Social-ecological dynamics at the livestock-wildlife interface in an African savanna



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Abstract

Amidst the global biodiversity crisis, eastern and southern Africa's rangelands stand out as one of the most critical regions for conservation attention. They contain much of the world's biodiversity and some of the only intact large mammal assemblages. However, over the next 50 years, these ecosystems will be disproportionally threatened by the global-scale impacts of land transformation and climate change. So far, the primary response to the global biodiversity crisis, both globally and within eastern and southern Africa, has been through an increase in the extent of protected areas (PAs). Yet, PA expansion has been unable to halt biodiversity loss. This thesis explores the factors driving this negative ecological trajectory at the livestock-wildlife interface in Africa's rangelands. First, I use a Kenyan case study to demonstrate that the current PA network inadequately represents biodiversity, indicating that conservation practice and policy need to extend across "working landscapes", such as rangelands and agricultural areas, to prevent loss. Second, I create a metric to show, for the first time, that PAs in eastern and southern Africa are under immense pressure along their boundaries, threatening their utility. Because of this, I argue that we must develop conservation strategies that cut across species and land-use boundaries to alleviate pressure on PAs and ensure that global biodiversity targets are met.

To understand how best to alleviate these pressures, I use a social-ecological systems (SES) lens to identify the drivers of biodiversity loss at the livestock-wildlife interface, using data collected across six ecosystems in southern Kenya. To do so, I compiled a wide variety of socio-economic and ecological data. This includes land price data collected from scraping websites, data from multiple sources of long-term changes in climate, rangeland productivity, and wildlife and livestock numbers, and the collation of data on ecosystem boundaries and land tenure. Specifically, I collected and synthesised one of the most extensive data sets on the status of any rangeland by mapping the extent of livestock enclosures, fencing, and agriculture across 35,000 km^2 in southern Kenya.

My analysis of these data demonstrates how the profit-driven turnover of ownership, subdivision and transformation of land in southern Kenya is rapidly underway, fragmenting ecosystems, changing governance structures, and degrading rangelands. This process is causing widespread detrimental impacts to savanna

biodiversity and the sustainability of the pastoral social-ecological system. Our comprehensive analysis exposes proximate anthropogenic stressors as overwhelmingly strong drivers of ecosystem-level change, currently eclipsing the impact of climate change, and confirms their importance for conservation within the rangelands of eastern and southern Africa. The lesson from southern Kenya is that African savannas can quickly flip from rain-driven to human-driven ecosystems. Thus, conservation solutions must focus on local drivers of change, which must be traced back to the higher-level socio-economic and political developments to which they are responding. In the face of global change, it is evident that economic incentives, underwritten by devolved management and governance of rangelands and wildlife, will be vital for conservation in this region. Ensuring there is an instrumental value of wildlife for landowners and national governments is critical, allowing landholders to convert wildlife and biodiversity from a short-term liability into a long-term asset. A landscape-based approach working across scales and sectors while incorporating and reacting to these SESs complexities is a critical step in addressing these shortcomings. I provide an example of this approach in southern Kenya, in what we term "inside-out" conservation. This broader perspective improves the chances that global biodiversity targets and sustainable development goals are aligned. It also ensures that limited conservation resources are used to benefit both people and wildlife through PAs and in the larger, more functional landscapes in which they are embedded.

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Publications and Contributions

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1 Introduction

1.1 A global biodiversity crisis

The Anthropocene epoch has arrived, and with it humanity has altered nearly every component of the natural world (Ripple et al. 2017; Balter 2013). As the human population, economies, and consumption of resources has continued to grow, the sixth mass extinction event in the last 500 million years has started (Barnosky et al. 2011). Of half the planet's known vertebrates, 32% are decreasing (Ceballos et al. 2017), and in the last 40 years, a global index of invertebrate abundance shows a 45% decline (Dirzo et al. 2014). In addition to the concern over species loss because of their intrinsic value, the biodiversity crisis is a significant driver of global ecological change, with cascading effects on ecosystem function and consequently human well-being (Dirzo et al. 2014). Therefore, conservationists must craft solutions that reduce or halt biodiversity loss and provide opportunities to recover ecosystem processes and function.

Nowhere else is this more applicable than across the tropical grasslands and savannas of eastern Africa, where, over the next 50 years, the terrestrial vertebrate diversity of these ecosystems is predicted to be impacted the most by the combined global-scale effects of land-use and climate change (Newbold 2018). These countries hold some of the worlds largest remaining populations of megafauna

and a considerable proportion of the world's vertebrate biodiversity (Jenkins et al. 2013). Yet, these wildlife populations are decreasing at massive rates in the light of land-use change and overexploitation (Ogutu, Piepho, et al. 2016; Craigie et al. 2010a; Veldhuis, Ritchie, et al. 2019).

1.2 Challenges for African protected areas

The primary response to the global biodiversity crisis, both globally and within Africa, has been the increase in the extent of protected areas (PAs), which now cover 14.7% of the world's terrestrial surface[1]. Despite significant increases in the PA network's size, the Aichi targets for terrestrial coverage of 17% are probably insufficient to protect biodiversity and ecosystem function at the landscape and global scales required (Venter et al. 2017; Larsen et al. 2014).

While there are several global estimates of the gaps in coverage of the PA network (Larsen et al. 2014), down-scaled estimates are also vital for national conservation policy and planning. In chapter 2, we downscale global gap analysis to investigate the PA network's ability to conserve biodiversity using a case study of Kenya, a country world-renowned for its natural capital. Here, we demonstrate that only a fraction of national biodiversity, as indicated by species ranges of mammals, birds, and amphibians, occurs within government-administered PAs. However, wildlife policy and conservation attention remain focused on megafauna in these areas, while the bulk of biodiversity outside of PAs receives minimal protection. We also use a biodiversity importance score that demonstrates the importance of rangelands and agricultural areas for biodiversity conservation. In Kenya, as in many parts of the world, it appears that the current extent of the PA network is inadequate to safeguard biodiversity at the national scale.

In addition to PAs inadequately representing biodiversity, over one-third of PAs are also under intense human pressures and may not be adequate to preserve biodiversity (Jones et al. 2018). Many PAs are not designed adequately to maintain

[1] www.protectedplanet.com

underlying ecological processes that sustain biodiversity and ecosystem functions, and most of them are too small to prevent the negative effects of isolation on biodiversity and conserve ecosystem process at the correct spatial scale (Western and Gichohi 1993; Fynn and Bonyongo 2011; Newmark 2008; Veldhuis, Ritchie, et al. 2019). This is particularly true for PAs in eastern and southern Africa, which hold some of the world's largest populations of large migratory mammals (Beale et al. 2013). The impact of people on ecosystem function is prevalent in not only small PAs, but is evident in the region's largest PAs complexes, such as the Serengeti-Mara ecosystem, where human pressures from livestock, development, and land-use change have negatively impacted grassland ecosystem function and water quality and flows (Veldhuis, Ritchie, et al. 2019; Mango et al. 2011).

In chapter 3, we demonstrate the scale of this problem for PAs in eastern and southern Africa for the first time. We show that at least 38% of all PA boundaries are 'hard' and thus transformed by human pressures, while only half of all buffer areas surrounding PAs remain intact for wildlife. Despite wide-spread attention (Newmark 2008; Veldhuis, Ritchie, et al. 2019), this represents the first large scale assessment of isolation and pressure on Africa's government-led PAs.

1.3 Conservation beyond protected areas

To address the shortcomings of PAs there is an appreciation that conservation efforts must increase their scope to include a greater percentage of the world's land area (Dinerstein et al. 2017; Watson and Venter 2017; Larsen et al. 2014). Initiatives such as the Half-Earth movement call for increasing PAs' coverage to at least 50% of each ecoregion (Wilson 2016). PAs, and primarily those that have separated wilderness from people, have been the cornerstone of conservation so far (Brockington 2002; Watson, Dudley, et al. 2014). But, as the number and size of PAs have increased, so has their scope, from protecting iconic landscapes and species in the early 20th century, to the conservation of biodiversity, preservation of ecosystems services, and incorporating social and community objectives in the 21st

century (Watson, Dudley, et al. 2014). It is increasingly acknowledged that the scale of the current conservation challenge will require integrating human-dominated landscapes and finding solutions that work with, rather than against people, to halt biodiversity loss and maintain and recover ecosystem functions (Sayer et al. 2013; Arts et al. 2017; Watson and Venter 2017; Dudley et al. 2018).

In addition to mapping pressures on eastern and southern Africa's government-led PAs, chapter 3 also highlights the potential for working with people to expand biodiversity conservation and improve the ecosystem function of PAs, given that there is still 1.2 million km^2 of intact habitat – primarily rangelands – within 40km of, and contiguous with, the current PA network.

Much of the area needed to protect biodiversity, as outlined in chapter 2, and the remaining intact habitat around PAs belong to one land use type in particular – rangelands – which hold great potential for fulfilling global conservation goals[2].

1.4 Rangelands and conservation

Rangelands – areas used for grazing livestock, including grasslands, shrublands, swamps, and savannas – cover more of the world's terrestrial surface (40%) than any other type of land (Galvin et al. 2008), and support nearly 30% of the world's population (Briske 2017). Additionally, rangelands provide roughly 70% of the forage consumed by ruminant livestock worldwide, primarily across landscapes that are poorly suited for agricultural production (Derner et al. 2017). This includes an estimate of nearly 1 billion camelids, cattle and small stock, in addition to other ungulates primarily belonging to pastoralists (Briske 2017). These pastoral people and their livestock have interacted with wild herbivores in rangelands for thousands of years (Western 1997; Reid et al. 2014; Reid 2012). While livestock production has been the historical focus of rangeland management and policy, there is increasing recognition of the importance of rangelands for both biodiversity conservation and for the provision of a comprehensive suite of ecosystem services, including regulating

[2]If local communities are positioned to be the drivers of change themselves – see Chapter 4.

and cultural services, alongside the provision of goods (Western 1997; Yahdjian et al. 2015; du Toit et al. 2017; Brown et al. 2018).

Rangelands are, therefore, of global importance for the conservation of biodiversity and protection of ecosystem services, and there is an urgent need to ensure that livestock production works synergistically with conservation (Du Toit, Kock, et al. 2012). Developing conservation strategies that support coexistence between large herbivores and wildlife is particularly important (du Toit et al. 2017). Some of the world's rangelands are protected under fortress conservation models where livestock and pastoralists are excluded (Brockington 2002), such as strictly protected areas (IUCN Categories I and II). Some areas are under less strict protection (IUCN Categories III to VI), including private and community-based conservation initiatives (Adams and Hulme 2001; Western 1997; Western, Waithaka, et al. 2015). However, most rangelands have no protection at all, and it is here that there can often be considerable interaction between people, livestock and wildlife.

These complex interactions are challenging to quantify, but essential to understand in order to craft solutions that ensure the sustainable protection of biodiversity, ecosystem services, and local livelihoods.

Chapter 4 outlines a conceptual framework for how conservation may be achieved across rangelands ecosystems, outside of government PAs, using a bottom-up process. We point out the need for, and the potential of, conservation in the human realm. In addition, this chapter serves as a comprehensive literature review, covering the evolution of conservation and the recent shift of focus to areas outside of government-led PAs, natural resource governance, and social and ecological drivers of rangelands systems.

1.5 Defining rangelands as a social-ecological system

To figure out how rangelands could contribute to higher-level biodiversity goals, it is important to acknowledge their complexity. Rangelands are complex social-

ecological systems (SES) where climate, ecology, management, culture, institutions, policy, individuals, and market forces all interact and influence conservation policy and management (Reid et al. 2014; Hruska et al. 2017). It is clear that conservation and management interventions in rangelands will fail when we do not consider this complexity and ignore economic, political, cultural and social well-being parts of the system alongside the ecological indicators (Reid et al. 2014; Mwangi and Ostrom 2009; Brehony 2020). In understanding and managing rangeland systems we must also appreciate that rangeland processes act at multiple scales, both temporal and spatial, and each scale has different dominant patterns and processes (Briske 2017; Brehony 2020). Conservation management interventions that do not appreciate the need to manage across multiple scales, incorporating the varying political, ecological and social dynamics, will often fail to meet their goals by missing critical factors affecting the system at a different scale to the one being observed (du Toit 2010; Cumming et al. 2013; Reid et al. 2014). In appendix A, we point out this challenge in justifying conservation success in a Tanzanian community-based conservation project.

1.6 Using a social-ecological systems lens for conservation planning

Considering rangelands as complex social-ecological systems is critical to address the root causes of biodiversity loss. Conservation, and particularly carnivore conservation, has at times suffered from a narrow scope of inquiry (Montgomery et al. 2018). However, it is becoming increasingly evident that broader, interdisciplinary approaches will be required to understand the challenges of achieving conservation goals (Pooley et al. 2017; Montgomery et al. 2018).

Understanding the critical social and ecological drivers of rangelands and the livestock-wildlife interface that characterises them (from livestock-dominated ecosystems to wilderness[3]) will ensure that we tackle the most important factors

[3] I use wilderness in the sense of a descriptive term for large areas of intact habitat, with lower human disturbance (Watson et al. 2016). While acknowledging the fallacies of the African

determining the diversity, resilience and abundance of wildlife communities. In particular, across rangelands, especially Africa's rangelands, livestock and their owners are the predominant ecological and social force in the SES (Hempson et al. 2017; Du Toit and Cumming 1999). Even in PAs that exclude livestock, the historical legacy of livestock is still apparent. Their influence at the fringes of these PAs can influence the ecology of the system (Vuorio et al. 2014; Veldhuis, Ritchie, et al. 2019), and the potential for conservation success (Muchiru et al. 2009; Western, Mose, Worden, et al. 2015; Broekhuis, Cushman, et al. 2017; Vuorio et al. 2014).

Considering rangelands as complex social-ecological systems is a critical step in broadening conservation to address the root cause of biodiversity loss and addressing inequalities brought about by conservation. In this thesis I use the southern Kenyan rangelands to investigate several vital gaps in our understanding of these SES and the interactions between humans, their livestock, and wildlife.

1.7 Study area

The rangelands of southern Kenya provide the opportunity to further our understanding of some of these key determinants of the livestock-wildlife interface. Here, pastoralists herd livestock across large landscapes in the presence of considerable populations of wildlife. The Kenya – Tanzania borderlands cover roughly 100,000 km^2 spanning the rangelands between southern Kenya and northern Tanzania. Because of the large range of biomes created by topographic and rainfall gradients, this region is one of the most biodiverse in the world (Jenkins et al. 2013). Additionally, the bimodal pattern of rainfall found in the East African regions contributes to some of the highest densities of large mammals found anywhere on the planet, including large migratory populations of grazing ungulates and elephants (Ahlering et al. 2013; Osipova et al. 2018) and considerable carnivore populations (Schuette et al. 2013; Dolrenry et al. 2014a; Elliot and Gopalaswamy 2016; Broekhuis and Gopalaswamy 2016). Because of this, the region also has some

wilderness paradigm that lead to the establishment of many fortress conservation initiatives (Adams & McShane 1992)

16 government-led national parks and forest reserves stretching from Serengeti and Maasai Mara in the west to Tsavo in the east (Fig. **ref**(fig:figure2SA)). These PAs protect wildlife but are also substantial foreign revenue earners for both Kenya and Tanzania (Balmford et al. 2015). Despite the importance of this region for wildlife conservation, the borderlands are dominated by livestock, and the region is the traditional home to Maasai pastoralists (Spear and Waller 1993).

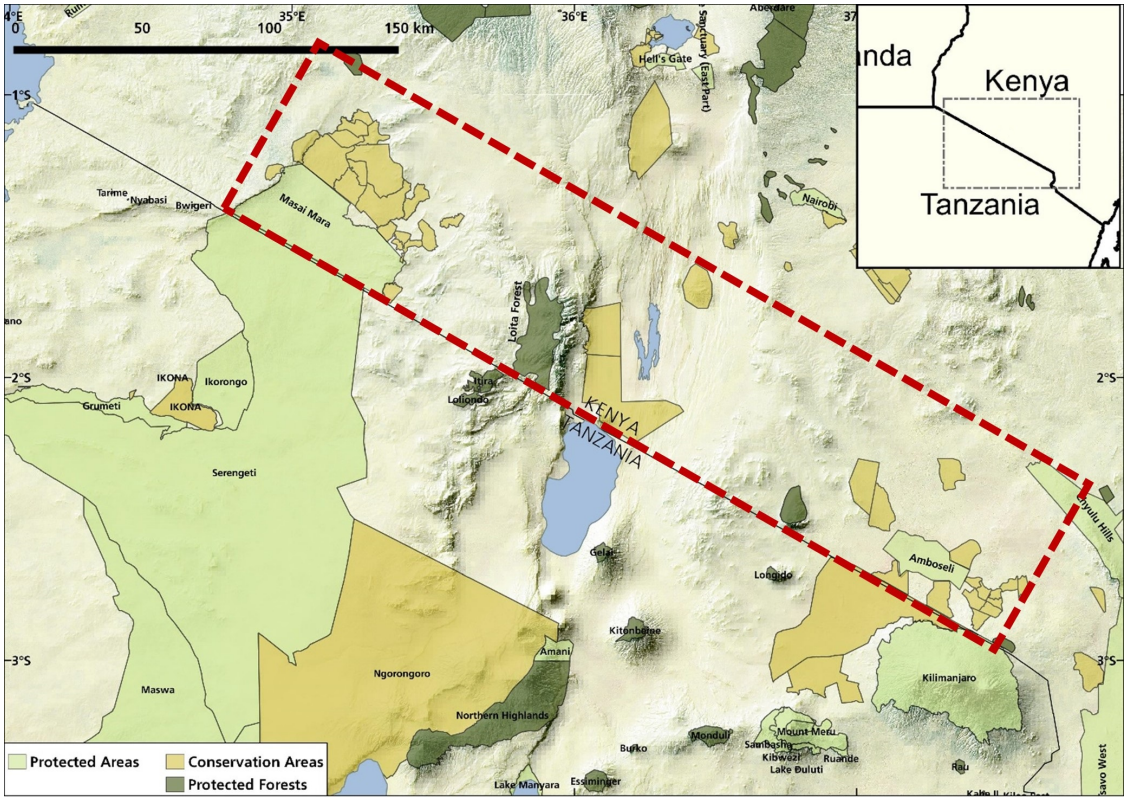

Figure 1.1: The Kenya - Tanzania borderlands areas. The southern Kenyan Rangelands investigated in this thesis are highlighted in red.

On the Kenyan side of the border (Fig1.1), land tenure and governance changes have eroded the resilience of these SESs over the last 100 years. Several policy shifts and economic pressures have driven these changes. First, in the mid-20th century, multiple publicly-owned national parks and reserves were established to conserve wildlife by excluding people and livestock (Mwangi and Ostrom 2009; Western, Tyrrell, et al. 2020). Second, historically Maasai areas were allocated into collectively owned group ranches (community land) in the 1970s (Mwangi and

Ostrom 2009; Galaty 2011). Yet, since then, government policies and economic forces have encouraged privatisation and subdivision of community land while encouraging the sedentarisation of pastoralists (BurnSilver and Mwangi 2007; Mwangi and Ostrom 2009; Sundstrom et al. 2012). This process is ongoing and accelerating. This has led to both pastoralism and wildlife conservation being jeopardised by the negative effects of fragmentation (Hobbs et al. 2008a; Reid et al. 2014), leading to wide-scale losses of wildlife (Ogutu, Reid, et al. 2005; Groom and Western 2013) and losses in rangeland productivity and heterogeneity (Western, Mose, Maitumo, et al. 2021; Western, Mose, Worden, et al. 2015). The changes have arisen because of policy decisions to encourage subdivision and fencing (BurnSilver and Mwangi 2007; Said et al. 2016; Løvschal et al. 2017). Fragmentation has also negatively impacted fire regimes, nutrient dispersal across landscapes, habitat structure and grassland productivity (Western and Gichohi 1993; Veldhuis, Ritchie, et al. 2019; Western, Mose, Maitumo, et al. 2021), and reduced the resilience of pastoral livelihoods (Boone et al. 2005; Hobbs et al. 2008a; Sundstrom et al. 2012). In addition, many areas have seen a loss in traditional grazing management structures, leading to further declines in rangeland productivity (Boone 2005). However, since the late 1990s multiple private and community-run conservation areas have been established to mitigate the negative impacts of fragmentation by providing an economic incentive, through ecotourism, to maintain open, connected landscapes to protect wildlife populations and improve livestock management and rangeland health (Western, Waithaka, et al. 2015) (Fig1.1). A more extensive outline of this region is provided in chapter 4.

1.8 Ecological implications of changing policy, impacting land tenure and management

While many studies have produced landscape-scale estimates of wildlife population changes in African rangelands, showing drastic declines in abundance (Western, Groom, et al. 2009; Craigie et al. 2010b; Ogutu, Piepho, et al. 2016), the link to the underlying drivers of change are rarely estimated, although often speculated. Much of the blame for losses in wildlife are attributed to increases in livestock

density and with-it rangeland degradation and losses in key resource areas for wildlife (Ogutu, Owen-Smith, et al. 2011; Veldhuis, Ritchie, et al. 2019). However, rangeland degradation is often more about limitations to mobility and changes in local livestock densities and land use management, which are driven by larger social and economic changes to the system (Hobbs et al. 2008b; Groom and Western 2013). In addition, changes in rainfall patterns and drought intensity, induced by climate change, have been hypothesised to be causing radical shifts in wildlife communities (Ogutu, Piepho, et al. 2016). However, little direct evidence exists to link climate change and changes to wildlife communities. Therefore, to achieve long-term sustainability of these systems for wildlife conservation, we must increase our understanding of the impacts of climactic and socio-economic factors on the system's ecological properties at the landscape scale.

The changes in livestock mobility across the landscapes is one of the most critical factors affecting livestock and wildlife resilience and abundance, particularly in the southern Kenya rangelands (Groom and Western 2013; Said et al. 2016; Løvschal et al. 2017). Mobility is increasingly limited by land subdivision, fencing and the increasingly sedentary lifestyle of pastoral people (Kimiti et al. 2018). These changes in livestock management result in the losses in rangeland productivity and functional heterogeneity - the spatial and temporal variation in the grass height (structure), productivity, phenology, composition and chemical attributes of grassland and savanna plant communities - which reduces the resilience and productivity of wildlife (Groom and Western 2013; Western, Mose, Maitumo, et al. 2021; Fynn, Augustine, et al. 2016). In addition, management changes can lead to changes in the abundance of certain wildlife species at the expense of others. Changes in livestock grazing intensity alter the species composition, height, productivity and nutritional content of forage resources, with ramifications for herbivore community composition (Augustine et al. 2003; Young et al. 2013; Linstädter et al. 2014). This occurs because herbivores differ in their forage requirements because of their differences in body size, gut morphology and mouth anatomy (Illius and Gordon 1992; Arsenault and Owen-Smith 2002; Fynn, Kirkman, et al. 2017).

To understand the changes occurring within the wildlife community in southern Kenya, we collected and analysed various data on the socio-economic changes occurring. This is documented in chapter 5 and chapter 6. Chapter 7 delves into the ecological ramifications of these changes, including investigating the role of climate change and drought frequency.

Chapter 5 fills an information gap by creating a databases which documents the anthropogenic structures influencing the mobility of livestock and wildlife. In the chapter, we describe a new, large scale database that extends across 30,000km^2 of rangeland in southern Kenya. We synthesised data from several research groups and conservation NGOs and created a spatial-temporal database to share outputs in an open-access format. This initial data release consists of 31,000 livestock enclosures, nearly 40,000 kilometres of fencing, and 1,500 km^2 of agriculture. We provide caveats and interpretation of the different methodologies used to collect these data. We believe this is one of the most extensive spatial datasets assembled that documents changes in mobility and fragmentation of rangelands.

Chapter 6 provides a brief, but timely, commentary and analysis of the importance of these data in quantifying the state of southern Kenyan rangelands and covers the key political and social changes influencing fragmentation.

Chapter 7 analyses 40 years of aerial wildlife and livestock aerial count data and 30 years of NDVI and rainfall across six ecosystems in southern Kenya covering over 40,000km^2. In general, studies on long term changes rarely consider the ultimate consequences of changes in rangeland management, changes in rangeland productivity and heterogeneity across a landscape, and how they affect wildlife community composition and abundance. To do this we used a unique spatially and temporally explicit approach to modelling wildlife abundance using hierarchical generalised additive models (Miller et al. 2013; Tyrrell, Russell, et al. 2017; Harihar et al. 2014; Pedersen et al. 2019). We used a variety of modelling approaches to understand changes in vegetation seasonality, rainfall and describe the link to changes in mobility from our data presented in chapter 5. The results show widespread changes in vegetation seasonality and declines in primary productivity,

but little change in annual rainfall. We find that the management of livestock has a large impact on wildlife communities and that this impact is likely due to the dampening effect that livestock management has on the production of grass biomass per unit rainfall. We also discuss how management and governance principles discussed in chapter 4 are vital to overcoming these ecological changes.

1.9 Economic factors at the human-wildlife interface

A combination of policy changes, globalisation, increasing local populations and local capitalist economies are driving changes in the management and governance of rangeland SES (Reid et al. 2014) which in turn drive ecological changes which ultimately impact wildlife.

One of these largest socio-economic drivers is the opportunity costs of maintaining wildlife-friendly landscapes (du Toit et al. 2017). To conserve wildlife landowners and national governments (who in eastern and southern Africa, have substantial debt and deficits) must forgo land-use opportunities which are not compatible with wildlife conservation and are potentially more profitable, such as agriculture or urban development (Norton-Griffiths et al. 2009). When opportunity costs cannot be met, previously wildlife-friendly land is transformed. Land price is a crucial indicator of the opportunity costs of a landowner resisting land transformation. However, reliable, spatially explicit databases of current land prices are generally lacking in developing countries.

In chapter 8, we use tools from data science to scrape land prices for southern Kenya from the internet. We find that land speculation from expanding urbanisation massively drives up the opportunity and acquisition costs of maintaining conservation buffer zones, corridors and dispersal areas. However, for the first time in Africa, we find high land values are also found adjacent to a world-famous tourist destination, the Maasai Mara. We show that profit-driven turnover of ownership, subdivision, and transformation of land is rapidly underway in the region, to the detriment of savanna

biodiversity and the sustainability of the pastoral social-ecological system. This suggests that economic solutions for conservation appear vital, and ensuring there is an instrumental value of wildlife for landowners and national governments is critical. We cannot rely on the intrinsic value of wildlife alone to carry their conservation.

Therefore, it is apparent that there is considerable need to develop both policies and economic opportunities that will allow for sustainable and competitive returns for land use options in rangelands within and beyond PAs that are compatible with wildlife conservation (Norton-Griffiths et al. 2009; du Toit et al. 2017). In appendix B we review the impact of COVID-19 on economies and international travel, which highlights (i) the lack of funding to offset opportunity costs and cover management costs for Africa's PAs and wildlands and (ii) the lack of long term resilience of these models to global shocks. We highlight potential areas of funding growth and mechanisms to improve the long-term sustainability of African conservation. Many of these points resonate with chapter 8.

At the moment, the primary mechanisms for generating income from wildlife are either consumptive use (for example through trophy hunting, and game meat), and non-consumptive use (such as ecotourism, payment for ecosystem services among others). In Kenya, for example, many of the community and private conservancies have focused on ecotourism as a primary financial mechanism to incentivise conservation (Western, Waithaka, et al. 2015). However, even in Kenya's most productive tourism environment, the Maasai Mara, conservancies may not provide adequate economic benefits to landowners to meet the financial costs of coexisting with wildlife (Bedelian and Ogutu 2017; Thompson et al. 2009), let alone the opportunity costs of forgoing agricultural development (Norton-Griffiths et al. 2009). In southern Africa, consumptive use of wildlife, through trophy hunting and game meat, has proven a viable and sustainable economic option to support wildlife as a land-use (Richardson 1998). In areas of lower agricultural potential, with lower opportunity costs, mixed livestock-wildlife ecosystems can be economically viable and successful when the cost of living with wildlife is mitigated (du Toit et al. 2017; Allan, Venter, et al. 2017).

These economic options for conservation are vital for the long-term sustainability of conservation. However, rarely do policy-makers, practitioners or academics address the social-ecological complexities of these economic policies. In chapter 9 we highlight the applicability of Ostrom's Social-Ecological Systems Framework (SESF) as a useful tool for informing conservation policy. In our case, we used the SESF to explore the barriers to the potential implementation of a policy of consumptive utilisation of wildlife in Kenya, a policy regarded as successful in several southern African countries. This chapter demonstrates how any economic solutions must be crafted for the SES in question, and we cannot assume that one funding solution will work in different SESs with different economic values, policies, governance, and cultures.

1.10 Conclusion

Following our SES lenses, in chapter 10, I will combine the knowledge from the empirical chapters of this thesis with knowledge and examples from the broader literature. In particular, I focus on conservation within southern Kenya, and its implication for conservation at the livestock-wildlife interface across eastern and southern Africa. Here, I will document the trajectory and status of biodiversity and large mammal community in our main study area, and explain the main ecological, social, and political drivers causing these changes. I then place these drivers of change in the regional perspective, and highlight the required interventions to mitigate large-scale biodiversity loss. I will also draw attention to existing gaps in knowledge, where more research may be necessary.

I have not provided a more extensive formal literature review in this introduction, as I review the relevant literature in Chapters 2-9.

2

Conservation beyond protected areas: Using vertebrate species ranges and biodiversity importance scores to inform policy for an east African country in transition

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Conservation beyond protected areas: Using vertebrate species ranges and biodiversity importance scores to inform policy for an east African country in transition

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Abstract

Conservation in eastern and southern Africa has historically centered on megafauna and protected areas (PAs), yet, in the face of rapid change, biodiversity outside of PAs is under threat. With policy changes underway in Kenya, we have performed an analysis that (a) quantifies how inclusive the current PA network is of the country's vertebrate diversity, and (b) identifies wildlife policy areas that need reform to achieve conservation targets. We found that species richness of mammals, birds, and amphibians is highest in areas of intermediate human pressures, whereas Kenya's current wildlife conservation policy focuses on land use (LU) types with the least human pressure. Percentage of range overlap for amphibians, mammals, and birds were all highest in rangelands followed by agricultural (cultivated) areas and then national PAs. Out of 1,535 terrestrial vertebrate species, 80 had no range overlap with national PAs. The current wildlife PA network adequately covers only 16% of amphibians, 45% of birds, and 41% of mammals. In addition, we used a biodiversity importance score which demonstrated the importance of rangelands and agricultural areas for biodiversity conservation. Finally, we observed that the distribution of current PAs, and the focus of Kenya's wildlife policy in general, is in areas of lowest human pressure, often with the highest large mammal densities. However, other biodiversity indicators - such as bird and plant species richness - show that areas under human-dominated LU currently support substantial biodiversity. Overall, our analysis demonstrates that formal PAs and wildlife policy presently cover only a small fraction of national biodiversity, which resides mainly in human-dominated landscapes that are undergoing rapid change. These findings echo global calls for a landscape-based approach to conservation policy and practice that promotes the coexistence of people and wildlife within social-ecological systems.

KEYWORDS

African wildlife, anthropogenic landscapes, conservation gap analysis, Kenya, landscape-scale conservation, megafauna

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1 | INTRODUCTION

Conservation, globally, and particularly in eastern and southern Africa, has historically centered on the protection of landscapes that provide habitat for charismatic megafauna (Adams & McShane, 1992; Watson, Dudley, Segan, & Hockings, 2014). A fortress-based approach to conservation, initiated from the middle of the 20th century, led to the large-scale creation of protected areas (PAs) across the African continent (Brockington, 2002). The policy framework for this national park system perpetuated the misunderstanding that "natural" African savannah ecosystems were wilderness areas lacking what was perceived to be the disturbing influence of people and their livestock (Adams & McShane, 1992). African wildlife policy was based on this wilderness notion, encouraging the separation of wildlife and people.

Despite the establishment of PAs and the exclusion of people, many of these PAs have failed to adequately conserve megafauna (Craigie et al., 2010; Western, Russell, & Cuthil, 2009) and few achieve their broader goals such as conserving regional biodiversity and ecosystem functionality, improving community livelihoods, or contributing toward national economic growth (Geldmann et al., 2013; Lindsey et al., 2014; Watson et al., 2014). These failures are attributable to several reasons, among which financial limitation is paramount, with underfunding and inadequate management of many PAs (Lindsey et al., 2018). Also, although PAs often have higher local species richness and abundance than adjacent unprotected areas (Gray et al., 2016), they are generally not big enough nor in the best places to independently conserve biodiversity and ecosystem services (Larsen, Turner, & Mittermeier, 2018; Venter et al., 2017), and they are seldom designed to protect ecosystem heterogeneity on a scale required by megafauna (Fynn & Bonyongo, 2010; Western & Gichohi, 1993). Finally, the focus on protecting megafauna has often led to a wildlife-versus-people paradigm, negatively influencing the attitudes of communities surrounding PAs and hindering conservation beyond PA borders (Brockington, Igoe, & Schmidt-Soltau, 2006).

Community-based conservation (CBC), is one mechanism that has been used to overcome the limitations with the PA network by incorporating local communities into natural resource management (Hackel, 1999). CBC effectively increases the coverage of the PA network by recognizing the value of ecosystem services, protecting wide-ranging wildlife populations, turning the burden of wildlife into an asset for local communities, and increasing local participation in and support for wildlife conservation (Naidoo et al., 2019; Western, Waithaka, & Kamanga, 2015). CBC establishment across eastern and southern Africa has largely been reinforced by national policies to create frameworks, including legislation, that support implementation (Muchapondwa & Stage, 2015). However, across the region, many policymakers continue to assume that biodiversity belongs in PAs that encompass wilderness areas, and this should be adequate. This assumption has limited the development of policies encouraging wildlife and biodiversity-friendly LU within human-dominated landscapes outside of PAs and CBC initiatives (Western et al., 2015).

The historical focus of wildlife policy on conserving a narrow segment of biodiversity—megafauna—exists for several reasons. First, charismatic large mammals attract an estimated 69 million visitors per year across Africa, generating much-needed foreign revenue through tourism (Balmford et al., 2015). Second, the charismatic nature of Africa's megafauna also attracts international donor funding and associated political pressure, which strongly influences national policy (Muchapondwa & Stage, 2015). Third, and more recently, megafaunal assemblages are considered to include umbrella and keystone species, so their protection should provide wider benefits for biodiversity and ecosystem services (Lindsey et al., 2018). Finally, with all conservation efforts in Africa being chronically underfunded, choices inevitably have to be made, and so there is little left for conserving the rest of biodiversity, especially outside of PAs (Lindsey et al., 2018).

The importance of Africa's PA network should not be undervalued, but it is evident that conservation practice and wildlife policy also need to incorporate LU options within the human realm (Sayer et al., 2013). Biodiversity within these human-dominated landscapes is under the greatest pressure (Di Marco, Venter, Possingham, & Watson, 2018), threatening ecosystem services and, therefore, human wellbeing (Donaldson, Wilson, & Maclean, 2017; Sayer et al., 2013). Widening the focus of conservation policy beyond PAs is essential for any country to reach global objectives such as the Aichi Biodiversity Targets and the Sustainable Development Goals (Kareiva & Marvier, 2012).

In this paper, we explore the scope for conservation in human-dominated landscapes using a biodiversity-rich country, Kenya, as a case study. Much of Kenya is of high priority for global goals of biodiversity conservation (Jenkins et al., 2013), but like the rest of Africa, is undergoing rapid human population growth, agricultural expansion, and urbanization. Kenya's diverse, charismatic, and abundant large mammal communities attract over 1 million tourists annually, contributing over 9% of the national GDP (Turner, 2017). Kenya is of particular interest among African countries because policy changes

in the 1970s, 1990s and, more recently, legal changes with the new Wildlife Act in 2013, have cemented community conservation into human-dominated landscapes (Western et al., 2015). Terrestrial government-administered PAs cover 11.7% of the country (Ministry of Tourism and Wildlife, 2018), yet 65% of Kenya's megafauna exist outside of those areas (Western et al., 2009). To protect wildlife outside of government-administered PAs 160 conservancies have been established within the last 20 years. An additional 11% of the country (both in private and community land) now has some level of protection of wildlife (KWCA, 2016; Ministry of Tourism and Wildlife, 2018).

Building on the conservancy movement and the associated policy direction, Kenya is developing a new wildlife policy and conservation master plan based on the national wildlife strategy, with the vision that: "Kenya's wildlife is healthy, resilient and valued by Kenyans", which is incorporating both biodiversity and development targets. Under this strategy, wildlife is defined broadly as: "any wild and indigenous animal, plant or microorganism or parts thereof within its constituent habitat or ecosystem on land or in water, as well as species that have been introduced into or established in Kenya" (Ministry of Tourism and Wildlife, 2018).

With these policy changes underway, we have explored the distribution of terrestrial vertebrates at the national scale. We used established global and regional practices (Coad et al., 2019; Riggio, Jacobson, Hijmans, & Caro, 2019) to explore which LU systems cover most species' ranges, how effective PAs are in including species' ranges, and how human impacts vary across LU systems. Finally, we used local data to ground-truth the assumptions made from these broad-scale datasets. This exercise enables us to present a discussion on which policy areas still need reform to achieve broad conservation goals through the inclusion of human-dominated landscapes across eastern and southern Africa, and doubtless more widely.

2 | METHODS

LU data were collated for Kenya from two datasets: MODIS MCD12Q1 500 m resolution land cover data from 2013 (accessible at https://lpdaac.usgs.gov/data_access/data_pool); and the World Database of Protected Areas shapefiles (WDPA; accessible at www.protectedplanet.net). The MODIS landcover raster layers were mosaicked and cropped to the Kenyan boundary and aggregated through nearest-neighbor resampling, to retain categorical classification, to a 1 km grid. Land cover categorical data (16 categories) from the MODIS data were reallocated to one of six LU categories, rangelands (livestock areas); forests, urban areas; agriculture; other; and water. The WDPA was used to categorize PAs into two classes recognized under the Wildlife Act 2013: national PAs (National Parks and National Reserves) and conservancies. Other PAs, primarily forest reserves, but also cultural forests protected through government gazettement, are covered under the Forest Act, 2016, rather than current wildlife legislation. Internationally designated PAs (UNESCO World Heritage Sites), were removed as they overlapped with other national-level designated areas. The WDPA data were converted into a raster and combined with the MODIS data to create a 1 km resolution grid of LU across Kenya. We removed water and "other" categories before data analysis.

We acquired human footprint index (HFI) data, which represents the level of human pressures on the landscape for the year 2009 (the index is derived from built environments, cropland, pastureland, human population density, night-time lights, railways, road, and navigable waterways), with values ranging from 0 (no impact) to 50 (highest possible impact), with a resolution of 1 km^2 (Venter et al., 2016).

Global gridded species richness data for three vertebrate classes—amphibians, mammals, and birds—were downloaded with a resolution of 10 km^2 from biodiversitymapping.org (Jenkins et al. Jenkins et al., 2013). We aggregated HFI to a 10 km^2 grid using bilinear resampling and plotted richness against HFI for all three classes. Generalized additive models were added to each plot to visualize trends.

Species range data for mammals and amphibians were acquired from the IUCN database (IUCN, 2017), and bird data were acquired from Birdlife International (BirdLife, 2017). These species distribution maps aim to provide the current known distribution of each species. Shapefiles were cropped to the Kenyan boundary and range polygons filtered to include only those polygons that were definitely extant, possibly extant, or possibly extinct, and either native or reintroduced. Percentage of range overlap (%RO) in each LU type was then extracted for each bird, mammal, and amphibian species.

To estimate the proportion of species with ranges that were adequately protected, we used a process (developed by Butchart et al., 2015; see also Coad et al., 2019) that defines individual species' "representation targets" scaled by species range size. A species with a small natural geographic range (<1,000 km^2) is considered to require 100% of that range protected, with the requirement decreasing to 10% for species with the largest ranges (>250,000 km^2). The values between these two thresholds are linearly

interpolated using a log-linear scale. We compared these representation targets to the extent of range under protection in areas covered under the current wildlife policy for national PAs and conservancies.

To identify the importance of each LU type in conserving biodiversity, we generated a biodiversity importance (BI) score. This score was based on the Flexibility Score of Macdonald et al. (2017).

$$\mathrm{BI}_{\mathrm{LU}n} = \sum_{s=1}^{n} \%\mathrm{RO}_s(\mathrm{EDGE}_s)$$

For each LU category the BI score was calculated by summing the percentage of the range overlap (%RO) for each mammal, amphibian, and bird species (s) multiplied by its Evolutionarily Distinct and Globally Endangered (EDGE) score (Isaac, Turvey, Collen, Waterman, & Baillie, 2007, available at www.edgeofexistence.com), which accounts for both endangerment and phylogenetic diversity as measures of conservation value. Many species within this study did not have an EDGE score due to missing global endangerment (GE) scores, but all species had an evolutionarily distinct (ED) score. We, therefore, recalculated the EDGE metric using the methodology described by Macdonald et al. (2017) and Dickman, Hinks, Macdonald, Burnham, and Macdonald (2015) by assigning GE scores according to each species red-list category: 1, least concern, data deficient, or data absent; 2, near threatened; 4, vulnerable; 8, endangered; 16, critically endangered (following the recommendation of doubling of extinction risk with each increment of red list category). To calculate our modified EDGE score, we summed the GE and ED score of each species. We also divided the BI score by area to adjust for the relative size of the different LU areas.

Two datasets were used as indicators to investigate megafauna bias in wildlife policy. First, the density of large mammals, given in tropical livestock units (TLUs) per square kilometer, on a 5×5 km grid, from a 1994 and 1996 aerial wildlife count in the arid and semi-arid rangelands by the Directorate of Remote Sensing and Resource Surveys, was downloaded from https://www.wri.org/resources/data-sets/kenya-gis-data. One TLU denotes the feed requirement of a standard animal of a weight of 250 kg. Second, a plant species-richness dataset from the R package *vegetable* was collected across 1946 sites in Kenya. The cumulative density of large mammals against the mean HFI for each cell, and plant species richness was compared to the HFI for the corresponding cell. All measurements of area were based on the Mollweide equal-area projection, and all analyses were conducted in R (R Development Core Team, 2008) using the *raster* package.

3 | RESULTS

3.1 | Species richness and human impact

All three vertebrate classes in our analysis (mammals, birds, amphibians) have highest species richness along the humid coastal belt, central and western highlands, and along the semi-arid southern border (Figure 1). Species richness is lowest in the very arid north-eastern area of the country. Generalized additive models (inset Figure 1) suggest that all three groups have the highest species richness at intermediate values of human pressures, with richness decreasing past this point. The entire East African region displays a similar trend, except the highest species richness continues to increase with the human footprint (Supporting Information).

3.2 | Land use

Data from WDPA and MODIS land cover (Figure 2b), show Kenya's LU to be overwhelmingly dominated by rangelands primarily used for livestock production, followed by agricultural land, national PAs, conservancies, and other PAs (which are not under the Wildlife Act., 2013), water, and urban areas. National PAs and conservancies are predominately found in areas with the lowest human pressure (Figure 2a), whereas agriculture, urban, forests, and other PAs show a much broader range of human pressures (Figure 2a). Removing the LU categories (built environments, cropland, pastureland) from the HFI (Supporting Information) indicates a similar pattern.

3.3 | Range overlap

Range overlap was calculated for all three vertebrate classes (Figure 3a–c, Supporting Information). There is a significantly higher range overlap for all three classes of species with rangelands than any other land-use type. The next highest range overlap for all classes is on agricultural land, with both amphibians and birds having a higher mean range overlap on agricultural land than do mammals. Mean range overlap with LU covered under the current wildlife policy (national PAs and conservancies) was considerably less for all classes. Other PAs had a similar mean percentage range overlap with conservancies for species across all classes, although birds had significantly less range overlap in other PAs than in conservancies. Forest LU covers as much range for amphibians as do conservancies but covers significantly less for the other two classes. Mean percentage of range

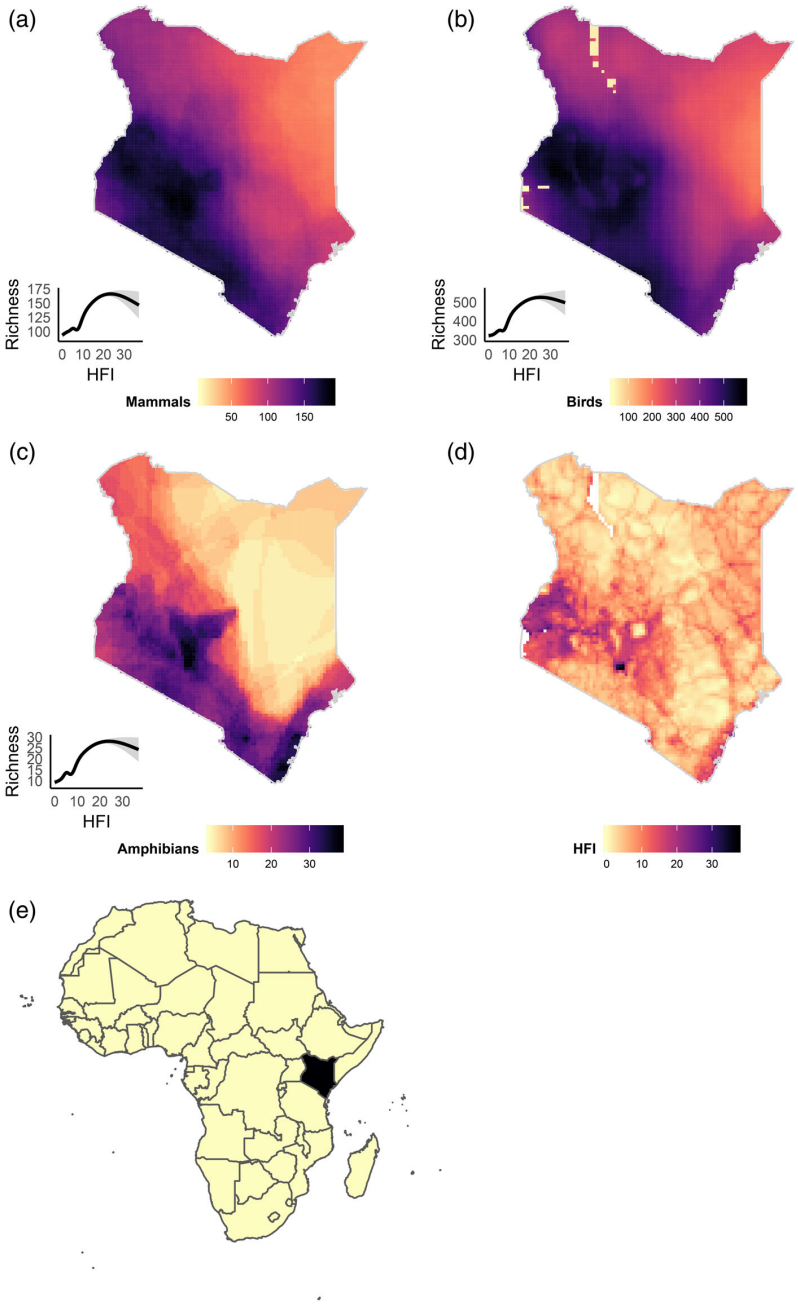

FIGURE 1 Maps of Kenya depicting variation in (a) mammal species richness; (b) bird species richness; (c) amphibian species richness; (d) human footprint index (HFI). The maps are plotted on a 10 × 10 km grid, with biodiversity data from biodiversitymapping.org (Jenkins et al., 2013) and HFI data from 2009 aggregated to a 10 × 10 km grid from Venter et al. (2016). HFI represents the level of human pressures on the landscape, ranging from 0 (no impact) to 50 (highest possible impact). Generalized additive model smooths (95% confidence intervals are shaded) of HFI and species richness are inset for all three classes. The location of Kenya within Africa is shaded in map E

in urban LU was the lowest for all three classes. These relationships are primarily consistent with the absolute size of each LU category (Figure 4). Of note, however, is that 80 species had no range overlap with national PAs (Supporting Information; 5.2% of all species analyzed), comprising 27 mammals (7.67% of total), 10 a.m.phibians (9.52% of total) and 43 birds (4.0% of total).

3.4 | Representation targets

For all three classes, over half the species had inadequate coverage by national PAs and conservancies (Figure 5). Only 16.2% ($n = 17$) of amphibian species met their representation targets. More, but not a majority, of mammal and bird species, had adequate protection under their

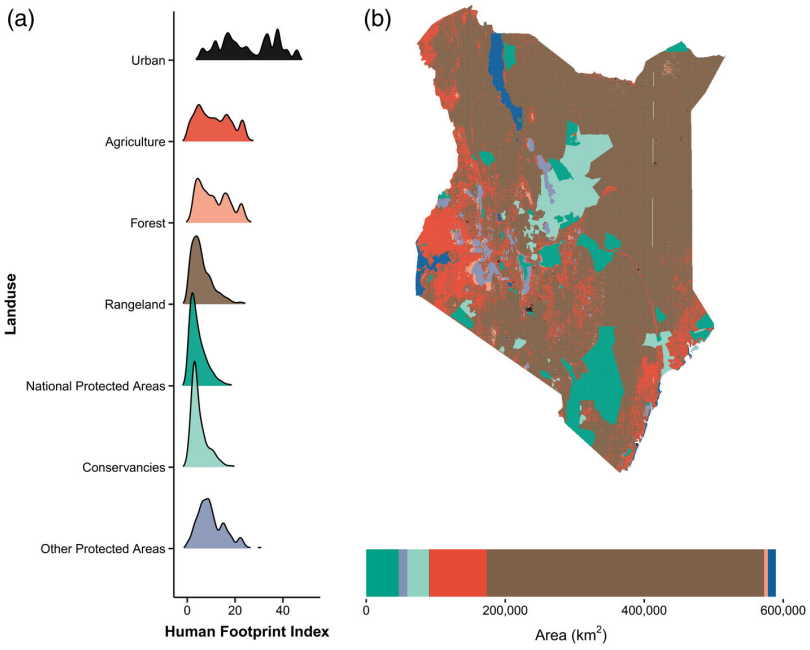

FIGURE 2 Kernel density curves (a) with the shaded area representing the distribution of human footprint index (HFI) values across land use categories in Kenya. A land use map of Kenya (b) was amalgamated from MODIS land cover data and the WDPA. Rangelands cover 399,029 km^2 (67.7%), followed by agricultural land covering 82,429 km^2 (14.0%). All PAs cover 90,694 km^2 (15.4%), broken down into: national PAs 46,751 km^2 (7.9%); conservancies, 31,640 km^2 (5.4%); and other PAs (which are not under the Wildlife Act., 2013), 12,303 km^2 (2.1%). Inland water bodies (dark blue) cover 11,343 km^2 (1.92%), much of which is Lake Victoria and Lake Turkana; urban areas cover 391 km^2 (0.07%)

representation targets, with 40.9% of mammals ($n = 144$) and 44.9% of birds ($n = 481$) having adequate protection.

