasmus Mundus scholarship to study a Master of Science degree in Geo-information Science and Earth Observation for Environmental Modeling and Management. This MSc. program was jointly offered by four European universities; University of Southampton (UK), Lund University (Sweden), University of Warsaw (Poland) and University of Twente-ITC (The Netherlands). He obtained his Msc. in 2010 and immediately started his PhD through a scholarship awarded by the Netherlands Organization for Scientific Research organization (NWO) under the auspices of the Earth Observation and Integrated Assessment of Lake Naivasha (EOIA) project.

ITC Dissertation List

http://www.itc.nl/research/phd/phd_graduates.aspx