3.5 | Biodiversity importance scores

Rangelands, followed by agricultural areas, have the highest biodiversity importance scores, as measured by range overlap and EDGE score, of all LU types in Kenya (Figure 6a). When scaled relative to LU area (Figure 6b), the relative importance of forest, agriculture, urban, and other PAs also becomes apparent, and the relative importance of rangeland decreases.

3.6 | Local data and taxonomic bias

Comparison of two indicators (Figure 7), shows the current bias in wildlife policy in Kenya toward areas of low human footprint and high large mammal density. Cumulative wildlife density (TLUs/km^2) drops off sharply as human pressures increase, whereas plant species richness increases up to intermediate values of the HFI (Figure 7a).

4 | DISCUSSION

Our Kenyan case study demonstrates that effective wildlife conservation at the national scale requires the development of new wildlife policy for human-dominated landscapes, extending way beyond the scope of the current PA and CBC network. Conservation efforts in human-dominated landscapes should not come at the expense of Africa's national park network, but human pressures are rapidly mounting across all LU categories, many of which are vital for biodiversity (Figure 2, Figure 5). These include urban areas, agricultural landscapes, and rangelands, where the current policy does not explicitly support wildlife conservation. Similar requirements for policy reform and implementation have been identified on other continents (Boakes, Fuller, & McGowan, 2018; Zisenis, 2017). Our analysis of species range data displays a similar result to an analysis of range data within the global PA estate (Coad et al., 2019), and for a regional analysis of endemic species coverage (Riggio et al., 2019).

The species range data used in this analysis represents the most up-to-date global distribution maps for species and, for data deficient countries like Kenya, it is the best biodiversity data available. These data are updated regularly to current range whenever possible for each species (https://www.iucnredlist.org/assessment/updates). However, these range maps include both past and potential habitat, whether occupied or not at present, including habitat within the matrix of human-dominated landscape. We nevertheless maintain that our findings provide important evidence for policy reform. A comprehensive wildlife conservation policy should protect both presently and previously occupied yet still intact

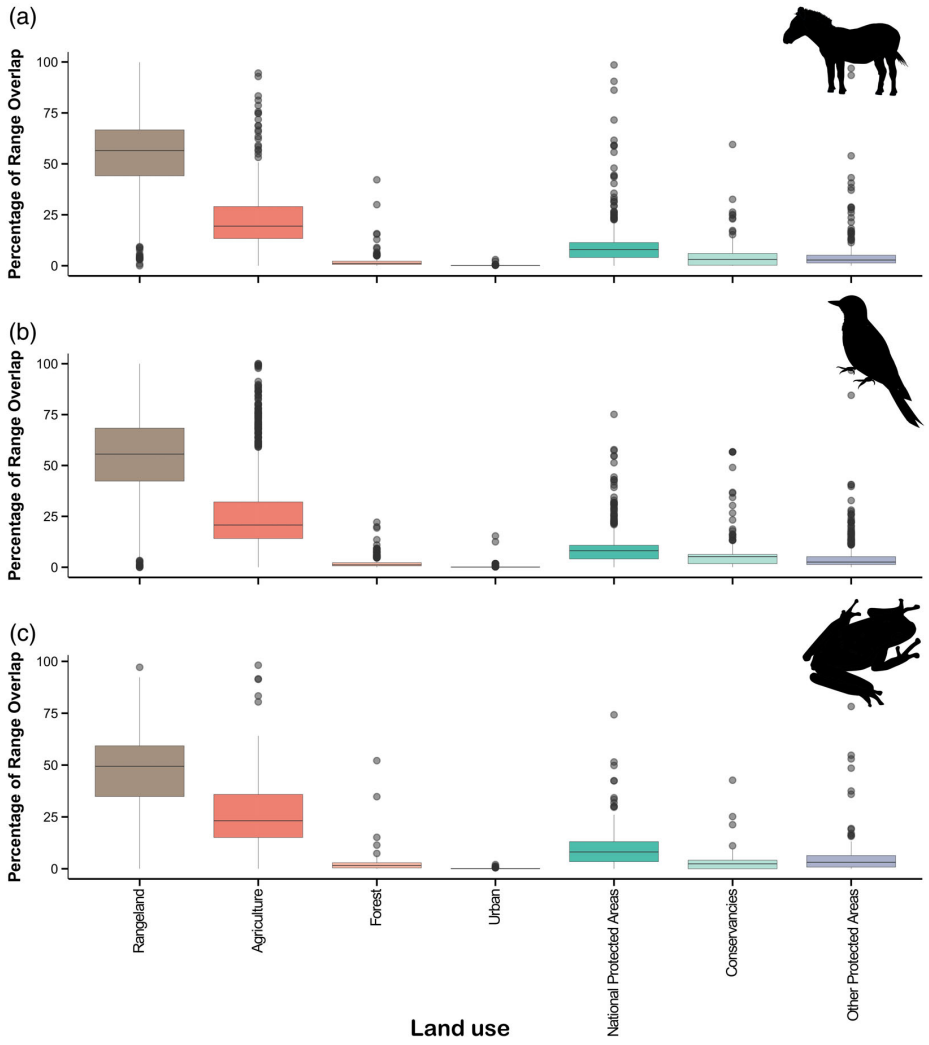

FIGURE 3 Boxplots of percentage species range overlap with the seven land use categories investigated, for three vertebrate classes: mammals, 352 species (a); birds, 1,078 species (b); amphibians, 105 species (c). Across all classes, 97 species are threatened with extinction. See Supporting Information for descriptive statistics

habitats, with attention to connectivity through the matrix between habitat patches. If only occupied habitat is considered worth protecting, then the total potential area of habitat and the connectivity between habitat patches will ratchet down inexorably as species are locally extirpated. A singular focus on occupied habitat is concerning considering the current inadequate representation of well over half of Kenya's terrestrial vertebrate species within the PA network (Figure 5). Many human-dominated landscapes support both wildlife and people. Rangelands in particular cover the largest area of the country (Figure 2b), have the highest range overlap (Figure 3) and biodiversity scores (Figure 6), and generally still support considerable biodiversity ranging from large mammals (Ogutu, Kuloba, Piepho, & Kanga, 2017; Tyrrell, Russell, & Western, 2017; Figure 7a) to avian scavengers (Sebastián-González et al., 2019) and invertebrates (Wilkerson, Roche, & Young, 2013). In addition, LU categories under medium-high human pressures, such as urban and agricultural areas classified at 1 km^2 resolution, might contain small patches of critical habitat for some species of plants (Figure 7b), foraging and dispersing primates (Anderson, Rowcliffe, & Cowlishaw, 2007), small-bodied vertebrates (Toth, Lyons, & Behrensmeyer, 2014), and invertebrates (Rogo & Odulaja, 2001). For example, central Nairobi, the area with the highest HFI in Kenya (Figure 1) and classified as

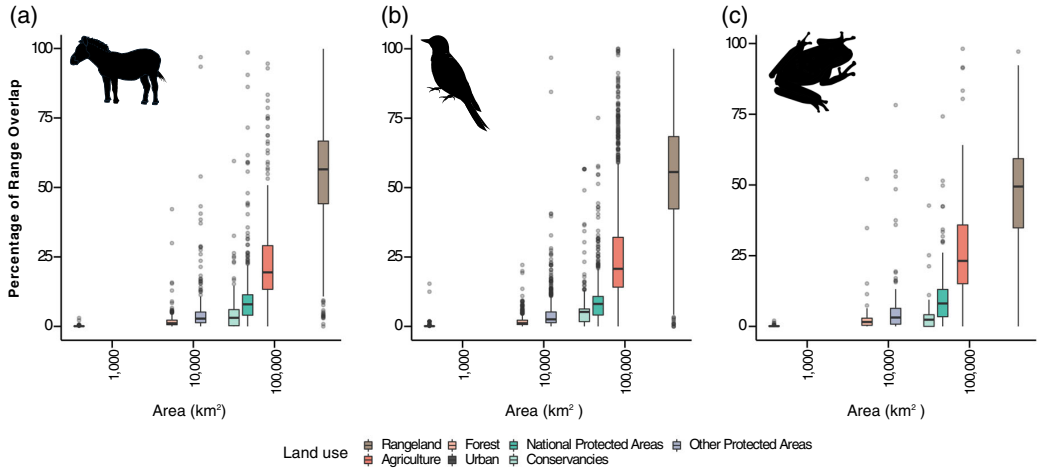

FIGURE 4 Boxplots of the percentage of species range overlap compared with the total size of the land use type across Kenya for the three groups investigated (a) Mammals (b) Birds (c) Amphibians. The total land use size is on a $\log_{10}$ transformed scale

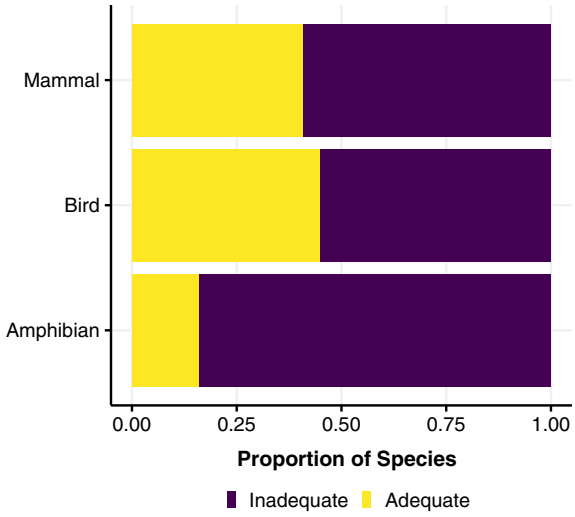

FIGURE 5 The proportion of species per vertebrate class that meet their representation targets (Butchart et al., 2015; Coad et al., 2019) in terms of PA coverage in Kenya, with PA in this analysis being national protected areas and conservancies

urban (Figure 2) at 1 km^2 resolution, has >257 species of bird recorded in the Kenya Bird Map (http://kenyamap.adu.org.za/).

4.1 | Species richness and human pressures

The highest species richness of the three classes investigated was found in areas of intermediate human pressure in Kenya and areas of highest human pressures across eastern Africa, similar to global patterns observed for vertebrates (Venter et al., 2016). Globally, the steepest biodiversity declines are within these areas (Di Marco et al., 2018), yet due to historical factors the wildlife conservation policy in Kenya (and other African countries) is focused on areas with the lowest human pressures and the highest densities of megafauna (Figures 2 and 7a). Obviously, megafauna needs special protection as keystone and umbrella species (Dickman et al., 2015; Dirzo et al., 2014), and they include the first species to be lost under increasing human pressure (Smith, Smith, Lyons, & Payne, 2018). Nevertheless, wildlife policy focused on megafauna provides diminishingly little protection to the larger segments of biodiversity remaining in areas under higher human pressures (Figure 7b).

4.2 | Beyond PAs

Our analysis demonstrates the importance of developing policies for wildlife conservation in human-dominated landscapes, beyond the scope of the current PA and CBC network, to close the gap in biodiversity conservation across Kenya. Only 16% of amphibian, 45% of bird, and 41% of mammal species meet their representation targets in terms of the percentage of their scale-adjusted range overlapping national PAs and conservancies (Butchart et al., 2015; Coad et al., 2019), being the two LU categories covered by the current wildlife policy (Figure 5). Those percentages are likely over-estimates, given the inadequate resourcing of many PAs and newly established conservancies (Coad et al., 2019). Additionally, PAs fail to protect 80 species that have no range

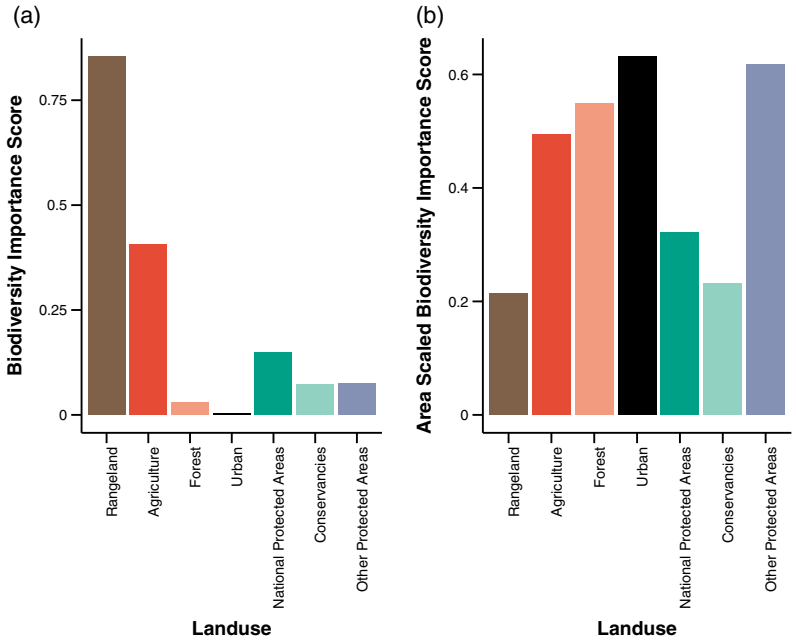

FIGURE 6 Biodiversity Importance (BI) scores calculated for each land use type showing (a) total scores, which reflect the importance of rangeland and agricultural areas to biodiversity, and (b) scores scaled by the area of each land use type

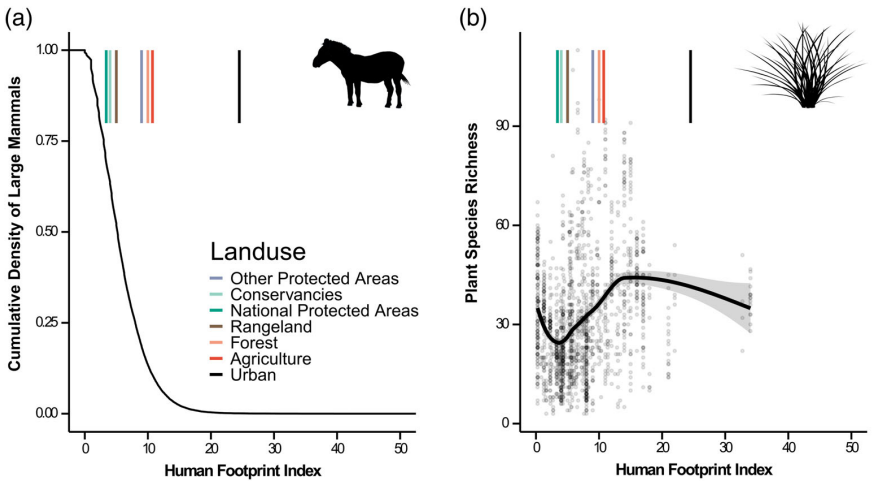

FIGURE 7 Comparison between two indicators used for conservation prioritisations relative to human pressures as indicated by the Human Footprint Index (HFI). The median HFI for each land use category is displayed for reference. The cumulative density of large mammals (A) is highest in areas with the lowest HFI, which is where Kenyan wildlife policy currently applies on the ground. In contrast, plant species richness increases up to intermediate HFI, because humans have settled mesic areas on fertile soils where historically high plant species richness still persists, but many wildlife species have been extirpated. Large mammal density was calculated from 1994 and 1996 aerial wildlife counts in the arid and semi-arid rangelands by the Kenyan Department of Remote Sensing and Resource Surveys, downloaded from https://www.wri.org/resources/data-sets/kenya-gis-data. Plant species richness comes from the R package *vegetable* using 1946 sites across Kenya, with data points fitted with a loess smooth and 95% confidence intervals (gray shading)

within PAs and many face immediate threats to their survival: one of these is critically endangered (Taita warty frog, *Callulina dawida*), seven are endangered, two are vulnerable, and five are near threatened (Supporting Information).

There is little scope for the expansion of government-administered PAs across Kenya to protect biodiversity due to limited funding opportunities and pressure for competing LU options, as applies throughout sub-Saharan Africa. However, a feasible path to protecting

more biodiversity is to integrate all PAs under a common policy framework. In doing so, coordinated efforts between currently disparate government agencies and policy sectors can be achieved, potentially increasing the effectiveness of conservation planning and implementation across different PA types. Integrating CBC into Kenyan wildlife policy and legislation was one step along that path and integrating forest reserves ("Other PAs"), which are administered by the Kenya Forest Service under the Forest Act of 2016, could be the next. Presently, clearing of forest for farmland is removing habitat for forest-obligate species such as the endangered Turner's eremomela (*Eremomela turneri*; BirdLife International, 2018). Despite high human pressure though (Figure 2), forest reserves appear to be as important for biodiversity conservation as conservancies (Figure 6a) and add an extra 2.1% of Kenya's land surface. Being situated primarily within or near to human-dominated landscapes, they form an important link between biodiversity and the Kenyan people while protecting ecosystem services for burgeoning urban areas. Human populations in urban areas across Africa totalled 395 million in 2010 and are predicted to reach 1.34 billion in 2050 (Güneralp, Lwasa, Masundire, Parnell, & Seto, 2018). Considering the link between the HFI and species richness (Figure 1; Figure 6; Supporting Information), and evidence from North America, conservation efforts in emerging urban centers will be important both for retaining some biodiversity (Ricketts & Imhoff, 2003) and for creating urban landscapes that enable human well-being.

The high biodiversity importance of rangelands is, in part, a function of their overwhelming area (Figure 4). When scaled by area, LU types found in areas of higher productivity, and thus higher human pressure (such as agriculture, urban and forests), gain local importance (Figure 6b; Balmford et al., 2001). Overall, however, rangelands are important as interfaces with PAs and as buffer areas for the megafauna within them (Beale et al., 2013). Yet, continued changes in tenure, management, and use of rangelands threaten biodiversity and human livelihoods across Kenya and much of the region (Reid, Fernández-Giménez, & Galvin, 2014). Additionally, agricultural expansion into rangelands involves habitat loss and widespread land subdivision, with fencing posing a major threat to movements of large mammals including the world-famous migration in the Serengeti-Mara ecosystem (Løvschal et al., 2017). Nevertheless, the coexistence of livestock and wildlife can be sustained in rangelands with production systems that promote functional heterogeneity at the landscape scale (Fynn, Augustine, Peel, & de Garine-Wichatitsky, 2016; Tyrrell et al., 2017). Such systems can provide benefits for biodiversity, ecosystem services, and local livelihoods, without the need for "top-down" administrative control (Keesing et al., 2018).

Under increasing food demands, agricultural landscapes are likely to both intensify production and increase in size at the costs of forest cover, which will drastically alter habitat availability for forest-dependent species(Laurance, Sayer, & Cassman, 2014). In our Kenyan example, this will have important ramifications (Figures 2 and 3) for many amphibian species, which are reliant on both agricultural and forest landscapes (Figure 3, Figure 5, Figure 6 & Supporting Information) and are poorly represented under the wildlife PA network (Figure 5). Policies to encourage and implement the restoration and preservation of remaining large forests patches within agricultural mosaics is of critical importance. Policies that support a continuum of land-sparing and land-sharing strategies, dependent on the local conditions, can protect biodiversity and ecosystems services in agricultural landscapes (Alvarado, Williams, Arroyo-Rodríguez, & Escobar, 2018; Baudron & Giller, 2014; Laurance et al., 2014). In southern Uganda, for example, land-sparing, through the preservation of remaining forest patches in intensive agricultural land, may benefit some bird species (Hulme et al., 2013). Land-sharing, through modifying agricultural LU and practices, can also have positive consequences for biodiversity conservation and ecosystem services (Haslem & Bennett, 2008; Phalan, 2018). Despite human pressures, well-managed agricultural landscapes can be important areas for biodiversity conservation and ecosystem service provision, which complement sustainable livelihoods (Scherr & McNeely, 2008).

4.3 | Policy reforms

Achieving transformative and effective policy reform for natural resources is especially challenging in developing countries such as Kenya, but we urge that our analysis should motivate progress in feasible steps. Prioritizing conservation interventions at the national level, across land-use types, is an important step. The development of National Red Lists, as has been done in Uganda and South Africa, could facilitate targeted regional conservation action for threatened species. Local programs to collect, collate, and periodically summarize temporally and spatially explicit data on biotic and abiotic environmental variables, LU, human demographics, and economic indicators, could contribute importantly toward national conservation goals (e.g., Xu et al., 2017).

Leveraging existing laws, and shaping cross-sector policy, could improve the scope for conservation in human-dominated landscapes. At present in Kenya, the

Agricultural Act of 2013, the Forest Conservation and Management Act of 2016, and the Environmental Management and Coordination Act of 1999 (revised in 2012) all work independently and influence biodiversity in different ways across different land-use sectors. Implementation and enforcement are problematic in each case while other policies, such as national spatial plans, urban development plans, and wide-scale infrastructural development, contradict conservation goals (Lambin & Meyfroidt, 2011; Laurance, 2018). Clearly, integration of biodiversity conservation policy across LU sectors is required, and the relevant agencies and institutions have to operate together at one appropriate scale, which is the landscape scale (Sayer et al., 2013).

Finally, to make conservation in human-dominated landscapes achievable there is a need for the empowerment of appropriate management structures, devolved governance systems, and coordination and consensus among stakeholders at various levels (Arts et al., 2017). The weak incentives for grass-roots conservation present a particular challenge with most landholders unable to convert wildlife and biodiversity from a short-term liability into a long-term asset (Norton-Griffiths & Said 2010). To overcome this problem, the exploration of innovative solutions to generate financial momentum across all LU types is required. Appropriate policy changes are urgently needed to encourage conservation incentives in human-dominated landscapes because prospects of large-scale restoration of biodiversity are difficult or unrealistic (Possingham, Bode, & Klein, 2015), as demonstrated by the rangelands of the USA (Reid et al., 2014) and the agricultural landscapes of Europe (Kleijn & Sutherland, 2003).

4.4 | Conclusions

This case study of Kenya, which is world-renowned for its natural capital, demonstrates that only a fraction of national biodiversity, as indicated by species ranges of mammals, birds, and amphibians, occurs within government-administered PAs. However, wildlife policy and conservation attention remain focused on megafauna in these areas, while the bulk of biodiversity outside of PAs receives minimal protection. PAs must be adequately supported, but innovative wildlife policies and practices are also needed to facilitate the transition of biodiversity from a short-term liability to a long-term asset for the burgeoning human populations living in the matrix of rangeland, cropland, and even urban sprawl. This echoes international calls for landscape-based approaches to conservation and policy reforms that integrate biodiversity conservation with all other sectors of LU (Sayer et al., 2013). Our analysis calls for the focus of national wildlife policy to widen beyond wilderness and megafauna and to include landscape heterogeneity, land-use diversity, key habitat patches (and dispersal among them) within the human-dominated matrix, and ecosystem services upon which people depend (Kremen & Merenlender, 2018). Nowhere else is this more applicable than across the tropical grasslands and savannas of eastern and southern Africa, where, over the next 50 years, the terrestrial vertebrate diversity of these ecosystems is predicted to be impacted the most by the combined global-scale effects of land-use and climate change (Newbold 2018).

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHORS' CONTRIBUTIONS

P.T. developed the ideas and methods for this research, conducted the analysis, and wrote the first draft of the manuscript. J.D.T and D.W.M edited and reviewed the subsequent drafts.

ETHICS STATEMENT

No ethics approval was required for this research.

DATA AVAILABILITY STATEMENT

All data used in this manuscript if freely accessible at the referenced sources.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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Measuring the hardness of protected area boundaries and buffers: implications for African conservation

Abstract

Protected areas (PAs) are the last bastions of global biodiversity. However, human pressures along their boundaries and in adjacent habitats impair connectivity and ecosystem function. Despite the importance of maintaining the integrity of PA networks within their surrounding landscapes, previous research has not measured the effects of human encroachment on PAs at the continental scale. Here, for eastern and southern Africa, we show that at least 38% of all PA boundaries are 'hard' and thus transformed by human pressures, while only half of all buffer areas surrounding PAs remain intact for wildlife. Human-wildlife conflict is generally high at hard boundaries, and >19,000km may need fencing. However, optimistically, there is still >1.2 million km^2 of intact habitat contiguous with the current PA network, approximately double the current PA extent. Policy reforms and economic incentives are required in these areas to prevent continued losses of biodiversity and ecosystem function.

Introduction

Protected areas (PAs) are the primary response to the current biodiversity crisis and cover ~15% of the world's terrestrial surface (UNEP-WCMC & IUCN 2020). The importance of PAs as a key conservation tool is enshrined in policy, with the Convention on Biological Diversity's Aichi Target 11 currently calling on nations to formally protect 17% of terrestrial land (United Nations 1992). Targets for the next decade are being negotiated, and it seems likely that the area requiring protection could increase to 30% by 2030, although recent estimates suggest it needs to be higher to adequately safeguard biodiversity (Allan et al. 2019).

Given their importance, PAs and Aichi Targets have both received much scientific attention. Studies have analysed the areas covered by PAs and their effectiveness in representing biodiversity and ecosystem services (Larsen et al. 2014; Butchart et al. 2015; Allan et al. 2019), the threats they face (Allan et al. 2016; Jones et al. 2018), and their management effectiveness and resourcing (Lindsey et al. 2018; Coad et al. 2020). This is all vital information (Visconti et al. 2020), but a less-studied element of Aichi Target 11 is the need for *"well-connected systems of protected areas and other effective area-based conservation measures, integrated into the wider landscape and seascape"*. This is important because a surrounding matrix of human-settled and transformed land impedes biodiversity conservation by compressing wildlife into PAs and preventing dispersal (Western & Gichohi 1993; Veldhuis et al. 2019). It also increases human-wildlife conflict and the exploitation of biodiversity while facilitating the spread of invasive species and pollutants into PAs, ultimately compromising ecosystem function and causing biodiversity loss (Western & Gichohi 1993; Newmark 2008; Fynn & Bonyongo 2011; Tucker et al. 2018; Veldhuis et al. 2019).

Increasing human pressure around PAs creates 'hard boundaries' for wildlife due to limited permeability through buffer zones, reducing physical and functional connectivity with the broader landscape. Integrative landscape-scale conservation that incorporates people into the process is, therefore, vital for PAs to maintain the underlying ecological processes that sustain biodiversity and ecosystem services (Western & Gichohi 1993; Newmark 2008; Kremen & Merenlender 2018). The problem of hard boundaries developing around PAs is especially acute given the current global PA network is not extensive enough to meet the CBD goals of safeguarding biodiversity and ecosystem services (Larsen et al. 2014).

A realistic assessment of progress towards achieving Aichi Target 11 requires quantification of the disjunction in habitat conditions at PA boundaries, which indicates the potential to expand a PA or integrate it into wider landscape-scale conservation efforts. Several studies

have assessed threats in buffer areas adjacent to PAs (e.g. Allan et al. 2016) and the connectivity of PA networks and habitat patches (Saura et al. 2018; Ward et al. 2020). However, to our knowledge, no study has specifically quantified the 'hardness' of PA boundaries and the buffer zones of accessible land surrounding them that have high conservation potential (Beale et al. 2013). Here, we quantify boundary hardness using the recently updated Human Footprint map of cumulative human pressures on the terrestrial environment (Venter et al. 2016). We first analyse spatial patterns of human pressure adjacent to government-administered PAs boundaries in eastern and southern Africa. PA boundary hardness is expected to increase with annual rainfall up to an asymptote at ~1000 mm, after which productivity and agricultural potential in African savannas is more limited by soil nutrients than soil moisture (du Toit et al. 2017). We, therefore, also identified boundaries that were harder or softer than expected from average annual rainfall. We then quantified the hardness of buffer areas surrounding PAs and the proportion of intact habitat remaining in the buffers, with sequentially larger buffer areas extending 10-40 km outwards from a PA boundary. We defined intact habitat as areas where anthropogenic land conversation has not occurred, and areas are still considered "natural"(Watson et al. 2016a). We calibrated the Human Footprint threshold using regional data on large ungulate abundance and connectivity.

We focus on eastern and southern Africa because this is where current conservation efforts are failing to halt biodiversity declines within the richest remaining wildlife assemblages on Earth (Western et al. 2009; Craigie et al. 2010; Ogutu et al. 2016). African megafauna plays a disproportionally large role in shaping ecosystem function, and consequently, species diversity and ecosystem services (Hempson et al. 2017; Goheen et al. 2018), yet are also disproportionally threatened by people (Smith et al. 2018). These threats, which include the increasing demand for bushmeat (Lindsey et al. 2017), illegal wildlife trade, human-wildlife conflict, and competition with livestock (Ogutu et al. 2016; Lindsey et al. 2017), also include the isolation of PAs within hard boundaries, yet this has not been monitored at a regional scale. Considering that land use and climate change threaten biodiversity in the savanna biomes of sub-Saharan Africa more than anywhere else (Newbold 2018), an analysis of boundary hardness is crucial for evaluating this PA network, in particular, to inform regional and local conservation efforts. It should also contribute to an improved framework for monitoring PA networks globally.

Methods

Protected areas

We obtained data on the terrestrial boundaries of eastern and southern African PAs from the World Database of Protected Areas (WDPA) in September 2019. All analyses were conducted using R version 3.5.1(R Core Team 2018). See S5 for additional details.

Human pressure as a measure of boundary hardness and buffer intactness

We used the updated Human Footprint (HF) that includes global data on built-up environments, human population density, electric infrastructure, croplands, pasture lands, roads, railways, and navigable waterways at 1 km^2 resolution (Venter et al. 2016). While any threshold is arbitrary to some extent, we used well-established global thresholds of HF, combined with locally acquired data, to indicate the likelihood of wildlife being able to move voluntarily and persist across PA boundaries. Our key definition is that boundaries with HF scores of >7 are classified as 'hard' because such scores indicate intensive agriculture or similar anthropogenic land transformation (Venter et al., 2016). Although large wild mammals can occasionally move through these landscapes, their mobility is greatly reduced (Tucker et al., 2018), and they are likely persecuted.

This follows established procedures to determine habitat intactness, defined as a "natural areas" that have not been converted to anthropogenic land uses (Watson et al. 2016a) We then validated this 'hardness' threshold against locally collected data. First, we compared the HF to an independent binary anthropogenic landcover for East Africa (Jacobson et al. 2015), which has been widely used to analyse connectivity for large mammals in the region (Masenga et al. 2016; Riggio & Caro 2017; Riggio et al. 2018). There is high concordance between a threshold of HF=7 and a transition to converted land-use unsuitable for wildlife mobility (S6). Second, we compared the relationship between cumulative population abundance and HF for 16 species of large herbivore across six diverse ecosystems covering 30,000km^2 of southern Kenya, ranging in size from elephant to gazelle (S7). We found that the majority of wildlife exists in areas scoring up to HF=7 (mean cumulative abundance = 67%; range 58% – 79%) with only remnant populations persisting at higher HF (e.g. for HF>10, mean cumulative abundance = 15%; range 0.08%-20%). Wildlife populations occurring in areas of HF>7 are close to roads, other infrastructural development and agriculture, where they are generally declining in abundance (Ogutu et al. 2016).

We note that there is no defined threshold for habitat conversion using the HF because there is no single value at which the properties we associate with habitat "intactness" are suddenly

lost (Watson et al. 2016a). We, therefore, explore the sensitivity of our results at more strict definitions of intactness (i.e. lower HF), using two other well-described thresholds to distinguish between those that are 'open' to wildlife and those that represent 'soft' and 'firm' barriers. HF scores <1 are associated with 'wilderness', being ecologically intact landscapes that are mostly free of human disturbance (but not necessarily free of people), and where anthropogenic pressures have limited impacts on biodiversity and ecological function (Watson et al. 2016b, 2016a; Di Marco et al. 2019). We classify these PA boundaries as 'open' to wildlife. An area with HF<4 has intact habitat where wildlife can still move freely (Tucker et al. 2018) and where biodiversity is at relatively low risk, so we classify these PA boundaries as 'soft' (Beyer et al. 2020). Areas with HF>4 but <7 are where land can be considered human-dominated, with biodiversity and ecosystem function threatened by habitat conversion and other anthropogenic impacts, and where conservation intervention is needed to prevent increasing extinction risk (Di Marco et al. 2018). Such PA boundaries present a 'firm' barrier to wildlife.

We broke down each PA boundary into 5km segments with an external width of 5km and calculated the mean HF in each segment (N=10,319 segments; 51,033 km in length).

Expected boundary hardness

We compared the HF value of each PA boundary segment with average annual rainfall (www.bioclim.org) using a Generalised Additive Model (GAM) and then used the residuals to identify boundaries that were harder or softer than expected from the potential for rain-fed agriculture in the region.

Buffer areas

We analysed contiguous intact habitat around PAs using the HF thresholds defined above, up to distances of 10, 20, and 40km outwards from the PA boundary. This spatial scale is based, first, on the finding of Veldhuis et al. (2019) that human activity outside the Serengeti-Mara PA system has reduced the abundance of multiple large herbivore species for >20 km inside the PA, and so an effective buffer would need to extend for >20 km *outside* the PA. Second, for a buffer area to support a resident population of the largest wildlife species, it would need to be at least as wide as the diameter of the home range of a savanna-elephant breeding group, which averages ~40 km (van Aarde, et al. 2008). We considered patches of intact habitat within 3km of each other as contiguous. This was primarily to reduce the effect of roads, for which HF=8, since many wildlife species can move across them unimpeded. Within each buffer distance around each PA boundary, we calculated the proportion of area comprised of contiguous habitat that was not in the 'hard' category. We then calculated the overlap of buffer areas with non-government PAs and with different biomes (S3).

Results

Boundary hardness

The mean human footprint within 5 km of a PA boundary in eastern and southern Africa was HF=6.36 (Figs. 1 & 2, S1), which is characteristic of human-dominated landscapes. There was a wide range in the hardness of boundary segments (5km segments with an external width of 5km) from HF=0 to HF=39.2 and, concerningly, 38% (length = 19,392.5km) of segments were hard (HF>7), being under intense human land-use pressure.

Predictably, we found that the 45.2% of all boundaries that were harder than expected from average annual rainfall were mostly in areas receiving 500-1000 mm annual rainfall (Fig. 2), thus being areas with high agricultural potential.

We found that nearly half (48.2%, n=79, S1&S2) of all individual PAs analysed had, on average, hard boundaries, indicated by a mean HF>7 within 5km of their border. In comparison, 40.2% (n=66) had firm boundaries (mean boundary HF of 4-7). Only 11.6% (n=19) of PAs had soft boundaries (mean boundary HF of 1-4), and none had entire boundaries that were, on average, open (mean boundary HF<1). Khutse-Central Kalahari, Botswana has the softest boundaries of all PAs (mean boundary HF = 1.5). In contrast, PAs with the hardest boundaries occurred adjacent to major cities or urban areas, including Table Mountain National Park, South Africa (mean HF = 30.0), and Nairobi National Park, Kenya (mean HF = 25.9).

Intactness of buffer areas

Almost half of all potential buffer areas were intact and thus available to wildlife in ‘firm’ or softer condition at 10km, 20km and 40km buffer distances from a PA boundary (46.4%, 47.7%, 47.3% respectively). Less than 20% of buffer areas were either ‘soft’ or ‘open’ (19.1%, 19.1%, 17.3%), and less than 3% were ‘open’ (2.7%, 2.2%, 1.5%;). Only 30 PAs (18.2%) had any intact buffer in the ‘open’ class, 97 (59.1%) had ‘soft’, and 152 (92.7%) had ‘firm’, whereas 12 (7.3%) had no buffer at all. Only half (n= 83) of the PAs had at least half of their boundary adjacent to a 40 km deep buffer area that was intact, i.e. ‘firm’ or softer for wildlife (Fig. 3&4, S4).

Despite the substantial human pressure around African PAs, it is important to note that at the 40km buffer distance, 1,246,308km^2 of buffer area was not ‘hard’ (HF<7), which represents 14.8% of the eastern and southern Africa’s land area and is 156% of the area (796,393 km^2) covered by PAs in that region. The Skeleton Coast set of parks (Namibia and South Africa) had by far the most extensive intact buffer area that is not hard at 78,343 km^2,

followed by Khutse-Central Kalahari (Botswana) at 43,473 km^2 and those around the Mikumi-Selous PAs (Tanzania) at 39,323 km^2.

Discussion

We have presented the first quantification of the boundary hardness of eastern and southern Africa's PA network and the availability of contiguous, intact buffer areas beyond PA boundaries. Our findings demonstrate that at least 38% of these PA boundaries are effectively 'hard' due to external human pressure (HF>7), and we have identified the boundaries that are harder or softer than expected based on the relationship between human pressure and average annual rainfall (Fig. 3). Our results support the concern that African savanna PAs are becoming increasingly isolated within a surrounding matrix of wildlife-incompatible land use. Hardening boundaries also have internal implications by squeezing wildlife deeper into PAs, which could negatively impact biodiversity, ecosystem functioning, and conservation action (Western & Gichohi 1993; Veldhuis et al. 2019). Hard boundaries further constrain the adaptive capacity of social-ecological systems to respond to external stressors such as climate change (du Toit et al. 2004).

Hard boundaries may need fencing

By identifying hard boundaries, our analysis highlights places where human-wildlife conflict and other threats are likely to be most pronounced (Buchholtz et al. 2020). Examples include the western boundary of Kruger National Park, south-eastern Hwange National Park, and western Serengeti National Park (Fig 2). There have been widespread calls for increased fencing of eastern and southern African PAs to mitigate human-wildlife conflict along hard PA boundaries (Packer et al. 2013), and it is likely that many of the hard boundaries revealed by our analysis, totalling >19,000km, are already fenced or will be soon. Fencing has faced criticism due to its potentially negative socio-economic and ecological impacts (Durant et al. 2015). Nevertheless, where dispersal routes of wildlife in and out of PAs are already severed, and the costs of human-wildlife conflict are high, strategic fencing can represent a useful last option. In southern Kenya, for example, fencing has maintained a narrow (100m wide) corridor through agricultural land to allow large mammals to move between Amboseli National Park and the nearby Chuylu and Tsavo PAs[1]. To ensure the long-term ecological integrity of these PAs, fencing is becoming increasingly common along sections of hard boundary but is expensive to erect and maintain and requires landscape-scale planning to protect the resilience of the wider social-ecological system.

[1] https://www.facebook.com/biglifefoundation/photos/a.178446792167011/2327506017261067/?type=3&theater

Ecological consequences of increasing isolation

Worryingly, we found that only half of the potential buffer areas around PAs were not hard, and very few buffer areas were open to wildlife with negligible human pressures (Fig. 5), reflecting the reality of shrinking wildlands on the African continent. The continued loss of buffer areas disproportionately affects wide-ranging species such as large herbivores and their predators by denying them access to seasonally required forage resources beyond PA boundaries, thereby reducing the productivity, resilience, and diversity of wildlife assemblages (Owen-Smith 2005; Fynn et al. 2014). , Many wildlife migration routes between seasonal foraging areas have already been severed or altered across eastern and southern Africa, including the Maasai Mara (Kenya), Karoo (South Africa), Nairobi (Kenya), Kruger (South Africa), and Tarangire (Tanzania) (Harris et al. 2009), as indicated by our analysis (Fig. 3 &4).

Crafting conservation solutions in buffer areas

The continued fragmentation of buffer areas will increase the difficulty of implementing the landscape-scale conservation initiatives. However, despite widespread human pressures, our results demonstrate there is still considerable scope for conservation within landscapes around current PAs, with half of all PAs having buffers that are >50% intact (Fig 3,4&5). Importantly, our analysis showed that intact buffer areas extending 40km from PA boundaries cover an additional 14.8% of land across eastern and southern Africa. These buffers represent important areas adjacent to PAs where the development of community-based conservation programs could alleviate ecological and social pressures on the PAs themselves. It is also often more practical, politically feasible, and faster to extend conservation efforts to cover some of these intact areas than to set up separate new protected areas (Pringle 2017). At present less than 30% of these buffer areas are under some form of protection. Strategically investing in these areas through community-based conservation and other effective area-based conservation measures would contribute to meeting the Aichi Targets by increasing both the effective PA area, ecological functionality, and keeping PAs "*integrated into the wider landscape".*

Some African governments have recognised the problem of PA isolation and are responding. Kenya, for example, has developed a "Dispersal Areas and Corridors Report" to identify areas critical for conservation outside PAs and is in the process of integrating them into government land-use planning. The key to the success of such initiatives is the generation of sufficient economic returns for landowners and the government to offset the opportunity costs of maintaining land for conservation. This requires appropriate rights and responsibilities to devolve to a local level to incentivise revenue-generating activities that are

compatible with wildlife conservation. These could include ecotourism, consumptive use of wildlife, payments for ecosystem system services, and conservation philanthropy, among others (Lindsey et al. 2020). Integrating wildlife conservation with livestock production is an integral component of this process since 95% of PA buffer areas in eastern and southern Africa fall within grassland and savanna biomes, where pastoralism is socially and economically essential to local communities (S3). The COVID-19 crisis highlights the insecurity of conservation funding from its primary source, international tourism, and stresses the need for multiple synergistic programs to increase PAs' economic and societal values to local populations.

Limitations

We recognise several caveats in our analysis. First, the Human Footprint (HF) is a globally derived layer not specifically designed to address the conservation of large mammals, and the thresholds we used are unavoidably crude. However, our calibrations with a local database, and the combined evidence of a close link between HF and the mobility and survival of large mammals, support our method. Our analysis is only as good as the HF and PA data, which are both the best available, yet updates will improve further analyses. We could not quantify the effect of fences on creating hard boundaries or limiting access to buffer areas because even reasonably accurate mapping of current fences is not available for the African continent. We also do not argue that areas with HF>7 serve no purpose for biodiversity conservation. Even though the potential for conserving large wild mammals in these transformed landscapes is minimal, many other native species still survive there and need policy and practice to support their conservation (Tyrrell et al. 2020). Finally, in addition to the human footprint, the distribution of biodiversity, functional resources, socio-economic factors, and the cost of conservation action should all be considered when prioritising local conservation efforts in the buffer zones around PAs (Western & Gichohi 1993; Naidoo et al. 2006).

Conclusions

As nations discuss post-2020 biodiversity targets, we can expect calls for effective conservation to extend over a significantly larger percentage of Earth’s terrestrial surface. However, it is increasingly difficult for countries to maintain connectivity across their existing PA networks or integrate PAs into landscape-scale conservation projects in the surrounding matrix, let alone proclaim new or expanded PAs. This is particularly true of countries in sub-Saharan Africa, where biodiversity conservation is under rapidly increasing socio-economic pressure (Tilman et al. 2017; Newbold 2018), and where the existing PA network is chronically underfunded (Lindsey et al. 2018). Our analysis, focusing on the landscape

integration element of Aichi Target 11, reveals that more than one-third of the summed edge-distance around these PAs is already a hard boundary. It may prove that to fulfil Aichi Target 11 entirely is too lofty a goal, as few terrestrial PAs can be considered "*integrated into the wider landscape".* This scenario is only likely to worsen while conservation in sub-Saharan Africa remains underfunded.

Nevertheless, we draw attention to the half of the PA boundaries that are not yet hard and to the remaining intact buffer areas extending for at least 40km beyond them, which represent almost 15% of the land area of southern and eastern Africa. We urge African governments and international development agencies to prioritise these areas for policy reforms and economic incentives to alter their current trajectories of change. There is still a window of opportunity to facilitate the social and ecological functioning of PAs by improving both rural livelihoods and wildlife conservation through frameworks that build resilient, community-driven social-ecological systems (Western et al. 2020).

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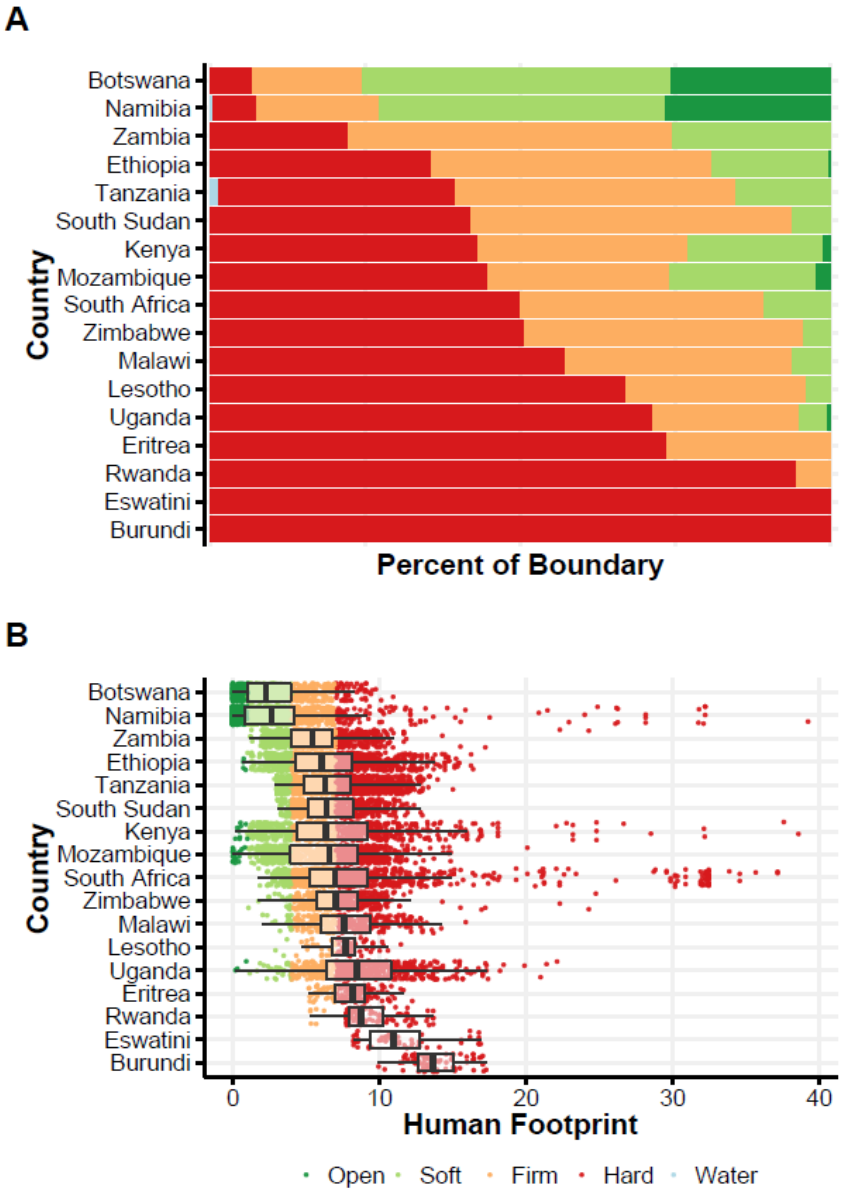

*Fig. 1 – A) The percent of protected area boundaries falling into each hardness category by country. 'Open' (dark green) boundaries have a mean human footprint (HF) scores of 0-1, 'soft' (light green) have scores of 1-4, 'firm' (orange) have scores of 4-7, and 'hard' (red) have scores >7. Several PAs share boundaries with water bodies. Both Burundi and Eswatini (formerly Swaziland) had 100% of boundaries falling in the 'hard' range (HF>7). Over half of the PA boundaries in Uganda, Rwanda, Eritrea, Malawi, Zimbabwe, and Lesotho had hard boundaries. Conversely, Botswana and Namibia had the highest percentage of 'open' PA boundary segments (mean boundary HF<1), with 25.6% and 26.7%, respectively. B) The distribution of boundary segment HF values for each country, including a boxplot of the distribution showing median value, first and third quartile. The upper whisker extends from the hinge to the largest value no further than 1.5 * IQR from the third quartile, where IQR is the inter-quartile range, or distance between the first and third quartiles. The lower whisker extends from the lower quantile to the smallest value at most 1.5 * IQR.*

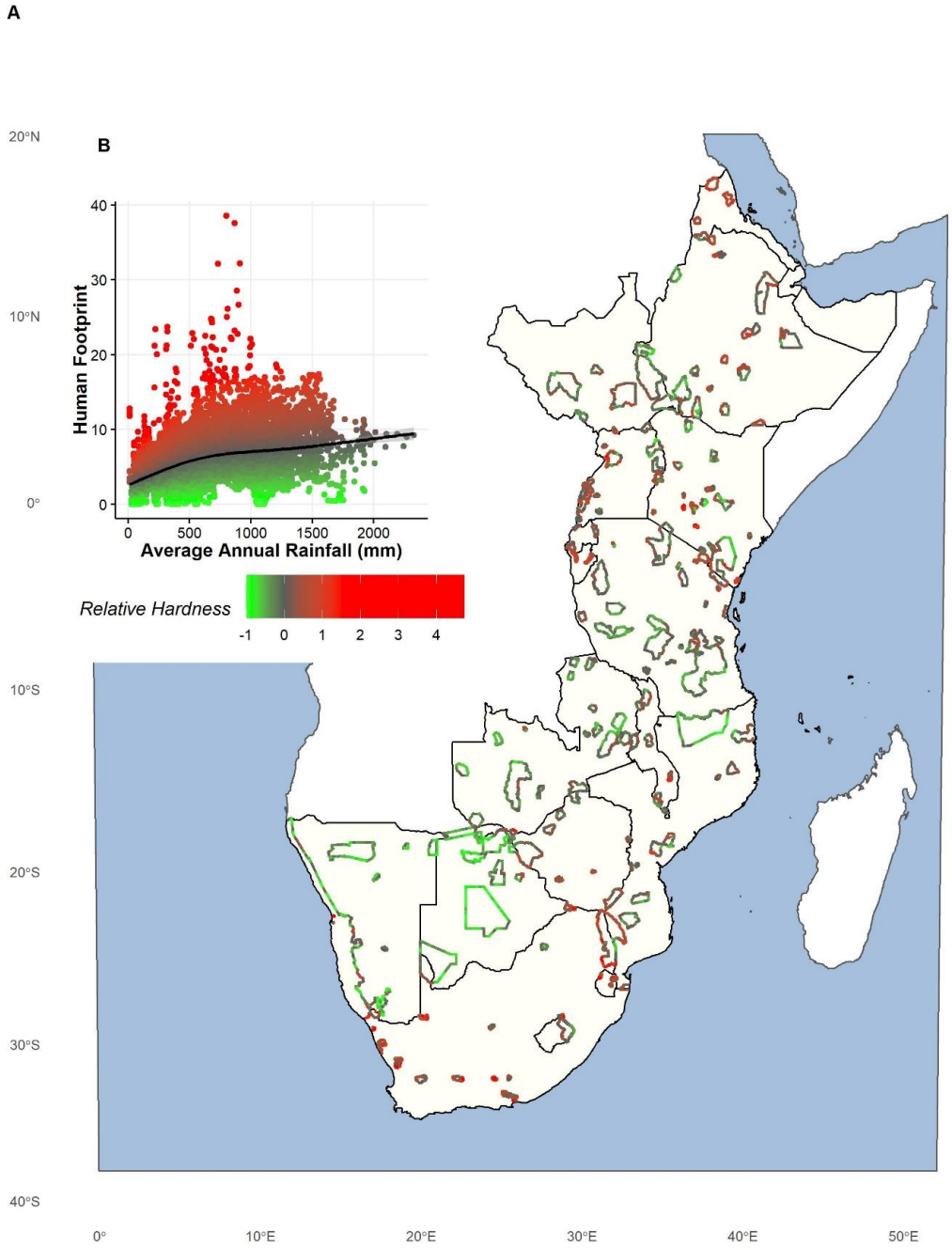

Fig. 2 – (A) Relative boundary hardness of eastern and southern Africa's protected areas. The inset (B) compares average annual rainfall with boundary hardness (the mean of the human footprint) in the 5km long and 5km wide boundary segments. The boundaries and the inset are colored to indicate boundaries that are harder (brighter red) or softer (brighter green) than expected compared to the generalised additive model fit to average annual rainfall and the human footprint.

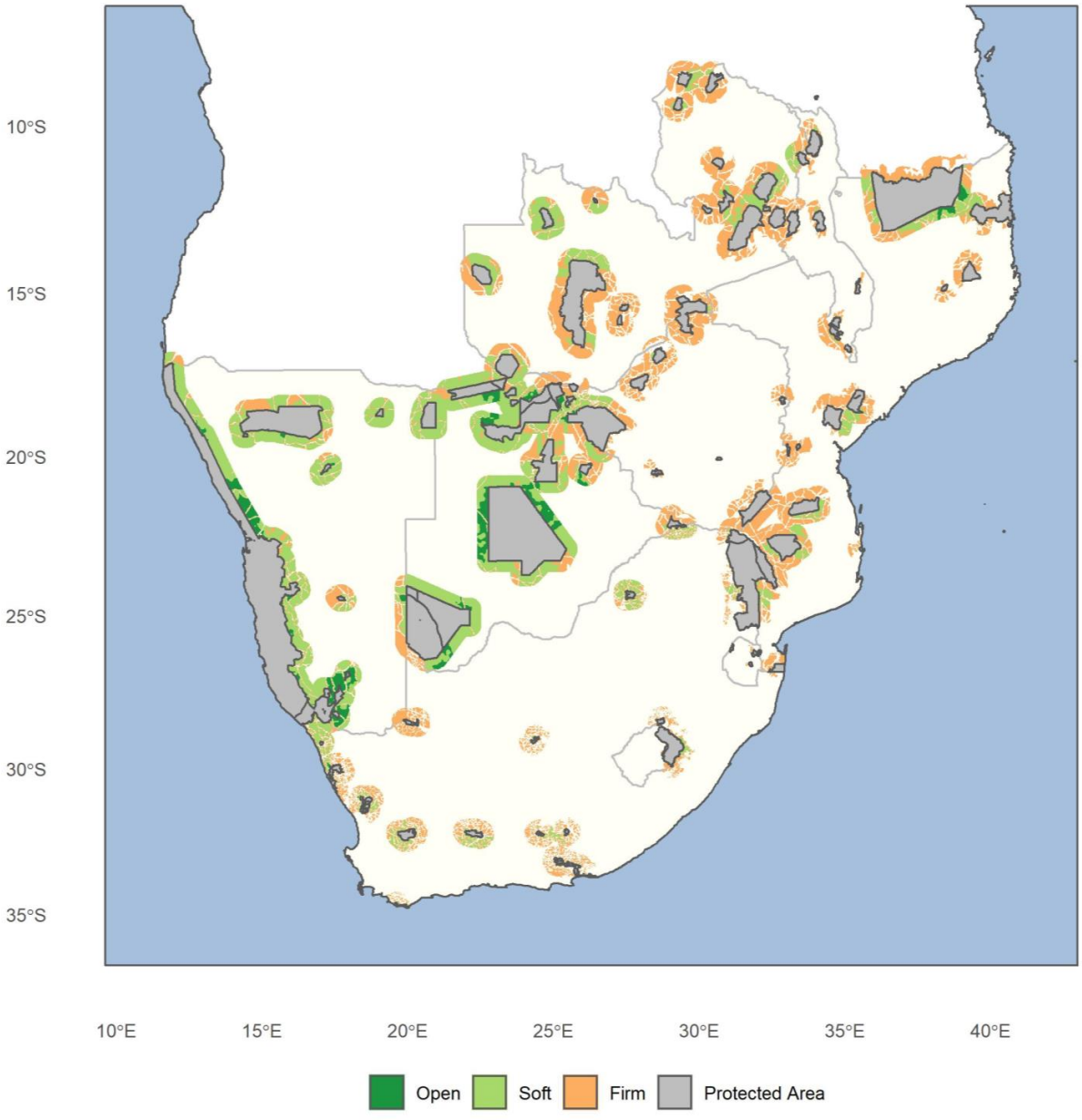

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Fig. 3 - The intact buffer areas around southern African PAs, from the analysis for the three different categories of Human Footprint: HF<1 is classified as "Open", HF 1-4 is "Soft", and HF 4-7 is "Firm". The buffer width shown here is 40km.

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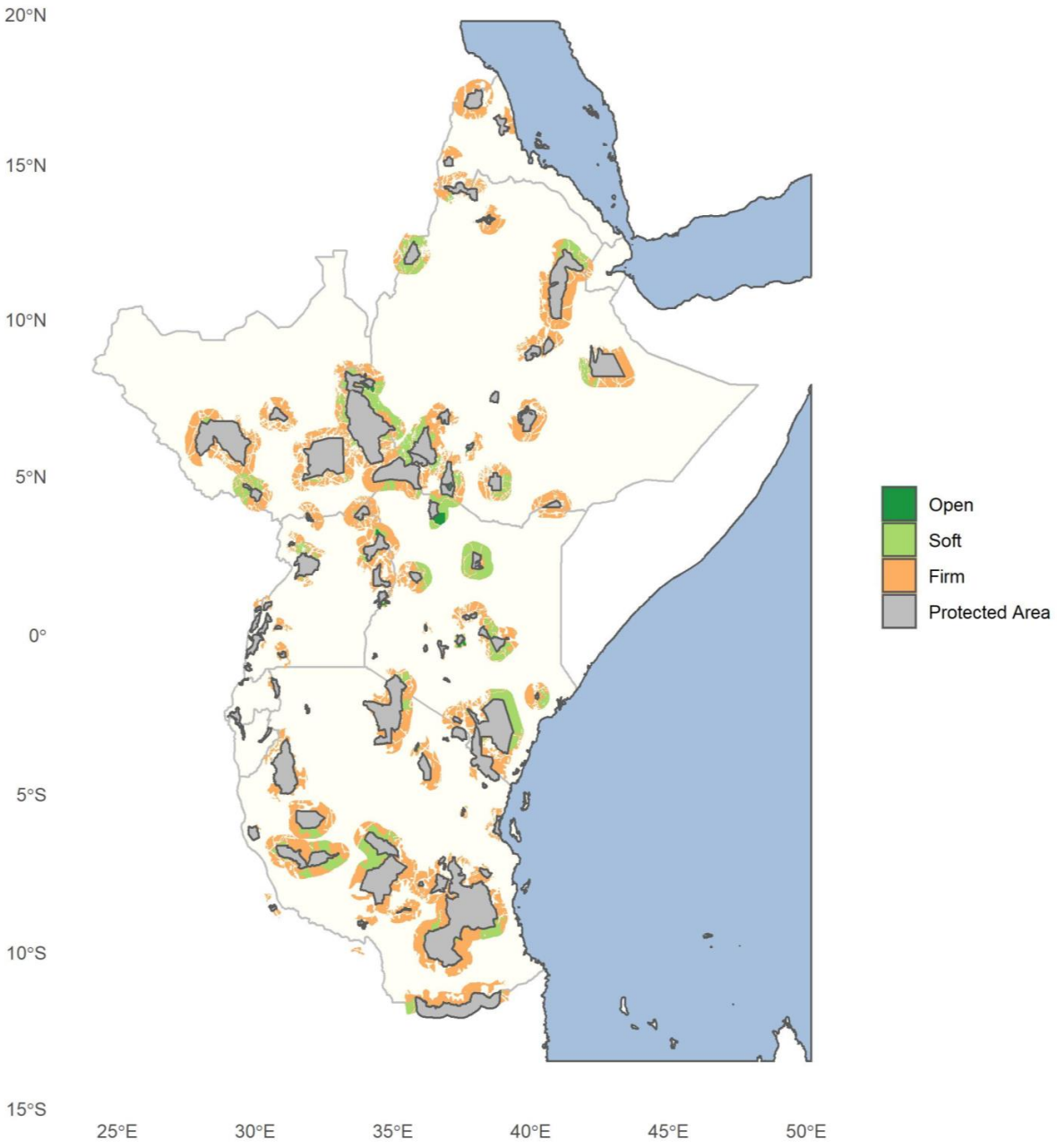

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Fig. 4 - The intact buffer areas around eastern African PAs, from the analysis for the three different categories of Human Footprint: HF<1 is classified as "Open", HF 1-4 is "Soft", and HF 4-7 is "Firm". The buffer width shown here is 40km.

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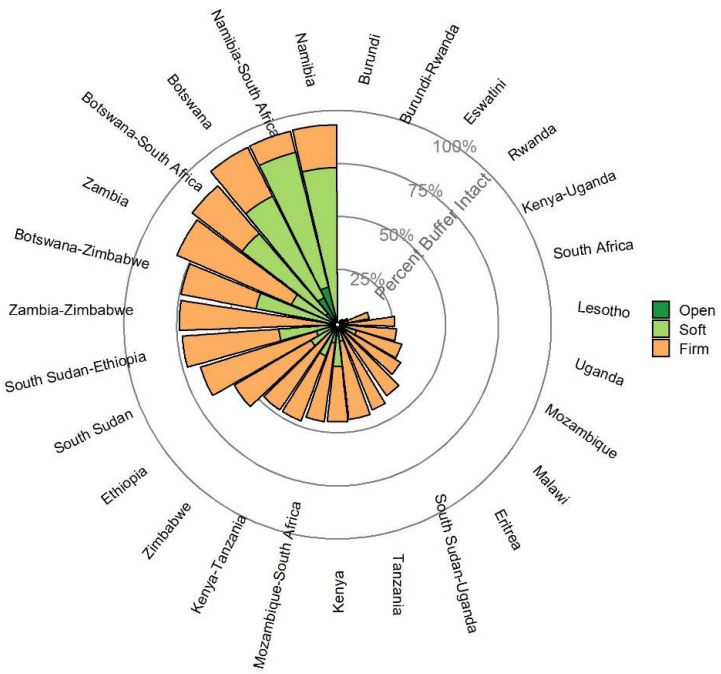
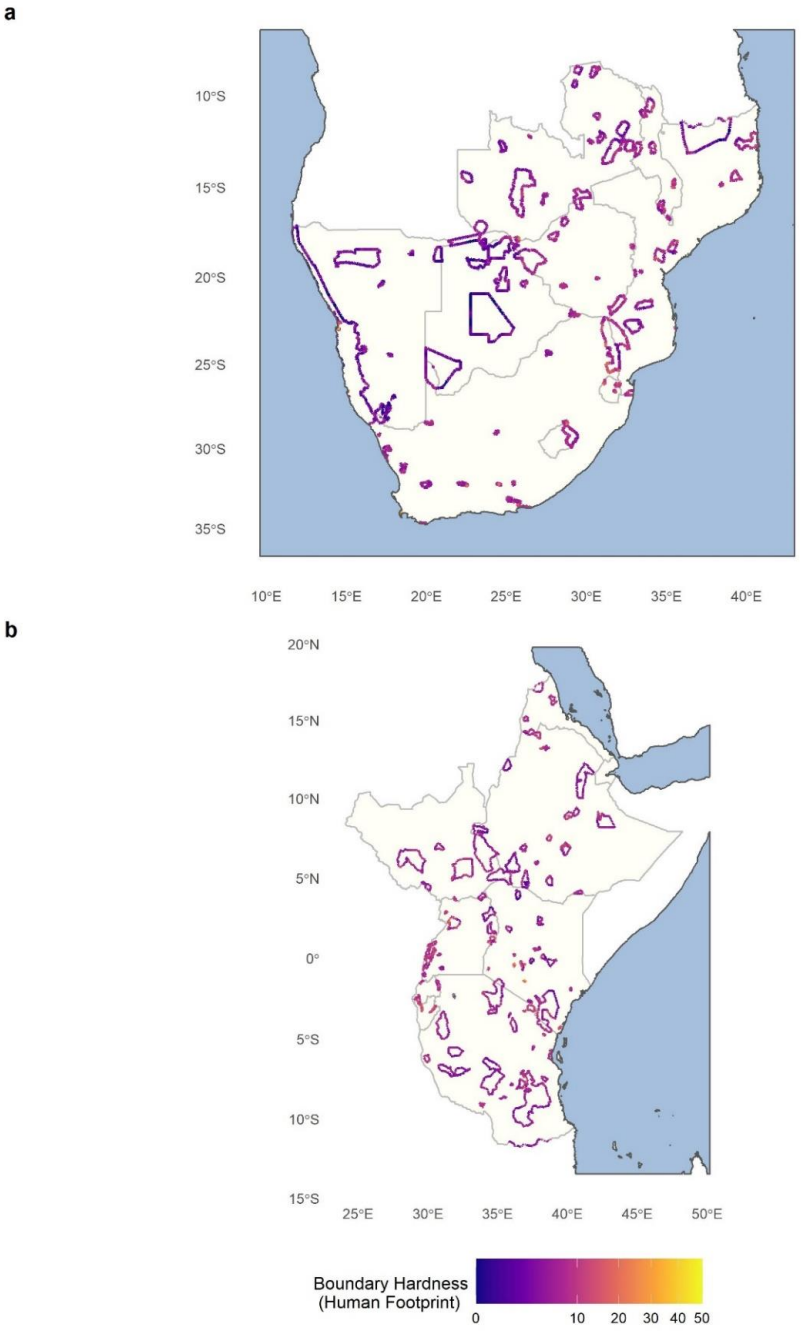


Fig. 5 - Coxcomb plot of the total percentage intactness of protected area buffers in each region and for the 40km buffer width. Some buffers are part of cross-border conservation areas, and the country names are amalgamated together. The percentage intactness - as calculated using the Human Footprint (HF) - of the generated buffer, relative to its theoretical size, is given for the three thresholds: 'Open'' <1 HF; 'Soft' <4; and 'Firm' <7. The width of each regions bar is proportional to the total size of the buffer area. Coxcomb plots for the other two widths show similar results and are provided in S8. Buffer areas around PAs in Namibia and Botswana, and the Namibian-South African cross border areas, were all >90% intact at all three buffer distances). Zimbabwe and Botswana-Zimbabwe PAs had buffers >75% intact at all three distances. South Sudan and the South Sudan-Ethiopia border fared best in eastern Africa, with >65% of buffer areas intact. Less than ten regions had 'open' buffers that were >1% intact, and only two regions had >10% of their buffers both intact and 'open' for wildlife movement. The Burundi-Rwanda region had no intact buffers of any width.

Supplementary Materials

S1 – Unadjusted Protected area (PA) boundary hardness for a) Southern Africa and b) East Africa. Boundary hardness is calculated as the mean Human Footprint score for 5x5 km buffer segments along the periphery of each PA. A square root transformation is used to adjust the scale.

S2 – Table of Protected area (PA) boundary hardness for each PA. Calculated as the mean Human Footprint score for 5x5 km buffer segments along the periphery of each PA.



PA Name	Mean Boundary HF Score	Median Boundary HF
Khutse-Central Kalahari	1.50	1.00
Naute Recreation Resort	1.70	0.78
Khaudum	2.10	1.95
Nkasa Rupara	2.18	1.95
Bwabwata	2.91	2.79
Sibiloi	2.99	2.81
Gemsbok-Kalahari Gemsbok National Park	3.02	2.97
Etosha	3.07	3.20
Rubondo Island National Park	3.12	3.12
West Lunga	3.16	3.14
North Luangwa	3.17	3.13
Mudumu	3.17	3.08
Waterberg Plateau Park	3.25	3.92
Tsau // Khaeb (Sperrgebiet)-Namib-Naukluft-Ai-Ais Hot Springs-Skeleton Coast Park-Dorob-Richtersveld National Park	3.36	2.38
Kasane-Chobe-Kasane Extension-Maikaelelo-Moremi	3.37	2.42
Hardap Recreation Resort	3.69	3.78
Mangetti	3.83	3.89
Nxai Pan-Makgadikgadi Pans	3.90	3.81
Alatish	3.90	3.77
Liuwa Plain	4.03	2.95
Niassa	4.12	3.78
Kazuma-Kazuma Pan	4.16	4.13
Lusenga Plain	4.19	3.63
Mt. Kenya	4.36	3.45
Tama-Omo-Mago	4.43	4.13
Katavi National Park-Rungwa River G.C.A.	4.59	4.58
Marakele National Park	4.60	4.30
Banhine	4.71	4.88
Bokora Corridor-Matheniko	4.86	4.78
Chelbi	4.89	4.36
Mweru-Wantipa	5.01	4.73
Ruaha National Park-Kizigo G.R. (C)	5.05	5.02
Tankwa-Karoo National Park	5.10	5.23
Lavushi Manda	5.12	4.77
Ugalla G.R. (N)	5.12	4.90
Gewane-Mille-Sardo-Yangudi Rassa	5.18	5.17
Zinave	5.42	5.77
Sioma Ngwezi	5.46	5.45

Kafue	5.52	5.31
Marsabit	5.56	4.83
Lantoto	5.57	5.53
Kora-Meru	5.61	5.15
Loelle	5.68	5.23
Lake Mburo	5.78	5.81
Luambe	5.80	5.83
Knersvlakte Nature Reserve	5.81	5.19
South Luangwa	5.84	5.68
Boma-Boma Extension-Gambella	5.85	5.91
Kisinga Lugaro	5.88	5.60
Lochinvar	5.92	6.19
Namaqua National Park	6.00	6.13
Nata	6.04	6.26
North East Undendeule-Mikumi National Park-Selous G.R	6.05	5.99
Blue Lagoon	6.07	6.19
Sibuyu-Hwange	6.11	6.37
Amboseli	6.24	6.39
Matusadona	6.24	5.93
South Turkana	6.27	7.11
Alledeghi	6.35	6.11
Nsumbu	6.38	5.77
Lower Zambezi-Mana Pools	6.39	6.14
Kasanka	6.44	6.06
Richtersveld National Park	6.49	6.40
Lukusuzi	6.50	6.06
Chimanimani	6.50	6.34
Mokala National Park	6.55	6.90
Vwaza Marsh Wildlife Reserve	6.58	5.97
Ts'ehlanyane	6.61	7.00
Mufindi Scarp	6.62	6.74
Pian Upe	6.63	6.24
Moribane	6.63	6.76
Selous G.R	6.66	6.75
Southern	6.72	6.44
Isangano	6.74	6.19
Shaba	6.76	6.56
Yob	6.76	6.58
Shambe	6.76	6.39
Moyowosi G.R (N)	6.77	6.68
Lake Manyara National Park	6.78	7.24
Kidepo Valley	6.78	6.28
Chyulu Hills-Tsavo East-Tsavo West-Mkomazi National Park	6.79	6.98

Babile Elephant	6.80	6.38
Tana River Primate	6.90	6.41
Masai Mara-Serengeti National Park-Maswa G.R. (N)-Maswa Kimali	6.92	6.49
Yabello	6.95	7.52
Mwabvi Wildlife Reserve	7.05	6.80
Nechisar	7.07	7.25
Agulhas National Park	7.22	6.65
Malka Mari	7.22	7.63
Chebera Churchura	7.23	6.73
Tarangire National Park	7.25	7.06
Lengwe National Park	7.29	7.36
Coutada Oficial N0. 12	7.35	7.58
Kasungu National Park	7.39	7.11
Nyika National Park	7.40	7.62
Gonarezhou	7.40	7.31
Nkhotakota Wildlife Reserve	7.46	6.58
Nguru North	7.49	6.89
Chizarira	7.53	7.93
Karoo National Park	7.55	5.83
Ukwiva	7.57	7.93
Majete Wildlife Reserve	7.63	6.94
Augrabies Falls National Park	7.63	7.86
Mountain Zebra National Park	7.68	7.72
Bwindi Impenetrable	7.70	7.69
MupaluÃƒ?Ã‚Â©	7.72	7.69
Northern Tuli-Mapungupwe National Park	7.90	7.55
Gorongosa	8.00	7.47
Unnamed Bird Sanctuary	8.01	7.21
Katonga	8.05	8.39
Nyaganje-Udzungwa Mountains National Park	8.07	7.85
Badingilo-Badingilo Extension	8.08	8.28
Quirimbas	8.13	8.55
Bale-Bale Mountains	8.19	7.33
Akagera	8.23	8.39
Mecuburi	8.33	8.45
Gash-Setit	8.41	8.43
Shire-Kafta-Shiraro	8.48	8.51
Addo-Elephant National Park	8.50	8.02
Rwenzori Mountains	8.57	8.14
Matopos	8.62	8.90
Volcans	8.62	8.53
Mahale Mts.National Park	8.65	8.87
Nakfa	8.71	8.71

Nyanga	8.76	8.72
Simien Mountains	8.80	7.77
Mushandike	8.82	8.57
Zona de Vigilancia da REM	8.87	9.14
Kitulo Plateau National Park	8.88	8.79
Saadani National Park	8.89	8.96
Limpopo-Pafuri Nature Reserve-Kruger National Park	8.90	8.46
Pomene	8.96	8.52
Buffalo Springs-Samburu	9.13	9.15
Semuliki	9.23	9.84
Toro-Semuliki or Toro-Semliki	9.56	9.74
Nimule-Otze Forest White Rhino	9.58	9.77
Lake Bogoria	9.93	9.87
Aberdare	9.98	10.46
Mkhaya Game Reserve	10.02	8.52
Mt. Elgon-Mount Elgon	10.06	10.12
Ajai	10.10	9.83
Kigezi-Kyambura-Kibale-Queen Elizabeth	10.13	10.29
Camdeboo National Park-Karoo Nature Reserve	10.14	9.47
Awash West-Awash	10.15	9.45
Shume Magamba	10.55	10.43
Liwonde National Park	10.69	10.96
Golden Gate Highlands National Park	10.79	8.86
Abijatta-Shalla	10.93	11.15
Murchison Falls-Bugungu-Karuma	10.98	11.88
Arusha National Park	11.06	11.57
Hlane Royal National Park-Mlawula Nature Reserve	11.19	10.42
Pala Mountains	11.47	11.70
Kilimanjaro National Park	11.69	11.52
Ruma	11.76	11.53
Nyungwe	11.91	11.91
Kibira-Nyungwe	12.49	13.04
Parc national du Ruvubu	12.91	12.81
Malalotja Nature Reserve	13.06	12.68
Zambezi	13.12	9.83
Kibira	13.98	13.92
Shimba Hills	14.71	14.60
Lake Nakuru	18.50	18.09
Nairobi	25.94	24.81
Table Mountain National Park	30.02	32.02

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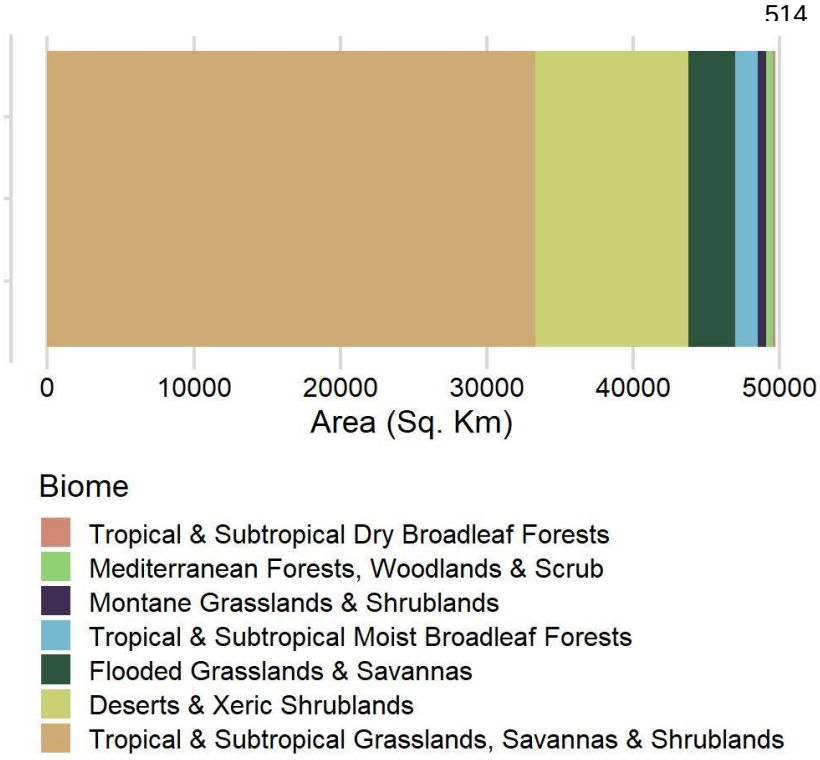

S3. The area of each biome encompassed in the 40km buffer which are "firm" or softer. (Dinerstein et al., 2017)

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S5 – Additional Methods

All analyses were conducted using R version 3.5.1 and several packages, including *raster, spdep, rnaturalearth, sf, exactextractr, fasterize,,* and *rgeos* (1–7).

Protected areas

Protected Areas (PAs) were cleaned to remove topological errors in the polygons, and PAs within 500m of each other were aggregated into a single PA polygon. The PA boundaries were simplified by using the Douglas-Peuker algorithm with a tolerance of 500m to remove excessive wiggliness (such as along rivers or other boundary features). Because of the cross-border nature of many PA complexes, the results are sometimes labelled with multiple countries.

Expected boundary hardness

We expected PA boundary hardness to increase with annual rainfall up to an asymptote at ~1000 mm, after which productivity in African savannas is more limited by soil nutrients than soil moisture(8). We, therefore, compared the HF value of each PA boundary segment with average annual rainfall (www.bioclim.org) using a Generalised Additive Model (GAM) to identify boundaries that were harder or softer than expected from the potential for rain-fed agriculture in the region.We used the package *mgcv* to fit a GAM with thin plate regression splines and a maximum basis size of five, which was fit using restricted maximum likelihood (9). We then calculate a relative hardness index for each segment using the ratio of the actual data to the predicted fit from the GAM. We excluded all PA boundary segments within five kilometres of ocean coastlines where they often abut to coastal cities.

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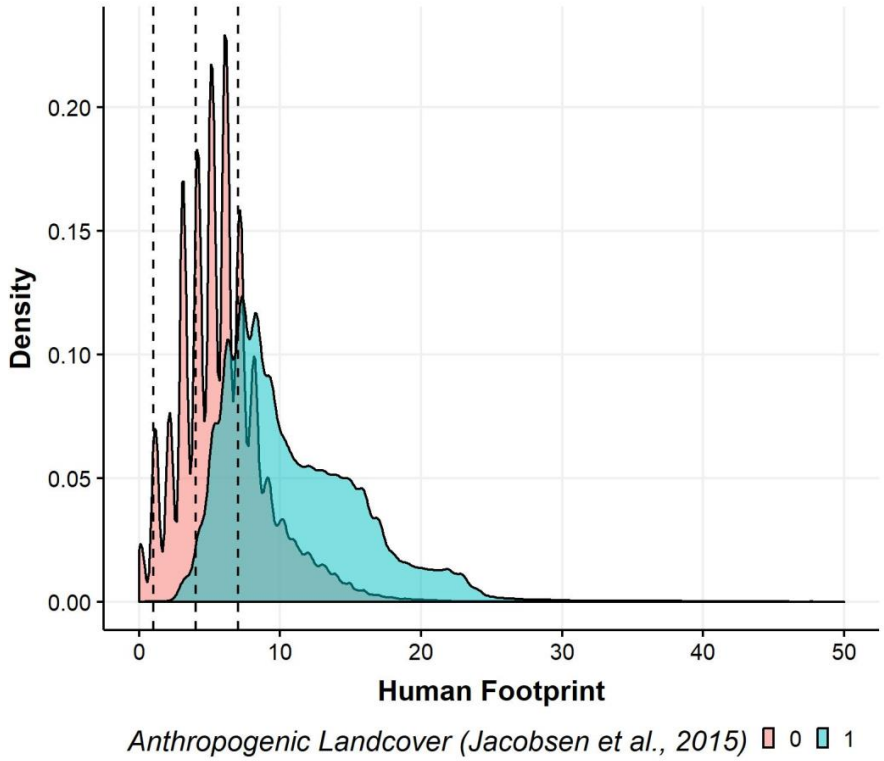

S6. A kernel density plot of the Human Footprint score for Eastern Africa (1x1km resolution), with the density fill colour determined by the landcover classification of Jacobsen et al., 2015, where 0 represents less than 50% human landcover in a 1x1km grid over a Google Earth image, and 1 represents greater than 50% human landcover. The vertical dashed lines represent the three thresholds used for the generation of the buffer intactness index, with values between 0-1 classified as 'open', 1-4 classified as 'soft', 4-7 classified as 'firm' and values greater than 7 as 'hard'.

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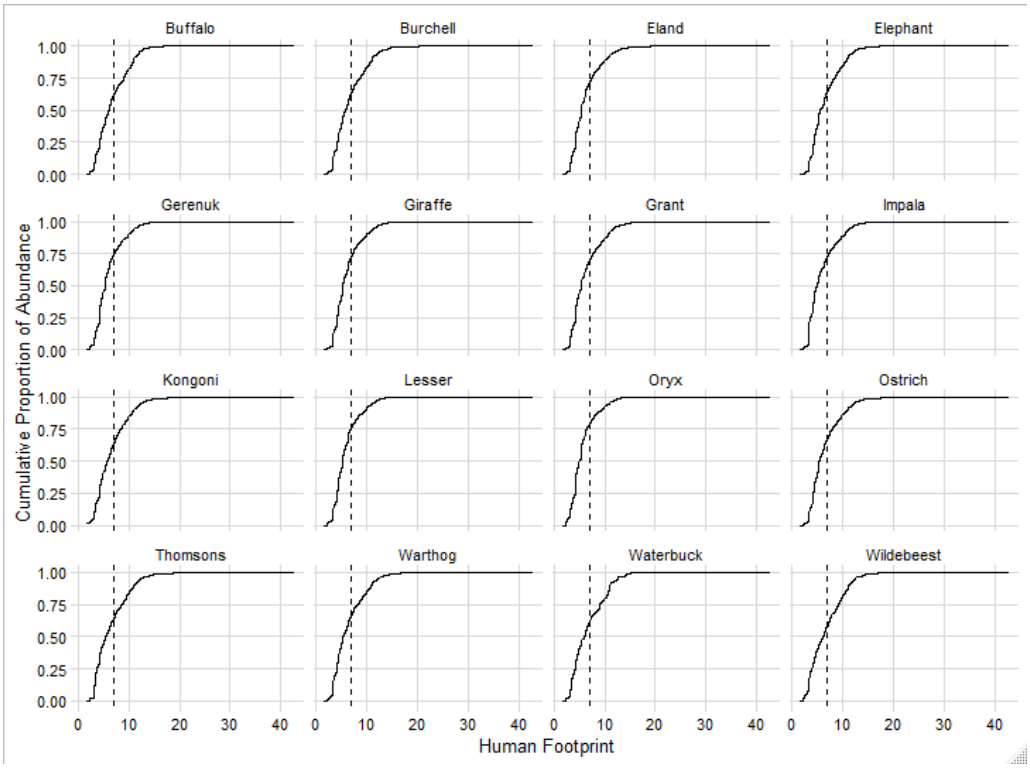
Jacobson, Andrew, Jasjeet Dhanota, Jessie Godfrey, Hannah Jacobson, Zoe Rossman, Andrew Stanish, Hannah Walker, and Jason Riggio. "A novel approach to mapping land conversion using Google Earth with an application to East Africa." Environmental Modelling *& Software* 72 (2015): 1-9.



S7, we compared the relationship between cumulative population abundance and HF for 16 species of large herbivore across southern Kenya, ranging in size from elephant to gazelle. The data is from Ogutu et al., 2016, and has been modelled using a spatially and temporally explicit framework to cover a 2x2km region across southern Kenya. The data is from the 2000s decade (Chapter 8). We found that the majority of wildlife exists in areas scoring up to HF=7 (mean cumulative abundance = 67%; range 58% – 79%) with only remnant populations persisting at higher HF (e.g. for HF>10, mean cumulative abundance = 15%; range 0.08%-20%). Wildlife populations occurring in areas of HF>7 are close to roads, other infrastructural development and agriculture, where they are generally declining in abundance (Ogutu et al. 2016).

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The art of land doctoring is being practiced with vigor, but the science of land health is yet to be born.

— Aldo Leopold: A Sand County Almanac.

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Conservation from the inside-out: Winning space and a place for wildlife in working landscapes

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Conservation from the inside-out: Winning space and a place for wildlife in working landscapes

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Abstract

1. Protected areas fall far short of securing the space needed to sustain biodiversity and ecosystem function at a global scale and in the face of climate change.
2. The prospects of conserving biodiversity in working landscapes help buffer the insularization effects of protected areas and hold great potential for biodiversity conservation on a landscape scale but depend on finding adequate space and a meaningful place in the lives of rural land users.
3. Using a case study in southern Kenya, we show that the conservation of large open landscapes, biodiversity and the coexistence between wildlife and livestock can be achieved indirectly by reinforcing pastoral practices that depend on open space, mobility, social networks and institutional arrangements governing common-pool resources.
4. Pastoral practices and wildlife both depend on large multiscale interactions within interlinked social and ecological systems, which are threatened by land fragmentation, alienation and degradation.
5. We show that large open spaces can be maintained by using a conservation approach starting from within community aspirations that emphasize the links between livelihoods, productivity, efficiency and resilience in pastoral economies and the secondary benefits of wildlife enterprises.
6. Scaling up from an ecosystem to multi-scale approach benefits pastoral communities by building resilience and new economic opportunities. In the process, the expanded scale conserves regional biodiversity and large free-ranging herbivore and carnivore populations underpinning ecosystem function and the nationally important tourism industry centered on the Kenya–Tanzania boundary.
7. The 'inside-out' approach to the conservation of wildlife and biodiversity is place-based, draws on local knowledge and informal governance arrangements and avoids the stigma of wildlife conservation driven by outside agencies.

The art of land doctoring is being practiced with vigor, but the science of land health is yet to be born. Aldo Leopold: A Sand County Almanac.

We protected wildlife from hunters and wildlife protected us from drought. Coexistence is the essence of survival for us both. Maasai elder noting why traditional livestock practices conserve wildlife.

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8. The human-centered approach reinforces land health and spatial connectivity and encourages multi-level and distributed governance arrangements embedded in large regional and national jurisdictions.

KEYWORDS
coexistence, community-based conservation, conservation governance, landscape conservation, natural resource management, pastoralism, wildlife, working landscapes

1 | THE EVOLUTION OF CONSERVATION

The scope of conservation has expanded continuously in the modern era, from natural resource management in the 18th century, to regulated hunting and protected area set-asides in the 19th century, and the conservation of species, biotic communities, ecosystems and biodiversity in the 20th century (Watson, Dudley, Segan, & Hockings, 2014). The expanded scope reflects changing human sensibilities, views and uses of nature (Nash, 1989; Thomas, 1983) and, more recently, the aspirations of modern states and the international community (Adams, 2005; Sitarz, 1993; United Nations, 1992; Watson et al., 2014; Western & Pearl, 1989; Western, Waithaka, & Kamanga, 2015; WWF, 1980). The philosophical and ethical foundations of conservation have in turn deepened from a largely utilitarian creed to encompass recreational, romantic, spiritual, educational, scientific, intrinsic and other values (Callicott, 1990; Meine, Soulé, & Noss, 2006; Vucetich, Bruskotter, & Nelson, 2015).

Changes in societal perceptions are echoed by the global perspective of the World Parks Congress (WPC) over the last half-century. The vision for national parks at the 1972 WPC projected the traditional view of areas set aside to protect natural wonders and wildlife for human recreation and enjoyment. The vision expanded to include parks for sustainable development at the 1982 WPC, and human well-being at the 2014 congress (McNeely, 1993; WPC, 2014). In the process six categories of internationally accredited protected areas have been recognized, ranging from Category I: strict nature reserves for scientific and wilderness protection, to Category V: land and seascapes where human uses have produced areas of distinctive aesthetic, ecological and cultural value, and Category VI: areas managed mainly for the sustainable use of natural ecosystems (Dudley & Stolton, 2008).

Although the WPC has raised the target for terrestrial coverage from 10% in the 1980s to 20% for 2020 (WPC, 2014), the coverage falls far short of the area needed to sustain biodiversity for several reasons. First, historically, most protected areas were set aside for scenic, recreational and aesthetic reasons and for specific wildlife attractions, rather than for biodiversity or conserving ecosystem viability (Bennett et al., 2009; Fynn & Bonyongo, 2011; Jenkins, Pimm, & Joppa, 2013; Western & Gichohi, 1993). Second, most protected areas were set aside in lands marginal for development, not to conserve biodiversity (Joppa & Pfaff, 2009; Pressey & Bottrill, 2008; Venter et al., 2017). Third, most protected areas are too small to avoid a loss of species due to insularization, habitat fragmentation and ecological disruption (Newmark, 2008). Fourth, over one-third of land user protected areas is degrading due to human pressures (Jones et al., 2018). Finally, the prospects of retrofitting protected areas to maximize biodiversity coverage are limited, given existing land tenure and uses (Pressey, Visconti, & Ferraro, 2015). Calls for allocating half the earth to protected areas, primarily free of human activity (Dinerstein et al., 2017; Wilson, 2016), face insurmountable political obstacles and fail to redress the systemic shortcomings of existing protected areas (Büscher & Brockington, 2017). The alternative is to consider finding space in lands used for human uses compatible with conserving biodiversity and maintaining the ecological health of the land.

2 | CONSERVATION IN THE HUMAN REALM

The prospects of conserving biodiversity within the human realm by sustaining the health of the land and its capacity for renewal has long been recognized as an evolutionary possibility and ecological necessity (Leopold, 1949). Leopold, in calling for a land ethic, noted that the art of land doctoring is being practiced with vigour, but the science of land health is yet to be born. The land ethic is gaining recognition as being essential for halting global losses of biodiversity (Kremen & Merenlender, 2018). The principles of the World Conservation Strategy (WWF, 1980), Agenda 21 (Sitarz, 1993), the Convention on Biological Diversity (United Nations, 1992) and the Millennium Ecosystem Assessment (Assessment, 2003) all underscore the importance of land health for sustainable development. Yet, land health also depends on cultural values and governance institutions (Brockington et al., 2019; Ostrom, 2009). Many traditional societies, referred to as biocultures by Nicolay Vavilov (Nabhan, 2012), evolved husbandry practices and cultures that have sustained the health of the land for generations in the face of environmental perturbations and climate change.

Conserving biodiversity in landscapes transformed by farming, ranching and other human uses depends on wildlife having access to their land and in their lives on terms favourable to them. The options for doing so include land sharing, land saving and land sparing (Fischer et al., 2014). The mixed-use and implicit coexistence in land sharing move biodiversity conservation beyond the sharp distinction between natural and human-modified landscapes implicit in protected areas to a land sparing-sharing continuum based

4. Conservation from the inside-out

on the intensity of uses (Phalan, 2018; Western & Pearl, 1989). The scale ranges from heavily transformed and intensively used lands such as monoculture farmlands with little biodiversity to extensive uses in less modified landscapes such as grass-fed ranching, agroecological farming, renewable forestry practices, recreational uses of wildlands rich in biodiversity and extensive mobile pastoralism (Kremen & Merenlender, 2018). Land sparing-sharing models can contribute significantly to biodiversity conservation, though not necessarily from a livelihood and social perspective (Phalan, 2018).

The expansion of nature conservation from the protection of habitats and species to sustaining biodiversity launched by the World Conservation Strategy in 1980 calls for large-scale planning across a broad range of land uses, users, jurisdictions and agencies (WWF, 1980). Biodiversity conservation in the human realm, especially at the scale needed to conserve species in the face of projected climate and land use changes in the 21st century (Newbold, 2018), must also fit in with other land uses and minimize or offset the socio-economic losses incurred (Donaldson, Wilson, & Maclean, 2017).

If scaling up biodiversity conservation has great potential, it also faces severe obstacles (Curtin, 2015; Western & Pearl, 1989). Community-based conservation, largely focused on ecosystem-level conservation, has shown some success in conserving wildlife and biodiversity in rural landscapes and in improving socio-economic development (Naidoo et al., 2016; Oldekop, Holmes, Harris, & Evans, 2016; Shahabuddin & Rao, 2010). Scaling up biodiversity conservation to a large landscape level calls for yet wider networks and jurisdictions cutting across varied land uses, user interests and jurisdictional boundaries (Arts et al., 2017; Sayer et al., 2013; Scarlett & McKinney, 2016).

Several such landscape approaches have emerged over the last few decades, ranging from the Yellowstone to Yukon Conservation Initiative (Merrill, 2005), Colorado River Initiative (Adler, 2007), Malpai Borderlands Group (Curtin, 2002), Kavango Zambezi Transfrontier Conservation Area (Cumming, 2008) and the Kenya–Tanzania Borderlands Conservation Initiative (BCI).[1] In many cases, the scale needed to secure sufficient space for biodiversity to accommodate large-scale migrations of species traverses several national boundaries. Many of these initiatives have struggled to reach their landscape-scale goals due to a limitation in economic resources for biodiversity conservation.

The tools for encouraging landscape biodiversity conservation are primarily economic in nature and include (a) conservation leases and easements, (b) payment for ecosystem services, (c) cost offsets, and (d) consumptive and non-consumptive uses of wildlife (Bedelian & Ogutu, 2017; Naidoo et al., 2016; Nelson et al., 2010). New economic accounting methods for valuing natural capital and ecological services, such the Total Economic Value (Costanza et al., 1997) and the System of Environmental-Economic Accounts (Jasch, 2003), emphasize the multiple benefits of conserving biodiversity. These tools complement the efforts of parks to expand the reach of nature conservation and alleviate human threats to biodiversity.

Large herbivores and carnivores have proven especially hard to conserve outside protected areas given a history of overhunting, displacement, the large spaces and intact habitats they need to survive and the dangers and competition they pose to people (Tilman et al., 2017). Smith, Smith, Lyons, and Payne (2018) show that a strong down-sizing of species has characterized the human impact on ecosystem structure and function over at least the past 125,000 years and is likely to continue to do so far into the future.

Despite these obstacles, there is considerable scope for conserving large herbivores and carnivores in the pastoral areas of Africa and rangelands around the world, far more than in protected areas (Western & Pearl, 1989). The East African savannas reflect the long co-evolution of humans and wildlife that survived both the Pleistocene megafaunal extinctions and colonial-era decimation of wildlife in other places (Adams & McShane, 1992). The reasons are due in part to the cultural and use values of wildlife (Western, 2019), the seasonal mobility of pastoralists and the milk-based pastoralist economy. If classified by the IUCN criteria, the pastoral-dominated savannas would be recognized as the equivalent of Category V landscapes where human uses have produced areas of distinctive aesthetic, ecological and cultural values, and Category VI areas managed mainly for the sustainable use of natural ecosystems.

In this article, we focus on wildlife and biodiversity conservation in the East African savannas but also draw broader inferences for the rangelands which cover 25% of the earth's surface and working landscapes more generally. Successfully conserving wildlife in the savannas depends on how herding people manage their lands (Groom & Western, 2013) and finding places for wildlife which fit within the livelihood needs and cultural values of communities (de Pinho & Ellis, 2009). We argue that the space and mobility for sustaining large mammals can be secured indirectly through an approach we term conservation from the 'inside-out'. By inside-out we mean drawing on husbandry and conservation practices used to maintain the productivity and resilience of pastoralism or other land uses that directly or indirectly maintain large free-ranging wildlife movements in the process. Though overlapping, inside-out conservation is distinguished from bottom-up approaches to wildlife conservation in using primary livelihood considerations to win space for wildlife indirectly rather than through direct incentive-based approaches.

Ultimately, the inside-out approach aligns biodiversity conservation to land health and sustainable husbandry practices, thus widening the scope for nature conservation to the majority of the earth's surface without necessarily relying on large capital investments or tackling biodiversity as the primary focus. Here, we use a case study that looks at the adaptation of traditional pastoral practices in East Africa to the fast-changing global age, and by doing so offers prospects for sustaining land health, improving livelihoods and conserving biodiversity.

3 | PASTORAL AND WILDLIFE LANDSCAPES

Maasai pastoralists occupy much of the 100,000 km^2 area that spans the Kenya–Tanzania borderlands and the Rift Valley (Figure 1). In this region, bimodal rainfall varies from 250 to 1,700 mm across altitudes ranging from 600 m on the floor of the Rift Valley to over 5,000 m on Kilimanjaro. The range of biomes cutting across the rainfall and altitudinal gradients make the Kenya–Tanzania borderlands one of the richest biodiversity regions in Africa and mammalian diversity centres on Earth (Jenkins et al., 2013). The region also has some 16 national parks and reserves stretching from Serengeti and Maasai Mara in the West to Tsavo and Mkomazi in the East (Figure 1). The continuous patchwork of grasslands, bushlands and woodlands reaching across this region also support the greatest abundance of pastoral livestock and wildlife in Eastern Africa (Ogutu et al., 2016).

The Maasai people are made up of 13 politically semi-autonomous sections, each sharing the same clan and age-set groupings. The overlapping clans and age-sets move seasonally between wet and dry season grazing areas, largely in synchrony with wildlife migrations (Western & Nightingale, 2005) by using reciprocal social ties that span the seasonal ranges and foster connections to adjoining Maasai sections (Spear & Waller, 1993).

The seasonally coordinated movements between wet and dry season ranges define the community of users and sustain their livestock herds except in extreme years when herders often move to distant refuges to evade droughts. Drought refuges are typically in the wetter regions of the landscape, such as highland pastures, wetlands and areas receiving recent rains (Fynn, Murray-Hudson, Dhliwayo, & Scholte, 2015). The drought movements expand the scale of use from the annual range of a few thousand square kilometres to tens of thousands, negotiated though their reciprocal arrangements (Western & Finch, 1986).

The conservation of the grazing commons to ensure herd productivity and resilience is deeply rooted in Maasai governance and herding practices (Spear & Waller, 1993). A family's survival and well-being are bound to the welfare of its livestock and the availability of pasture and water. The Maasai nevertheless have no word for conservation. The link between rainfall, pasture production, herd productivity, family welfare and the maintenance of commons resources is, instead, incorporated in the concept of *eremata*re. Akin

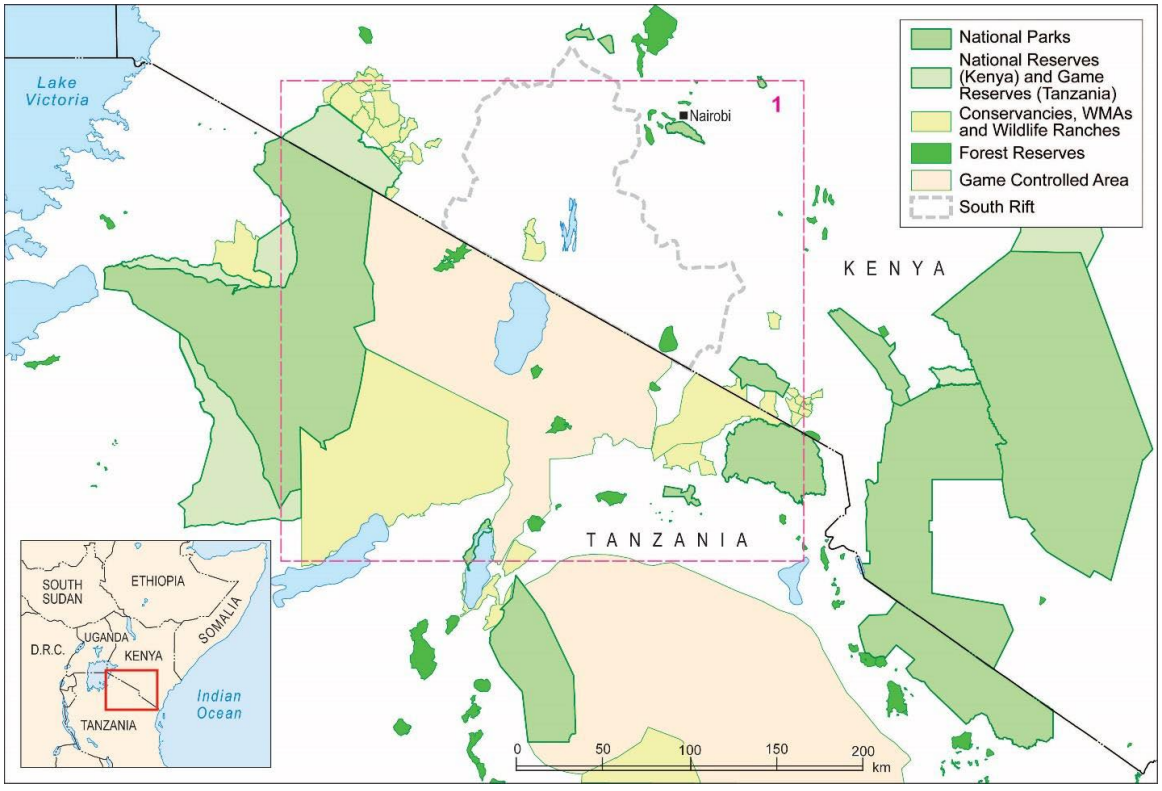

FIGURE 1 Map of the conservation and protected areas network in the Kenya–Tanzania borderland, highlighting the location of our case study within the region. Our case study looks at three scales: Shompole and Olkiramatian conservancies in the centre of the map, the South Rift at the landscape level and the regional level across the whole map. The red box indicates the extent of Figure 3. Data are from the World Database of Protected Areas (www.protectedplanet.org), South Rift Association of Landowners (www.soralo.org), Maasai Mara Wildlife Conservancies Association (www.maraconservancies.org) and BigLife Foundation (www.biglife.org)

to Vavilov's biocultures and Leopold's land ethic, *eramatare* is an ethos embedded in husbandry practices, cultural customs and the governance of Maasai society. *Eramatare* linkages stretch across the landscape through social networks, giving families access to the resources needed to sustain them through the seasons and in times of drought. *Eramatare* also extends to wildlife, which holds many values and uses among the Maasai, including food, clothing, medicine, ornamentation, utensils, clan symbols and aesthetic appeal (Western, 2019). Many species, including eland and buffalo, are regarded as 'second cattle' and are used as a standby food source in times of drought (Western, 1997).

4 | HUMAN-DRIVEN CHANGES IN EAST AFRICA

Starting in the 1940s, concerns over the impact of population growth, land transformation and poaching of wildlife led to the creation of national parks and reserves presently covering 15% of Tanzania and 8% of Kenya. By the 1970s recognition that national parks are too small to avoid extinctions and insufficient to protect the wildlife migratory routes led to policies for engaging communities in wildlife conservation through tourism and hunting revenues (Western & Pearl, 1989). In the ensuing decades the policy shift resulted in an expansion of wildlife conservation onto community lands by encouraging the creation of wildlife conservancies in Kenya and Wildlife Management Areas in Tanzania (KWCA, 2016).

Despite the spread of community-based conservation in Africa's rangelands, its success hinges on the future of pastoral economies and cultures. Pastoralism, the dominant form of land use in the sub-arable savannas, accounts for over 90% of the large mammal biomass in Kenya (Ogutu et al., 2016). Despite the economic potential of tourism and sport hunting, wildlife revenues contribute to only a small portion of household income (Kristjanson & Trench, 2009). The strong cultural identity and social bonds rooted in livestock also make it likely that pastoralism will remain the primary form of livelihood even where wildlife revenues are a significant portion of family incomes.

Pastoralism nevertheless faces many of the same threats as wildlife, namely the loss of space and mobility; land use changes and land degradation; a loss of livestock production; and decreasing resilience to droughts (Boone, 2005; Hobbs et al., 2008). The loss of ecological adaptability to environmental perturbations is further compounded by a breakdown in the traditional governance institutions rooted in social reciprocity which regulate pasture use and minimize local risks of drought, disease and other hazards (Mwangi & Ostrom, 2009). The breakdown stems from several factors arising from pre- and post-colonial government policies, including government-mandated regulations of the rangelands, the creation of wildlife parks and reserves, forced eviction of pastoral communities for agricultural development, sedentarization and subdivision policies for rangelands and the replacing and breakdown of traditional decision-making practices (Mwangi & Ostrom, 2009). Because of these common threats, redressing the threats to pastoralism and pastoral lands indirectly alleviates the same threats to wildlife. Further, conserving the cultural and governance practices underpinning the mobility and resilience of pastoral herds also reduces human-wildlife conflict and the prospects for continued coexistence (Western, 2019).

Here we look at an example of how two adjacent Maasai communities in Kenya's South Rift (Figure 1) are drawing on both traditional and contemporary knowledge of husbandry and governance practices to sustain pastoralism and conserve wildlife. We then look at how the expansion of such ecosystem-level efforts can benefit from increased scales of governance and management to not only build livestock production and resilience but scale up to large landscapes to conserve biodiversity.

5 | CONSERVATION FROM THE INSIDE-OUT

5.1 | The benefits of landscape scale to pastoralists and wildlife

Among pastoral communities free-ranging movements give livestock access to resources over large regions where forage and water sources are patchy and ephemeral. Mobility allows herders to track the richest pastures through the season and minimizes exposure to drought, disease, local pasture degradation and perturbations in semi-arid areas where rainfall is highly variable in time and space (Ash, Gross, & Smith, 2004; Boone, 2005; Hobbs et al., 2008; Wang et al., 2006; Western, 1982; Western & Finch, 1986). These ecological benefits of large-scale mobility in areas where resource availability is highly stochastic are reflected in the energy bonus of improved digestive efficiency, growth rates and milk yields for pastoral livestock and wildlife alike (Illius & O'Connor, 2000; Owen-Smith, 2004; Wang et al., 2006). In the case of pastoralists, the scale of use is tied to the scale of social networks allowing free and safe movement (Western, 2019). Large social networks have in turn been shown to increase the benefit to individuals through a 'return to scale' across a range of societies from hunter-gatherers to agrarian and urban economies (Hamilton, Milne, Walker, & Brown, 2007; West, 2017).

The ecological benefits of mobility in offsetting stochastic resource availability apply widely regardless of habitat and landscape variability. The benefits become far more beneficial, however, in landscapes varying in elevation, climate, soils, hydrology, habitat and plant nutrition. In such varied landscapes, the functional heterogeneity at scale adds the productivity, diversity and resilience of large herbivores (Fynn, Augustine, Peel, & Garine-Wichatitsky, 2016; Owen-Smith, 2002, 2004).

In the case of the African savannas, wildlife survival, abundance and resilience to seasonal flux and drought are also scale-dependent, and like livestock, they depend on the ecological benefits accruing across large functionally heterogeneous landscapes (Fryxell et al., 2005; Owen-Smith, 2004; Western & Gichohi, 1993). Species such

4. Conservation from the inside-out

as elephants, lions, wild dogs, giraffe and migratory wildebeest, zebra and gazelle in the Kenya–Tanzania borderlands cover thousands of square kilometres in the course of seasonal movements (Dolrenry, Stenglein, Hazzah, Lutz, & Frank, 2014; Fryxell et al., 2005; Mose, Nguyen-Huu, Western, Auger, & Nyandwi, 2013; Osipova et al., 2018). In that species richness, habitat diversity and ecosystem integrity all increase with landscape heterogeneity (Peterson, Allen, & Holling, 1998; Figure 3), conserving metapopulations of landscape species—species using a large geographic area which includes a wide variety of other species—conserves biological diversity and integrity in the process. Large open landscapes also avoid the compression effects of large mammals on biodiversity (Western & Maitumo, 2004) and rangeland health (Hobbs et al., 2008; Western, Mose, Worden, & Maitumo, 2015) through seasonal movements and population dispersal (Mose & Western, 2015).

Scale and mobility in increasing functional heterogeneity also facilitate coexistence between livestock and wildlife by increasing foraging options, minimizing competition (Fynn et al., 2016; Tyrrell, Russell, & Western, 2017) and expanding the scope for the spatial and temporal separation of wildlife and livestock. Temporal separation in turn reduces pathogen transmission, crop-raiding and livestock depredation (Valls-Fox et al., 2018; Western, 2019).

Finally, scale and mobility increase the structural and functional heterogeneity of landscapes through disturbance effects created by the differential grazing and browsing impacts (Fuhlendorf et al., 2016; Fynn et al., 2016) important to conserving the richness and integrity of ecosystems. Examples of patch dynamics caused by the seasonal movements of livestock and wildlife to optimize foraging include the interaction of elephants and livestock in creating a shifting mosaic of habitats (Asner, Vaughn, Smit, & Levick, 2016), the intensity, timing and scale of fires influencing biodiversity and forage quality (Fynn et al., 2016; Morrison et al., 2018) and abandoned settlements in creating nutrient hotspots and habitat succession (Muchiru, Western, & Reid, 2009; Vuorio, Muchiru, Reid, & Ogutu, 2014). The expanded scope for coexistence linked to scale also favours ecotourism, hunting and recreation activities that diversify pastoral economies and sustains ecological services such as carbon sequestration, nutrient cycling, and water supplies at local, national and global scales (Yahdjian, Sala, & Havstad, 2015).

Expanding the scale of landscape management from an inside-out approach is driven by the vested interests of pastoralists and agro-pastoralists in sustaining their livelihood productivity and resilience and, incidentally, avoids the negative impacts of fragmentation of rangelands (Groom & Western, 2013; Hobbs et al., 2008). Conservation approached from the self-interests of herders and their social networks shift the focus from top-down outside-driven programs to culturally embedded and community-based approaches to conservation (Figure 2).

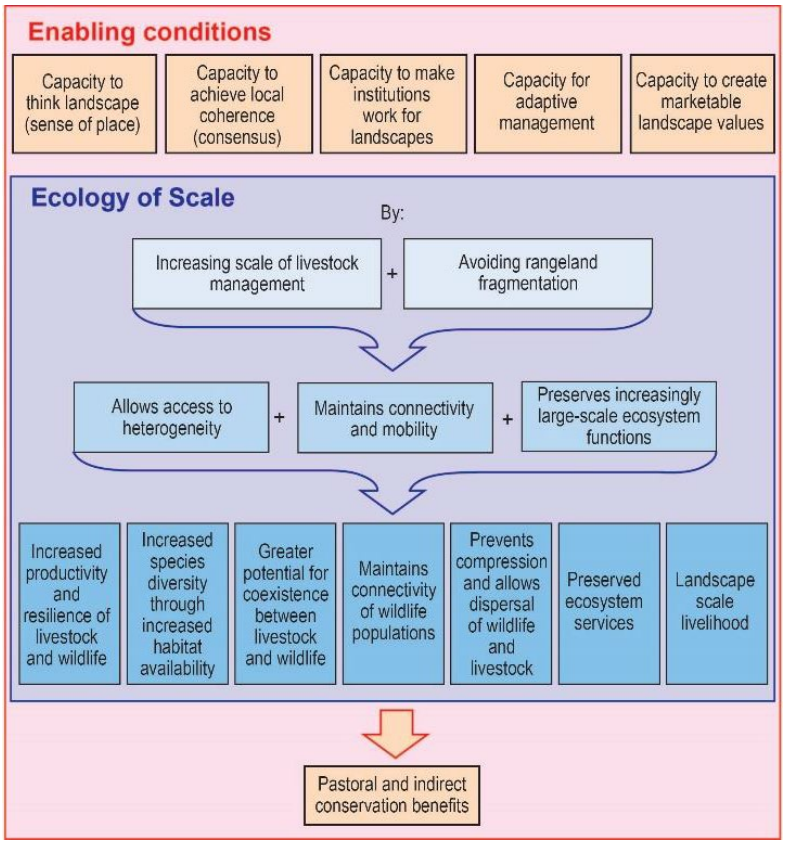

FIGURE 2 A diagrammatic representation of conservation from the inside-out for rangeland and pastoral systems. Successful resource governance of the pastoral rangelands depends on enabling conditions (Arts et al., 2017) linked to the ecology of scale and social networks (Cumming, Olsson, Chapin, & Holling, 2013). Scale benefits pastoralists through increased mobility, herd production, resilience and the maintenance of land health and, in the process, conserves biodiversity and ecosystem services. The benefits and implications of the ecology of scale can act across multiple scales (ecosystem, landscape, region)

Social-ecological system theory (SES) and landscape governance theory recognize that successful management of common property resources depends on managing the commons through social networks and ruled-based institutions with coherence at the appropriate social and ecological scales, the capacity for adaptive management through devolved management rights and marketable landscapes (Figure 2; Cumming et al., 2013; Ostrom, 2007; Reid, Fernández-Giménez, & Galvin, 2014).

Our case study demonstrates that fundamental principles of SES theory and landscape governance theory are integral to but fading in traditional Maasai communities. The traditional grazing practices and land use practices, social networks and governance arrangements are changing but remain central in sustaining natural resource management from an ecosystem to landscape and regional level.

5.2 | Ecosystem scale

The pastoral lands of Kajiado and Narok counties in Kenya cover 40,000 km^2 along the border with Tanzania. The traditional common grazing grounds were divided into group ranches under the Group Ranch Representatives Act (CAP 287) in the 1960s and 1970s. Two of the group ranches in the southern Rift Valley of Kajiado County, Shompole and Olkiramatian, cover 1,500 km^2 (Figure 1) stretching from the forested Nguruman Escarpment to the semi-arid grasslands and bushland flats of the Rift Valley floor. The pre-colonial occupants of the Shompole–Olkiramatian ecosystem are predominantly members of the Lodokilani section of Maasai. The section includes a small group of settled farmers along the base of Ngurman Escarpment and a transhumant population of approximately 20,000 pastoralists who move seasonally.

Shompole and Olkiramatian communities have maintained their traditional collective herding practices to avoid the subdivision and fragmentation of their common grazing grounds arising from the subdivision and privatization of group ranches (Mwangi & Ostrom, 2009; Russell, Tyrrell, & Western, 2018). The two group ranches have, however, adapted traditional husbandry practices and livelihoods in response to the emerging opportunities in the market economy and to conform to national land, governance and development policies. The adaptations include diversifying the traditional livestock economy through commercial livestock production, farming, wildlife and tourism enterprises and pursuing new opportunities through education, social services and rural development (J. Kamanga, pers. commun.).

Both Shompole and Olkiramatian incorporate national legal requirements in group ranch governance statutes by appointing government chiefs alongside traditionally selected age set leaders responsible for overseeing the use of common-pool resources. Among other functions, the group ranch committees regulate the movement of livestock and seasonal pastures (Russell et al., 2018; Tyrrell et al., 2017; Western, 2019) and arbitrate herding arrangements within and between clans and with adjoining group ranches and Maasai sections (ibid.). The traditional late-season pastures double up as wildlife conservancies attracting tourism enterprises, including lodges, cultural visits and nature walks (J. Kamanga, pers. comm.). The group ranch committees also oversee livestock markets and guide development activities through land planning and zoning to ensure complementarity in land and resource use.

The regulation of livestock movements among community members ensures optimum use of pastures, the conservation of late-season grass reserves and minimum conflict with wildlife over pastures and water (Tyrrell et al., 2017). The governance practices afford community members access to grazing grounds, a variety of habitats for sustaining herd productivity and the mobility required to capitalize on patchy rains, avoid both disease outbreaks and competition with wildlife (Russell et al., 2018). The ability of herders to live alongside wildlife and benefit through tourism enterprises and traditional values (Roque de Pinho, 2009) depends on their rich knowledge of wild herbivores and carnivores and their skills in averting conflict (Western, 2019).

The role of traditional deployment of community scouts termed *ele'enore* is to gather the information the community needs to weigh its grazing options and reach collective decisions on herd deployment, watering regimes and the avoidance of serious conflicts with wildlife (Western, 2019). Olkiramatian, drawing on the *ele'enore* tradition, set up a Lale'enok Resource Centre which trains and deploys resources assessors to gather a wide variety of ecological, social and market data relevant to collective herd management, land planning, resource management and market access. The resource assessors use automated data collection platforms to enter and analyse information for rapid dissemination and decision-making (Mose & Western, 2015; Tyrrell et al., 2017).

The mix of traditional and contemporary knowledge, herding practices and governance arrangements maintains the seasonal scale of livestock movements on Shompole and Olkiramatian, ensuring that wildlife and livestock can benefit from seasonal migrations and adaptability to droughts (Russell et al.,; Tyrrell et al., 2017). In contrast to the sharp wildlife declines in pastoral areas which have been subdivided (Groom & Western, 2013; Ogutu et al., 2016; Said et al.,), wildlife populations on Shompole and Olkiramatian have been more resilient. Elephant numbers have increased sharply, wild dog sightings have increased, cheetahs are resident and the lion population has spread into the surrounding ranches (Ahlering, Maldonado, Fleischer, Western, & Eggert, 2012; Schuette, Creel, & Christianson, 2013; Tyrrell et al., 2017). The area remains an important bird area with several threatened species (BirdLife International, 2019).[2]

5.3 | Landscape-scale

The success of the Olkiramatian and Shompole conservation efforts encouraged the African Conservation Centre (ACC) to create a landowner network connecting Amboseli National Park and Maasai Mara National Reserve across the Rift Valley, aimed at forging a new tourist link and conserving the biodiversity-rich landscape (Figures 1 and 3). ACC partnered with the Olkiramatian and Shompole leaders in 2007

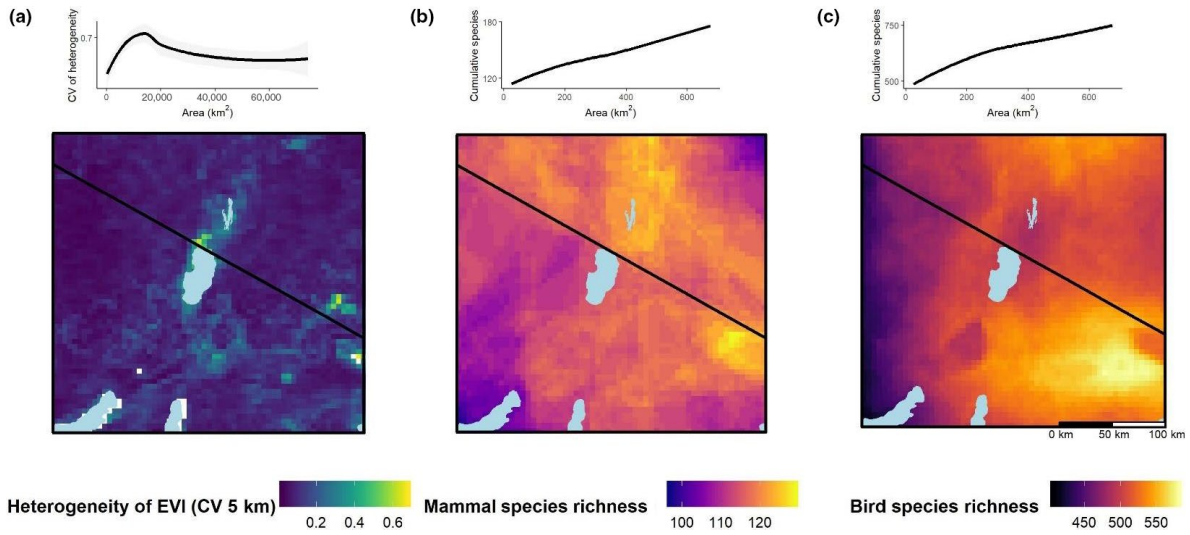

FIGURE 3 5 × 5 km grid maps of the Kenya–Tanzania borderlands (border - black line) and major lakes (light blue) showing: (a) Habitat heterogeneity based on the coefficient of variation of Enhanced Vegetation Index (EVI) from Tuanmu and Jetz (2015). The accompanying graph shows heterogeneity increasing steeply with area coverage from a central pixel to a peak at 15,000 km^2. The accompanying graphs to maps (b) and (c) show respectively species richness in mammals using the Digital Distribution Maps of Red List Species (IUCN, 2016) and birds based on Bird Life Digital Distribution Maps (BirdLife International, 2019) both increasing steadily from a central pixel

to establish the South Rift Association of Landowners (SORALO) incorporating the 16 current and former group ranches spanning the 15,000 km^2 landscape. The common goals of the SORALO members include land security, raising and diversifying livelihoods, sustaining natural resource use and land health, developing ecotourism enterprises and conserving the open rangelands and rich wildlife assemblage.

The governance of SORALO's membership builds on the existing social networks and reciprocal grazing arrangements connecting adjacent Maasai clans and sections. SORALO is registered as a land trust and like Shompole and Olkiramatian, incorporates traditional and contemporary governance institutions and practices. The SORALO board includes representatives of regional group ranch clusters and draws on strong community inputs and the political influence it has with county and national agencies.

The geographic reach and group ranch network SORALO covers scales up Shompole and Olkiramatian ecosystem-level governance to take advantage of the expanded benefits accruing from a landscape scale, including access to drought refuges, the conservation of watersheds and ecosystem services they depend on beyond their boundaries, the protection of wildlife corridors, joint wildlife scouting operations, ecotourism planning and access to country, national government and NGO services.

5.4 | Regional-scale

The Kenya–Tanzania borderlands are globally important as a vertebrate biodiversity hotspot and regionally as a centre of plant diversity accounting for a quarter of all the plants recorded in Kenya and Tanzania (Ministry of Environment Natural Resources and Regional Development Authorities, 2015; Figure 3). The borderlands also support large populations of endangered and threatened species, including one of the largest free-ranging elephant populations, richest carnivore assemblages in Africa, and among the largest remaining large herbivore migrations world-wide (Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009; Jenkins et al., 2013). Coupled with sixteen protected areas and a $1.5 billion annual tourism industry, the borderlands have attracted international attention as one of the earth's last great natural wonders.

Despite the attention and large well-equipped government ranger forces, wildlife has declined sharply in national parks both sides of the border in the last few decades (Craigie et al., 2010; Western, Russell, & Cuthil, 2009). The declines stem from the same threats confronting the future of free-ranging pastoralists at an ecosystem and group ranch level; land conversion, subdivision, settlement and growing pressures on the open rangelands. Species dependent on large-scale migrations to access seasonal forage and sustain large populations are especially vulnerable to land compression and fragmentation. Both the Tarangire and Nairobi National Park herbivore populations are threatened by a lack of collaboration and incentives at the regional scale (Newmark, 2008; Western & Gichohi, 1993).

In the case of elephants, the main cause of the decline in the 1970s and 1980s arose from a ten-fold rise in ivory prices in the world market creating a surge in poaching and compression of remaining herds into the relative safety of national parks (Mose & Western, 2015; Stiles, 2004). The compression reduced woody

habitats and biodiversity in national parks and most severely in small parks like Amboseli. Here, the extreme compression and habitat loss (Western & Maitumo, 2004) spurred efforts in 2006 to reestablish the elephant's range to reduce the pressure on the park and recolonize the elephant's former wide-ranging movements. The first step involved training and deploying community scouts and promoting conservancies and tourism enterprises in Shompole and Olkiramatian where resident herds were driven out by poachers in the 1980s.

Following the natural repopulation of Shompole and Olkiramatian, ACC and SORALO expanded the elephant recovery program to connect the isolated Mara and Amboseli population with the aim of creating a metapopulation across the Rift Valley. The recovery involved monitoring elephant movements and deploying community scouts along dispersal routes. The program, premised on the inside-out model of conservation, evolved into the BCI in 2012.

The initial goal of BCI was to halt elephant poaching by using SORALO-like community linkages to create space for the fragmented park populations and recreate a viable metapopulation in the pastoral lands spanning the Kenya–Tanzania borderlands. BCI used the endangerment and charismatic appeal of elephants to create a coalition of local NGOs, conservation organizations, researchers and government agencies to support the pastoral community initiatives. The BCI collaboration soon expanded from the initial focus on elephants to conserving lions, other large carnivores, giraffe and other threatened and charismatic species to obviate the impacts of land restrictions on large scale movements and the fragmentation of metapopulations critical to their genetic and ecological viability. Recent evidence from the Serengeti-Mara ecosystem shows that even the largest of national parks are threatened by surrounding human pressures (Veldhuis et al., 2019) and are in need of mitigating conservation measures aimed at sustaining free-ranging movements.

5.5 | Inside-out conservation as a way forward

Conservation in working landscapes connected from small land management entities to large multiscale landscapes holds untapped potential for alleviating the insularization and other human impacts on protected areas as well as conserving biodiversity in rural landscapes. Global warming is adding urgency to conserving species beyond protected areas as their ranges shift in response to climate change (Thomas et al., 2004). The threats call for new approaches to conserving biodiversity in the rural landscape. Solutions range from creating buffer zones for protected areas, protected areas that include working landscapes, conservation easements, leases and direct land purchases. Conservation opportunities in the agrarian landscape include creating space through land-sparing intensified agriculture; conservation subsidies to farmers to protect wetlands, rivers and woodlands and financial offsets for converting inimical uses to conservation-compatible uses.

Conservation emanating from within communities based on sustaining livelihoods which are dependent on large open landscapes widens the scope for nature conservation in the rural lands which cover 75% of the earth's terrestrial surface. Contrary to both top-down and bottom-up approaches which are focused primarily on conserving wildlife as the priority, an inside-out approach builds on existing practices that maintain open landscapes and wildlife by patching together networks of livelihoods and interests with compatible objectives. Unlike debates around land sparing and land sharing, this approach is centered on people rather than wildlife (Phalan, 2018) and allows for a range of land use options along the sharing to sparing continuum. As our case study shows, the productivity and resilience of pastoral communities are linked to the ecological and functional benefits of scale, heterogeneity and land health, which if sustained, make space for large free-ranging wildlife populations and biodiversity. While the inside-out approach is applicable to rangelands, it has relevance to other large complex systems that benefit from increasing the scale of management to larger landscapes, such as marine fisheries (Curtin, 2015).

Finding such space also depends on finding a place for biodiversity within a community's aspirations and economic options. To succeed, biodiversity conservation in rural lands must expand to a landscape scale and cut across national, jurisdictional, institutional and cultural boundaries, and create network connections between them (Scarlett & McKinney, 2016). The feasibility of using an inside-out approach to conserve large open spaces becomes more feasible when linked to existing theories connecting landscapes among multiple jurisdictions using a polycentric and devolved approach to governance (Ostrom, 2007), landscape theory based on sustainable practices (Arts et al., 2017; Curtin, 2015) and a sound ecological understanding using functional heterogeneity theory (Fuhlendorf, Fynn, McGranahan, & Twidwell, 2017; Fynn et al., 2016).

Of particular use is the SES framework (McGinnis & Ostrom, 2014; Ostrom, 2007, 2009), which allows for the analysis of relationships among multiple levels of complex SESs at different spatial and temporal scales. It also helps us understand how specific parts of the systems are related and interact. Applying the SES framework to natural resource management reveals several important elements affect the likelihood of users' self-organizing to sustainably manage a resource, including: (a) the existence of institutions that work at the correct social and ecological scales; (b) governance that is multi-scale and multi-level, (c) communities who have clear devolved autonomy over resource management; (d) communities who see an importance of the resource, and see a benefit (through economic and non-economic values) from their natural resources; (e) strong social norms of collaborative governance and management (Cumming et al., 2013; Ostrom, 2007, 2009; Reid et al., 2014).

Our case study shows that these conditions are achievable for the management of pasture (and subsequently wildlife), and when they are conceptually twinned with a capacity for effective landscape

governance (see Arts et al., 2017 for landscape governance as a capacity; Figure 1) and locally appropriate ecological principles, the results are mutual benefits to people, livestock and wildlife.

Biodiversity and livelihoods dependent on land health converge in the rangelands more than in most other biomes. The convergence stems from two formerly disparate objectives. First, the ambit of protected areas for conserving biodiversity has widened from the strict protectionism of IUCN Category I parks to include Category VI areas accommodating a range of compatible human values and uses. Second, land users, including pastoralists, private commercial ranchers, fishing, hunting and forestry communities are finding common ground in conserving healthy, open landscape for their inclusive values. These include not only primary livelihoods but also other uses and values as nature sensibilities expand and international commitments to sustainable development deepen. These include a sense of place, a healthy environment and the range of ecological services it provides (Arts et al., 2017; Sayer et al., 2013).

The inside-out approach to winning space and a place for wildlife and biodiversity is place-based and draws on local knowledge and informal governance arrangements. It avoids the bottom-up wildlife-centric approaches which are driven from the outside and that alienate communities working on the land for a living. Instead, conservation approached from the inside outward promotes a human-centered approach that reinforces land health and spatial connectivity. It also encourages a shift from colonial and post-colonial central government command-and-control policies that have hampered wildlife and natural resource management towards devolved rights and ownership emerging with political and economic liberalization trends around the world.

Expanding conservation benefits from the inside-out is especially pertinent to conserving large herbivores and carnivores which need large open landscapes, pose considerable threats and costs to rural communities and are the most vulnerable of all species to farming, ranching and resource extraction (Tilman et al., 2017). Given that the downsizing of large herbivores and carnivores will have the biggest impact on ecosystem structure and function in coming decades, finding places for such landscape species will avert trophic cascade effects and the ecological impoverishment arising from the loss of keystone species (Dirzo et al., 2014; Smith et al., 2018).

Unlike much of East Africa's privately protected areas, conservancies and Wildlife Management Areas which 'buy' tolerance through tourism, trophy hunting or other land leases, the inside-out approach to conserving large open landscapes and wildlife expands self-interests and shared community livelihoods, social networks and cultural values. In the case of the Maasai, *eramatare* linkages at the individual levels between family and herds, and at the community level for land access and land health through common pool governance arrangements, these connections promote both traditional intrinsic and instrumental values for wildlife. The linkages also reduce conflict and increase the prospects for coexistence with wildlife. Nevertheless, governments, NGOs and other conservation agencies have a large supporting role to play in offsetting the opportunity costs of wildlife and mitigating conflict as subsistence economies erode with population growth and market economies.

Collaboration at large scales and across human-dominated landscapes faces enormous challenges and at best will only complement and not supplant the need for protected areas and other conservation tools. Yet, as Leopold recognized, the extension of ethical values to include the health of the land is an evolutionary possibility and ecological necessity. By drawing on lessons from cultural institutions, principles and practices which have maintained the commons for generations, combined with ecological, political and social sciences, we see the possibility of landscape doctoring evolving into the science of land health.

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CONFLICT OF INTEREST

J.K., G.W. and S.R. work for SOLARO and D.W. works for the African Conservation Centre. All authors have engaged in conservation within the region outlined in the case study.

AUTHORS' CONTRIBUTIONS

D.W., S.R. and P.T. developed the original concept for this manuscript. D.W. led the writing. P.T. and P.B. produced the figures and analysed the data and assisted D.W. with the drafting of the manuscript alongside S.R., G.W. and J.K. All authors revised the manuscript critically for important intellectual content, approved the version to be published and agree to be accountable for the aspects of the work that they conducted.

DATA AVAILABILITY STATEMENT

All data in this manuscript are avalaible through their referenced sources.

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ENDNOTES

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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5

Landscape Dynamics (landDX): first release of an open-access spatial-temporal database for the Kenya-Tanzania borderlands

Abstract

The savannas of the Kenya-Tanzania borderland cover >100,000 km^2 and is one of the most important regions globally for biodiversity conservation, particularly large mammals. The region also supports >1 million pastoralists and their livestock. In these systems, resources for both large mammals and pastoralists are highly variable in space and time and thus require connected landscapes. However, ongoing fragmentation of (semi-)natural vegetation by smallholder fencing and expansion of agriculture threatens this social-ecological system. Spatial data on fences and agricultural expansion are localized and dispersed among data owners and databases. Here, we synthesized data from several research groups and conservation NGOs and present the first release of the Landscape Dynamics (landDX) spatial-temporal database, covering ~30,000km^2 of southern Kenya. The data includes 31,000 livestock enclosures, nearly 40,000 kilometres of fencing, and 1,500 km^2 of agricultural land. We provide caveats and interpretation of the different methodologies used. These data are useful to answer fundamental ecological questions, to quantify the rate of change of ecosystem function and wildlife populations, for conservation and livestock management, and for local and governmental spatial planning.

Background & Summary

The Kenya – Tanzania borderlands cover roughly 100,000 km^2 spanning the rangelands between southern Kenya and northern Tanzania (Fig. 1). This region is one of the most biodiverse in the world and contains some of Earth's highest densities of large mammals[1,2]. Because of this, and the value they generate through tourism, the region also has some 16 national parks and forest reserves stretching from the Serengeti and Maasai Mara in the west to Tsavo and Mkomazi in the east. Adjacent and between these government-protected areas are scores of non-government run conservancies, wildlife management areas, wildlife ranches, and game controlled areas. Despite the importance of this region for wildlife conservation, the borderlands are dominated by livestock[3]. This region is predominantly home to the Maasai people, who are traditionally transhumant or seasonally moving pastoralists[4]. Maasai herding practices and relative tolerance towards wildlife have allowed for continued cohabitation of wildlife and people[2].

However, extensive pastoralism and wildlife are under threat, particularly on the Kenyan side of the border. Both suffer from the negative effects of fragmentation[5]

driven by complex processes including policy change, economic drivers, and globalization, which have encouraged and driven subdivision and fencing, and the expansion of subsistence and mechanized agriculture[6–8]. This has halted migrations of wildlife and livestock, leading to wide-scale decreases in wildlife numbers [7,9–11], decreases in connectivity between populations and increasing genetic isolation[12], and losses in rangeland productivity and heterogeneity[13]. Additionally, many areas have experienced the loss of traditional grazing management structures, including increasing rates of sedentarisation (permanent settlement of transhumant pastoralists), causing rangeland degradation[14].

There have been many attempts to map these changes, including mapping of fencing, livestock enclosures (bomas), wildlife numbers, agricultural expansion, and habitat change[7,8,15–18]. These data are useful for a range of applications: to answer fundamental ecological questions, to quantify the rate of change of ecosystem function, pastoralists strategies, and wildlife populations - especially wildlife mobility, for conservation planning and mitigating threats to wildlife, for livestock management and planning, and local and governmental spatial planning. However, much of these data have remained inaccessible, disparate, or at smaller spatial or temporal scales than required to address regional challenges. Across the region, there have been calls to increase data sharing and collaborations between data owners, involving initiatives such as the Borderlands Conservation Initiative[1], SOKNOT WWF[2], One Mara Research Hub[3], and Amboseli-Tsavo-Kilimanjaro Spatial Data Infrastructure (ATK-SDI)[4].

Here we present a first step towards providing a regional scale open-access spatial (and temporal) database, through a permanent and updatable web server for the Kenya-Tanzania borderlands. The authors have initially compiled data for three of the most important anthropogenic structures covering an area of over 30,000 km^2, focusing on the rangelands of southern Kenya the extent of fencing across the region, the distribution of livestock enclosures (*enkangs* or bomas), and the extent of agricultural land use. Unlike previous efforts to collate this type of data, we have now synthesized

[1]https://www.accafrica.org/our_work/explore_programs/conserving-biodiversity-in-east-africa/kenya-tanzania-borderland-conservation-initiative/
[2]https://wwfke-giscoe.wwfkenya.org/portal/home/group.html?id=f6d50eae471e4937a3d0c0f7ab9f8847#overview
[3]https://www.kenyawildlifetrust.org/wp-content/uploads/2020/07/KWT-2019-Annual-Report_Web-Version.pdf
[4] https://www.ifaw.org/eu/projects/amboseli-tsavo-kilimanjaro-landscape

data at a scale large enough to be relevant for addressing and understanding the fragmentation in the region. The data from this study are accessible through the Landscape Dynamics (landDX) database hosted by the Mara Elephant Project (MEP). The landDX database is based on the ArcGIS online data infrastructure (https://www.arcgis.com/home/search.html?q=landDx), where it will be updated as and when new imagery, data, and project funding become available. A static version of this data is also made available through the Oxford Research Archive.

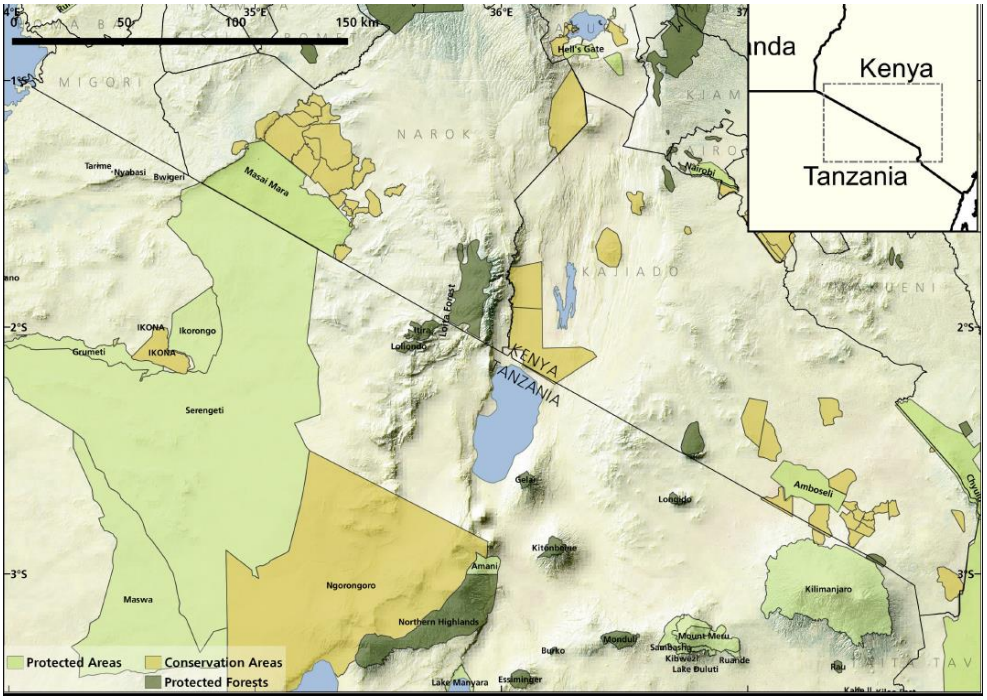


Figure 1 - The Kenyan-Tanzania borderland area (roughly 100,000 km^2), is the focus of this data release. Our initial dataset covers most of Kajiado and Narok counties in Kenya. This region is one of the most important areas globally for conservation. The area consists of 16 national parks and reserves (light green), protected forests, including forest reserves and community protected forests (dark green) and many conservancies, wildlife management areas, game management areas, and conservation areas (orange).

Methods

Data Collection

Data were collected from a variety of partners and sources across the region: South Rift Association of Land Owners, Aarhus University, Kenya Wildlife Trust, and the Mara Elephant Project. The study area covers the majority of the Kenyan counties of Kajiado and Narok (Fig. 2). The data extend into parts of Machakos and Nakuru counties, and the dataset is clipped to the Siria Escarpment and Nyakweri forest to the west, and the extensive farms along the Mau Escarpment to the north (Fig. 2). Beyond these limits, the land use is predominantly agricultural.

Aarhus University

Løvschal et al., 2017 mapped the changes in fences located within the Greater Mara (5,771 km^2), using Landsat satellite images between 1985 and 2016 with a resolution of 30m (Table 1; Fig. 2). In this study, only Landsat satellite images with similar optical sensors and spatial resolution were used, and images with a cloud cover of <1% were retained. All images were from mid-January to late-February to minimize the effect of changing seasons. The digitization of fences was done manually (by a single individual) based on visual interpretation using ArcMap 10.3.1, by looking at characteristic homogeneous areas using three different colour composites as well as a version based on normalized difference vegetation index (NDVI). When an assessment of one year was conducted, it was compared to the mapped fences from previous years to ensure that fences from previous years would not be overlooked due to difficulties in detecting them in later years.

South Rift Association of Land Owners Data (SORALO)

In 2019 and 2020, SORALO collected data for the entirety of Kajiado county, parts of Machakos and Nakuru county, and a considerable portion of east Narok county, totalling 25,000 km^2 (Table 1; Fig 2). Using QGIS[19], a Google Earth layer was used to digitize bomas, visible fence lines, and agricultural land use using a 1x1km search grid. These data were digitized in collaboration with Ramani Geosystems Ltd. (www.ramani.co.ke).

Brush fences are easily distinguishable from Google Earth imagery due to their width and dark brown colour (Fig. 3). These types of fences represent the majority of fencelines present in this semi-arid region. However, this imagery alone is not accurate enough to identify the thin wire fences more common to agricultural land. Instead, an abrupt change in land use, especially if it is in a straight line, likely indicates a wire

fence. In this manner, digitization of these types of fence lines used a similar method to the Aarhus University team, searching for homogenous areas of vegetation, urban development, or agriculture, distinct from the surrounding vegetation, which must have resulted as a consequence of fencing (Fig. 3). We converted these v digitized fence lines into polygons and manually searched through them to identify areas of agricultural production identifiable from the Google Earth imagery.

Livestock enclosures (bomas) vary across the region, ranging from permanent settlements to more traditional temporary and permanent bush enclosures (Fig. 4). We therefore only digitized areas which were clearly used to hold livestock at the date the satellite image was collected, rather than the full extent of a settlement. This is clear from the distinctive colour of manure and a continuous fenced perimeter delimiting the boma.

A date layer was generated from Google Earth imagery by manually digitizing the underlying imagery data boundaries for the study region, and the corresponding imagery dates spatially joined to the fencing data (See Validation).

Kenya Wildlife Trust (KWT)

Klaassen and Broekhuis (2018)[18] collected data on the human footprint in the Maasai Mara ecosystem by manually digitizing all anthropogenic structures using QGIS in a similar way to SORALO. We created a 1x1 km grid layer covering over 6,000 km^2 (Table 1; Fig. 2), which included the Maasai Mara National Reserve, the surrounding conservancies and community land. Within this grid layer, we documented all human settlements using the OpenLayers for both Google Earth and Bing maps. The human settlements included agricultural land, settlements, livestock enclosures (bomas), settlements with adjacent livestock enclosures, towns, dams, tourist camps, and other and unknown developments. Here, we present the livestock enclosures (boma) data, settlements with adjacent livestock enclosures, and agricultural land. No date attribute is provided with this layer, although all data were collected using imagery that was available up to 2017.

Mara Elephant Project (MEP)

Beginning in November 2019, MEP identified fences on the ground using a custom mobile mapping application '*Njia'* based on the Esri Android SDK (https://github.com/walljcg/njia). Three field assistants using motorbikes have mapped 1787 km of fencing as of November 2020 (Table 1). Fences are classified by type

(Electric, Wire, Stone, Wood post, Cactus, Other) and based on strand count for wire/electric fences. Data collection is ongoing using other datasets (see Table 1) to target ground collection.

Data amalgamation

All data were amalgamated and processed using R[20] and the *sf* package[21]

a) **Agricultural data:** we combined the agricultural polygon data from the KWT and SORALO.
b) **Fence Polylines:** we combined the fenceline data from SORALO and Aarhus university into a single database. We used the 2016 Aarhus data, the MEP data, and the SORALO fencing data to present our best estimate of the current extent of fencing across the region. The spatial-temporal nature of the dataset will allow for future comparison of the Aarhus data across years (1985 - 2020). The Aarhus data were converted from a polygon to a polyline to match the format of the SORALO data.
c) **Boma Polygons:** we combined the boma polygon data from the KWT and SORALO.
d) **Boma Points:** we calculated the centroids of the boma polygon data from KWT and SORALO. In some bomas, there are multiple holding areas for livestock (Figure 4c). To produce a single point for each boma we create a buffer of 12.5m around each polygon and unioned any overlapping polygons before finding the polygon's centroid.

Data Records

We provide an initial four types of data that extend across southern Kenya (Figure 5): fences demarcated as polylines, polygons of livestock enclosures, centroids of points from the boma polygons layer, and agricultural polygons. These data are accessible from the Landscape Dynamics data portal (https://www.arcgis.com/home/search.html?q=landDx_export), under a Creative Commons Attribution ShareAlike 4.0 International (CC-BY-SA). This data portal is hosted on Esri ArcGIS Online and provides a web map service in addition to available data.

These data are stored as three feature collections on ArcGIS online, dependent on the geometry type of the data: polylines; polygons; or points. A Python script is run whenever the database has been updated from a Jupyter notebook on ArcGIS online, to produce a timestamped set of ESRI shapefiles and File Geodatabases from these feature collections. Publicly available data are searchable through the ArcGIS Online website.

Each geometry feature type (point, polyline, polygon) share a standardized data table format:

1) *type*: the type of feature represented by the geometry (e.g. Fence_Other or Fence_Electric_Unknown)
2) *name*: if available the name of the feature
3) *short_name:* if available the shortened name of the feature
4) *active:* a binary field indicating whether the data should be considered currently relevant for the landscape (1), only data with an active level is exported to the end-user in this release
5) *collect_user:* the person or organization responsible for the data collected
6) *collect_method:* the methodology used for data collection (such as Google Earth Digitisation, Landsat Digitisation, or GPS)
7) *collect_date:* when known the date of the data acquisition, including the date of imagery used during digitization or field data collection (UTC)
8) *ground_verified:* indicates whether the data has been confirmed on the ground.
9) *spatial_feature_owners:* the owner of the spatial feature
10) *spatial_data_owners:* the owner of the spatial data
11) *data_availabiltiy: an* indicator of the open-access format

12) *other_id*: attribute data passed in JSON format containing information specific to the data contributor
13) *attributes*: a javascript object notation (JSON) column to store additional attribute, type or labels for a given feature
14) *globalid*: a globally unique identifier (guid) value for the feature
15) *parent_guid*: This describes a parent-child relationship between different features (even across geometry types) and allows the comparability of the connected features mapped across different years but whose geometry and attributes might vary.

Table 1 provides the details of the public data records released with this data descriptor. This includes the data geometry type, format, the data source, the total area covered (linked to the area of interest files), number and/size of the objects in the method used to collect the data, and the projection of the data.

235 **Table 1: Metadata for the data currently publicly available from the data portal**

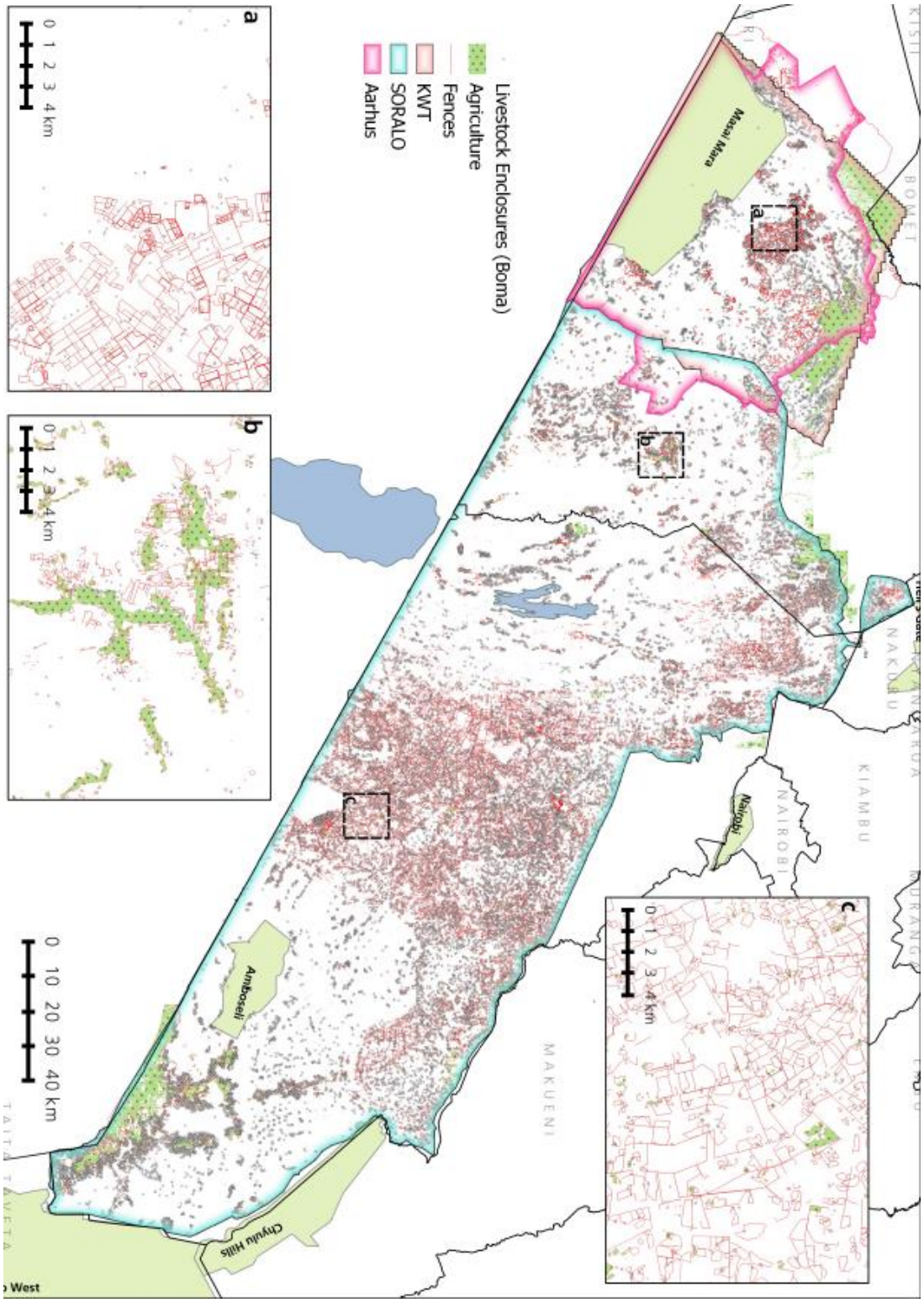
Data Type	Data Geometry Type	Data Contributor	Total Area covered	Number of objects/size	Methods	Projection
Livestock Enclosures (Boma)	Point	SORALO	25,041 km^2	26,309	Google Earth Digitization	WGS84
		KWT	6,373 km^2	4,714	Google Earth and Bing maps Digitization	
		Total	*31,414 km^2*	*31,023*		
	Polygon	SORALO	25,041 km^2	32,592	Google Earth Digitization	WGS84
		KWT	6,373 km^2	5,118	Google Earth and Bing maps Digitization	
		Total	*31,414 km^2*	*37,710*		
Fences	Polylines	SORALO	25,041 km^2	37,847.5 km	Google Earth Digitization	WGS84
		Aarhus University	5,771km^2	2,104.7km (2016 data)	Digitization of Landsat Imagery	
		Mara Elephant Project		1,787 km	Ground collection	
		Total	*30,527km^2*	41,739.2 km		
Agriculture	Polygon	SORALO	25,379km^2	785.9km^2	Google Earth	WGS84

					Digitization	
		KWT	6,373 km^2	676.6 km	Google Earth and Bing maps Digitization	
		Total	*31,414 km^2*	*1,462.5km^2*		

Overview of data

Fig. 2 provides an overview of the geographical location of the data sources collected, contained in the area of interest shapefile. In total, we collected data from over 31,000 km^2. In total our database consists of 37,710 livestock enclosure polygons; 31,023 livestock enclosure points; 41,739 km of fencing; and 1,465.5km^2 of agricultural areas.

Figure 2 (below) - A map of the dataset presented in the first release of this database. Including the rough area covered by each data-collection method (no area is given for MEP as data collection is ad-hoc), and the three datasets released livestock enclosures (bomas), agricultural land use, and fencing.


Livestock Enclosures (Boma)
Agriculture
Fences
KWT
SORALO
Aarhus
a
b
c
0 1 2 3 4 km
0 10 20 30 40 km
Masai Mara
Amboseli
Chyulu Hills
Nairobi
KIAMBU
NAIROBI
MAKUENI
NAKURU

Technical Validation

Aarhus University, SORALO and KWT digitized bomas, fences and agriculture in a systematic manner using available satellite imagery (see methods). All digitization was re-checked by supervisors, to ensure that no data had been missed, and was adjusted following quality control where and when required. All data were then manually checked by conservation practitioners knowledgeable of the study area. Both the spatial resolution and temporal sampling of the data may present limitations to its accuracy and usage.

Spatial resolution

For both the KWT and SORALO datasets collected using Google Earth, we used the latest Google Earth imagery. Additionally, for KWT's dataset, we also used the latest Bing maps imagery. However, the spatial resolution of this Google Earth and Bing maps data varies. Resolution can be as high as ~0.5 m, while a few remaining areas still rely on Landsat Imagery with a resolution of 30m. However, the quality of the Google Earth and Bing maps imagery was generally high enough across the study area to accurately delineate bomas, fencelines and agricultural land. Figs. 3 & 4 provide examples of areas that would be digitized, with the boundaries of the boma and fence lines clearly visible.

The fencing data collected by Aarhus University used Landsat Imagery at 30m resolution and smaller fences may be missing from the dataset as they are harder to distinguish. This is also true for wire fence (the predominant type of fencing around the Maasai Mara; Fig. 3c). Vegetation differences used to identify these fence lines may take some time to develop. Therefore, there may be an underestimate of the fences mapped, especially in those regions with high usage of wire fences.

It must be noted that images from Google Earth have an overall positional root mean squared error of 39.7 m, which may impact the interpretation of this dataset[22]. We believe that these errors are acceptable for our first attempt at collecting landscape-scale data, and will be refined over time with improved imagery and ground-truthing. Landsat data has a root mean squared error usually below the size of a pixel, with 90% of pixels having less than 12m deviation[5].

[5] https://www.usgs.gov/media/videos/landsat-collections-rmse

Temporal variation

The most likely discrepancies in data quality will arise from temporal variation in fencing placement, boma usage and placement, and agricultural change. Google Earth data were used for SORALO, using data available up to February 2020. Google Earth and Bing maps data were used for KWT, with data up to 2017. The weighted mean imagery date for SORALO (weighted by the area covered) was the 9th of September 2016 and ranged from 15th of December 2000 to 12th of February 2020 (Fig. 5). Where possible we have added a date-time stamp to the boma, agriculture and fencing dataset to best match the date the satellite imagery was acquired, or when it was collected on the ground. However, KWT and some SORALO data lack date attribute, the latter because no date stamp was found in Google Earth, and the former because no date was recorded for any data. The Aarhus University fencing data are from a Landsat Image from January 2016, and the MEP data are from on-the-ground collection. Our database is built so that as new or updated data become available, from both new satellite imagery and ground-based identification, the data layer can be adjusted (see below).

Livestock enclosure validation

We used data on the location of SORALO livestock enclosures from the Magadi region[23] (collected using handheld GPS devices), to estimate the accuracy of our data collection. The SORALO ground-truthed database contains 668 bomas, which have been occupied at least once during 2014-2017. In the same area, our boma points database contains 573 bomas (85%) of which 41.2% (n=275) are within 100m of ground-truthed points and 87.7% (n=586) are within 500m of the ground-truthed points. These ground-truthed points may have inaccuracies from their data collection. Also, many livestock enclosures distant from ground-truthed points are newer than the ground-truthing dataset.

Agricultural land validation

We compared our agricultural data layer to a commonly used global open source data layer, the 2015 GFSAD30AFCE 30-m for Africa: Cropland Extent Product (www.croplands.org). Our layer agreed with the Cropland Extent Product across 856km^2 of cropland. However, our layer demarcated 455 km^2 (34.4% of the total extent) more agricultural land than was found in the 30m Cropland Extent Product, because many small areas of subsistence farming had not been detected by this global layer. Additionally, the Cropland Extent Product contained 468km^2 (35.3% of the Cropland Extent Product) of agricultural extent not captured in our layer. Much of this was on the

periphery of large continuous agricultural areas and appears inaccurately mapped by the global product.

Continual validation and improvement of database

Ongoing ground-truthing exercises by the Mara Elephant Project and other partners will improve the quality of the database over time, particularly the datasets on wire fencing in the Mara region. To do so the Njia app (see above) combined with a QuickCapture app (to validate fence lines and boma locations using aerial reconnaissance) are integrated into the ArcGIS online framework, and following validation both manually and using automated Python script, can be used to update the features collection database.

Additionally, any data currently held in the private domain can be easily integrated into this database, and made available to the public domain with approval. Linking these features using a parent ID allows for not only the addition of new features, but improved spatial accuracy of old features, and temporal changes to features to be captured.

This database will be continually improved over time. For example, current efforts from conservation partners in the region have resulted in large scale acquisition of high resolution, up-to-date, satellite imagery which will be further used to refine this database.

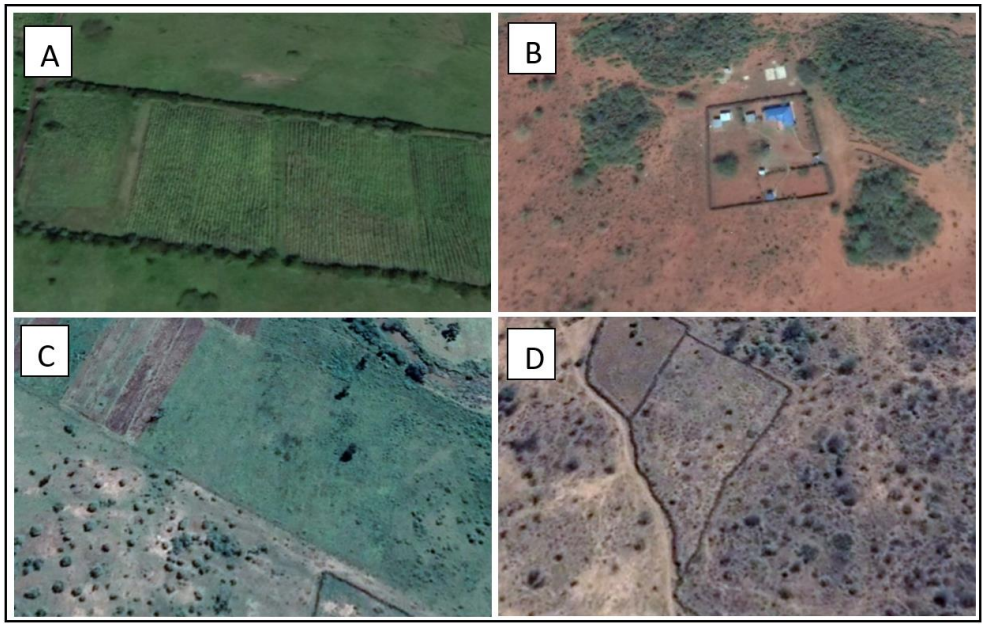


Figure 3 - Example of the fence lines that are visible with Google Maps imagery and which were digitized by SORALO.

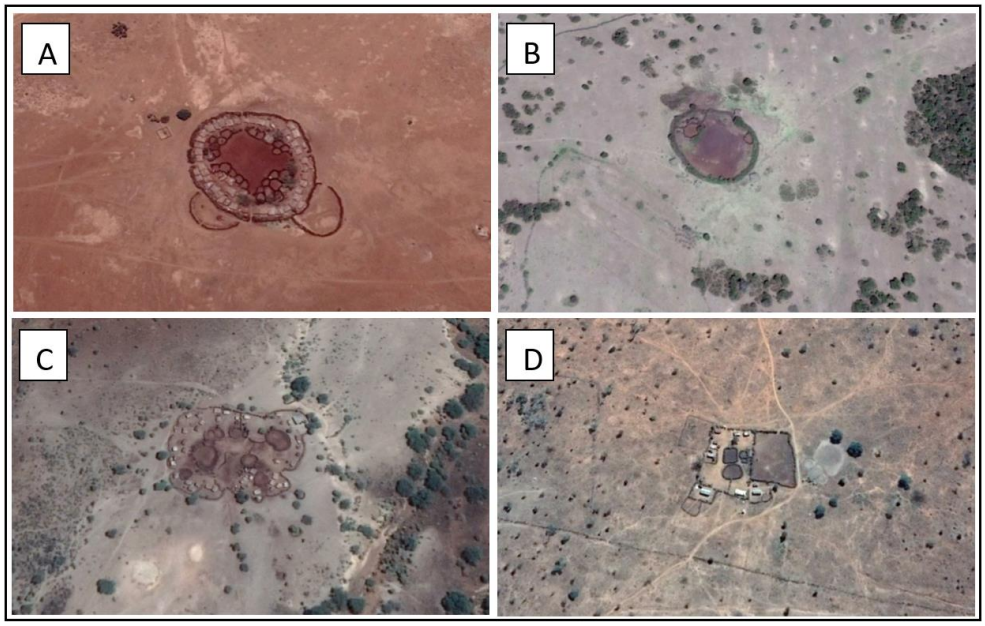


Figure 4 - Example of the different livestock enclosure types (bomas) that are visible with Google Earth and Bing maps imagery and which were digitized by SORALO and KWT. Note the visible change in terrain colour and texture where livestock is held and the surrounding brush fences.

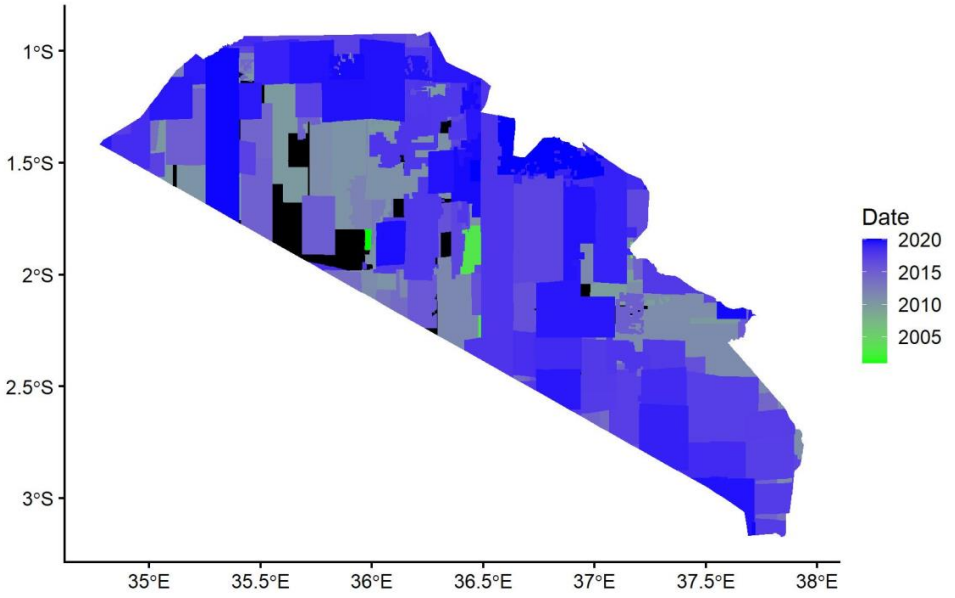


Figure 5 - The date of acquisition of satellite imagery from Google Earth used in the SORALO mapping process. Black polygons have no date attribute.

Usage Notes

We aim to provide a comprehensive layer of the most recent anthropogenic impacts for use at regional scales. These data, however, still require the end-user to interpret any results based on the method used to collect it, as well as the temporal dynamics of each data type. This is particularly relevant for areas under change where fencing is rapidly increasing. Temporal aspects of the data are also important for interpreting the occupancy of livestock enclosures (bomas) which are likely to change seasonally as forage and water distribution change, but also over longer periods as socio-economic pressures alter livestock management and governance practices (see validation above). Data collected through digitization of Google Earth and Landsat imagery may likely underestimate the extent of fencing where wire, rather than brush fencing is used, and where visible changes in vegetation condition are not apparent. Continual field-based data collection from the MEP team, and other project partners, will improve the accuracy of the digitization products. In addition, some datasets may overlap in the public release, including the Aarhus and MEP data. We provide all datasets in one release so that the end-user can make their own decision on filtering and combing data, based on their requirements. The area of each study is provided for this purpose.

This database will be updated and continually validated as new imagery, external data sources, and ground-truthed data are collected. The end-user should note this and expect changes to the database over-time. This includes the addition of other data sources such as land-use and land-cover maps, protected area boundaries, rivers, and roads. For example, already 3828 km of roads in the Mara region have been mapped. These data, and updates, will be made available by download through ArcGIS online.

While other options exist to host open access data, such as Open Street Map (OSM), we chose to create our database and host it through ArcGIS online for several reasons. First, we want to capture the temporal dynamics of change within this region, which we are unable to do in OSM. Second, we want to have control over the contributions into this database so that only verified data, matching our required gaps in the database, are added. Third, it allows contributors to share data under varying degrees of access, dependent on the data's sensitivity and ownership rights. Finally, our database allowed meta-data specific to the datasets we are collecting, as opposed to conforming to other standard tags.

Data owners who are interested in contributing open-access data to this database are welcome to reach out to the lead author. Our initial data release provides some of the most important features for determining the level of fragmentation and losses of mobility in the region. Over time, we hope to grow the geographic range of the database

and the data sources. We anticipate that this initiative will encourage data-sharing in the Kenya-Tanzania borderlands area (and more widely in East Africa, with this approach already being adopted in northern Kenya) and provide easy access to updatable data sources, which are critical to the conservation, management, and understanding of this region. In addition, we hope the landDX database structure encourages more frequent and better standards of data sharing in the broader conservation and landscape management communities.

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Author contributions

PT – led the compilation of the data, wrote the manuscript, conducted the validation, worked on the database, and supervised the collection of the SORALO data
IA – contributed to the collection and dissemination of data
KB – collected SORALO data
FB – supervised and collected the KWT data and contributed towards writing the manuscript
RB – provided the Aarhus data and contributed towards writing the manuscript
SC – collected MEP data, contributed towards the manuscript, maintained database
NH –collected MEP data, contributed towards the manuscript, maintained database
DH – collected SORALO data
BK– supervised and collected the KWT data and contributed towards writing the manuscript
ML– supervised and collected the Aarhus data
DM– contributed towards the design of data collection and towards writing the manuscript
KM– collected SORALO data
HM– collected SORALO data
NM– contributed to the design of the database
CO– collected SORALO data
EO– collected SORALO data
VO– collected SORALO data
JR– collected SORALO data

FP– contributed to the design of the database and contributed towards writing the manuscript
SR – supervised the SORALO data collection and contributed towards writing the manuscript
WS – collected MEP data and database maintenance
KS– collected SORALO data
JAS – contributed towards the design of data collection, the database, and towards writing the manuscript
JCS – supervised and collected the Aarhus data
ES– collected SORALO data
JdT – contributed towards the design of data collection and towards writing the manuscript
G.Western – supervised the SORALO data collection and contributed towards writing the manuscript
G.Wittemyer – contributed to the design of the database and contributed towards writing the manuscript
JW – supervised the MEP data collection, contributed towards the manuscript, designed and built the database and its associated tools, helped to lead and host the data amalgamation processes

Competing interests

The authors declare no competing interests.

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6

Wide-scale subdivision and fencing of pastoral commons jeopardises biodiversity conservation and pastoral livelihoods in Southern Kenya

6. Sbdivision and fencing jeopardises biodiversity conservation and pastoral livelihoods

Abstract

1. Globally rangelands are undergoing rapid social-ecological changes, yet the scale of these changes are rarely measured.
2. Fencing, sedentarisation, and land conversion limit wildlife and livestock access to vital resources such as water and seasonal forage and lead to rangeland degradation. In addition, these changes limit connectivity between wildlife populations creating a range of detrimental impacts.
3. Moreover, the combination of land privatisation, sedentarisation and fencing endangers pastoral livelihoods by reducing resilience to drought and diminishing livestock holdings per person.
4. We provide a unique, urgent, and vital snapshot across >30,000 km^2 of southern Kenya's rangeland, covering four ecosystems renowned for their rich megafauna and pastoral people.
5. We document and explore the drivers of extensive fencing (~40,000 km), the proliferation of livestock enclosures (>27,000), and the cultivation of rangelands (~1,500 km^2).
6. Fencing is generally more prolific in areas that have been converted from community tenure to private individual titles, especially in areas with the highest land value, driven by proximity to Kenya's capital, Nairobi, and areas with high agricultural value. These factors can result in land sale by rural landowners to speculators and the eventual transformation of land into agricultural, industrial and urban land use.
7. Space for wildlife and livestock is limited in private, subdivided land. Here, livestock enclosures are at higher densities, and less space exists between than in community land or conservation areas.
8. Conflicting planning incentives, policies, and economic forces are driving unsustainable and potentially irreversible social-ecological transitions at unprecedented scales. A ranger of financial, policy and governance-related interventions are required.

Main Body

Rangelands cover >30% of the world's terrestrial surface, supporting billions of people and nearly half of all livestock and sustaining biodiversity and vital ecosystem services (Briske, 2017). Yet many rangelands are undergoing radical social and ecological transitions, jeopardising global plans to *"prevent, halt, and reverse the degradation of ecosystems worldwide*" during the upcoming UN Decade of Ecosystem Restoration[1] (Reid, Fernández-Giménez, & Galvin, 2014). Biodiversity is decreasing mainly through land conversion and fragmentation (Hobbs et al., 2008; Reid et al., 2014), although East Africa is one region that still hosts pastoralist social-ecological systems in which the rangeland is shared with a high abundance and diversity of large mammals (Western et al., 2020a). However, these systems face profound degradation due to widespread agricultural expansion, sedentarisation of pastoral people, and accelerating fencing, which is fragmenting ecosystems and threatening their sustainability (Reid et al., 2014; Western et al., 2020a).

The scale of these changes are poorly understood, primarily because of a lack of large-scale spatial data (Hobbs et al., 2008). Recently, we synthesised and published one of the largest known datasets for rangelands on the extent of fencing, agricultural land use, and the location of livestock enclosures, mapped over 30,000 km^2, across four large, adjacent ecosystems in southern Kenya with comparable social-ecological dynamics: Maasai Mara, Loita Hills, the South Rift Valley and Amboseli (Fig. 1a; Tyrrell et al., 2020). We identified nearly 40,000 km of linear fencing—enough to circle the globe—and 1,500 km^2 of former rangeland converted to agricultural land, and 27,000 livestock enclosures. This indicates severe landscape fragmentation since the 1960s, when fences were virtually absent, with much of these changes occurring very recently (Løvschal et al., 2017). We hope that these data will form the basis for new studies that seek to address the multicausal and highly complex social and environmental challenges to the sustainability of rangeland ecosystems.

Critically, fencing and land conversion alter the mobility of wildlife and livestock, including their access to vital resources such as water and seasonal forage, which are patchily distributed in rangeland ecosystems (Hobbs et al., 2008; Homewood et al., 2001; Said et al., 2016; Western & Gichohi, 1993). In addition, these changes limit connectivity between wildlife populations, preventing wildlife from entering new areas, preventing genetic exchange, exacerbating human-

[1] https://www.decadeonrestoration.org/

wildlife conflict, squeezing wildlife and livestock into smaller areas, altering ecosystem function, and preventing wildlife and biodiversity from adapting to climate change (Newmark, 2008; Osipova et al., 2018; Veldhuis et al., 2019; Western & Maitumo, 2004; Western, Waithaka, & Kamanga, 2015). Sedenterisation, resulting in a homogeneous year-round spread of livestock enclosures, reducing livestock mobility, and increases local livestock densities and grazing pressure, which reduces forage productivity and creates deeper annual and seasonal deficits in grass biomass than from rainfall-induced droughts alone (Groom & Western, 2013; Western, Mose, Maitumo, & Mburu, 2021; Western, Mose, Worden, & Maitumo, 2015). These localised high stocking rates and lack of mobility alter the species composition, height, productivity, and nutritional content of forage resources, with ramifications for wildlife and livestock composition and productivity (Augustine, Mcnaughton, & Frank, 2003; Boone, BurnSilver, Thornton, Worden, & Galvin, 2005; Groom & Western, 2013; Western, Groom, & Worden, 2009; Young et al., 2013). Moreover, the combination of land privatisation, sedentarisation, and fencing endangers pastoral livelihoods by reducing resilience to drought and diminishing livestock holdings per person (Bedelian & Ogutu, 2017; Boone et al., 2005; Kimiti, Western, Mbau, & Wasonga, 2018), with these negative trajectories likely to increase with continued global climate change (Funk, 2020).

The scale of fencing, sedenterisation, and land conversion in southern Kenya

We quantified the extent of fencing, sedenterisation, and land conversion across four iconic ecosystems with comparable but unique social-ecological dynamics. First, Amboseli, a 10,000km^2 area, is home to several thousand elephants, hundreds of lions, and thousands of wildebeest and zebra. Private land in this area is now heavily fenced (21,150 km), with a mean density of 1.78 km.km^{-2} (Fig. 1&2), with high densities of livestock enclosures, and agriculture covers 42,809 ha or 3.4% of the area (Fig.1). This proliferation of fencing, sedenterisation, and land transformation has fragmented the ecosystem, with severe implications for pastoral livelihoods (Kimiti et al., 2018), wildlife populations (Groom & Western, 2013), and the connectivity for large mammals (Osipova et al., 2018). Yet, considerable areas of unfenced land remain around the Amboseli National Park (Fig. 1& 2), especially in areas where communities have set aside parts of their land for conservation. Many of these communities are paid annual lease fees by conservation NGOs, supporting wildlife's persistence around the National Park[2], although subdivision and fencing are also underway here.

Second, the South Rift Valley, an 8000km^2 area, is primarily under communal ownership with a diverse and abundant wildlife community. Here, there is a high density of livestock enclosures and fences in private land in parts of the ecosystem (1.3 km.km^{-2} on average, 11,152 km in total: Fig. 1). Some areas in the south and west of the ecosystem remain unsettled and unfenced, including community conservation areas (Fig.1&2). In these areas, wildlife and livestock still maintain considerable mobility, which is vital for their long-term survival (Tyrrell, Russell, & Western, 2017). This region's arid nature and strong community governance structures that manage the landscape to maintain mobility for pastoralism have protected the land from subdivision and conversion to agricultural (0.9% of total area) or urban land use (Western et al., 2020b).

Third, the Loita ecosystem (~3000 km^2) has undergone considerable fencing, sedenterisation, and conversion to agriculture (8006 ha, 2.3% of total area, 3029 km total, 0.901 km km^{-2}; Figs. 1&2), which now limits the mobility of large mammals between the Maasai Mara and South Rift Valley. The Loita Forest is a vital part of this ecosystem, where considerable areas remain unfenced and unsettled (adjacent to the South Rift Valley). It is an important water tower for both the Mara-Serengeti and South Rift Valley ecosystems, a central connection for large mammal movement across the greater Kenya-Tanzania borderlands region, a critical area for carbon sequestration, and a biodiversity hotspot (Broekhuis et al., 2018).

Finally, the Maasai Mara ecosystem (~7000 km^2), world-renowned for its large wildlife populations, still has a comparatively low extent of fencing and livestock enclosures due to the Maasai Mara National Reserve and the surrounding conservation areas, supported by eco-tourism lease fees (3039 km total, 0.477 km.km^{-2} on average). However, as reported by Løvschal et al. (2017), there has recently been a rapid expansion of fencing around the Maasai Mara National Reserve and within surrounding 'conservation areas' (Fig. 1&2), with associated wildlife declines, including the near complete collapse of the Loita Plains migration of over 300,000 wildebeest (Løvschal, Håkonsson, & Amoke, 2018). Large-scale conversion to agriculture has occurred in key wet season grazing areas for wildlife, extending south from private lands in the north (8.3% of the ecosystem; 57974 ha; Fig. 2).

Economic, social, and policy drivers

Across southern Kenya, pre-and post-colonial government policies have continually encouraged the privatisation and subdivision of unfenced communally-owned land and the sedenterisation of pastoralists (Mwangi & Ostrom, 2009). When coupled with a combination of structural forces,

including Kenya's fast-growing economy and population, land commodification and demands for land, this has led to wide-scale fencing of privatised land to secure ownership (Mwangi & Ostrom, 2009; Rutten, 1992; Weldemichel & Lein, 2019) (Fig. 4b). Shrinking space for pastoralism due to these policies, in addition to the expansion of government-protected areas and conservancies, has perversely incentivised fencing on private land to protect individual property rights and resources (including forage for livestock) and to avoid human-wildlife conflict (Fig. 4b) (Løvschal et al., 2018; Said et al., 2016; Weldemichel & Lein, 2019).

Fencing has escalated most rapidly in areas with rapidly increasing land prices (Fig. 4a), driven by proximity to Kenya's capital, Nairobi, and areas with high agricultural value (Tyrrell, Naidoo, Macdonald, & du Toit, n.d.). These factors can result in the sale of land by rural landowners to speculators and the eventual transformation of land into agricultural, industrial and urban land-use (Fig. 4a)(Rutten, 1992; Tyrrell et al., n.d.). The Nairobi National Park and Athi-Kapiti ecosystem, adjacent to Nairobi, are now almost completely fragmented with a collapse of the previously rich migratory system of wildlife and pastoralism (Nkedianye et al., 2020; Said et al., 2016). Economically, subdivision into private parcels may empower landowners, at least in the short-term, allowing them entry into the cash economy through land sales, loans on title deeds, and subsistence agriculture. However, land sales are often driven by wealthy and powerful investors external to the local community (Rutten, 1992). Without access to grazing land, pastoralists will eventually be forced to abandon their traditional lifestyle and culture, risking a poverty trap (Rutten, 1992). Poor planning and weak local leadership during the subdivision process itself, often led by local elites or government officials, can exacerbate inequalities within communities and worsen fencing and land conversion's ecological impacts.

Using a point process model (PPM) with a Poisson distribution, we found that livestock enclosures (total n = 29,467) density were lowest in protected areas followed by conservation areas, community land, and private (subdivided) land (Fig. 3b). Rainfall and land-tenure both explained the distribution of livestock enclosure density (PPM, df= 4, p-value < 0.0001). Private land in Amboseli, the South Rift and the Mara ecosystem showed some of the highest average densities (Fig. 3b). Conservation areas have the largest large spaces between livestock enclosures (Fig. 3c). On the other end of the spectrum, private subdivided has the least open space between livestock enclosures. This greater homogeneity and lack of space between bomas in private landscapes are related to the sedenterisation of pastoral households during privatisation and has likely negatively impacted rangeland health (Groom & Western, 2013).

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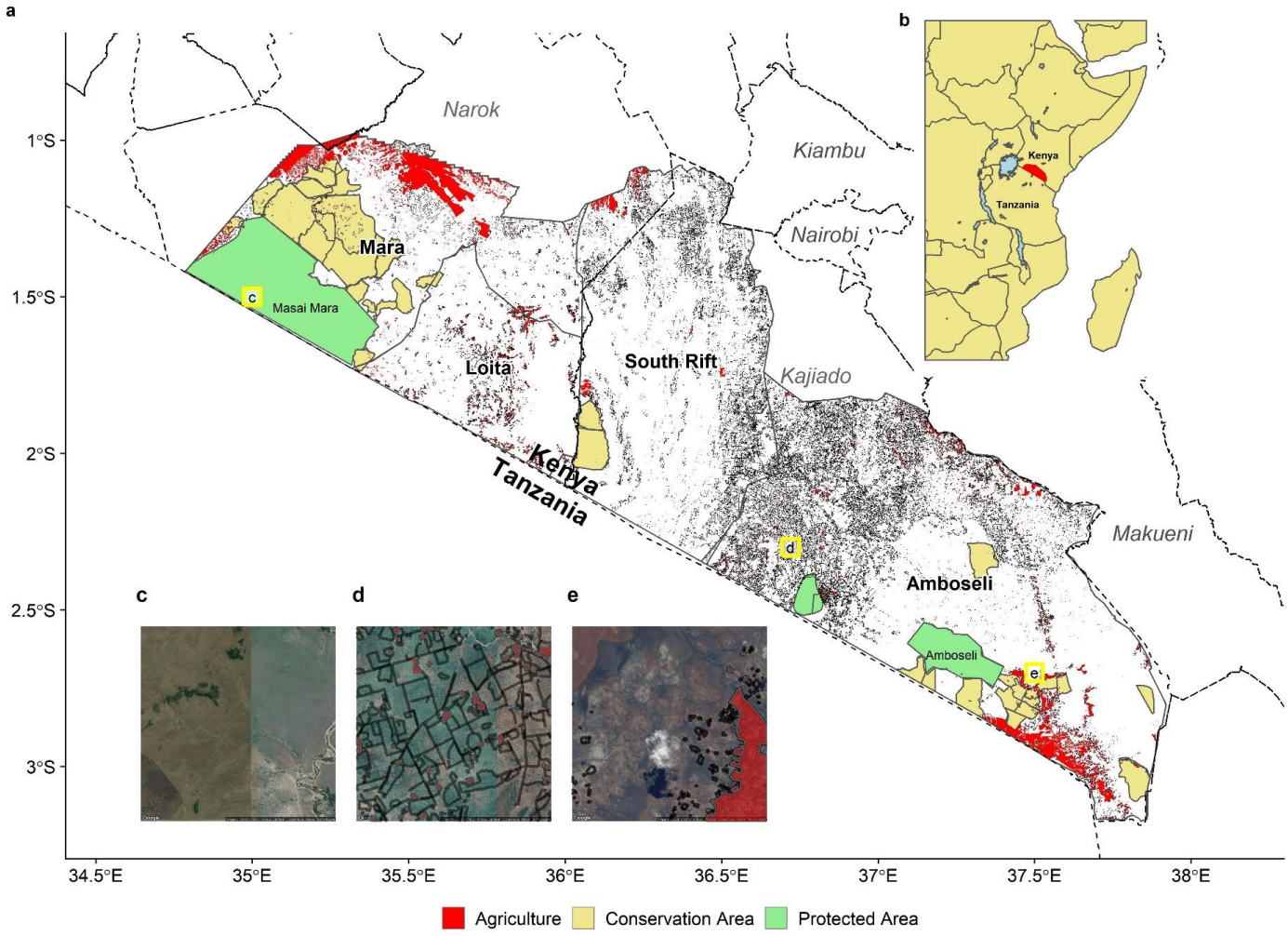

Figure 1: a) ~40,000km of fencing (black lines) and ~1500km^2 of agriculture (red polygons) across four southern Kenya ecosystems (left to right: Maasai Mara; Loita, South Rift Valley, Amboseli). Kenya county boundaries are shown for reference (dashed lines). b) The location of the study area (red), within East Africa; c-e) zoomed in panels of three areas under different states of fencing and agricultural development, with Google Maps imagery for reference.

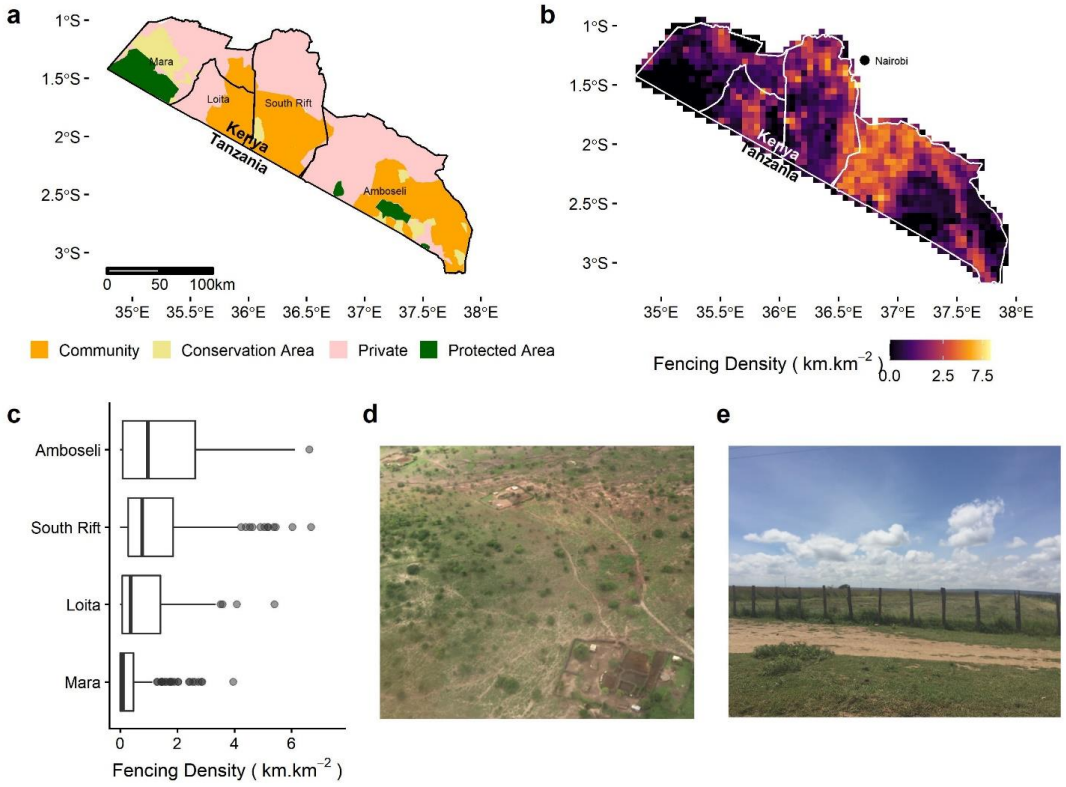

Figure 2 a) The four ecosystems in southern Kenya: Amboseli, South Rift (Valley), Loita (Hills), and (Maasai) Mara. Those areas with government-run protected areas (Protected Areas) in dark green, established community and private conservation areas (Conservation Area), the remaining land is subdivided and individually titled private land without conservation efforts (Private) and collectively owned or managed community land (Community) b) fence density calculated as the km.km^{-2} calculated on a 0.05-degree grid (~5 km). Nairobi, Kenya's capital city, is displayed for reference; c) Boxplot of fence density within each ecosystem, with median (line), first and third quartiles (box) and 1.5 times the interquartile range (whiskers); d) example of brush fences around settlements; c) wire and post fencing to demarcate property in the Loita plains (north-east of the Mara ecosystem)

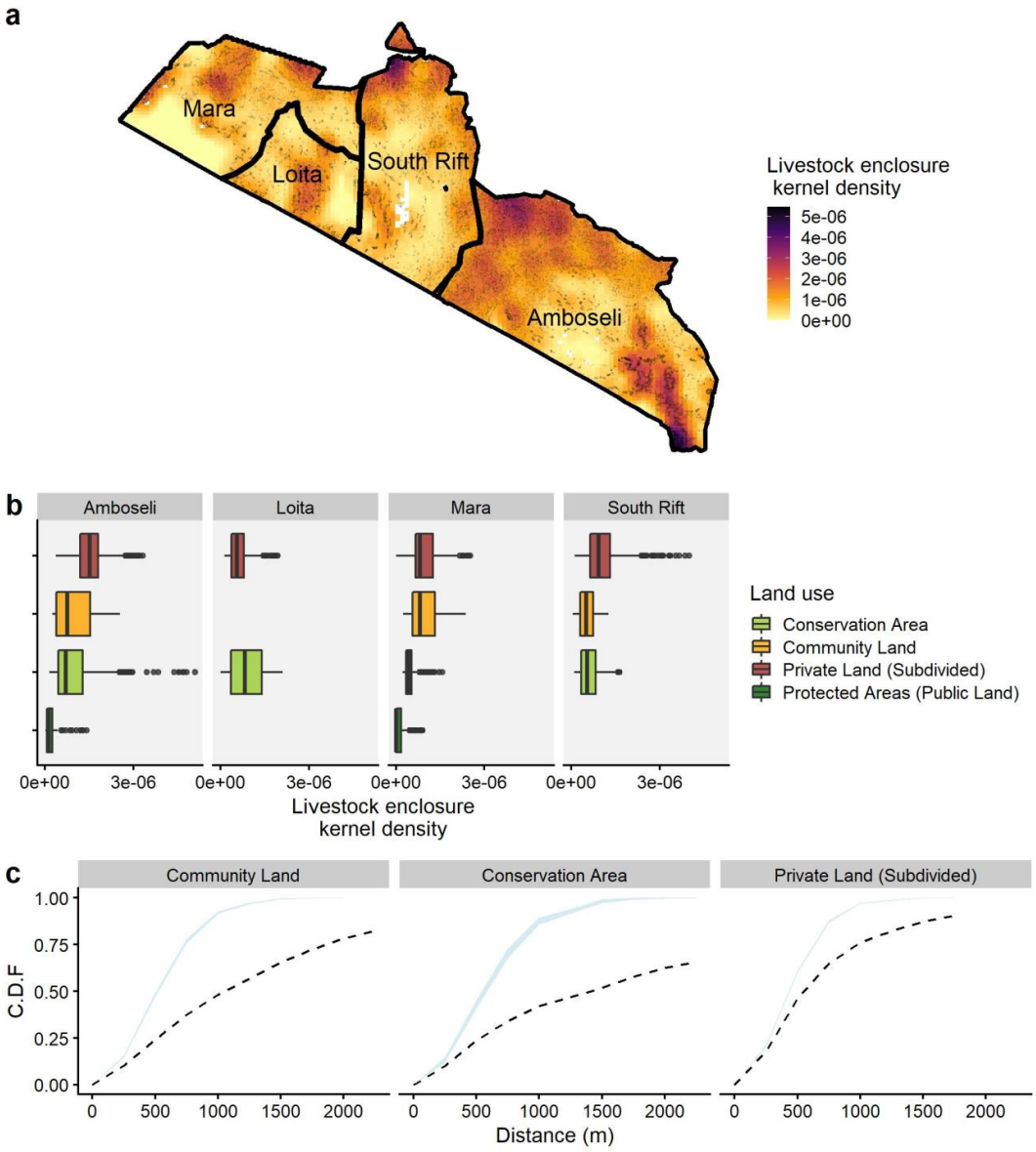

Figure 3: In southern Kenya, space for wildlife and livestock is limited in private, subdivided land. Here, livestock enclosures are at higher densities, and less space exists between than in community land or conservation areas. a) Livestock enclosure kernel density calculated using 29,467 boma locations (light black dots). b) A boxplot showing the frequency of the different livestock enclosure kernel density values for the four ecosystems and four land use types. d) This shows the cumulative distribution function (CDF) of the distance from a fixed point in space to the nearest livestock enclosures, calculated using the empty space function F of a stationary point process for each land use type. Protected areas are excluded. They have few or no

settlements within their boundaries. The blue ribbon represents the 96% point-wise intervals of the theoretical distribution of livestock enclosures under a stationary Poisson process of the same estimated intensity. Conservation areas have the shallowest slopes, indicating large spaces between livestock enclosures. On the other end of the spectrum, private subdivided land shows a curve that quickly increases to an asymptote, indicating that little open space is available.

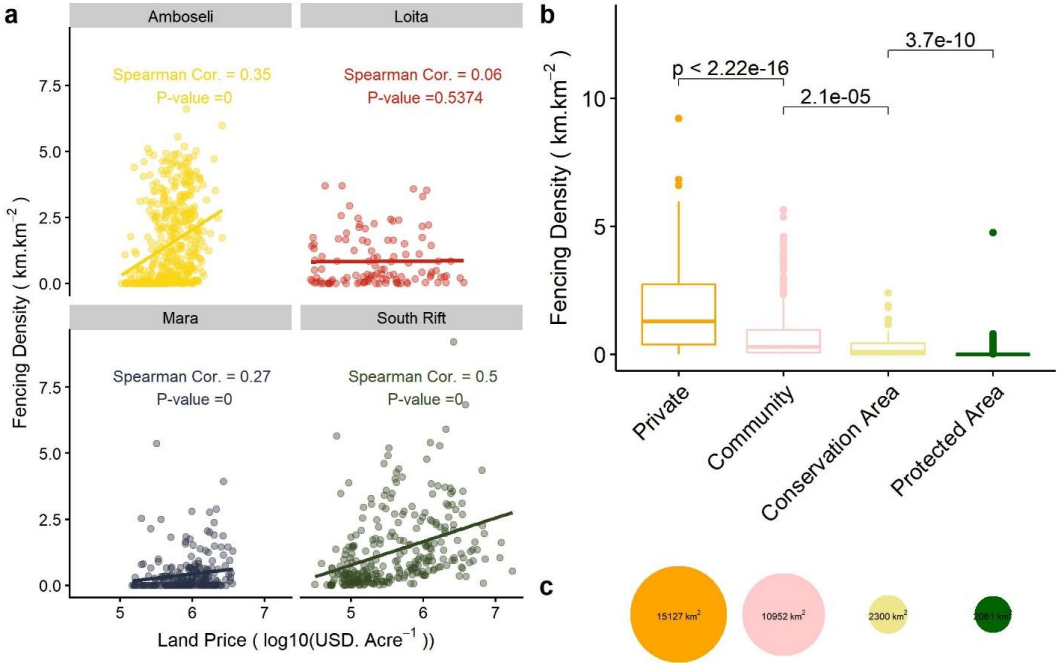

Figure 4: a) The density of fences is positively correlated with the price of land in Amboseli, Mara and South Rift. The effect is strongest in Amboseli and the South Rift, where prices and land conversion are high and driven by the proximity to Nairobi, Kenya's capital, and main roads. b) Boxplots of fence density in each land-tenure type across the region. Private areas have the highest fence density, followed by community areas, conservation areas, and protected areas. The comparison text indicates p-values from a Kruskal-Wallis test between groups. c) Bubble plot comparing the total area of each land-tenure type.

Solutions to prevent negative social-ecological trajectories

To maintain social-ecological systems with land-sharing between wildlife and local communities, land use planning for the remaining areas, particularly those currently undergoing subdivision, is vital and pressing. This must allow for people to equitably benefit from their land while maintaining the space and mobility required for livestock and wildlife (Western et al., 2020a). In Amboseli, a comprehensive ecosystem management plan and a locally developed subdivision plan are indeed guiding the process of subdivision to ensure equitable and social - ecologically sensible allocations of land[3]. In the community-owned and fertile Loita ecosystem, where conversion to private holdings are underway, bottom-up processes are underway to incorporate and adapt current community and regional government spatial plans.

[3] http://www.amboseliconservation.org/news--commentaries/the-subdivision-of-ogulului-group-ranch-does-it-spell-doom-for-amboselis-wildlife

In the longer term, however, the response to these changes must be driven by regional (county) governments in collaboration with local communities, with significant support from the national government, local and international civil society stakeholders, and where relevant, tourism stakeholders (like the lucrative Mara). This support includes policy reforms of planned fencing schemes and land subdivision, coupled with diversifying and expanding economic incentives for maintaining open rangelands, to ensure the social-ecological sustainability of these ecosystems, including their human and nonhuman inhabitants (Lindsey et al., 2020; Norton-Griffiths & Said, 2009). This would avert the current situation, where there is *ad hoc* propagation of fences encircling land subdivided into small parcels.

Ultimately the highest costs of wildlife and conservation are borne by local communities, and this must be addressed (Norton-Griffiths & Said, 2009; Weldemichel & Lein, 2019). Solutions may include investments in and recognition by national and regional governments of the economically and culturally important livestock industry; increasing the payment for ecosystem services; and restructuring and expanding the lucrative eco-tourism industry, ensuring that local communities receive a greater benefit (Lindsey et al., 2020; Western et al., 2020a). In some areas, it appears that these types of mechanisms may provide incentives for the removal of fencing and prevent sedenterisation (Western et al., 2020a). Reducing the direct and indirect costs of co-existing with wildlife is also critical (Norton-Griffiths & Said, 2009).

Immediate investment to support leases and land purchases for areas that are under imminent threat of fragmentation and conversion, yet critical for ecological integrity, may be required, as well as co-created, long-term solutions for people currently living in and managing these areas. The scale of these investments needed in the coming years is vast and may amount to millions of dollars per year in southern Kenya alone (Norton-Griffiths & Said, 2009). For example, in the private land around the Maasai Mara Reserve, over $6 million is already invested in conservation areas through land leases to offset the opportunity costs of conservation. However, this may not be enough to ensure equitable and sustainable livelihood options for the local community (Bedelian & Ogutu, 2017).

Any support garnered would need to be underpinned by strong and accountable local leadership and governance, along with devolved benefits and decision-making rights to local people, in order to ensure its ultimate effectiveness and sustainability (Western et al., 2020a). Kenya has one of the more proactive policies for devolving the benefits and management rights of natural resources in eastern and southern Africa, including the benefits of wildlife (Western, Waithaka, et al., 2015). More is needed to make these efforts sustainable, fair, and effective, at the landscape scale (Weldemichel & Lein, 2019). For the remaining areas not yet subdivided, there is a need to maintain and empower community tenure and governance systems, including adopting the recent Community Land Act, allowing for an alternative to uncontrolled and unequitable subdivision (Fig. 4b).

Conclusions

Our data and analysis, across >30,000km^2 of southern Kenya, provides a unique, urgent, and vital snapshot of the social-ecological changes occurring across rangelands. Similar changes are occurring at different rates across eastern and southern Africa, North America, Australia, South America, and central Asia, yet few of these changes have been documented at the spatial scale we have covered (Reid et al., 2014). As we enter the UN Decade on Ecosystem Restoration, global efforts must be strengthened to conserve and sustainably use rangelands. This requires swift and thoughtful action by governments and appropriate support to local communities to avoid irreversible losses of habitat, wildlife, ecosystem services, and the cultural heritages of pastoralist societies.

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Methods

Data on land tenure in Southern Kenya were collected and split into four categories as defined by the Constitution[1] and Wildlife Conservation and Management Act, 2013[2]: (i) Protected area (State Forest Reserves, National Parks, and National Reserves), land where human settlement is limited and the land is under public ownership; (ii) Conservation Areas, private and community land which has been set aside for wildlife conservation; (iii) community land, land under de facto or de jure community ownership; and (iv) private land, land which has been subdivided with land title deeds issued to individuals. These data were collated from multiple sources including BigLife Foundation, Maasai Mara Conservancies Association, South Rift Association of Land Owners, Kenya Wildlife Conservancies Association, and the African Conservation Centre. Due to the many conflicting land claims, and potentially inaccurate boundaries, these data represent the best estimate of land tenure at a broad scale and are by no means definitive.

Ecosystem boundaries were digitised from original drawings of the Kenya Rangeland Ecological Monitoring Unit (KREMU), who split Kenya into 44 ecosystems (ecological units), based on topography, vegetation, wildlife migration patterns, and seasonality[3]. We adjusted the boundaries of the ecosystem to split the Nairobi and Amboseli ecosystems based on wildebeest collar data and evidence from the literature[4–7].

Generally, spatial data on fences and agricultural expansion are localised and dispersed among data owners and databases. Here, we synthesised data from several research groups and conservation NGOs into a spatial-temporal database[8]. The data include 31,000 livestock enclosures, nearly 40,000 kilometres of fencing, and 1,500 km^2 of agricultural land. When data overlapped between research groups, the features with the newest date were selected. We clipped all our data layers to the extent files provided with each data source.

We generated several metrics to determine the distribution and total impact of fencing and agricultural land use within each ecosystem. First, we calculated the extent of agriculture within each ecosystem. Second, we calculated the length of fencing in each ecosystem. We then calculated the density of fences within non-agricultural land. We did this because the data we collected did not demarcate fences within agricultural land use. To demonstrate the spatial distribution of fencing within ecosystems, we created a 0.05° grid and calculated fence density, as kilometre of fencing per square kilometre, for each cell.

We performed a Spearman correlation test between fence density within the 0.05° grid to log10 transformed land price. Land prices (in USD) were calculated in Tyrrell et al., (in press) using scraped internet adverts of land sales from January 2018, which were modelled using a Generalised Additive Model with socio-economic and ecological covariates[9]. We assigned the dominant land tenure category to each 0.05° grid and conducted non-parametric Kruskal-Wallis tests on fence data between groups, sequentially ordered by median fence density.

For each land use type, we calculated the cumulative distribution function (CDF) of the distance from a fixed point in space to the nearest livestock enclosures, calculated using the empty

space function F of a stationary point process(Baddeley, Rubak, & Turner, 2015). Protected areas are excluded because they have few or no settlements within their boundaries. We then fit a model that assumes that the point process' intensity (livestock enclosure) is a function of land use and compared it to the null model and a model with mean annual rainfall in addition to land use and evaluate the best fitting models using log-likelihood.

These analyses were all conducted in R version 3.5.1[10], with the packages sf, tidyverse, raster, furrr, and exactextractr[11–14].

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7

Immediate human pressures outpace climate change in driving community dynamics at the livestock-wildlife interface.

Abstract

Across global rangelands, both inside and outside of protected areas, wildlife communities are changing and populations have plummeted. Disentangling the ultimate and proximate drivers of change is essential for predicting their effects on social-ecological systems. Here we show how immediate human pressures outpace climate change in driving community dynamics at the livestock-wildlife interface in six southern Kenya ecosystems, a region world-renowned for its wildlife and coexisting pastoral system. Over the last 40 years, the wild-herbivore community has seen decreases in all functional types except for non-ruminants, has undergone down-sizing reduced diversity, and homogenisation within and across ecosystems. In contrast, there has been a substantial proportional increase in shoat (sheep + goat) abundance relative to cattle within the livestock assemblage. There has been no discernable trend towards declining mean annual rainfall in southern Kenya, although drought events driven by changes to livestock management and its consequence impacts on grass biomass, are strong drivers of change in the large-herbivore community.

Introduction

Across global rangelands, both inside and outside of protected areas, wildlife numbers have plummeted in recent decades[1–3]. Large mammals are ecological linchpins[4], with their declining abundance leading to losses in ecosystem functions and services[3,5,6] that can cascade into co-extinction events across landscapes[7]. In addition, losing charismatic wildlife means declining foreign revenue, particularly for some African governments[8], jeopardy of the global biodiversity heritage[9], and a dwindling source of local livelihoods and employment[8] for some of the world's poorest people. There is a global synchrony to this phenomenon, which applies across wildlife species whether they are trafficked or not, implicating ecosystem-level effects of Anthropocene stressors, such as climate change, exacerbating various proximate and immediate human pressures. Disentangling these ultimate and proximate drivers of ecological change is essential for predicting their effects on social-ecological systems. Here, we describe and discuss how immediate human pressures outpace climate change in driving community dynamics at the livestock-wildlife interface in southern Kenya, a region world-renowned for its wildlife and coexisting pastoral system.

The main abiotic determinants of large-herbivore community composition in African savannas are rainfall and soil type[10–12]. Increased aridity due to climate change has been proposed as a reason for the changing composition of mixed wildlife-livestock assemblages in Kenya, with a relative increase in smaller-bodied species (sheep and goats) resulting from their drought tolerance[13]. However, in East Africa it is unclear whether there are any changes in rainfall patterns and seasonality attributable to climate change as of yet [14,15]. Rather, the frequency of drought events, measured by forage deficits, increase in areas where the sedentarisation and fragmentation of pastoral commons restrict livestock mobility[14,16]. Reduced livestock mobility is a result of the increasing abandonment of the traditional Maasai pastoral system and a proliferation of fencing. These developments are in turn associated with increasing rangeland homogeneity, changes in forage species composition, lower primary productivity per unit rainfall, increased frequency of forage deficits[14,17–19], and reduced diversity, productivity, and resilience of wildlife assemblages.[14,19]

Global trafficking of wildlife products, such as ivory, is a serious threat to wildlife conservation but international policing and intensive in-country protection has resulted in the elephant (*Loxodonta africana*) population increasing in southern Kenya[16]. Meanwhile, however, the large-herbivore community has undergone a dramatic decline in abundance of larger-bodied wild ruminants and an increase in smaller-bodied domestic ruminants[1,20]. We investigated the causes of these changes using data from six ecosystems across southern Kenya (Fig. 1). We specifically explored patterns of change in the mixed wildlife-livestock assemblage and its resource base, comparing the effects of ultimate (climatic) and proximate (changing pastoral management) drivers of that change at the wildlife-livestock interface. Our methodology involved analyses of long-term datasets on rainfall from satellite monitoring and gauge

readings, NDVI, vegetation monitoring plots, and regular aerial surveys of the mixed wildlife-livestock assemblage since the 1970s.

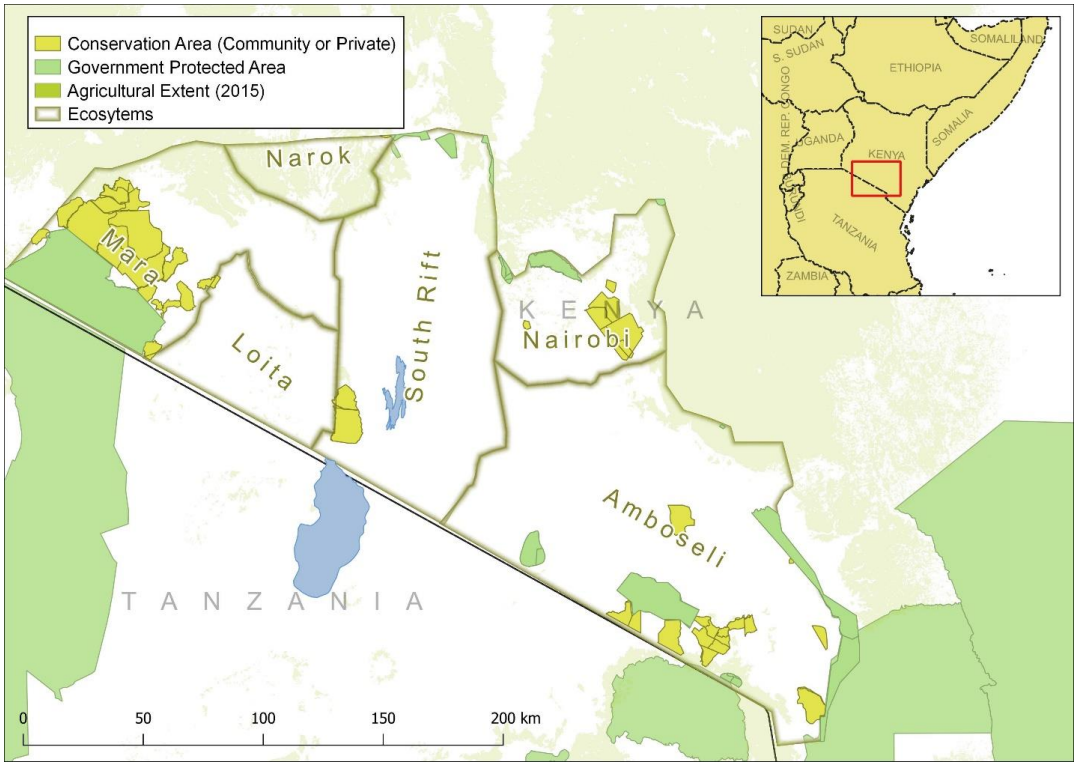

Figure 1 – The six study ecosystems (Mara, Loita, Narok, South Rift, Nairobi, and Amboseli) within the southern Kenyan landscape. Protected areas are displayed for reference, as is the extent of agriculture (light green) as of 2015, which is currently extending southward but is not accurately mapped.

Results and Discussion

Decreases in wild herbivores and cattle with increases in sheep and goats

We used a hierarchical Generalised Additive Model (HGAM) framework to model spatial and temporal correlation of aerial counts of wildlife density for 16 of the most common large herbivore species, spread across 40 years, using penalised spline-based smoothing. Overall, our HGAMs fit the data relatively well (median deviance explained was 50%, range 22%- 75%; S1), and we used these models to predict wildlife and livestock densities across four decades (the 1970s, 1980s, 1990s, 2000s) at a 4km^2 resolution covering 36,144km^2, and six ecosystems (S1).

It is common to convert species abundance or density estimates into mass-scaled values (e.g. metabolic biomass) for comparisons across differently-sized species in an assemblage. In our case, we are interested in the ways in which changes in ungulate community composition and abundance influence forage consumption in relation to forage availability at the ecosystem level. That requires quantifying the plant tissue passing through each herbivore species population per unit area per unit time. Therefore, we used species biomass to calculate dry matter intake (DMI). We used the unit body mass (M) of each species, multiplied by its population density estimate, in the equation $y=aM^b$ with b= 0.885, and a= 0.026, to produce daily DMI per km^2.[21]

During the study period, livestock (in particular cattle) has continually been the dominant consumer in most of these ecosystems, increasing in proportion from ½ of total DMI in the 1970s to ¾ in the 2000s, although total livestock DMI decreased from 2.21mT.yr^{-1} to 1.98 mT.yr^{-1} (Fig. 2). The proportional (and total) DMI by sheep and goats ('shoats') increased over time from 8.0% (0.31mT.yr^{-1}) to 15.5% (0.42 mT.yr^{-1}), while the proportional DMI of cattle increased slightly from 46.4% to 56.8% but the total DMI of cattle decreased from 1.82mT.yr^{-1} to 1.52mT.yr^{-1}. The reason for the proportional increase in livestock DMI despite an absolute decrease is that DMI by wild herbivores decreased substantially across most areas (Figure 2), from 43.6 % (1.72mT.yr^{-1}) of total DMI in the 1970s to 26.0% (0.70mTyr^{-1}) in the 2000s. Two protected areas show the greatest declines in wild herbivore DMI from 1.17 mT.yr^{-1} (72.4%) to 0.46 mT.yr^{-1} (45.0 %) in Maasai Mara National Reserve, and from 0.15mT.yr^{-1} (52.4%) to 0.03 mT.yr^{-1} (18.0%) in Nairobi National Park. Of all functional types, water-dependent wild grazers declined the most in DMI from 6.53 mT.yr^{-1} (30%) in the 1970s to 2.16 mT.yr^{-1} (14.6%) in the 2000s, largely in the Mara and Nairobi ecosystems. Among wild ruminants, large browsers, mixed feeders, and small browsers all showed major declines whereas non-ruminants also experienced some decline in DMI but with little proportional change, from 2.26 mT.yr^{-1} (6.24%) to 1.63 mT.yr^{-1} (6.61%).

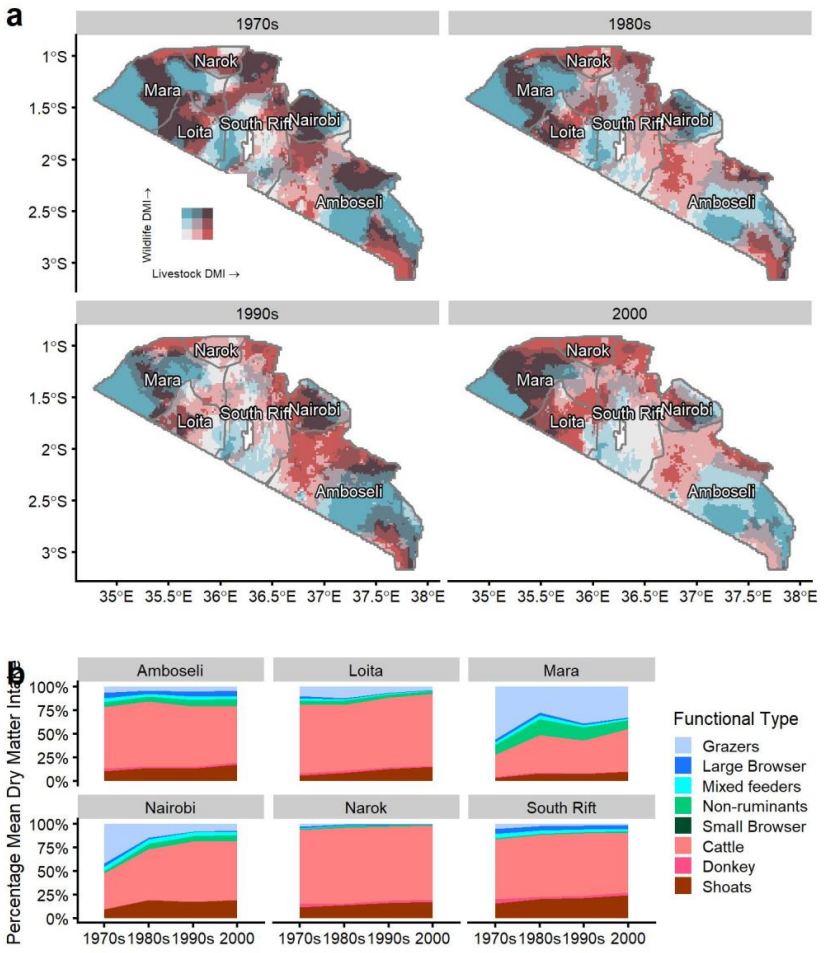

Figure 2: Predicted changes in dry matter intake (DMI) across four decades (1970s, 1980s, 1990s, 2000s) and six ecosystems (Mara, Loita, Narok, South Rift, Nairobi, and Amboseli) in southern Kenya covering 36,144km^2 for livestock species (cattle, donkey, and sheep and goats combined as 'shoats') and wild herbivore functional types. The total predicted DMI for wild herbivores and livestock is compared using a bivariate colour scheme (a). Higher livestock DMI is represented by darker red, higher wildlife by darker blue, with different shades representing DMI values in equal quantiles for each of the two groups. Changes in mean percentage of DMI are shown with wild herbivores grouped by functional type (b).

Widespread changes in the large-herbivore community

Between the 1970s and 2000s, there was a large, significant drop in both diversity and in the mean body mass of species in the assemblage in all six ecosystems (S1). The drop in mean body mass is concerning considering the disproportionate importance of large herbivores in maintaining ecosystem functions[5]. Weighted mean body mass dropped the most where wild herbivores were closer to major towns in Amboseli ($p < 0.001$, Pearson's correlation = -0.17), Nairobi ($p < 0.001$, Pearson's correlation = -0.38), Narok ($p < 0.001$, Pearson's correlation = -0.24), and South Rift ($p < 0.001$, Pearson's correlation = -0.24). This pattern reflects the extirpation of large wild herbivores close to human settlement, which can be due to the bushmeat trade, human-wildlife conflict, and the loss of migratory corridors due to land conversion for agriculture and urban development.

In 40 years, the large herbivore community has drastically changed in composition, having homogenised (both within and between ecosystems) with increased dominance of livestock (shoat, donkey and cattle). SIMPER analysis shows a 70.5% difference in wild herbivore species composition, and a 45.6% difference in wild herbivore functional trait composition (S1). Non-Metric Multidimensional Scaling (NMDS) and PERMANOVA analysis indicate changes in wildlife community composition for all ecosystems except Narok, with the PERMDIP analysis showing decreases in beta-diversity in Nairobi, Mara, and Loita ecosystems (S1). The strength of correlations of the two rainfall related variables (drought, aridity) with the NMDS ordination decreased from the 1970s to the 2000s. These findings were supported by a Permutational Multivariate Analysis of Variance (PERMANOVA) using the same variables for the 2000s (S1), with livestock species DMI accounting for more variation in wildlife species composition than the environmental variables. Ordination plots and PERMANOVA plots of functional trait level composition data provide similar results.

Ecosystem changes driven by people and their livestock

Dissimilarity in wild herbivore species-level community composition between the 1970s and 2000s varied considerably across the region (mean = 0.29, range = 0.04 – 0.79; Figure 4a). The Nairobi and Mara ecosystems had the highest median dissimilarity (both 0.35) and Narok the lowest (0.18). We used a generalised additive model (GAM) to understand the drivers of wild herbivore dissimilarity between each consecutive decade from the 1970s to 2000 (Fig.3). This GAM explained 38.6% deviance and found evidence that proportional increases in total livestock DMI, proximity to urban and agricultural land, and drought cycles are all related to differences in wild herbivore community compositions across the decades (Fig. 3).

First, change in proportion of livestock dry matter intake (DMI) had the largest effect on changing wildlife community composition, particularly from the 1980s to 1990s, and partially in the 1970s to 1980s transition (effective degrees of freedom = 7.0, p <0.001, Figure 3b). Second, decades with more intense droughts, measured by deficit from the NDVI and Rainfall Standardized Precipitation Index, increased wildlife community dissimilarity between decades (edf = 1.78, p< 0.001, Figure 3c). Third was the direct human effect represented by agricultural land conversion and travel times to towns. Between the 1970s and 1980s, larger changes in the wildlife community occurred closer to major towns, in areas with and without substantial future changes in agricultural landcover (edf = 4.7, p<0.001, Figure 3d). Such a pattern was recorded in the Mara and Nairobi ecosystems in particular, where habitat loss and ecosystem fragmentation led to wide-scale changes in large-herbivore community composition at that time[22,23]. Between the 1980s and 1990s, we observed a small impact close to towns in non-agricultural areas (edf = 1.58, p< 0.01, Figure 3e). In the 1990s-2000s, larger dissimilarity occurred in areas close to towns and in areas that underwent conversion of land to agriculture (edf = 5.2 p<0.001, Figure 3f). Finally, there was slightly higher dissimilarity in relatively humid areas with fertile soils (edf = 7.8, p<0.001, Figure 3g), which is where land conversion is underway for agriculture. We also modelled dissimilarity between the 1970s and 2000s only as the dependent variable, again using a GAM. This model explained 73.1% of the deviance and fit the data well (S1). We found the largest change in community composition in areas with the highest proportional increases in livestock DMI as well as the largest mobility losses caused by migratory corridor blockages in areas with significant numbers of large wild herbivores (Mara and Nairobi).

This is all consistent with evidence for agriculture as a major driver of large-herbivore community change in this period in the Amboseli, Mara, and Nairobi ecosystems.[6,24,25]. These results, coupled with the decrease in mean body mass of wildlife species, demonstrates a down-sizing of the community (despite an increase in elephant numbers) with the effect being greatest closer to major towns, which is consistent with the long-term global trend of down-sizing in wildlife communities.[26] Larger-bodied species are targets for both retaliatory killings in human-wildlife conflicts and for the bushmeat market, both of which tend to increase with proximity to agricultural and urban areas[27].

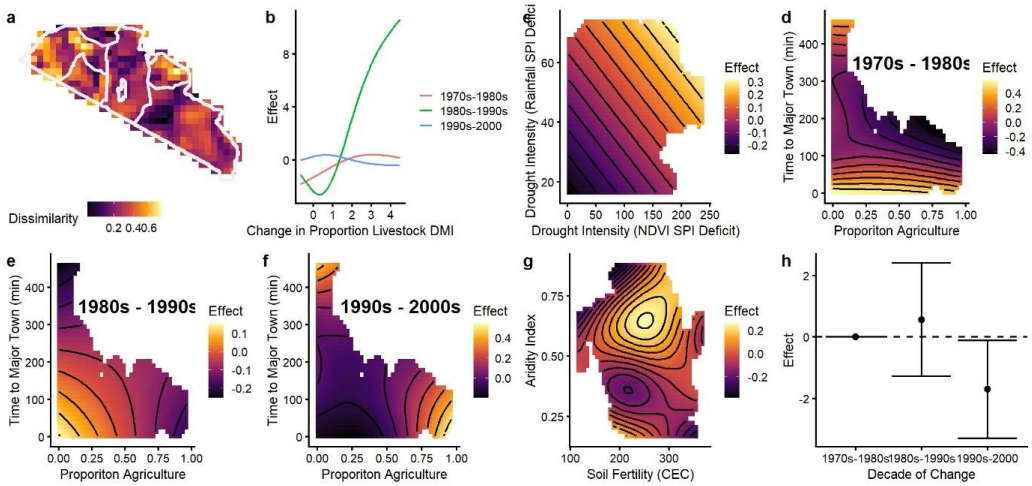

Figure 3: Dissimilarity of wild herbivore species composition between the consecutive decades from the 1970s to the 2000s in Southern Kenya, within the six ecosystems. (b-h) the drivers of dissimilarity identified by a Generalised Additive Model (GAM). (a) Dissimilarity in wild herbivore species composition for each sampling units between the 1970s and 2000s, with ecosystems outlined. (b) The model response curve for the change in the proportion of livestock dry matter intake (DMI) for each change period. (c) The model response curve for the intensity of drought in the decade, measured by NDVI and rainfall data, which were transformed using the Standardised Precipitation Index and the total deficit for each decade summed. (d-f) The tensor product relationship between the proportion of agriculture per pixel and travel time to major towns for each change period. (g)The tensor product of soil fertility measured by the cation exchange capacity and aridity index. (h) the fixed effect of the period of change.

Little evidence of long-term climatic effects on rangeland productivity

Analysis of our data reveals that drought (measured both by rainfall and NDVI) has affected the wild-herbivore community as expected for systems with low grazing pressure from livestock, where rainfall variation is likely the key driver of wild herbivore abundance and composition[12,28]. For example, changes in wild-herbivore composition in the 1980s and 1990s in the Mara were previously attributed to drought[29], and so increasing drought intensity and frequency is potentially a wide-scale driver of change in wild-herbivore communities across separate ecosystems[13]. Indeed, some evidence from southern Kenya suggests changes in annual and seasonal rainfall and drought frequency and intensity, but the combined evidence is inconclusive when different spatial and temporal scales are used[15,30]. We analysed two rainfall data sets: (1) CHIRPS (Climate Hazards Group InfraRed Precipitation with Station data), a 39+ year quasi-global rainfall dataset at 0.05° resolution; and (2) the GPCC (Global Precipitation Climatology Centre of the World Meteorological Organization, V2018) dataset V2018 at 0.5° resolution including monthly records from 1891-2016 (S2 for details).

We found inconclusive evidence for changes in overall rainfall or increases in the frequency, intensity, or length of droughts - measured using the Standardised Precipitation Index (SPI) - for both datasets (S2). Using CHIRPS data from 1981-2020, most regions actually had small annual rainfall increases (Figure 4a). However, this was only significant, using a Sen's Slope test, in small areas in the north-west of the study area, particularly in the Narok ecosystem (81% of pixels significant; Sup Table). Here rainfall has increased by 5.3mm - 23.5mm per year across the study period (mean - 14.5mm), whereas a small decrease has occurred in the Amboseli region (mean = -0.40mm per year; 1.5% of pixels show significant declines). Perhaps more importantly, there were some larger changes in the seasonality of rainfall (sup material).

Our analysis of CHIRPS data, using quantile regressions on the SPI, suggests that there has been an increase in the intensity of extreme high-rainfall events across much of the region (S2). Low-rainfall events have decreased in severity for the Mara but have increased in Amboseli and parts of the South Rift (S2). However, when taking a longer-term perspective, the GPCC data suggests that drought severity has decreased in all ecosystems since the end of the 19th Century (S2). These data also show that high-rainfall events have decreased in Amboseli and Nairobi ecosystems but increased in Loita, Mara, and Narok.

Previous research has highlighted an increased frequency of meteorological droughts across the East African region in recent years (2000-2010) and suggests that climate change may be responsible[31]. This leads to the speculation that climate-change-induced drought events are a significant driver of wild herbivore decline[1]. Our results show that aridity and drought appear to be the significant drivers of wild-herbivore community composition, particularly in the 1970s, and the change in composition is partially

related to drought intensity (Figure 2). However, our analysis of the long-term rainfall datasets reveals a variable pattern of change that makes it difficult as yet–at least for southern Kenya–to identify a consistent trend attributable to global climate change.

Changes in rangeland productivity as a result of changing livestock management

The effect of increased livestock herbivory (measured as dry matter intake, DMI) on wildlife community composition operates through two main processes. First, livestock and their associated human presence may directly cause spatial and temporal displacement of wildlife, especially at key grazing and water points [32,33]. Second, when competition occurs between wildlife and livestock for forage resources, supplementary feeding and watering of livestock typically results in wildlife being out-competed[1,6,12]. To understand the link between changing livestock DMI, rainfall patterns, and long-term availability of forage resources, we conducted a series of analyses using long-term NDVI data from the Global Inventory Monitoring and Modeling System (GIMMS, 1981-2015) and long-term monitoring of 24 vegetation plots in the South Rift ecosystem (S2).

Despite the general increase in rainfall since the 1970s across many East African ecosystems, NDVI–an indicator of grass biomass during the growing season[14]–has decreased. Using a pixel-wise Sen's Slope test, this decrease was significant in many parts of Amboseli, South Rift, Nairobi, and the edge of the Mara ecosystems (Figure 4b). NDVI variations generally coincided with drought events, which occurred with increasing severity in the South Rift and Nairobi and less severity in the Mara (S2). Seasonal time-series analysis of NDVI also indicated more significant variation in seasonality over time (S2). Many regions had seasonal NDVI profiles with deepening troughs during dry months and declining NDVI peaks during the growing season (S2). Our bivariate copula GAMS models showed that despite recovery from severe droughts in the early 1980s and 2009, there was a consistent weakening of the correlation between NDVI and rainfall during the growing seasons (measured by Kendall's Tau) for most ecosystems (Figure 5a). Areas displaying the greatest weakening of this correlation now have high densities of livestock enclosures (Figure 5b) and occur in regions with intermediate soil fertility (Figure 5c). These results are corroborated by long-term ground monitoring data from Amboseli, where a 30% decline in herbaceous productivity is linked to a three-fold increase in livestock grazing driven by socio-economic and land-use changes[16]. Further support comes from our generalised additive mixed model (GAMM) and random forest model of 12 years of data collected across 24 long-term monitoring vegetation plots in the South Rift. There, grass biomass is driven primarily by rainfall (S2) but we found that the prevailing level of chronically-intense livestock grazing had a stronger influence on available grass biomass than soil texture or nutrient content (S2

We found some evidence that drought events have caused changes in the wildlife community, particularly in the 1980s period of drought and low correlation of NDVI to rainfall in many ecosystems. (Fig 6), This,

coupled with our modelled results of drivers of dissimilarity (Fig 4), suggests that drought contributed to a change in large-herbivore community composition in the 1970-1980s period. There was probably a density-dependent effect involved in that too, because the combined livestock-wildlife abundance was exceptionally high when the drought commenced, following a wet period during the 1960-70s. Apart from discrete drought events, however, we found little support for any continuous climatic trend, such as declining annual rainfall, being a driving factor behind the long-term changes observed in the large-herbivore community. Our long-term analysis of NDVI and rainfall data supports this by demonstrating how the correlation between both is decreasing, especially in areas with the highest density of livestock enclosures. Increased stocking rates reduce the grass biomass per unit rainfall and create deeper annual and seasonal deficits in grass biomass than from rainfall-induced droughts alone, the frequency of which could be increasing in some areas[16,30]. High stocking rates also alter the species composition, height, productivity, and nutritional content of forage resources, with ramifications for herbivore community composition[34,35] These local changes are in turn driven by larger-scale changes affecting the pastoral social-ecological system. A set of interlinked political, economic, and governance factors has led to a wide-scale proliferation of permanent livestock enclosures, decreased seasonal mobility of livestock, and intensification of livestock grazing in certain areas[36] (Figures 5&6).

Although total livestock DMI has decreased across the region since the 1970s, there has also been a dramatic decline in livestock mobility due to sedentarisation and compression in rangelands that are increasingly fragmented by land transformation, inevitably driving up local DMI in the remaining matrix[14,17]. In a separate Omni-directional connectivity analysis (S3 for details) across five ecosystems (excluding Narok), we found overall reductions in livestock mobility when considering the locations of agriculture, urban areas, livestock enclosures and fencing. These results demonstrated that rangeland area in all ecosystems has shrunk (Nairobi 49.5% of its original size; Amboseli 60.2%; South Rift 70.1%; Mara 75%; and Loita 87.1%). Long-term monitoring of the South Rift vegetation plots shows that grazing intensity is positively associated with livestock enclosure density (Fig 6a, r-squared 0.17, p-value = 0.015) and, as theorised elsewhere[20], the substantial proportional increase in shoat (sheep + goat) abundance is an additional factor. Dry season shoat abundance was positively correlated with the mean proportion grazed in each plot (Fig 6b, r-squared 0.22, p-value =0.014).

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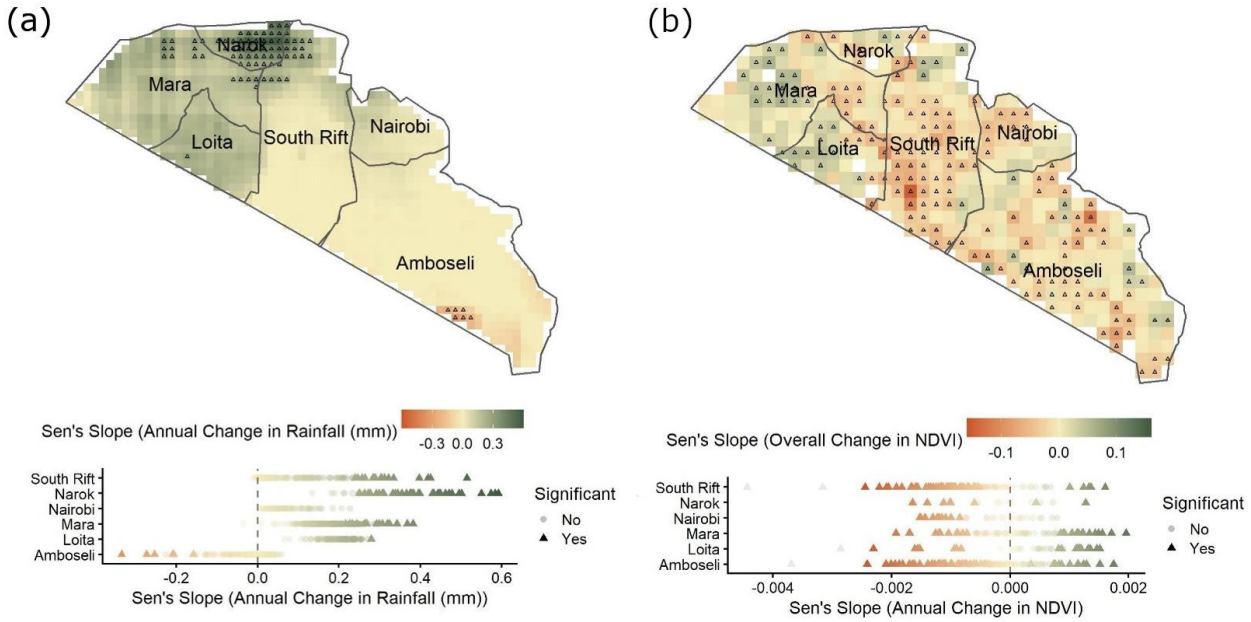

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282 Figure 4 (a-b) Changes in rainfall estimated using Sen's Slope between 1981-2020 in southern Kenya at
283 0.05° resolution. (c-d) Changes in NDVI estimated using Sen's Slope between July 1981-2015 in
284 southern Kenya at 0.083° resolution. Significant differences at each pixel are highlighted as triangles in all
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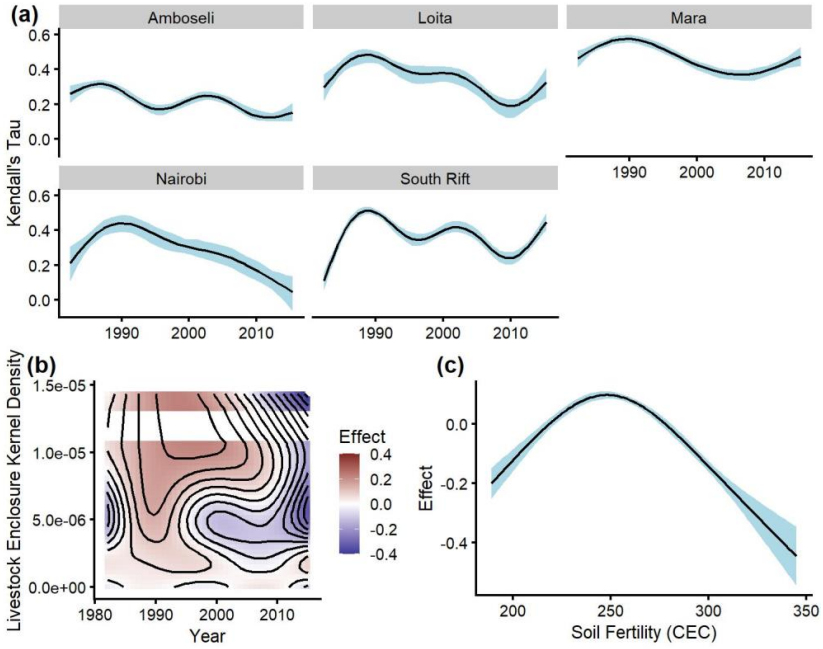

Figure 5: (a) Estimates and 95% intervals for Kendall's Tau over time from a Gaussian copula model with gaussian margins fitted to NDVI and rainfall data during the growing season, independently for each ecosystem (Copula Model 1). (b) The estimated smooth effect size of year and livestock enclosure kernel density in 2020, (c) and soil fertility (Cation Exchange Capacity) on the association parameter from a Gaussian copula model with gaussian margins fitted NDVI and rainfall data during the growing seasons. In (c), the shaded area is 95% confidence intervals.

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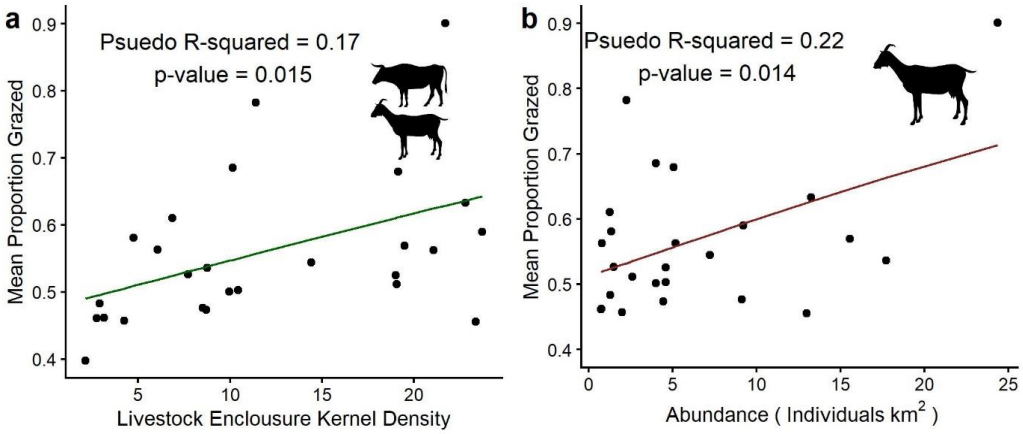

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300 Figure 6: Beta-regressions explaining the relationship between the mean proportion of grass grazed
301 across 25 vegetation monitoring plots in the South Rift and A) Livestock enclosure kernel density; B)
302 Shoat abundance in the dry season.
303

304 **Conclusions**
305
306 Across six ecosystems in southern Kenya, there have been major changes in large-herbivore community
307 composition over the last 40 years, with decreases in all wild-herbivore functional types except for non-
308 ruminant grazers. The wild-herbivore community has undergone down-sizing, reduced diversity, and
309 homogenisation within and across ecosystems. In contrast, within the livestock assemblage there has
310 been a substantial proportional increase in shoat (sheep + goat) abundance relative to cattle. This is due
311 to the ability of shoat populations to recover and be restocked quickly after die-offs in droughts, and the
312 entry of traditional pastoralists into a cash economy in which shoats are preferentially traded as a quick-
313 cash commodity[20].
314
315 Over the past four decades there has been no discernable trend towards declining mean annual rainfall in
316 southern Kenya, although drought events have proved to be important drivers of large-herbivore
317 community dynamics. Our comprehensive analysis exposes proximate anthropogenic stressors as
318 overwhelmingly strong drivers of ecosystem-level change and confirms their importance[37] in an East
319 African region that is world-renowned for its wildlife. While the ultimate driver of savanna ecosystem
320 change is rainfall, and with frequencies and intensities of droughts expected to increase with ongoing
321 global climate change, their effects will be additive to those of proximate drivers operating at a shorter
322 time scale[38,39]. The lesson from southern Kenya is that African savannas can quickly flip from rain-driven
323 to human-driven ecosystems. Thus, conservation solutions must focus on local drivers of change, traced
324 back to the higher-level socio-economic and political developments to which they are responding.
325

Methods

Study Area

Ecosystem boundaries were digitised from original drawings of the Kenya Rangeland Ecological Monitoring Unit (KREMU), who split Kenya into 44 ecosystems (ecological units), based on topography, vegetation, wildlife migration patterns seasonality[3]. We adjusted the ecosystem's boundaries to split the Nairobi and Amboseli ecosystems based on wildebeest collar data and evidence from the literature[4–7]. These ecosystems experience bimodal rainfall (April-June and October-November), and vary from arid to semi-arid, including Maasai Mara (Mara; annual rainfall 855mm, 15% annual rainfall CV), Loita (Loita Hills and Forest; 877mm, 22% CV), Narok (900mm, 19% CV), South Rift Valley (South Rift; 600mm, 24% CV), Amboseli (593mm, 22% CV), Nairobi (675.4mm, 21.6% CV).

Wildlife Poupulation Data

Aerial surveys of wildlife and livestock populations had been conducted for 40 years from 1977 to 2010 by the Kenyan Department of Resource Surveys and Remote Sensing (DRSRS). The surveys were conducted using systematic reconnaissance, flying the same fixed aerial transects and sampling units measuring 5km^2 (S1 for details). Our analysis used the most common wildlife (n=16) and livestock (n=3) species.These are buffalo (*Syncerus caffer*), Burchell's zebra (*Equus quagga*), cattle (*Bos taurus*), donkey (*Equus africanus asinus*), eland (*Tragelaphus oryx*), elephant (*Loxodonta africana*), gerenuk (*Litocranius walleri)*, giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Nanger granti*), impala (*Aepyceros melampus),* kongoni (*Alcephalus buselaphus*), lesser kudu (*Tragelaphus imberbis),* oryx (*Oryx beisa*), ostrich (*Struthio camelus),* shoats, a combination of domestic sheep and goats (*Capra aegagrus hircus* and *Ovis aries*) that are indistinguishable from an aircraft, Thomson's gazelle (*Eudorcas thomsonii*), warthog (*Phacochoerus africanus*), waterbuck (*Kobus ellipsiprymnus),* and wildebeest (*Connochaetes taurinus).* We averaged the number of animals per sampling unit over all of the surveys conducted in four decades comprising the 1970s, 1980s, 1990s and 2000s. In total, 124 surveys were flown: 21 in the 1970s; 42 in the 1980s; 38 in the 1990s; 23 in the 2000s (S1).

We use a hierarchical GAM (HGAM)[40] framework to model spatial and temporal correlation in decadal wildlife density data collected across 40 years of aerial monitoring, using penalised spline-based smoothing. We modelled the impact of four important covariates influencing wildlife density, in addition to modelling an explicit spatial-temporal component. The four covariates – human population density, slope, distance to water, and mean NDVI were incorporated as smooths using penalised thin-plate regression splines[41]. We used a Tweedie model to account for many zeros from the density data, with these types of models now widely used in GAM[42]. We used the package *mgcv*[43] in R[44], to facilitate model fitting, model selection and model checking. We used this model to predict species densities across the region and the four decades at a 2km^2 resolution totalling 9036 cells, covering 36,144km^2. (See S1 for additional details). We converted density to species biomass to calculate dry matter intake (DMI) by using the unit body

mass (M) of each species, multiplied by its population density estimate, in the equation $y=aM^b$ with b= 0.885, and a= 0.026, to produce daily DMI per km^2.[21]

We subsequently calculated changes in diversity (Simpson Diversity index) and a weighted mean mass (individual mass weighted by density) per pixel over time in each ecosystem. The Simpson diversity index was calculated using the package *vegan*[45]. We compared diversity and weighted mean mass in each ecosystem between the 1970s and 2000s using a non-parametric test, the paired Wilcoxon test. We also conducted a set of non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA), using a Bray-Curtis dissimilarity with DMI data per pixel for all species and independently for wildlife-only. We used permutational multivariate analysis of variance (PERMANOVA) and an analysis of multivariate homogeneity of group dispersions (variances; PERMDISP) to test the variability and differences of species composition between the 1970s and 2000s as an independent test for each ecosystem. We used similarity percentage analysis (SIMPER; the *simper* function in vegan) to determine species and functional groups' identity contributing most to community dissimilarity among plots in the start and end decade and used 500 permutations to calculate pseudo-P values[46].

We calculated the Bray-Curtis dissimilarity of the species-level community composition for wildlife species only between each sampling unit between the 1970s-1980s, 1980s – 1990s, 1990s-2000s, and the total change between 1970s-2000s. We then used a Generalised Additive Model (GAM) to determine the drivers of dissimilarity[42]. We fit two GAM models. Both used a beta distribution with a logit link structure to model univariate and bivariate smooths of *a priori* selected drivers of dissimilarity, including anthropogenic, abiotic and biotic factors. The models were implemented using the *mgcv* package[47].

See S1 for more details.

Long-term changes to rainfall and grassland productivity

We downloaded data from CHIRPS (Climate Hazards Group InfraRed Precipitation with Station data), a 39+ year quasi-global rainfall data at 0.05° resolution, and monthly rainfall data from the World Meteorological Organization Global Precipitation Climatology Centre (GPCC) monthly rainfall data V2018 at a 0.5° resolution. This data includes monthly records from 1891-2016.

We downloaded the Normalised Difference Vegetation Index (NDVI) 3rd generation product using the Global Inventory Monitoring and Modeling System (GIMMS). The dataset covers July 1981 to December 2015 with a bi-weekly temporal resolution and a 1/12 degree spatial resolution (roughly $8km^2$).

For the three datasets we calculated change in rainfall or NDVI using a non-parametric Sen's Slope test (Theil–Sen test) to determine the magnitude of these changes at the pixel level using the *trends* pacakge[48]. We calculated the Standardised Precipitation Index (SPI), a climatic proxy widely used for drought quantification and monitoring[49]. We used *quantreg*[50] to conduct quantile regression on the SPI data to understand changes in periods with higher rainfall or NDVI and lower rainfall or NDVI events.

Also, we used the SPI to calculate specific metrics per decade, including the overall intensity of drought events, the number of drought events, and the length of drought events. We performed a Sen's slope analysis on the monthly NDVI data, but the results provided literal clarity on how changes in seasonal patterns of NDVI have occurred over time. We, therefore, performed a three-step time-series clustering process at the pixel-level to identify these patterns (S2 for details).

We also calculated the change in ecosystem size using Circuitscape[51] with a moving window analysis, implemented in Omniscape[52] in Julia 1.5. We compare two scenarios. First, a model with no anthropogenic impact only incorporating slope as a key limitation to movement. Second, we used the data from Chapter 5, which provides a database for livestock enclosures, agricultural land use, and fences for over 30,000 km^2 across Southern Kenya to model mobility changes as caused by humans. (S3 for details)

We estimate the time-varying correlation between the CHIRPS rainfall and GIMMS NDVI time series using a bivariate copula distribution model, an extension of generalised additive models for location, scale and shape (GAMLSS)[53]. We fit two copula models to this data (S2 for details).

We used a Generalised Additive Mixed Model (GAMM) with a negative binomial logit link structure to determine the abiotic, biotic and anthropogenic drivers of grass biomass at 24 plots across the last 12 years[54] within the South Rift ecosystem. To account for temporal autocorrelation, we used an autocorrelation-moving average correlation structure of order three, with the correlation structure nested at the plot level[42]. We also performed a random forest analysis using the package *randomForest*[56] to determine the importance of these factors in predicting grass biomass[55] (S2 for details).

Finally, we compared the mean proportion of grass grazed at each plot to several variables using beta-regression models[57]. These variables were the seasonal abundance of wildebeest, zebra, shoats (sheep and goats), and cattle[58]. These four groups are the ecologically dominant species in the ecosystem[59], and we extracted plot level abundance from the explicit spatial estimates of seasonal abundance for each species from[58].

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Supplementary Text – Hierarchical Generalized Additive Model covariates (HGAM), and community composition analysis

Aerial Count Data

The management and conservation of wildlife and livestock rely on an accurate understanding of species representation in space and time. This is needed to pinpoint the social (e.g. economic, political, land tenure) and ecological pressures (e.g. climate change and degradation) impacting species abundance. Monitoring efforts have provided a baseline for understanding regional trends in wildlife numbers. For example, many studies have pointed to precipitous drops in abundance across the region, both inside and outside protected areas, with large ramifications for conservation planning and management[1,2]. A common approach to estimate changes in abundance is to use spatially referenced data to produce spatially stratified abundance estimates, assuming independence between stratum [1,3–5]. This approach neglects the correlation in abundance between nearby locations in space, assuming that abundance is homogenous in each stratum, which means that the abundance estimates in each stratum may be less accurate and imprecise than they could be.

Additionally, these estimates are often at a broad spatial scale, yet most abiotic and biotic drivers of wildlife distribution and abundance occur at much finer scales. While it has become increasingly common to use spatially reference data to model wildlife distribution and occupancy in relation to biotic, abiotic, and human variables, it is still rare to do this for abundance estimates at an appropriate spatial scale[6]. However, several studies have recently predicted spatially explicit estimates of wildlife abundance on a scale that is relevant to underlying ecological and anthropogenic variables[7–10]. We use a hierarchical GAM (HGAM)[11] framework to model spatial and temporal correlation in wildlife density data collected across 40 years of aerial monitoring, using penalised spline-based smoothing. The flexible nature of GAMs allows for modelling smooth patterns across space and over time, with the amount of smoothing controlled within the GAM framework to prevents over-fitting. We used the package *mgcv* to facilitate model fitting, model selection and model checking.

Study Area

Our study spanned six well-defined ecosystems, originally defined in the 1970s by the Kenya Rangeland Ecological Monitoring Unit (KREMU). These ecosystems experience bimodal rainfall (April-June and October-November), and vary from arid to semi-arid, including Maasai Mara (Mara; annual rainfall 855mm, 15% annual rainfall CV), Loita (Loita Hills and Forest; 877mm, 22% annual rainfall CV), Narok (900mm, 19% annual rainfall CV), South Rift Valley (South Rift; 600mm 24% annual rainfall CV), Amboseli (593mm 22% annual rainfall CV), Nairobi (675.4mm, 21.6% annual rainfall CV).

Data Collection

Aerial wildlife and livestock count data was collected by the Department for Resource Surveys and Remote Sensing (DRSRS). The data covered the period 1977 to 2010. The surveys were conducted using systematic reconnaissance, flying the same fixed aerial transects and sampling units measuring 5km^2 (see Ogutu et al., 2016 for details.) The data consisted of the estimated

number of animals of each species in each 5 x 5 km^2 sampling unit. On transects, animals are counted by two rear set observers, only within observation strips defined on the ground, and calibrated pre-flight, by two parallel rods (streamers) attached to the wing struts of the aircraft[1].

Our analysis used the most common wildlife (n=16) and livestock (n=3) species.These are buffalo (*Syncerus caffer*), Burchell's zebra (*Equus quagga*), cattle (*Bos taurus*), donkey (*Equus africanus asinus*), eland (*Tragelaphus oryx*), elephant (*Loxodonta africana*), gerenuk (*Litocranius walleri)*, giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Nanger granti*), impala (*Aepyceros melampus),* kongoni (*Alcephalus buselaphus*), lesser kudu (*Tragelaphus imberbis),* oryx (*Oryx beisa*), ostrich (*Struthio camelus),* Shoats, a combination of domestic sheep and goats which are indistinguishable from an aircraft (*Capra aegagrus hircus* and *Ovis aries*), Thomson's gazelle (*Eudorcas thomsonii*), warthog (*Phacochoerus africanus*), waterbuck (*Kobus ellipsiprymnus),* and wildebeest (*Connochaetes taurinus).*

We averaged the number of animals per sampling unit over all of the surveys conducted in four decades comprising the 1970s, 1980s, 1990s and 2000s. In total, 124 surveys were flown - 21 in the 1970s, 42 in the 1980s, 38 in the 1990s, 23 in the 2000s (Sup Table 1).

612

YEAR	NAROK	KAJIADO	MASAI MARA	ATHI-KAPUTIEI	TOTAL	Decadal Flights
1977	1	1	2	1	5	
1978	1	1	2	1	5	
1979	0	0	11	0	11	21
1980	1	1	1	1	4	
1981	0	1	4	1	6	
1982	0	1	4	1	6	
1983	1	1	4	0	6	
1984	0	0	2	0	2	
1985	2	0	2	0	4	
1986	3	1	3	1	8	
1987	1	1	1	1	4	
1988	0	0	0	0	0	
1989	1	0	1	0	2	42
1990	1	1	1	1	4	
1991	2	2	2	2	8	
1992	2	1	2	3	8	
1993	1	0	1	2	4	
1994	1	1	1	1	4	
1995	0	0	0	0	0	
1996	1	0	1	1	3	
1997	2	0	1	1	4	
1998	0	1	0	1	2	
1999	0	0	0	1	1	38
2000	1	1	1	1	4	
2001	0	0	1	0	1	
2002	1	0	0	1	2	
2003	0	0	0	0	0	
2004	1	0	1	0	2	
2005	2	0	2	0	4	
2006	0	1	0	1	2	
2007	1	1	1	1	4	
2008	1	0	1	0	2	
2009	1	0	1	0	2	**23**
Total	29	17	54	24	124	

613 Supplementary Table 1. The occurrence of DRSRS aerial systematic reconnaissance flights
614 across the study region and used in this analysis[1].
615

Hierarchical GAM Modelling

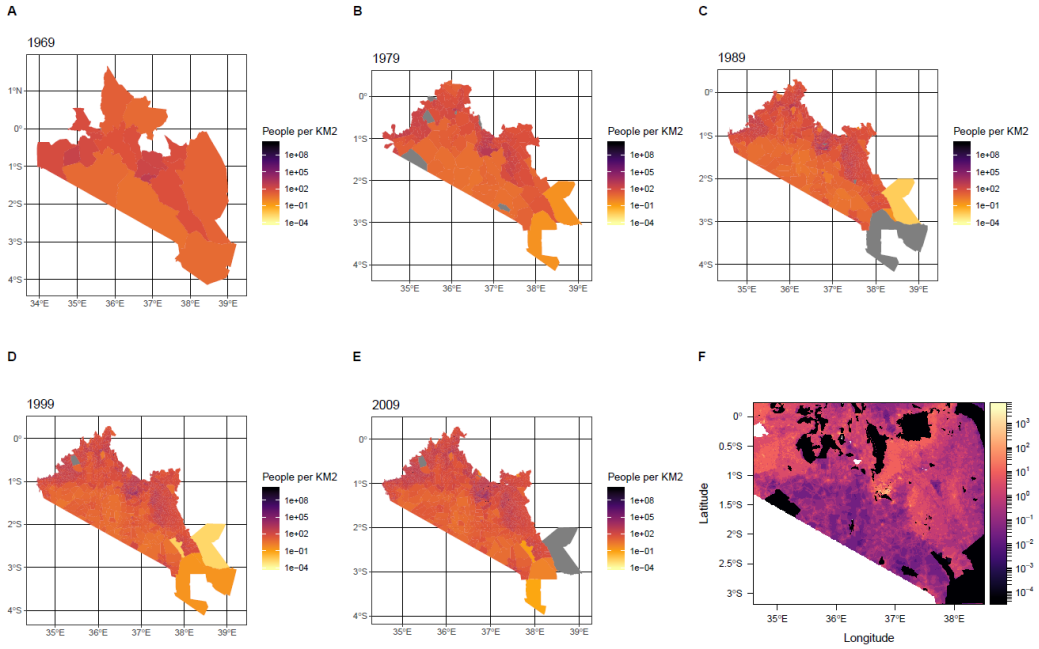
We used a hierarchical generalised additive model (HGAM) framework to model the spatial and temporal distribution of wildlife and livestock density using penalised spline-based smoothing[11]. We used this model to predict species densities across the region and the four decades. While GAMs have begun to be widely used in modelling the spatial distribution of wildlife[12], there have been limited attempts to incorporate temporal replicates of data into the modelling framework[13]. The flexible nature of GAMs allows for modelling smooth patterns across space and over time, with the amount of smoothing controlled within the GAM framework to prevents over-fitting[11,14]. We fit an individual HGAM for each focal species to explain their density over time and across the four sampled decades. We modelled the impact of four important covariates influencing wildlife abundance, in addition to modelling an explicit spatial-temporal component. To do this, we use a spatial HGAM with a global tensor product of the x and y coordinates of the sampling's units, plus group-level smoothers per decade, allowing for differing wiggliness and penalties between decade[11]. These were modelled using thin plate regression splines[15]. This modelling approach increases the model's computational cost (as there are more smoothing parameters to estimate), but it means that information is shared between groups through the global smoother, the common smooth terms, the common error term, and the random effect for group-level intercepts[11]. We allow the model to penalise the squared first derivative of the function rather than the second derivative. This reduces collinearity between the global smoother and the group-specific terms, which occasionally leads to high uncertainty around the global smoother[11]. We modelled four covariates – human population density, slope, distance to water, and mean NDVI as smooths using penalised thin-plate regression splines[16]. The penalised spline has a modified smoothing penalty, and the whole term can be shrunk to zero, effectively acting as a model fitting process. For each term, the maximum basis complexity was set, and the penalty controlling the degree of smoothing was selected using restricted maximum likelihood (REML)[17]. we used a Tweedie model to account for many zeros from the density data, with these types of models now widely used in GAM[17]. A hurdle model, an alternative modelling approach, would identify zeros' underlying causes, but accounting for these zeros using a Tweedie model is appropriate for our aims[18]. The model was built in R[19] using the *mgcv* package[20].

Covariates

In addition to modelling the temporal and spatial dynamics of density using an HGAM, our model also included several additional covariates that influence our study species' density. We collected five different covariates for each decade of data: normalised difference vegetation index (NDVI), the coefficient of variation of NDVI, human population, distance to permanent water, and slope. All spatial data were projected into the UTM 37 projection and cropped to the study area's extent (Sup Figure 3). We resampled the data to the 5x5km sampling units using the *extractr* package[21]. When potential predictor variables were correlated by 0.7 or more (Spearman rank correlation coefficient), just one was used in the modelling process (Sup Fig. 4).

Human Population

We included human population density because it generally indicates areas of higher human use for livestock grazing, settlement, natural resource extraction, agriculture and urban areas[22,23]. These may all influence the distribution and abundance of wildlife (e.g Tyrrell et al., in press). To generate decadal estimates of human population density, we re-adjusted spatial data from government censuses for 1979, '89, '99, and 2009. These data have human population information collected at various spatial scales, which varies between censuses. We resampled each population estimate to a 100m resolution to adjust the population to a standard spatial resolution. To do this, we downloaded a 100m resolution human population raster for the year 2015 from WorldPop (www.worldpop.org). For each census year, we redistributed the population within an individual polygon by using the human population's distribution for that polygon using the 2015 raster layer as a weighting layer for the polygon's estimated population from the census. This process mirrors the process used by WorldPop to generate this spatial data[24]. Due to this data layer's highly skewed nature, we log10 transformed population after adding a small value (+ 0.000001) to avoid the log10 transformation of zeros (Sup. Fig. 1).



Supplementary Figure 1: Human population data for southern Kenya used to generate covariates for the analysis. A) 1969 census results for southern Kenya; B) 1979 results; C)1989 results; D)1999 results; E) 2009 results; F) WorldPop 2015 human population data at 100m resolution plotted for the region. This layer was used as a weighting layer to create 100m res grids for each census period.

Normalised Difference Vegetation Index

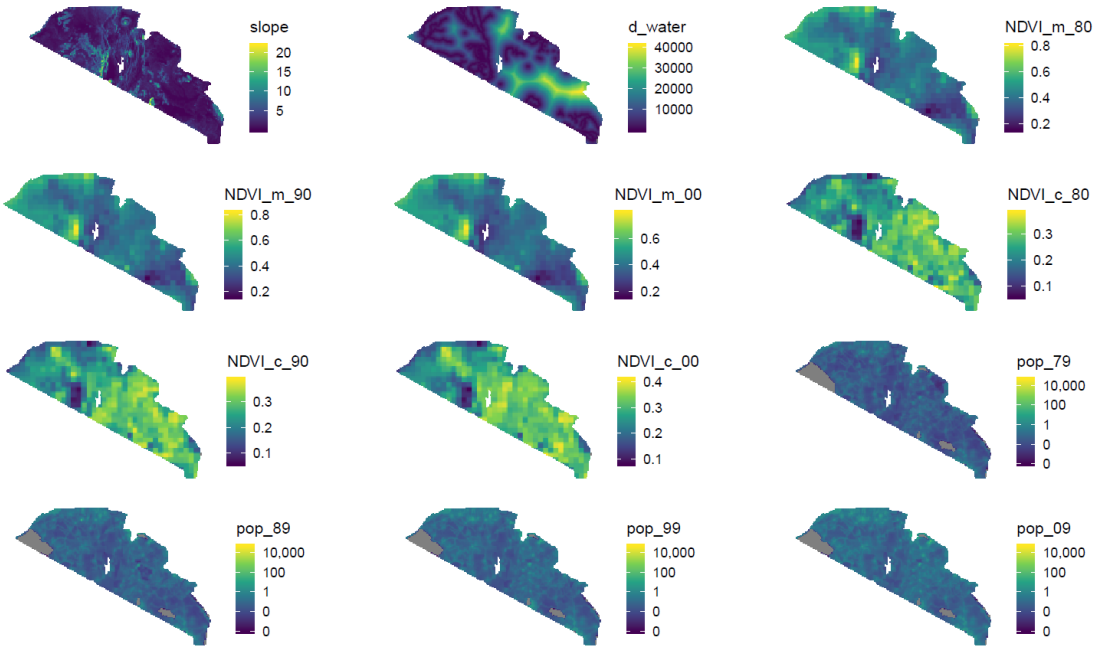
We downloaded the Normalised Difference Vegetation Index (NDVI) 3rd generation product using the Global Inventory Monitoring and Modeling System (GIMMS)[25]. This index is generated using Advanced Very High-Resolution Radiometer (AVHRR). The data covers July 1981 to December 2015 with a bi-weekly temporal resolution and a 1/12 degree spatial resolution (roughly 8km^2). We used mean NDVI and the decadal coefficient of NDVI as proxies for habitat type, capturing overall productivity and seasonality[7,10]. We calculated these values independently for each decade for which we had available data. We did not have data for the late 1970s, and therefore we used the 1980s mean.

Slope

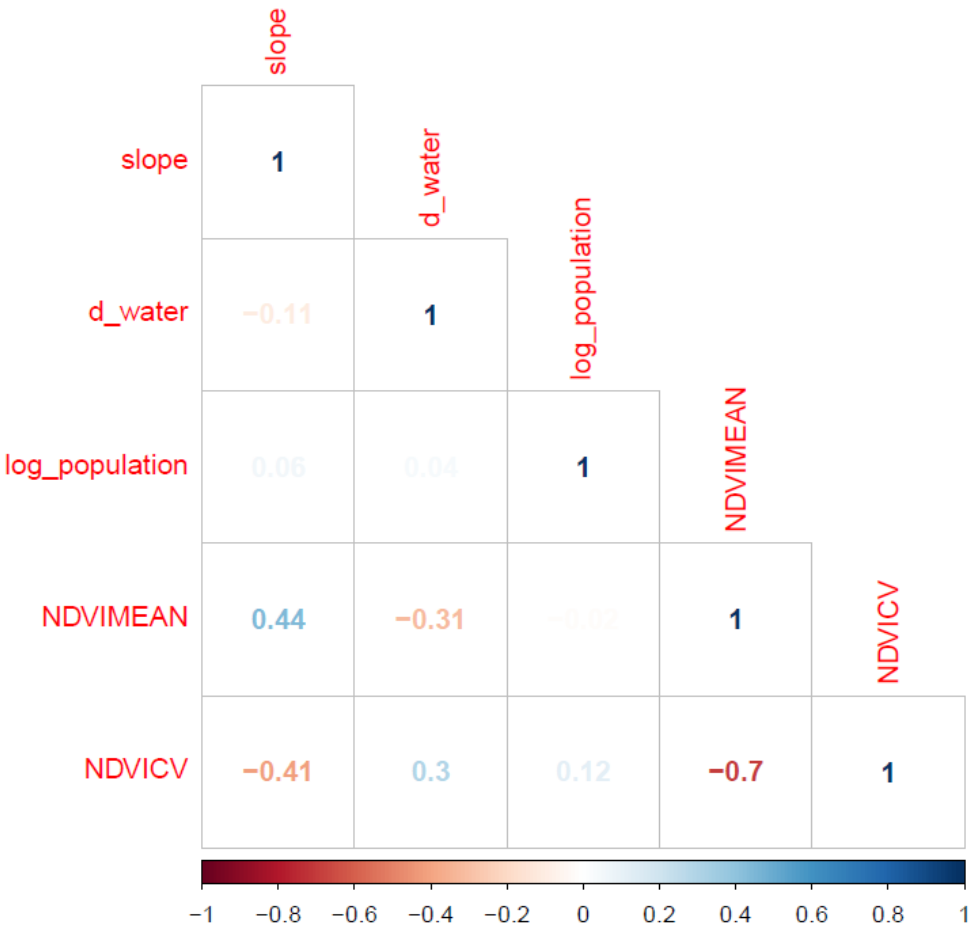
We downloaded Shuttle Radar Topography Mission (SRTM) Digital Elevation Model data at an aggregated 300m resolution using the package *elevatr*[26]. We calculated slope using the *raster* package[27]. The slope is known to influence wildlife density and distribution by limiting wildlife mobility and habitat in areas with the highest slopes[7]. Also, some species may prefer areas with a slighter steeper slope.

Distance to Permanent Water

Water is a key determinant of wildlife distribution, although the effect varies between species and guilds[28–30]. We created a layer of distance to permanent water by digitising perennial rivers from Google Earth, as identified by the authors and other sources[10,31,32]. To account for surface water availability, we downloaded data from https://global-surface-water.appspot.com/[33]. This layer provides a global database of surface water collected using Landsat 30m resolution data, from 1984-Present. We filtered the dataset defining permanent water as any surface water that has more than 50% occurrence. We then polygonised this layer and combined it with the perennial rivers layer to generate a distance to water raster at a 1km resolution.



Supplementary Figure 3: The covariates used in the modelling process to create the prediction grid. From top-left: Slope, Distance to Permanent Water, Mean NDVI 1980's, Mean NDVI 1990's, Mean NDVI 2000's, Coefficient of variation NDVI 1980s, Coefficient of variation NDVI 1990s, coefficient of variation NDVI 2000s, redistributed human population density for 1979, 1989, 1999 and 2009.



Supplementary Figure 4: The spearman rank correlation coefficient between covariates used in the HGAM modelling processes. Because of the strong negative correlation between NDVI Mean and NDVI-CV, we used only NDVI Mean in the models.

Prediction Grid

To estimate wildlife densities for each decade, we created a prediction grid at a 2kim resolution totalling 9036 cells, covering 36,144km^2. We used this size grid to use information from the 5x5km grids to downscale our population estimates to a smaller resolution at which variation in density is likely to occur due to human population, slope and habitat variation. We excluded Lake Magadi and Lake Natron from this grid. From each of the covariates, we extracted the mean value for each grid using *exactextractr*.

Conversion to ecologically relevant units

It is common to convert species abundance or density estimates into mass-scaled estimates to compare different species' impacts on an ecosystem. This allows for species' effects on various ecosystem functions to be evaluated, rather than just population abundance. Often, studies use the average adult mass to estimate its relationship to other ecological properties. However, body mass and metabolic functions do not necessarily scale with isometry. Therefore, allometric relationships have been used to explain how variation in body mass (M), can explain variation in multiple factors including basal metabolic rate (BMR), gut passage rate, dry matter intake rate (DMI), dry matter gut contents, and secondary production[34–38].

For mammalian macroecology, it is often assumed that BMR scales allometrically with M according to the ¾ power rule[39,40]. However, there is considerable debate on the exact scaling exponent within mammals, with some arguing for a 2/3 power rule[34,35]. It has also been assumed that DMI is directly proportional to BMR and should also scale with M to the ¾ power, assuming all animals eat roughly similar food[41,42]. However, even this relationship is contended[43]. However, for the same-sized animal, there is variation across taxa and regions in BMR. It appears that large African herbivores have higher-than-expected BMR, perhaps due to the need for constant vigilance and rapid response to a high predation threat[44]. Evidence from Lovegrove suggests that for BMR, the assumption scaling with M to the ¾ power is inaccurate, and so assuming that DMI scales similarly is also inaccurate. Lovegrove's (2000) analysis suggests that an exponent of 0.9 for BMR of large Afrotropical mammals. However, for Lovegrove's estimates for large Afrotropical, of the 11 largest species, 6 are carnivores and five ruminants which may impact estimates, especially when the whole sample size for this group was just 31, and we have no understanding of the underlying data quality or margins of error. White et al., for example, note the inaccuracy of BMR data for ruminants, and that temperature must be accounted for in calculating BMR[35,40]. It appears that for large mammals, limited data is available to derive an accurate scaling relationship. Other work by Western (1983) suggests that secondary production, derived independently of BMR, and based on field calibrated data, suggests the energetic turnover per year in a herbivore community is scaled using a 2/3 exponent[37]. It appears that traditional allometric scaling equations for metabolic indices and related life-history parameters can be contested, and do not always scale allometrically[45].

The selection of an allometric scaling equation and its resultant quantity depends on the question being asked, and the interpretation of the specific equations used to calibrate these data points. In our case, we are interested in the change in community composition and

abundance and its relationship to available forage. Therefore, we wish to quantify the plant tissue passing through each herbivore species population per unit area per unit time. Estimates by Muller et al. (2013) for mammals >10 kg found the M exponent for the scaling of DMI is 0.844-0.885[46]. They also found M exponents for dry matter gut content of 0.924-0.959. Therefore, we use the unit body mass (M) per species (Sup. Table 2), the species population density estimate, and the DMI exponent of 0.885, and coefficient of 0.026 from Muller et al., 2013.

Species	Latin Name	Individual Body Mass (kg)	Functional Type	Domestication	Short Name for Functional Type	Daily Dry Matter Intake ($kg.d^{-1}$)
Buffalo	*Syncerus caffer*	486.3	Medium-large, social, water-dependent grazers	Wildlife	Grazers	9.44
Burchell's zebra	*Equus quagga*	208.4	Large, water-dependent, non-ruminants	Wildlife	Non-ruminants	4.46
Cattle	*Bos taurus*	231	Medium-large, social, water-dependent grazers	Livestock	Grazers	4.89
Donkey	*Equus africanus asinus*	256.7	Large, water-dependent, non-ruminants	Livestock	Non-ruminants	5.37
Eland	*Tragelaphus oryx*	511.2	Small-medium, social, non-water reliant mixed feeders	Wildlife	Mixed feeders	9.87
Elephant	*Loxodonta africana*	4101.8	Large, water-dependent, non-ruminants	Wildlife	Non-ruminants	62.34
Gerenuk	*Litocranius walleri*	39.1	Small, non-social, water independent browser/frugivores	Wildlife	Small Browser	1.01
Giraffe	*Giraffa camelopardalis*	1117.5	Large, social, water-dependent browsers	Wildlife	Large Browser	19.72
Grant's Gazelle	*Nanger granti*	57.4	Small-medium, social, non-water reliant mixed feeders	Wildlife	Mixed feeders	1.43
Impala	*Aepyceros melampus*	49.1	Medium-large, social, water-dependent grazers	Wildlife	Grazers	1.24
Kongoni	*Alcephalus buselaphus*	150.3	Medium-large, social, water-dependent grazers	Wildlife	Grazers	3.34
Lesser Kudu	*Tragelaphus imberbis*	86.3	Small-medium, social, non-water reliant mixed feeders	Wildlife	Mixed feeders	2.04
Oryx	*Oryx beisa*	168.6	Small-medium, social, non-water reliant mixed feeders	Wildlife	Mixed feeders	3.70
Ostrich	*Struthio camelus*	105	Small-medium, social, non-water reliant mixed feeders	Wildlife	Mixed feeders	2.43
Shoats	*Capra aegagrus hircus*	30	Medium-large, social, water-dependent grazers	Livestock	Grazers	0.80
Thomsons Gazelle	*Eudorcas thomsonii*	19	Small-medium, social, non-water reliant mixed feeders	Wildlife	Mixed feeders	0.54
Warthog	*Phacochoerus africanus*	70	Large, water-dependent, non-ruminants	Wildlife	Non-ruminants	1.70
Waterbuck	*Kobus ellipsiprymnus*	211.8	Medium-large, social, water-dependent grazers	Wildlife	Grazers	4.53
Wildebeest	*Connochaetes taurinus*	220.1	Medium-large, social, water dependent grazers	Wildlife	Grazers	4.68

Supplementary Table 2: The study species and their attributes used during analysis. The mass of an individual (kg) and functional type is taken from Hempson et al., 2015[47]. Daily dry matter intake of an individual ($kg.d^{-1}$) is calculated using an allometric scaling equation from Muller et al., 2013, $0.026.BodyMass^{0.885}$.

Community Composition Analysis

We calculated changes in diversity (Simpson Diversity index) and a weighted mean mass (individual mass weighted by density) per pixel over time in each ecosystem. The Simpson diversity index was calculated using the package *vegan*[48]. We compared diversity and weighted mean mass in each ecosystem between the 1970s and 2000s using a non-parametric test, the paired Wilcoxon test.

To understand how beta-diversity changes over time we visualised variation in species composition as a 2D ordination using non-metric multidimensional scaling (NMDS) using a Bray-Curtis dissimilarity on the DMI data per pixel, where all data across the four decades and six ecosystems were ordinated as a single data set. Distances between points represent how similar pixels are in species composition. To reduce the generation of the NMDS and dissimilarity matrix's computational complexity, we aggregated all data to a 10km resolution grid.

We aimed to examine the changes in wildlife community composition and functional types, as a function of the impact of livestock, drought events, and other abiotic factors (Sup Table 2). Therefore, we conducted another NMDS and permutational multivariate analysis of variance (PERMANOVA), a non-parametric multivariate statistical test[49], for wildlife data only, independently for both the 1970s and 2000s. We conducted this analysis on both the wildlife species-level DMI, and the aggregated DMI for functional types. We fit several factors onto the ordination (using 999 permutations) and while fitting the PERMANOVA model including the decadal aridity index, soil fertility, livestock DMI (shoats and cattle) and the intensity of droughts in the decade on community composition (Sup Table 3). Pseudo-*F* and *P* values were calculated based on 999 permutations of the data using the *adonis* function.

We used permutational multivariate analysis of variance (PERMANOVA) and an analysis of multivariate homogeneity of group dispersions (variances; PERMDISP), to test the variability and differences of species composition between the 1970s and 2000s as an independent test for each ecosystem. PERMANOVA tests the null hypothesis that the centroids and dispersion of the groups; in this case, decades, are equivalent for all groups[49]. PERMDISP test compares within-group spread among groups using the average value of the distances from individual observations to their group centroid[50]. All PERMANOVA and PERMDISP used 999 permutations.

We used similarity percentage analysis (SIMPER; the *simper* function in vegan) to determine species and functional groups' identity contributing most to community dissimilarity among plots in the start and end decade and used 500 permutations to calculate pseudo-P values[51].

Supplementary Table 3: Covariates, their sources, a description of their importance to driving community composition, and the analysis they were used: MDS ordination, PERMANOVA, or the GAM to understand the drivers of dissimilarity between the 1970s and 2000s.

Covariate	Description	Source	Analysis
Decadal Aridity Index	Aridity is the ratio of the precipitation in an area to the amount of evapotranspiration. It is a crucial predictor of community composition in African savannas[52–54]. We created a decadal aridity index using the estimated monthly precipitation and evapotranspiration index data created by TerraClimate (~4km resolution)	[55]	NMDS, PERMANOVA, GAM
Soil Fertility	Soil fertility is a crucial predictor of wildlife community composition[53,54]. We used Cation Exchange Capacity at a 250m resolution as an indicator of soil fertility form soilgrids.org	[56]	NMDS, PERMANOVA, GAM
Livestock Dry Matter Intake (Shoats, Cattle, and Donkeys)	The impact of livestock grazing can have an impact on the wildlife community composition[57]. We used the Dry Matter Intake calculated for each decade and each species.	This manuscript	NMDS, PERMANOVA, GAM
Total Dry Matter Intake	The sum of all DMI in each pixel.	This manuscript	GAM
Intensity of Droughts	We calculated droughts' intensity using monthly 0.05° World Meteorological Organization Global Precipitation Climatology Centre (GPCC) monthly rainfall data. We calculated the Standardised Precipitation Index (SPI) a climatic proxy widely used for drought quantification and monitoring[58]. We calculated the index at the 12-month time scale and summed the SPI deficit for each decade investigated	[59]	NMDS
Travel time to Major Towns	Using data from the Malaria Project Atlas, we calculated travel time for each pixel to major towns. The impact of large human populations, and ready access to market, can be in indicator of bush-meat poaching and other threats.[60]	[61]	NMDS, PERMANOVA, GAM
Change in NDVI	We downloaded the Normalised Difference Vegetation Index (NDVI) 3rd generation product using the Global Inventory Monitoring and Modeling System (GIMMS). This	[25]	GAM

	index is generated using Advanced Very High-Resolution Radiometer (AVHRR). The data covers July 1981 to December 2015 with a bi-weekly temporal resolution and a 1/12 degree spatial resolution (roughly 8km^2). We calculated the overall change in NDVI from 1981-2010 using a Sen's Slope estimator from the package *trend*[62]. We also calculated the change in NDVI associated droughts over time, be using the Standardised Precipitation Algorithm[58]. We calculated the index at the 12-month time scale. We used a 0.05 quantile regression[63] of SPI over time and extracted the slope as an indicator of changing the intensity of NDVI droughts.		
Change in Rainfall	We downloaded the 0.05° World Meteorological Organization Global Precipitation Climatology Centre (GPCC) monthly rainfall data. We calculated the overall change in rainfall at each pixel from 1975-2010 using a Sen's Slope estimator from the package *trend*[62]. For the same period, we calculated the Standardised Precipitation Index (SPI), a climatic proxy widely used for drought quantification and monitoring[58]. We calculated the index at the 12-month time scale. We used a 0.05 quantile regression[63] of SPI over time and extracted the slope as an indicator of changing the intensity of rainfall droughts.	[59]	GAM
Changes in Connectivity (Current Flow)	In S3, we used Circuitscape[64,65] with a moving window analysis, implemented in Omniscape, to quantify the connectivity and mobility changes in Southern Kenya. We generated a raster showing the percentage change in current flow (an indicator of mobility) from a scenario with and without anthropogenic structures such as livestock enclosures, fences, agricultural land-use, and buildings.	S3	GAM
Proportion of Agriculture	Generally, spatial data on fences and agricultural expansion are localised and dispersed among data owners and databases. We synthesised data from several research groups and conservation NGOs into a spatial-temporal database[8]. The data includes 1,500 km^2 of agricultural land. When data overlapped between research groups, the features with the newest date were selected. We clipped all our data layers to the extent files provided with each data source. Beyond the limits of this database we supplemented this data with a commonly used global open source data layer, the 2015 GFSAD30AFCE 30-m for Africa: Cropland Extent Product (www.croplands.org)	Chapter 5	GAM

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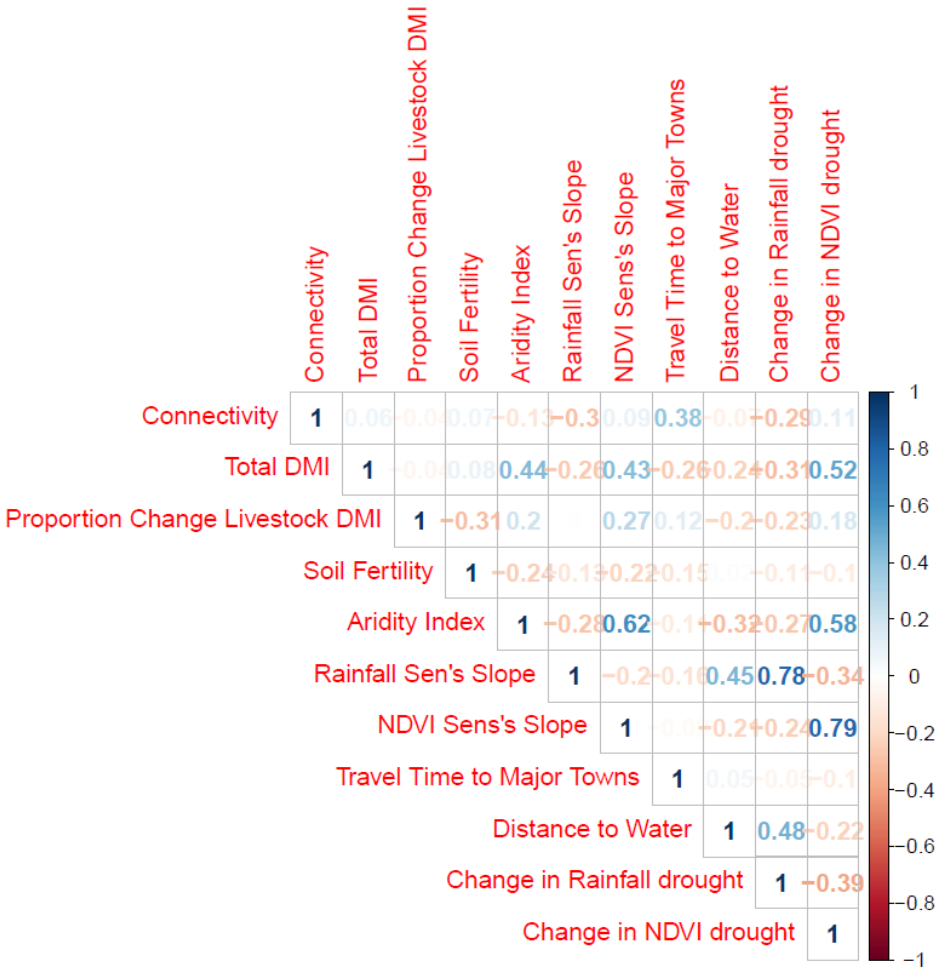

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810 Supplementary Fig 5. The spearman rank correlation coefficient between covariates used in the first GAM
811 modelling processes to identify drivers of dissimilarity in species-level community composition. Because
812 of the strong negative correlation between Rainfall and NDVI Sen's slope and the Change in Rainfall and
813 NDVI drought, we kept only the Sen's Slope estimates.
814

Dissimilarity

We calculated the Bray-Curtis dissimilarity of the species-level community composition for wildlife species only in each sampling unit between the 1970s-1980s, 1980s – 1990s, 1990s-2000s, and the total change between 1970s-2000s. We then used a Generalised Additive Model (GAM) to determine the drivers of dissimilarity[17]. We fit two GAM models. The first GAM looked at overall dissimilarity between the 1970s and 2000s. It used a beta distribution with a logit link structure to model univariate, and bivariate smooths of *a priori* selected drivers of dissimilarity, including anthropogenic, abiotic and biotic factors. These were:

(i) The change proportional change in Dry Matter Intake of livestock species between the 1970s and 2000s.
(ii) The travel time to major towns.
(iii) The distance to permanent water.
(iv) A tensor product smooth of the Sen's slope change in rainfall from the 1970s-2000s, and the Sens's slope of NDVI from 1983-2010. Both slopes were calculated at the sampling unit level.
(v) A tensor product smooth of proportion change in current flow (a measure of connectivity, see S3) and the total Dry Matter Intake in the 1970s. Both measured at the sampling unit level;
(vi) A tensor product smooth of cation exchange capacity (a proxy for soil fertility) and aridity index.

The second GAM modelled dissimilarity between each decade. It also used a beta distribution with a logit link structure to model univariate and bivariate smooths of *a priori* selected dissimilarity drivers, including anthropogenic, abiotic and biotic factors. These were similar to the first model but adapted to the temporal nature of the data:

(i) The proportional change in Dry Matter Intake of livestock species each decade. We allowed the smooth to vary with the change period, but each smooth has the same smoothing parameter[11].
(ii) Due to concurvity issues between travel time and major towns, we did not treat these variables independent. Instead, we created a tensor product of travel time to major towns and the proportion of a cell occupied by agriculture in 2015. We also allowed these smooths to interact with the change period but did not constrain the smoothing parameters.
(iii) A tensor product interaction of cation exchange capacity (a proxy for soil fertility) and aridity index.
(iv) The overall intensity of drought events in each decade measured using GIMMS NDVI and the SPI.
(v) The overall intensity of drought events in each decade measured using CHIRPS Rainfall and the SPI.
(vi) The change period as a fixed parametric effect[11].

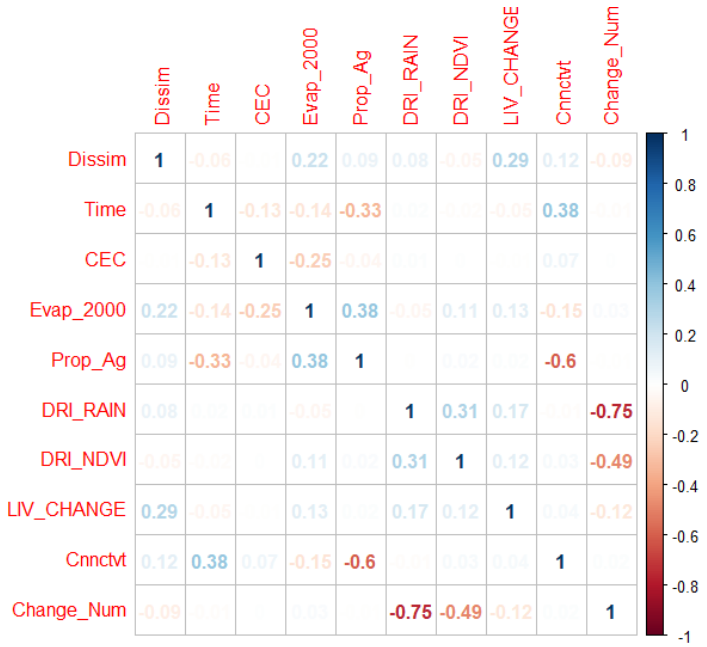
We did not include the covariate changes in connectivity due to its strong correlation with the proportion of a cell covered by agriculture (Sup Fig. 6).

In both models, all univariate and tensor product smooth used penalised thin plate regression splines[15]. With these splines, the null space is also penalised slightly, and the whole term can therefore be shrunk to zero. We also allowed an extra penalty to be added during model fitting to each term to be penalised to zero[16]. This means that the smoothing parameter estimation part of fitting can altogether remove terms from the model. The smoothing parameters were fit using restricted maximum likelihood (REML)[17]. We

checked the final models for concurvity between smooths and found no problems. The models were implemented using the *mgcv* package[20].

Ecosystem Boundaries

Ecosystem boundaries were digitised from original drawings of the Kenya Rangeland Ecological Monitoring Unit (KREMU), who split Kenya into 44 ecosystems (ecological units), based on topography, vegetation, wildlife migration patterns seasonality[3]. We adjusted the ecosystem's boundaries to split the Nairobi and Amboseli ecosystems, based on wildebeest collar data and evidence from the literature[4–7].



Supplementary Fig 6. The spearman rank correlation coefficient between covariates used in the second GAM modelling processes to identify drivers of dissimilarity in species-level community composition.

Results

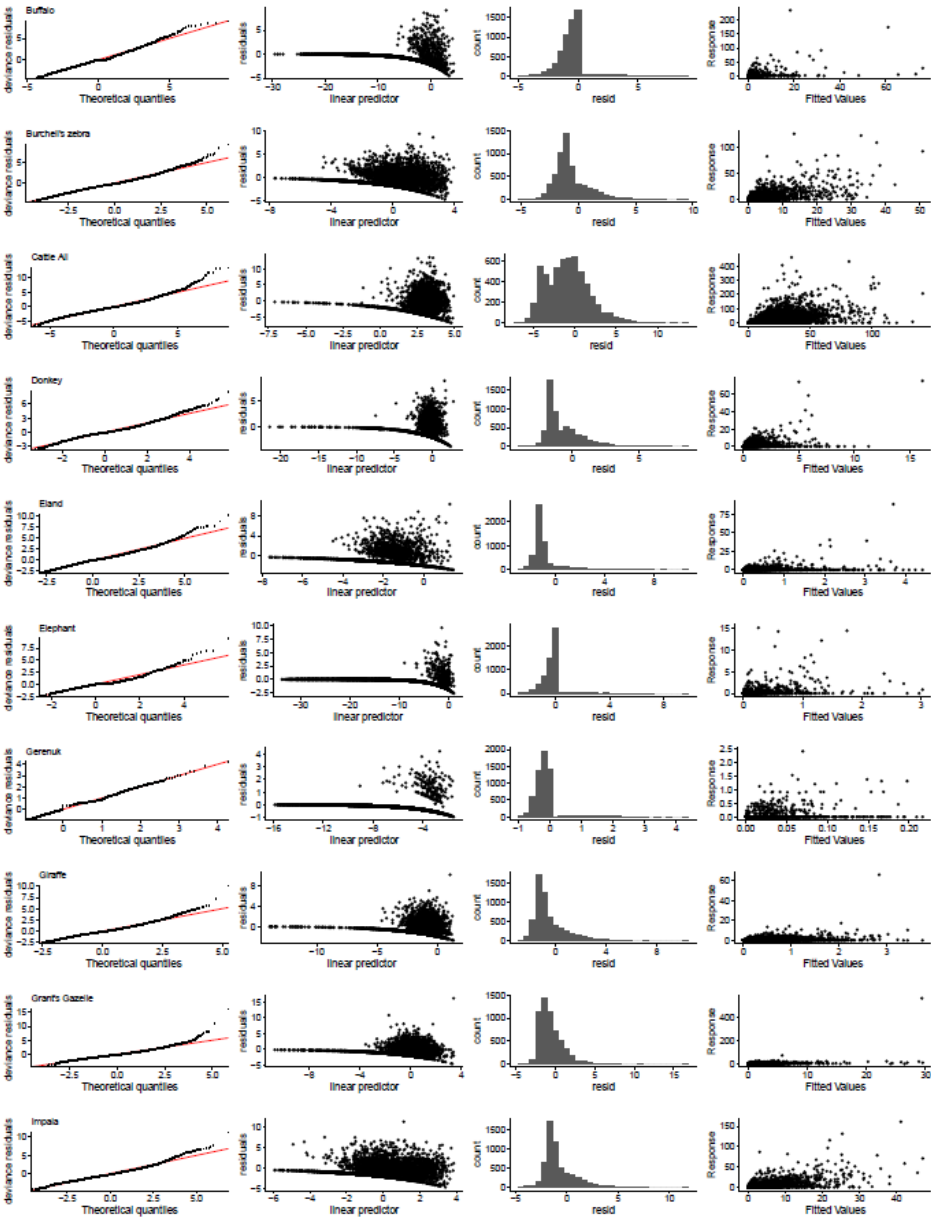
HGAM Model Fit and Checking

Overall, our HGAMs fit the data relatively well, and the median deviance explained of 50%, and a range from 22% (shoats) to 75% (wildebeest) (Sup Table 4). Q-Q plots and analysis of the residuals suggested that the Tweedie model generally fits the data well, although there is slight overdispersion at higher densities for some species (Sup Fig. 7&8). The linear predictor vs residual plots generally indicates a lack of heteroskedasticity.

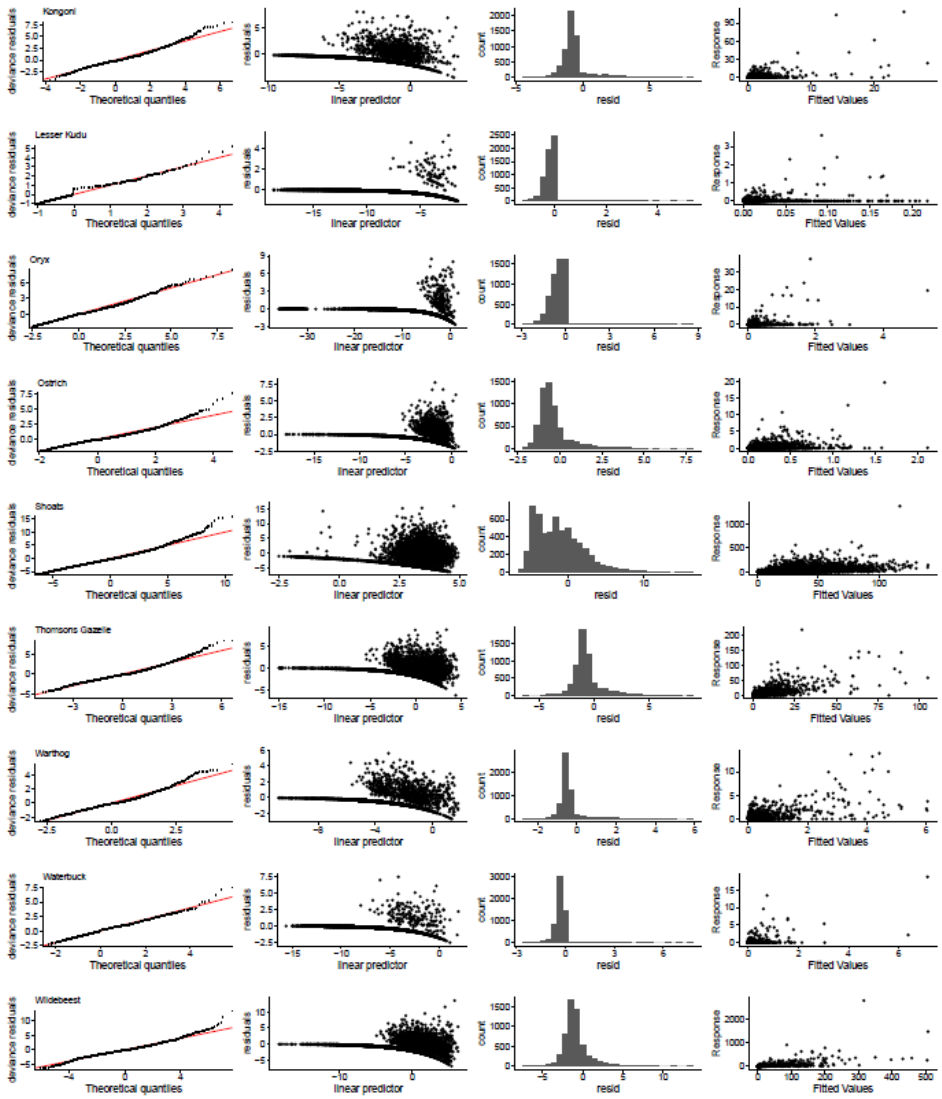
The majority of species (n=11) had a negative effect from the slope, with lower densities found at higher slopes. Notables are the species that have no relationship to slope; elephants, buffalo, gerenuk, kongoni, lesser kudu, ostrich, warthog, and waterbuck (Sup Fig 9). Distance to water had a linear negative effect on the density of cattle, donkeys, and shoats. The impact of water for most species was more complex and non-linear, with elephants showing large densities far from permanent water. Buffalo, eland, giraffe, elephant, kongoni, impala, warthog and waterbuck densities were all strongly negatively related to human population density. Shoats, donkeys, and cattle density generally increased with human population density. Burchell's zebra, donkeys, eland, giraffe, impala, ostrich, shoats, Thomson's gazelle, warthog and wildebeest density peaked at lower to intermediate values of mean NDVI. Thomson's gazelles and then wildebeest showed the highest effect size at low mean NDVI. Waterbuck, elephant, and buffalo had higher densities at higher mean NDVI.

Supplementary Table 4 – The descriptive statistics of Hierarchical Generalised Additive Models fir for each species.

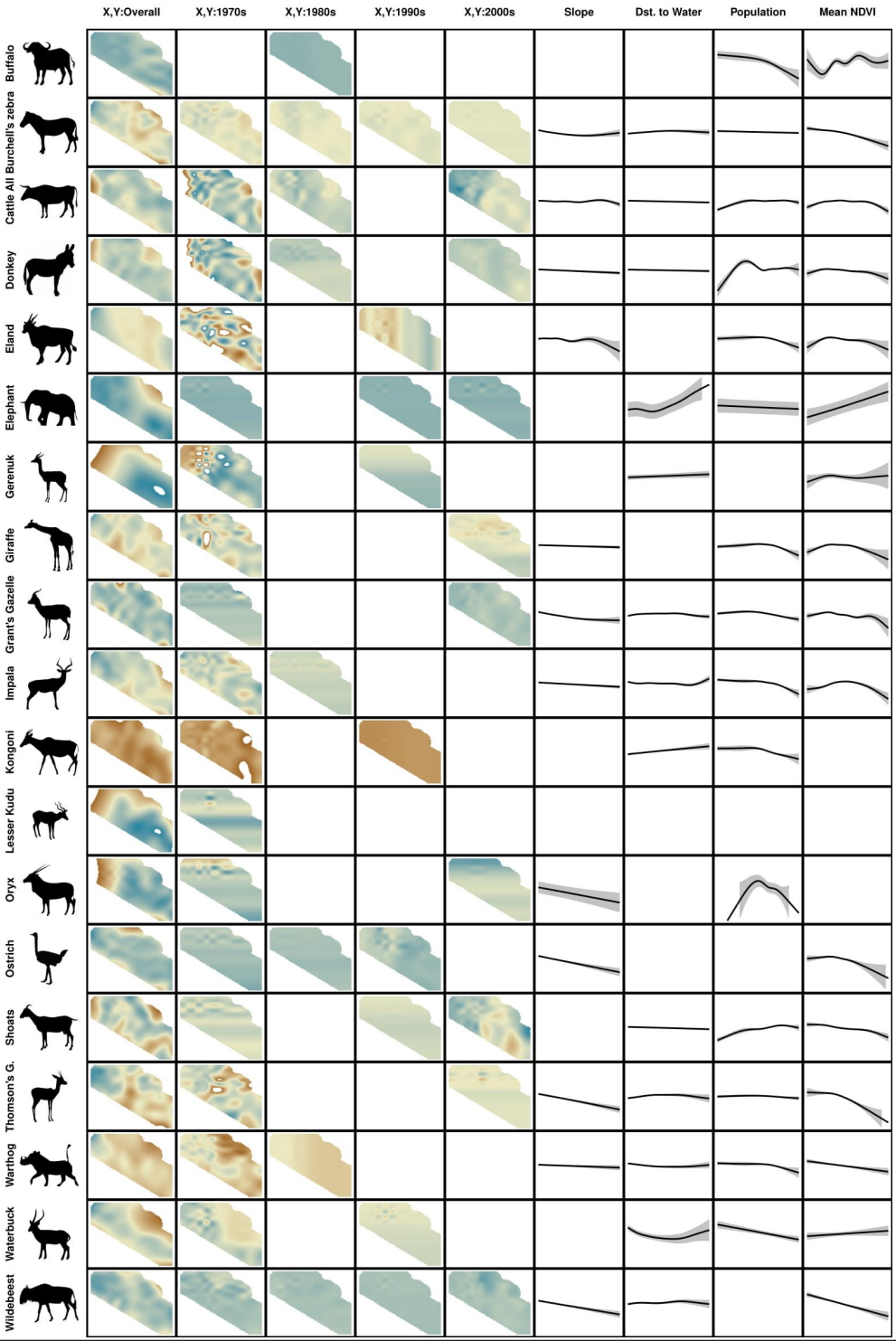
Species	Degrees of freedom	Log-likelihood value	Akaike's Information Criterion	Bayesian information criterion	Deviance	Residual Degrees-of-freedom	Dispersion	R-squared	Deviance Explained
Buffalo	89.19	-3560.32	7332.02	8034.67	8621.30	5610.81	8.10	0.15	71%
Burchell's zebra	202.41	-8482.02	17403.18	18862.85	14458.02	5495.59	3.17	0.39	56%
Cattle All	194.43	-21532.97	43486.94	44885.81	41715.47	5490.57	6.37	0.16	24%
Donkey	166.07	-6705.13	13787.44	15041.05	13799.86	5528.93	2.98	0.13	26%
Eland	104.55	-4384.43	9029.63	9896.59	13334.19	5600.45	5.13	0.06	25%
Elephant	72.76	-2945.89	6077.56	6695.14	2957.41	5630.24	3.57	0.12	66%
Gerenuk	44.35	-2705.16	5527.38	5916.60	981.01	5662.65	1.27	0.07	38%
Giraffe	155.97	-5217.39	10776.72	11913.28	9686.25	5542.03	2.21	0.08	27%
Grant's Gazelle	137.68	-8724.69	17753.33	18763.47	14152.70	5555.32	2.54	0.08	34%
Impala	167.75	-8444.23	17255.17	18474.08	16933.99	5529.25	3.59	0.39	50%
Kongoni	120.12	-4011.11	8291.98	9188.57	8594.35	5574.88	3.83	0.28	53%
Lesser Kudu	35.69	-2756.11	5609.25	5931.80	794.75	5669.31	2.17	0.05	50%
Oryx	57.43	-2994.74	6133.14	6610.76	4626.67	5650.57	7.26	0.11	58%
Ostrich	112.96	-3417.40	7105.58	8005.71	5395.85	5589.04	1.76	0.10	34%
Shoats	122.37	-21459.78	43188.97	44083.99	59432.19	5556.63	9.32	0.15	22%
Thomson's Gazelle	171.43	-6641.62	13647.29	14857.61	11984.18	5534.57	3.55	0.51	70%
Warthog	102.57	-3183.16	6600.40	7378.47	3696.24	5595.43	1.75	0.40	55%
Waterbuck	66.09	-2838.29	5841.91	6391.51	2069.29	5634.91	3.69	0.29	63%
Wildebeest	237.40	-8085.24	16694.56	18436.69	18200.41	5463.60	5.24	0.33	75%



Supplementary Figure 7: Residual plots for the HGAM models for the following species: buffalo, Burchell's zebra, cattle, donkeys, eland, elephant, gerenuk, giraffe, Grant's gazelle, and impala. In general, the Tweedie model has performed well at addressing multiple zeros. However, some species still have slight overdispersion at higher values, particularly those with a few large values.



Supplementary Figure 8: Residual plots for the HGAM models for the following species: kongoni, lesser kudu, oryx, ostrich, shoats, Thompson's gazelle, warthog, waterbuck and wildebeest. In general, the Tweedie model has performed well at addressing multiple zeros. However, some species still have slight overdispersion at higher values, particularly those with a few large values.



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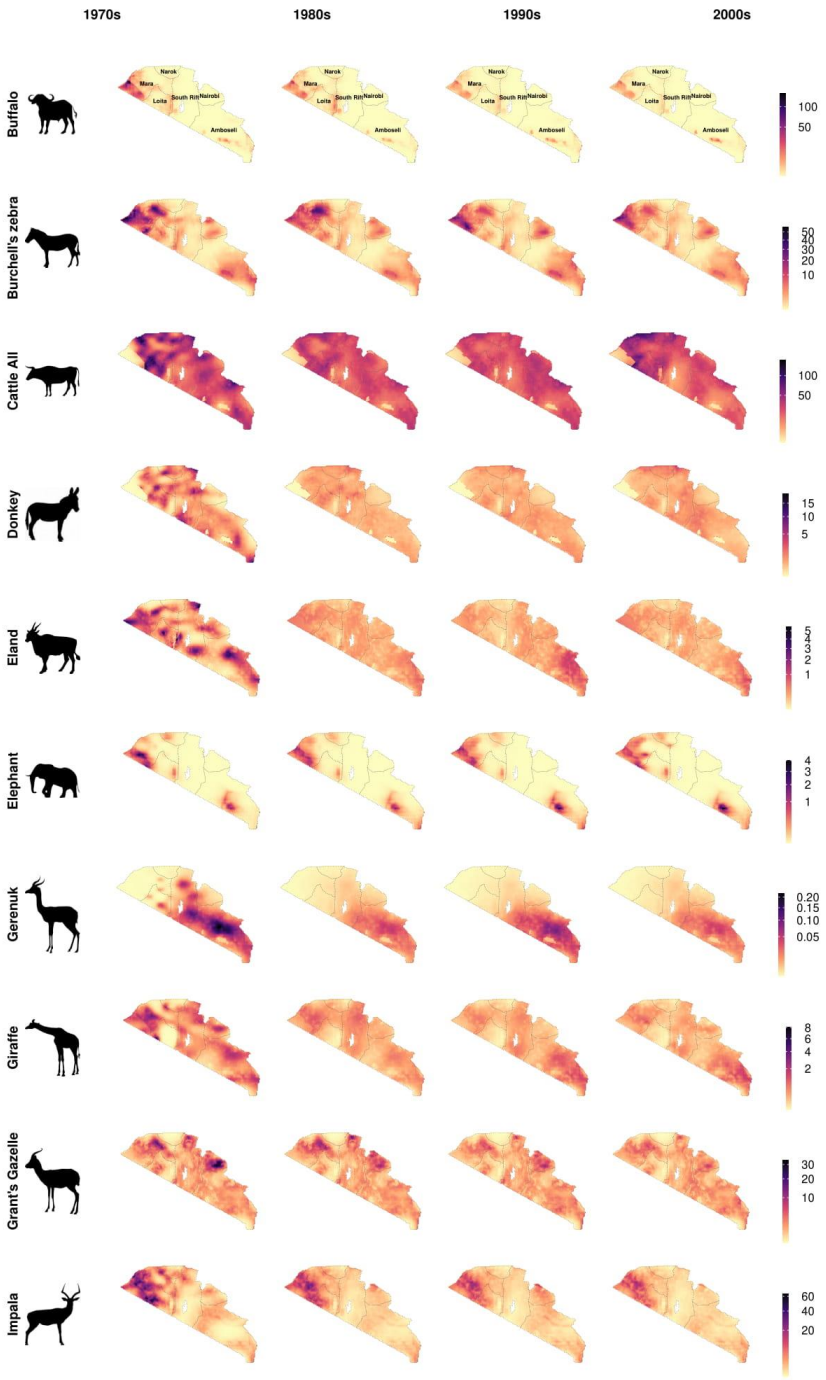
Supplementary Figure 9: Hierarchical generalized additive model effect size for each species model. The first four columns display the hierarchical spatial-temporal model. The first column is the global smoother of density across X and Y coordinates. The subsequent columns are different smooths for each decade. Blue colors are higher effect sizes and brown colors are lower. Only those smooth terms which are significant (p-value <0.05) are shown. For the univariate's smooths, solid lines represent effect size (all on the same scale) with 95% confidence intervals (grey bounds) presented for each of the covariates used in the final fitted models.



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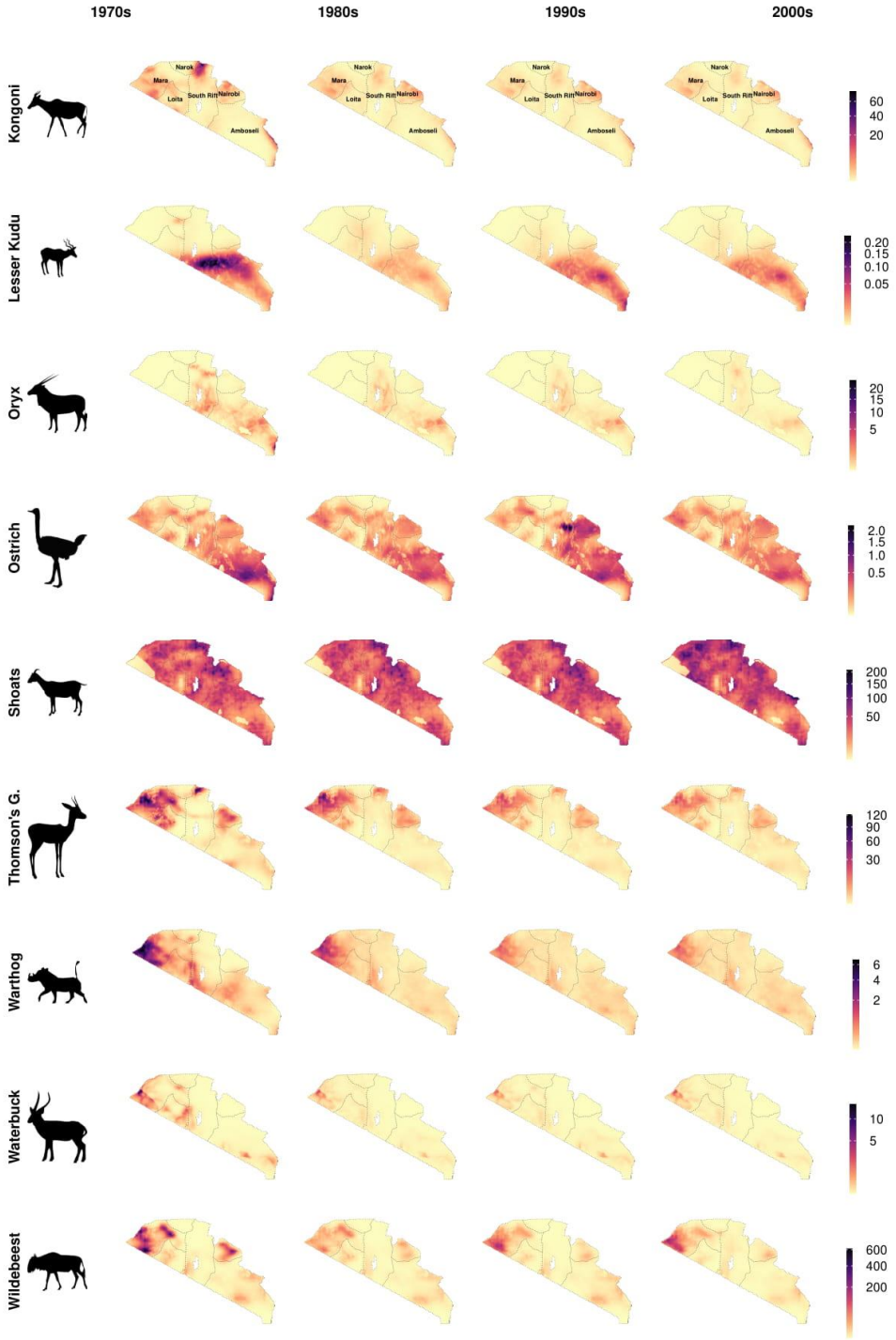
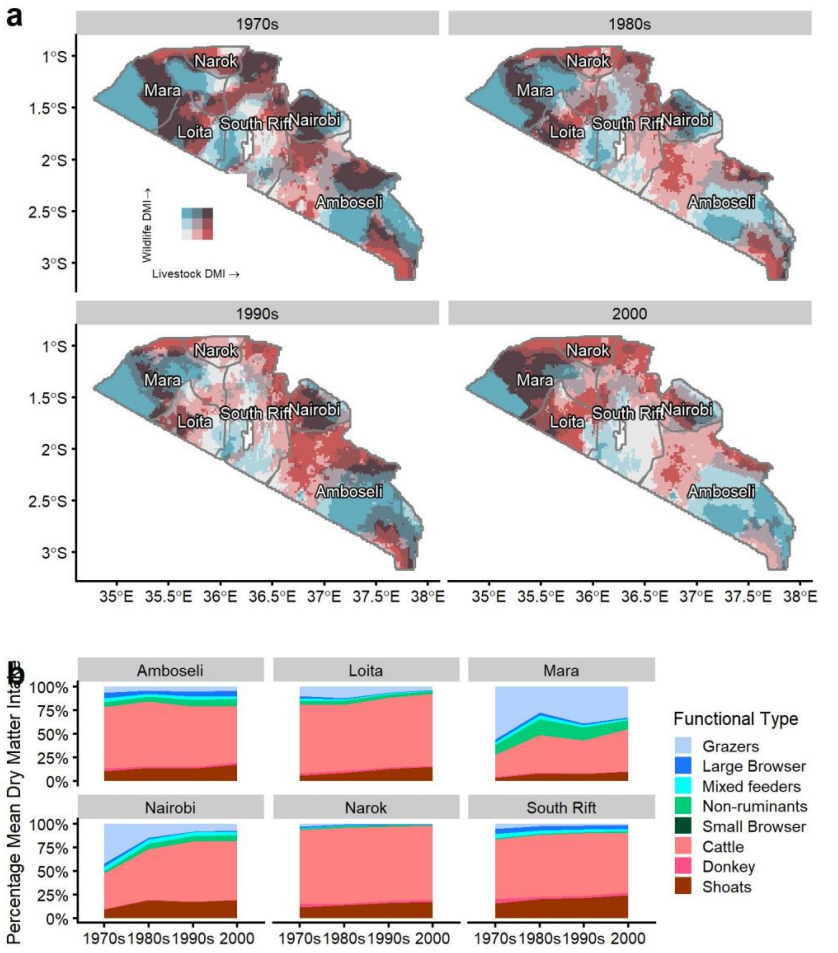
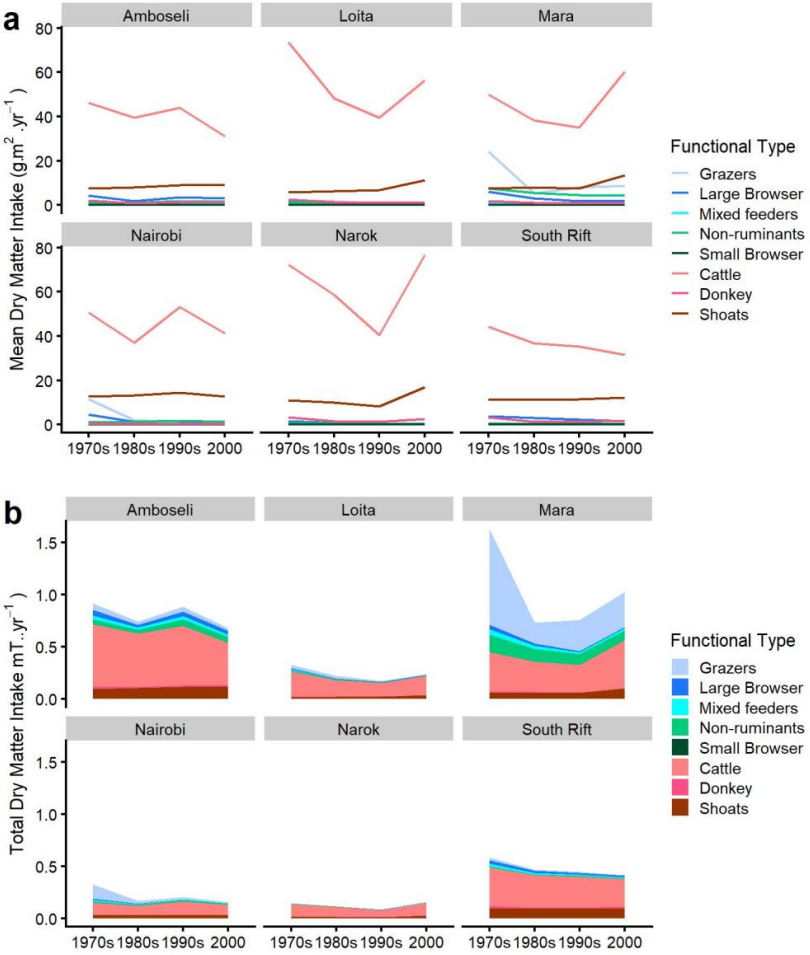
Supplementary Figure 10: Predicted density estimates across the 2kmx2km resolution prediction grid for the first ten species. Density is predicted for each decade. The 6 ecosystems in the study region (Mara, Amboseli, Narok, Nairobi, Loita, and South Rift are displayed with dotted lines. Colour scales are square root transformed.



Supplementary Figure 11: Predicted density estimates across the 2kmx2km resolution prediction grid for the last nine species. Density is predicted for each decade. The 6 ecosystems in the study region (Mara, Amboseli, Narok, Nairobi, Loita, and South Rift are displayed with dotted lines. Colour scales are square root transformed.



Supplementary Figure 12: Predicted changes in Dry Matter Intake (DMI) over time for all livestock and wildlife species in Southern Kenya. a) The predicted DMI for wildlife and livestock species is compared using a bivariate colour scheme. Darker red colour represents higher livestock DMI, and higher wildlife by darker blues. The colour scheme was created by splitting the DMI values into equal quantiles for each of the two groups b) the change in mean percentage of DMI for each functional type in the six highlighted ecosystems across the four decades. Wildlife species are grouped by functional type, and livestock are shown as each species.



Supplementary Figure 13: Changes in Dry Matter Intake (DMI) over time for the six ecosystems across the four decades. Wildlife species are grouped by functional type, and livestock is shown as each species. a) Change in mean DMI in each ecosystem using the mean for each grid cell; b) Changes in total DMI, summing the intake per year in each ecosystem.

Changes in Dry Matter Intake

Livestock (in particular cattle) has continually been the dominant ecological force in most of these ecosystems (Sup Fig. 10-13). Livestock dominance increased over the period from 56.3% of total DMI to 74.0%, although total livestock DMI decreased from 2.21mT.yr^{-1} to 1.98 mT.yr^{-1}. The total DMI and proportion of DMI from shoats increase over time from 8.0% (0.31mT.yr^{-1}) to 15.5% (0.42 mT.yr^{-1}), while the proportion of cattle DMI increases slightly from 46.36% to 56.80% although the total DMI of cattle decreases from 1.82mT.yr^{-1} t0 1.52mT.yr^{-1}.

In the 1970s, wildlife DMI was high, and livestock DMI was low in the Mara National Reserve, Loita Plains, Loita, parts of the South Rift, parts of the Nairobi ecosystem, and the central part of Amboseli ecosystem. By the 2000s mean wildlife DMI has decreased across many areas (Figure x a and b), from 43.6 % (1.72mT.yr^{-1}) of total DMI in 1970s to 26.0% (0.70mTyr^{-1}). The Nairobi and Maasai Mara ecosystem show the greatest declines in wildlife DMI from 1.17 mT.yr^{-1} (72.4%) to 0.46 mT.yr^{-1} (45.0 %) in the Mara, and 0.15mT.yr^{-1} (52.4%) to 0.03 mT.yr^{-1} (18.0%) in Nairobi. Overall Grazers total DMI declined the most from 6.53 mT.yr^{-1} (30%) in the 1970s to 2.16 mT.yr^{-1} (14.6%) in the 2000s, largely in the Mara and Nairobi ecosystems. Large browsers, mixed feeders, and small browsers all showed large declines. Non-ruminants experienced declines in DMI, but not as large and with no proportional change, from 2.26 mT.yr^{-1} (6.24%) to 1.63 mT.yr^{-1} (6.61%).

Changes in Community Composition

Species Diversity and Mean Mass

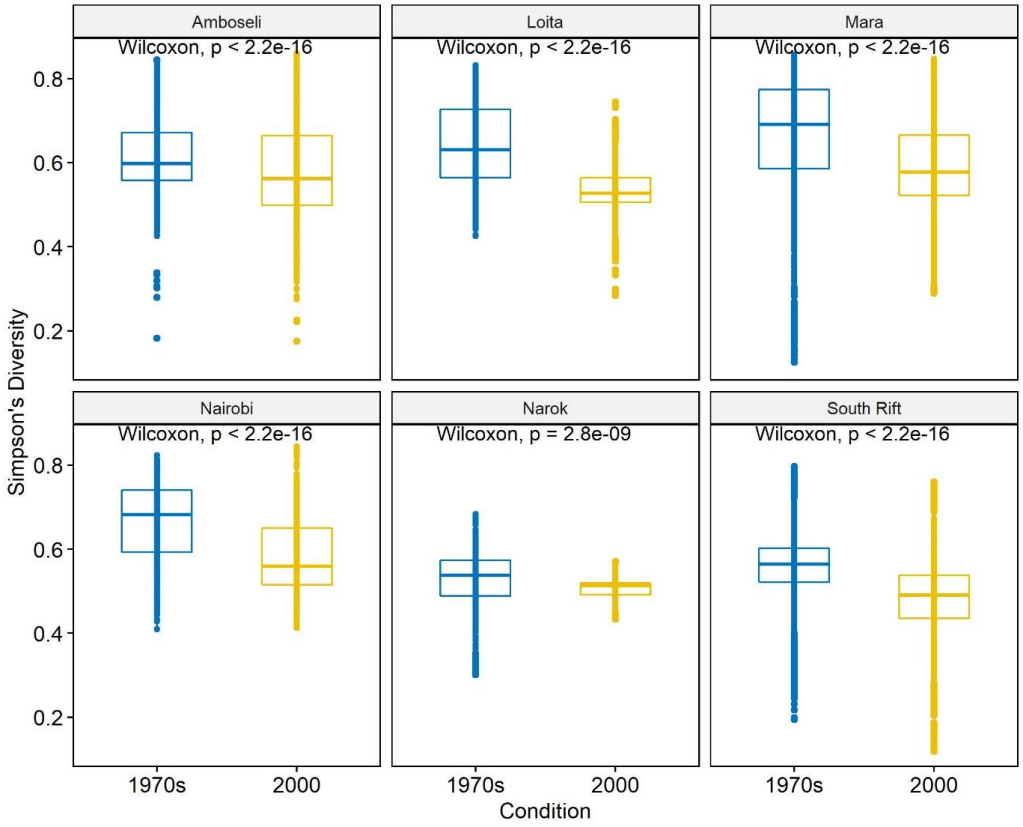
Between the 1970s and 2000s a highly significant drop in diversity and weighted mean body mass occurs all six ecosystems (Fig. 15 & 16 and Sup Table 5 & 6). Weighted mean body mass dropped the most in areas within closer travel time to major towns for Amobseli ($p < 0.001$, Pearson's correlation = -0.17), Nairobi ($p < 0.001$, Pearson's correlation = -0.38), Narok ($p < 0.001$, Pearson's correlation = -0.24), and South Rift ($p < 0.001$, Pearson's correlation = -0.24). In the Mara weighted mean body mass decreased the most when further from major towns ($p < 0.001$, Pearson's correlation = 0.15).

Supplementary Table 5 – Mean Simpsons Diversity for each ecosystem in the 1970s and the 2000s.

Ecosystem	1970s Mean Diversity	2000s Mean Diversity
Amboseli	0.62	0.58
Loita	0.64	0.53
Mara	0.66	0.59
Nairobi	0.66	0.59
Narok	0.52	0.51
South Rift	0.56	0.48

Supplementary Table 6 Weighted mean body mass (kg) for each ecosystem in the 1970s and 2000s

Ecosystem	1970s Weighted Mean Body Mass (kg)	2000s Weighted Mean Body Mass (kg)
Amboseli	156.68	142.78
Loita	179.44	141.80
Mara	170.42	146.41
Nairobi	135.00	110.08
Narok	135.91	119.84
South Rift	126.09	100.57



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955 Supplementary Figure 15: Box plots displaying Simpson's Diversity for each predicted pixel for and the
956 1970s and the 2000s and faceted by each ecosystem. The comparison indicates p-values from a non-
957 parametric paired Wilcoxon tests comparing the two decades.

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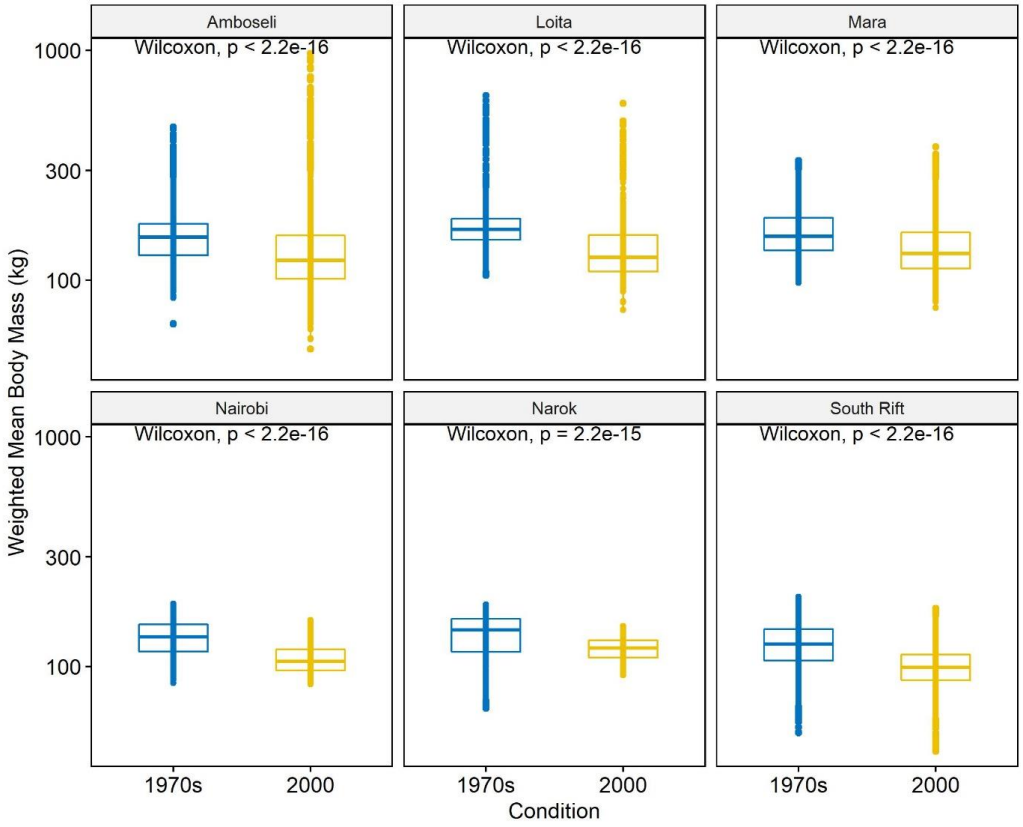


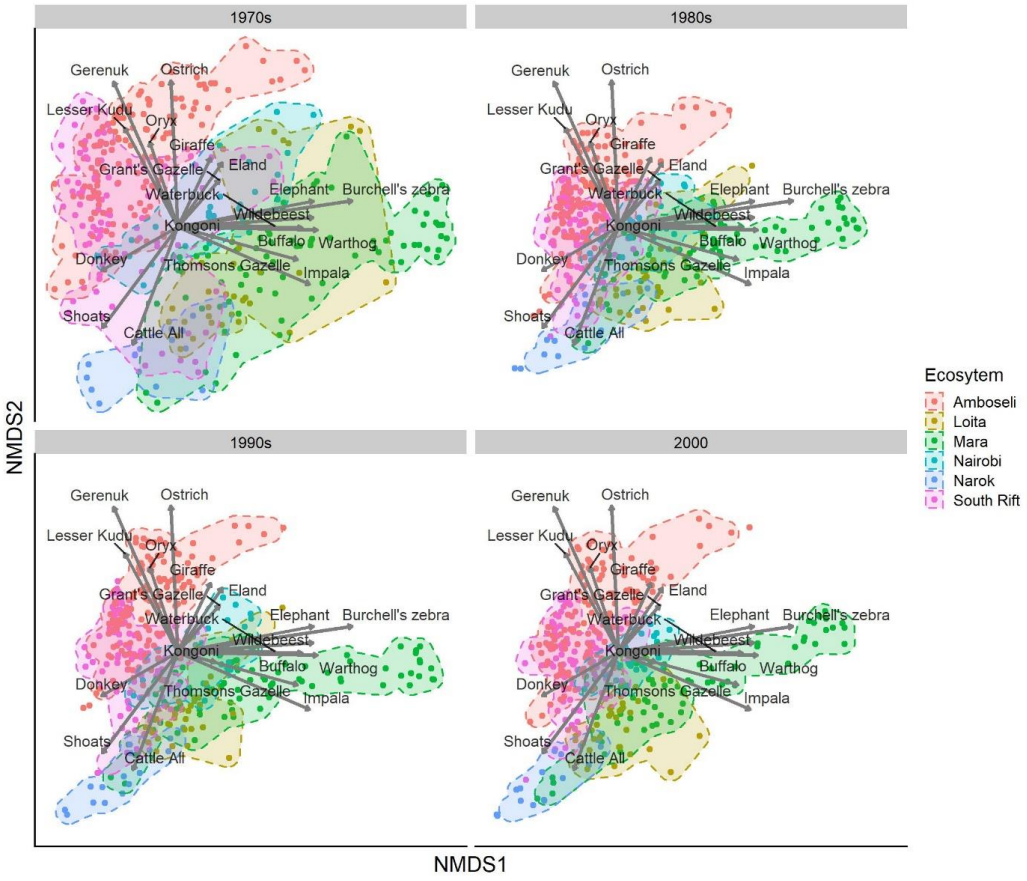
Supplementary Figure 16: Box plots displaying weighted mean body mass (kg) for each predicted pixel for and the 1970s and the 2000s and faceted by each ecosystem. The comparison indicates p-values from a non-parametric paired Wilcoxon tests comparing the two decades.

Non-Metric Multidimensional Scaling (NMDS)

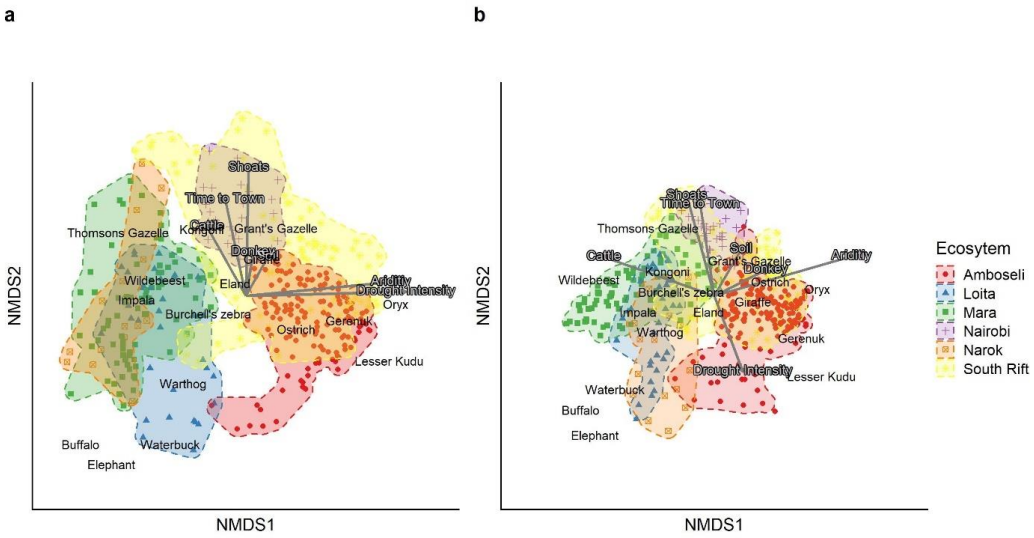
The NMDS of all the data had a stress of 0.154. This provides a measure of the degree to which the distance between samples in reduced dimensional space (usually 2-dimensions) corresponds with the samples' actual multivariate distance. Lower stress values (<0.2) indicate greater conformity and therefore are desirable.

Two-dimensional NMDS ordination of species composition (Sup Fig. 17) shows differences in species composition variability in each ecosystem over time. More variability exists in the 1970s for nearly all ecosystems than in any other decades, and this is substantially reduced during the 1980s. In the 1970s there is considerable similarity between the South Rift and Amboseli, dominated by browsers, and between the Loita and Mara ecosystems dominated by water-dependent grazers. Across the study area, homogeneity increases from the 1970s, with a shift to more livestock (shoat, donkey and cattle) dominated ecosystems. This is supported by the PERMANOVA which indicated significant differences in the centroids of the 1970's and 2000s data for, Amboseli ($F_{1,280} = 17.4$, $R^2 = 0.06$, $p<0.001$), Loita ($F_{1,64} = 7.9$, $R^2 = 0.11$, $p<0.001$), Mara ($F_{1,156} = 10.5$, $R^2 = 0.06$, $p<0.001$), Nairobi ($F_{1,54} = 13.0$, $R^2 = 0.19$, $p<0.001$), and South Rift ($F_{1,178} = 15.1$, $R^2 = 0.08$, $p<0.001$). Narok shows no significant difference ($F_{1,30} = 1.78$, $R^2 = 0.06$, $p<0.153$).

The NMDS suggests that beta-diversity within many ecosytems has also reduced, and PERMDIP, testing for changes of within group dispersion, an indication of changes in ecosytem beta-diversity, showed significant changes for Loita ($F_{1,64} = 16.33$, $p<0.001$), Mara ($F_{1,156} = 14.3$, $p<0.001$), and Nairobi ($F_{1,54} = 20.7$, $p<0.001$). No significant differecens where found in the South Rift ($F_{1,178} = 0.6$, $p=0.46$), Narok ($F_{1,30} = 0.6$, $p=0.07$), and Amboseli ($F_{1,280} = 1.5$, $p=0.22$).



Supplementary Figure 17: Results of the NMDS of species community composition across the four decades. Each ecosystem is highlighted using a convex hull. The length of the arrows is proportional to the strength of the correlation.



Supplementary Figure 18: Results of the independent NMDS of species community composition in the 1970s (stress = 0.172) (a) and 2000s (stress = 0.168) (b). Each ecosystem is highlighted using a convex hull. The length of the arrows are proportional to the strength of the correlation with the environmental variables.

At the species-level, in the 1970s all covariates had significant correlations with the ordinations (Sup Figure 18): shoats DMI (p-value <0.001, r^2 = 0.35), cattle DMI (p-value <0.001, r^2 = 0.13), drought intensity (p-value <0.001, r^2 = 0.55), aridity (p-value <0.001, r^2 = 0.46), soil fertility (p-value <0.001, r^2 = 0.04), travel time to towns (p-value <0.001, r^2 = 0.20), and donkey DMI (p-value = 0.006, r^2 = 0.04). Similar correlations occur in the 2000s, with significant correlations with the ordination for shoats DMI (p-value <0.001, r^2 = 0.23), cattle DMI (p-value <0.001, r^2 = 0.30), drought intensity (p-value <0.001, r^2 = 0.14), aridity (p-value <0.001, r^2 = 0.28), soil fertility (p-value <0.001, r^2 = 0.06), travel time to towns (p-value <0.001, r^2 = 0.18), and donkey DMI (p-value = <0.001, r^2 = 0.07). The strength of correlations of the two rainfall related variables, drought and aridity, decreases from the 1970s to 2000s. From both ordinations it is clear that buffalo, elephant, waterbuck, zebra, wildebeest, and kongoni father humid environment, while oryx, gerenuk, ostrich, and kudu are present in more arid areas.

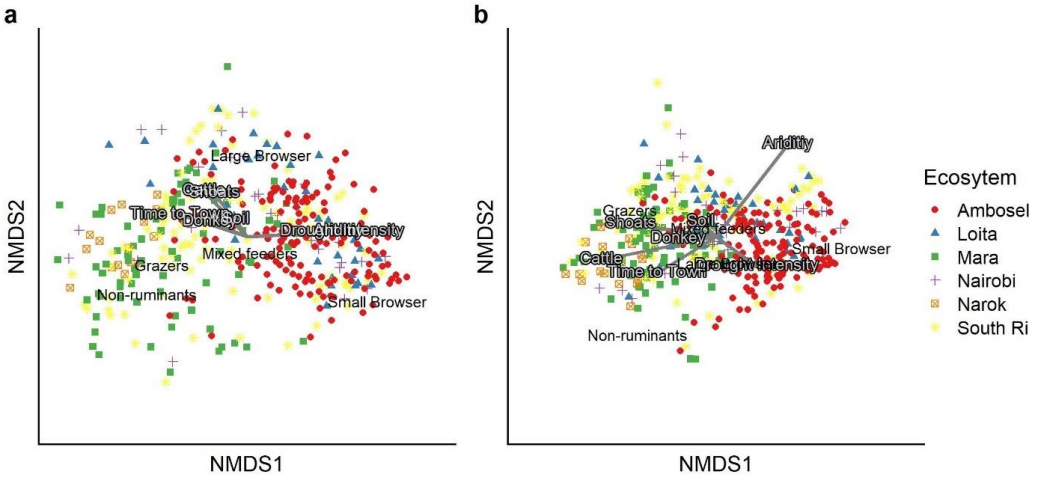
These conclusions are supported by a Permutational Multivariate Analysis of Variance (PERMANOVA) using the same variables (Sup Table 7&8), with livestock accounting for more variation in species composition in the 2000s than the environmental variables.

Supplementary Table 7 – Result of a Permutational Multivariate Analysis of Variance for the wildlife species composition data for the 1970s. All terms are significant at the 0.05 significance level. No multi-collinearity was found between variables.

Term	df	SumOfSqs	R2	statistic	p.value
Shoats DMI	1	2.696	0.025	12.559	0.001
Cattle DMI	1	3.283	0.030	15.294	0.001
Donkey DMI	1	1.808	0.017	8.423	0.001
Drought Intensity	1	8.113	0.074	37.797	0.001
Aridity	1	4.441	0.041	20.689	0.001
Soil	1	1.769	0.016	8.243	0.001
Time to Town	1	2.188	0.020	10.191	0.001

Supplementary Table 8 – Result of a Permutational Multivariate Analysis of Variance for the wildlife species composition data for the 2000s. All terms are significant at the 0.05 significance level. No multi-collinearity was found between variables.

Term	df	SumOfSqs	R2	statistic	p.value
Shoats DMI	1	2.190	0.025	14.638	0.001
Donkey DMI	1	9.921	0.115	66.318	0.001
Cattle DMI	1	4.396	0.051	29.387	0.001
Drought Intensity	1	1.664	0.019	11.126	0.001
Aridity	1	4.000	0.046	26.739	0.001
Soil	1	3.605	0.042	24.097	0.001
Time to Town	1	1.021	0.012	6.827	0.001



Supplementary Figure 19: Results of the independent NMDS of wildlife functional type composition in the 1970s (stress= 0.158) (a) and 2000s (stress = 0.144)(b). The length of the arrows are proportional to the strength of the correlation with the environmental variables

In the functional type NMDS (Sup Fig. 19), in the 1970s most covariates had significant, but weak correlations with the ordinations: shoats DMI (p-value =0.002, r^2 = 0.04), cattle DMI (p-value <0.001, r^2 = 0.05), drought intensity (p-value <0.001, r^2 = 0.12), aridity (p-value <0.001, r^2 = 0.11), travel time to towns (p-value <0.001, r^2 = 0.07), and donkey DMI (p-value = 0.012, r^2 = 0.02). Soil fertility was not significantly correlated.

Similar correlations occur in the 2000s, with stronger relationships for both shoats DMI (p-value <0.001, r^2 = 0.10), and cattle DMI (p-value <0.001, r^2 = 0.18), and similar correlations for drought intensity (p-value =0.003, r^2 = 0.03), aridity (p-value <0.001, r^2 = 0.18), travel time to towns (p-value <0.001, r^2 = 0.07), and donkey DMI (p-value =0.023, r^2 = 0.02). Soil fertility was non-significant (p-value = 0.281, r^2 = 0.01).

It is clear that small browsers dominate communities in more arid areas from both ordinations, and non-ruminants and grazers dominate humid areas. The increased correlation of shoat DMI and cattle DMI in the 2000s indicates a more considerable impact on defining functional composition. The change in the overlap between non-ruminants and grazers is also evident between the two decades. These conclusions are supported by a Permutational Multivariate Analysis of Variance (PERMANOVA) using the same variables (Sup Table 9&10), with livestock accounting for considerably more variation in the functional composition in the 2000s than in the 1970s.

In the 2000s grazers have a more identifiable axis, distinct from non-ruminants. Also, large browsers (giraffe) change from having a strong relationship with the ordination in the 1970s to a weak one in the 2000s, representing their wide-scale declines.

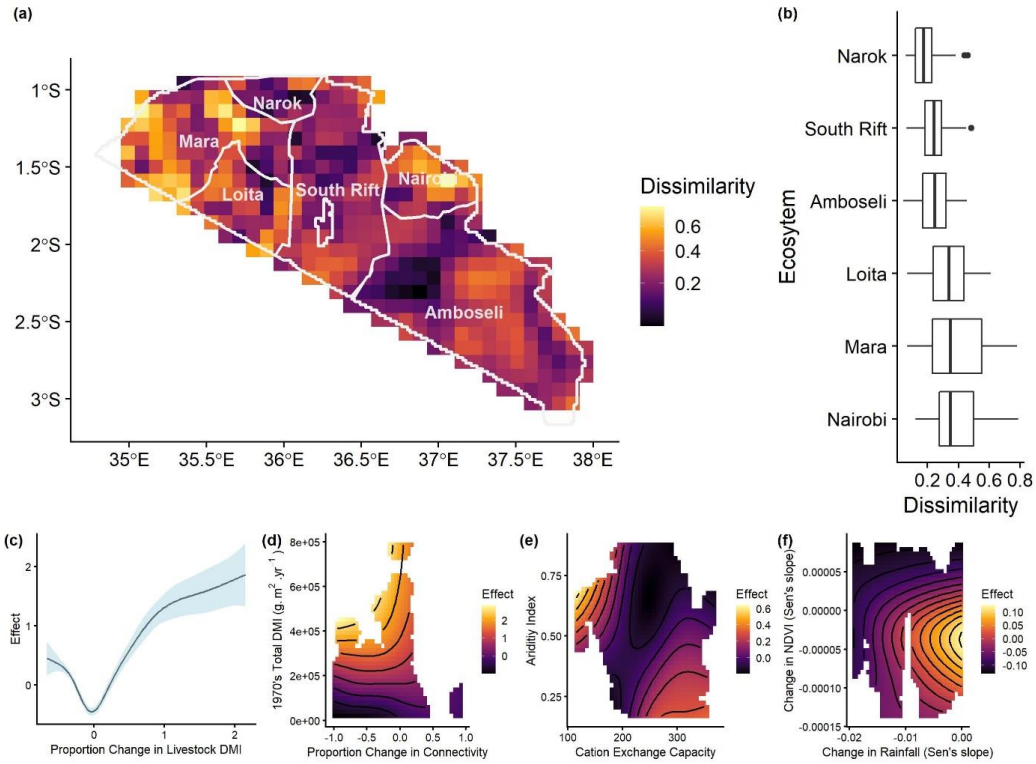
Simper analysis between decades shows 70.5% difference in wildlife species composition between 1970's and 2000s. The five species contributing most to dissimilarity between the decades are wildebeest (average proportion = 0.21, p = 0.002), giraffe (average proportion = 0.11, p = 0.002), zebra (average proportion = 0.10, not significant), eland (average proportion = 0.05, p = 0.002), and elephant (average proportion = 0.04, not significant). Simper analysis which included the livestock species shows a 46.7% difference. The five species contributing most to dissimilarity between the decades are cattle (average proportion = 0.19, p = 0.002), wildebeest (average proportion = 0.10 p = 0.002), sheep and goats (average proportion = 0.05, p = 0.002), zebra (average proportion = 0.03, p = 0.002), and giraffe (average proportion = 0.02, p = 0.002). Simper analysis between 1970's and 2000's for functional traits shows a 45.6% difference in composition. This is broken down into grazers (average proportion = 0.27, p = 0.004), non-ruminants (average proportion = 0.09 non-significant), large browsers (average proportion = 0.06, p = 0.002), mixed feeders (average proportion = 0.04, p = 0.002), and small browsers (average proportion = 0.00, p = 0.002).

Supplementary Table 9 – Result of a Permutational Multivariate Analysis of Variance for the functional traits composition data for the 1970s. All terms are significant at the 0.05 significance level. No multi-collinearity was found between variables.

Term	df	SumOfSqs	R2	statistic	p.value
Shoats DMI	1	2.137	0.037	16.390	0.001
Donkey DMI	1	0.791	0.014	6.066	0.003
Cattle DMI	1	0.351	0.006	2.695	0.046
Drought Intensity	1	1.162	0.020	8.916	0.001
Aridity	1	1.879	0.032	14.416	0.001
Soil	1	0.066	0.001	0.504	0.662
Time to Town	1	0.186	0.003	1.425	0.225

Supplementary Table 10 – Result of a Permutational Multivariate Analysis of Variance for the functional traits composition data for the 2000s. All terms are significant at the 0.05 significance level. No multi-collinearity was found between variables.

Term	df	SumOfSqs	R2	statistic	p.value
Shoats DMI	1	2.840	0.068	35.037	0.001
Donkey DMI	1	1.580	0.038	19.492	0.001
Cattle DMI	1	2.467	0.059	30.438	0.001
Drought Intensity	1	0.363	0.009	4.475	0.006
Aridity	1	1.469	0.035	18.119	0.001
Soil	1	0.553	0.013	6.826	0.001
Time to Town	1	0.108	0.003	1.332	0.245

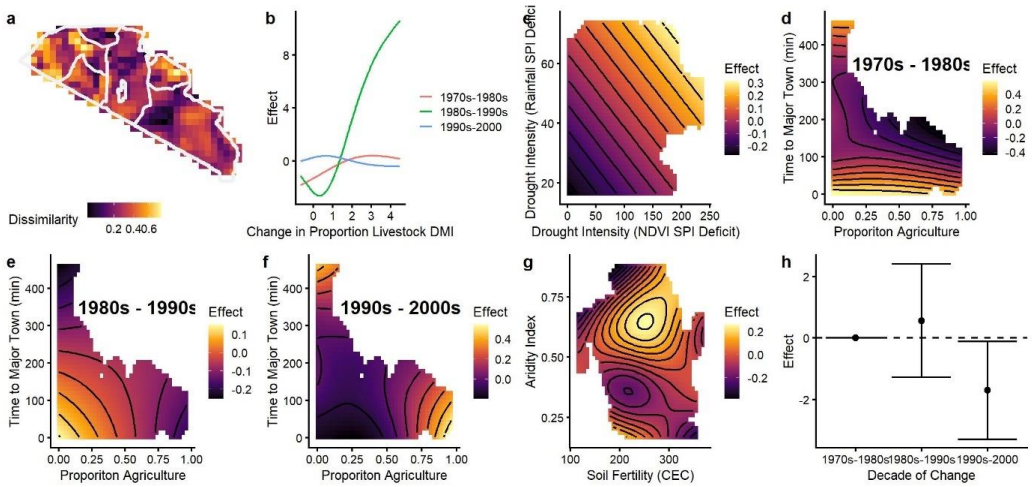


Supplementary Figure 20: Dissimilarity of wildlife species composition between the 1970s and 2000s in Southern Kenya within the six ecosystems (a-b), and the dissimilarity drivers identified by a Generalised Additive Model (c-f). (a) Dissimilarity in wildlife species composition for each sampling units between the 1970s and 2000s, with ecosystems, labelled; (b) boxplot of dissimilarity per ecosystem; (c) response curve for the proportion change in livestock dry matter intake (DMI) between 1970s and 2000s; (d) the tensor product relationship between the proportion change in current flow (connectivity) based on anthropogenic obstructions to mobility and the total dry matter intake in the 1970s; (e) tensor product of soil fertility measured by the cation exchange capacity and aridity index; and (f) tensor product of the change in rainfall in NDVI over the study period. (c) has the most considerable effect on dissimilarity, which decreases down to (f).

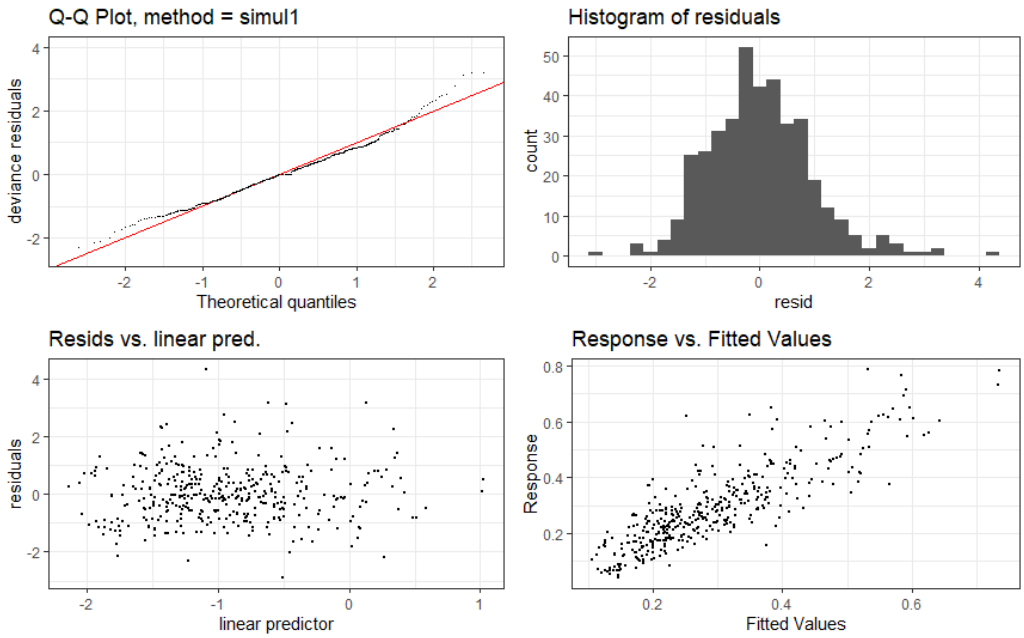
Dissimilarity in wildlife species-level community composition between the 1970s and 2000s varied considerably across the region (mean = 0.29, range = 0.04 – 0.79).The Nairobi and Mara ecosystems had the highest median dissimilarity (both 0.35) and Narok the lowest (0.18).

Our Generalised Additive Model (GAM) that modelled dissimilarity between the 1970s and 2000s as the dependent variable explained 73.1% of the deviance and fit the data well (Sup Fig 20). Two terms were removed during the model fitting during penalisation the travel time to major towns and distance to water. A large effect was found for the proportion change in livestock DMI between 1970s and 2000s (effective degrees of freedom 6.62, = $p < 2e\text{-}16$; Sup Fig 20c) with the largest impact occurring when livestock DMI increases, but also small impacts on dissimilarity when livestock DMI decreases. The effect on dissimilarity was highest when the current flow (connectivity) - based on anthropogenic obstructions to mobility – had reduced and when the total DMI in the 1970s was large (e.d.f. = 9.00, $p < 2e\text{-}16$; Sup Fig 20d). A moderate effect of soil fertility (measured by the cation exchange capacity) and aridity index was found (e.d.f= 6.56, p =4.42e-06, Sup Fig 20e), with the highest dissimilarity in low fertility humid areas or higher fertility arid areas. A small effect of the interaction between change in rainfall and NDVI was identified (e.d.f 3.44, p = 0.00886, Sup Fig 20f), with the highest effect on dissimilarity in areas which had seen a decrease in NDVI, but only a marginal decrease in rainfall.

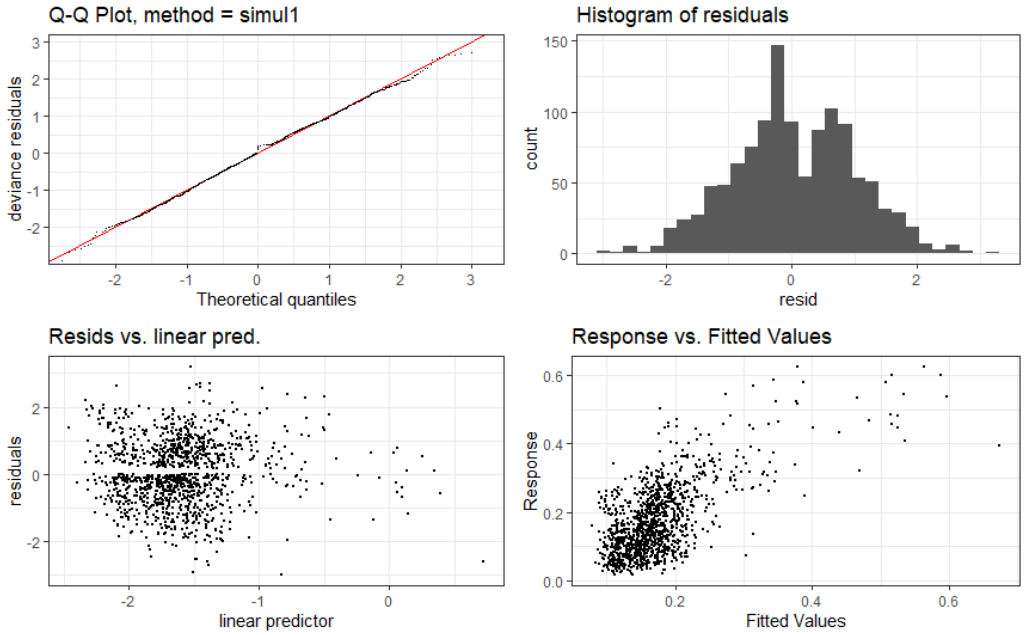
Our second model modelled wildlife dissimilarity between each consecutive decade from the 1970s to the 2000s as the dependent variable explained 38.6% of the deviance (Sup Fig 21). No terms were removed during model fitting. The model shows that: (i) Change in proportion of livestock Dry Matter Intake (DMI) is an essential driver of wildlife community composition change, particularly from the 1980s to 1990s, and partially in the 1970s to 1980s transition (effective degrees of freedom = 7.0, $p < 0.001$). (ii) Decades with more intense droughts, measured by deficit from the NDVI and Rainfall Standardized Precipitation Index, increase wildlife community dissimilarity between decades (edf = 1.78, $p < 0.001$). (iii) Between the 1970s and 1980s changes in the wildlife community occurs close to major towns, in areas with and without future agricultural change, (edf = 4.7, $p<0.001$). Between the 1980s and 1990s, we observed a small impact closet to towns in non-agricultural areas (edf = 1.58, $p < 0.01$). In the 1990s-2000s, larger dissimilarity occurs in areas close to towns and large proportions of a sampling unit converted to agricultural (edf = 5.2 $p<0.001$). (iv) Slightly higher dissimilarity in relatively humid areas with reasonably fertile soils (edf = 7.8, $p<0.001$); (v) and slightly lower changes in dissimilarity between the 1990s and 2000s (estimate = -1.7, $p<0.05$).



Supplementary Figure 21: Dissimilarity of wildlife species composition between the consecutive decades from the 1970s to the 2000s in Southern Kenya, within the six ecosystems. (b-h) the drivers of dissimilarity identified by a Generalised Additive Model (GAM). (a) Dissimilarity in wildlife species composition for each sampling units between the 1970s and 2000s, with ecosystems outlined. (b) The model response curve for the change in the proportion of livestock dry matter intake (DMI) for each change period. (c) The model response curve for the intensity of drought in the decade, measured by NDVI and rainfall data, which were transformed using the Standardised Precipitation Index and the total deficit for each decade summed. (d-f) The tensor product relationship between the proportion of agriculture per pixel and travel time to major towns for each change period. (g)The tensor product of soil fertility measured by the cation exchange capacity and aridity index. (h) the fixed effect of the period of change.



Supplementary Figure 22: Q-Q plots and analysis of the residuals for the generalised additive model explaining dissimilarity in wildlife species community composition between the 1970s and 2000s. This suggested the beta regression model generally fit the data well, although there is still slight overdispersion at higher densities.



Supplementary Figure 23: Q-Q plots and analysis of the residuals for the generalised additive model explaining dissimilarity in wildlife species community composition between each consecutive decade from the 1970s and 2000s. This suggested the beta regression model generally fit the data well.

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Supplementary Text 2 – Changes to Rainfall, NDVI and Grass Biomass

Landscape-scale changes

Rainfall

We downloaded data from CHIRPS (Climate Hazards Group InfraRed Precipitation with Station data), a 39+ year quasi-global rainfall data at 0.05° resolution. Due to the CHIRPS data's temporal limitations, we also downloaded monthly rainfall data from the World Meteorological Organization Global Precipitation Climatology Centre (GPCC) monthly rainfall data V2018 at the 0.5° resolution. This data includes monthly records from 1891-2016. Both the GPPCC and CHIRPS data have reasonable accuracy for predicting rainfall at the monthly level across Africa and Kenya [12].

We used the CHIRPS data to calculate changes in rainfall from January 1981 - September 2020. We calculated change in rainfall using a non-parametric Sen's Slope test (Theil–Sen test) to determine the magnitude of these changes at the pixel level using the *trends* pacakge[3]. This test is more robust to outliers and temporal autocorrelation than simple linear models. We performed the test across the entire temporal length of the data and each month to determine seasonal changes in rainfall. Using CHIRPS and GPCC data, we calculated the Standardised Precipitation Index (SPI), a climatic proxy widely used for drought quantification and monitoring[4]. The functions standardise a variable following a log-Logistic distribution function. We calculated the index at the 12-month time scale for the long-term mean monthly rainfall in each ecosystem. We used *quantreg*[5] to conduct quantile regression on the SPI data to understand changes in periods with higher rainfall and lower rainfall events. We choose two extreme quantiles to represent heavy rainfall conditions (0.95 quantile) drought conditions (0.05 quantile)[6]. In addition, we used the SPI to calculate specific metrics per decade, including the overall intensity of drought events, the number of drought events, and the length of drought events.

GIMMS NDVI

We downloaded the Normalised Difference Vegetation Index (NDVI) 3rd generation product using the Global Inventory Monitoring and Modeling System (GIMMS). This index is generated using Advanced Very High-Resolution Radiometer (AVHRR). The data covers July 1981 to December 2015 with a bi-weekly temporal resolution and a 1/12 degree spatial resolution (roughly 8km^2). We calculated the overall change in NDVI from 1981-2010 using a Sen's Slope estimator from the package *trend*[3]. We also calculated the change in NDVI associated droughts over time be using the Standardised Precipitation Algorithm[4]. We calculated the index at the 12-month time scale. We used *quantreg*[5] to conduct quantile regression on the SPI data to understand changes in periods with higher rainfall and lower rainfall event. We choose two extreme quantiles to represent heavy rainfall conditions (0.95 quantile) and drought conditions (0.05 quantile)[6]. In addition, we used the SPI to calculate specific metrics per decade, including the overall intensity of drought events, the number of drought events, and the length of drought events.

Time-series clustering

We performed a Sen's slope analysis on the monthly NDVI data, but the results provided literal clarity on how changes in seasonal patterns of NDVI have occurred over time. We, therefore, performed a three-step process at the pixel-level to identify these patterns. First, we split the data into three even periods (1/7/1981 –15/11/1992, 15/11/1992 - 04/01/2004, 04/01/2004 – 30/12/2015) to compare patterns of seasonality across the data period. We settled for these periods because it represented a trade-off between understanding long-term seasonality changes while ensuring that enough data was present to calculate seasonality accurately. Second, for each pixel, we created a simple generalised additive model (GAM) [7], which had a univariate smooth of the month using a cyclic cubic regression spline and a basis complexity set to twelve. Third, we extracted this seasonal pattern in the data from the GAM and performed hierarchical time-series clustering for all seasonal data using dynamic time warping distance

and subsequently ward distance to perform the clustering[8]. We performed a series of diagnostics tests to determine the optimum number of clusters and split the data into fifteen clusters.

Bivariate Copula Distribution Model

We estimate the time-varying correlation between time series using a bivariate copula distribution model, an extension of generalised additive models for location, scale and shape (GAMLSS)[1]. Copulas represent a new technique for analysing ecological data[9], allowing for the specification of a copula dependence and marginal distribution parameter to be estimated simultaneously[1]. In our case, we wanted to understand how the relationship between NDVI, which is related to grass biomass in the growing season[10], and rainfall has changed over time. Previous work from Amboseli has shown a reduction in the grass biomass per unit rainfall over time[10]. This method allows the estimation of a Kendall Tau statistic of correlation between rainfall and NDVI over time. We filtered the GIMMS NDVI and CHIRPS rainfall data to include the sum of NDVI and precipitation in the two annual growing seasons, April-June, and October-December from 1982-2015. We removed any grid cell with greater than 50% agricultural cover by 2020.

We fit two copula models to this data. In the first model, we used the Gaussian distributions for both the margins of rainfall and NDVI. We fit a model where the scale and location parameters and the single association parameter were allowed to independently vary over time for each of the five ecosystems. We constrained the number of basis functions to six for the theta parameter to remove excessive wigglyness to represent overall changes in time. Initially, the algorithm failed to converge. We removed the Narok ecosystem data points which had a low sample size, and this problem was fixed. In the second model, we again used Gaussian distributions for both the margins of rainfall and NDVI terms. We fit a model where the scale and location parameters were related to a smooth of year. The association parameter was represented as a tensor product of the densities of bomas (livestock enclosures) in 2020, year, and a univariate smooth of soil fertility, measured by the cation exchange capacity. We originally included aridity as a tensor product smooth with soil fertility but removed it due to concurvity issues associated with livestock enclosure densities. We constrained the tensor products basis dimensions to five along each axis to prevent overfitting. This data does not cover the Narok or Nairobi ecosystems, so we removed them from the analysis. All smooths used penalised thin plate regression splines[11]

The boma data was collected and described in Chapter 5.

Local Scale

Grass Biomass Data

We used data from a 1000km^2, the Shompole and Olkiramatian area, within the South Rift ecosystem to determine the relationship between grass biomass, rainfall, and grazing pressures. Pasture characteristics were measured using the pin – intercept across 24 plots every few months across the Shompole and Olkiramatian area since 2008. A simple linear regression was calculated to predict grass biomass (g/m^2) based on the mean hits per pin[12]. We calculated the percentage of plant material grazed at the time of data collection and the mean percentage grazed in the previous six months.

Soil

In July 2018, we collected soil samples from the 24 plots. One plot was excluded because it was transformed into agriculture by the time data was collected. At each plot, we used an auger to extract up to 500g of soil from the top 30cm of soil. The samples were analysed by a commercial provider (www.cropnuts.com) using protocols from agrocare[1] . They use a Mid-Infrared (MIR) scanner, X-ray fluorescence, and machine learning to identify soil texture, pH, and macro and micronutrient content.

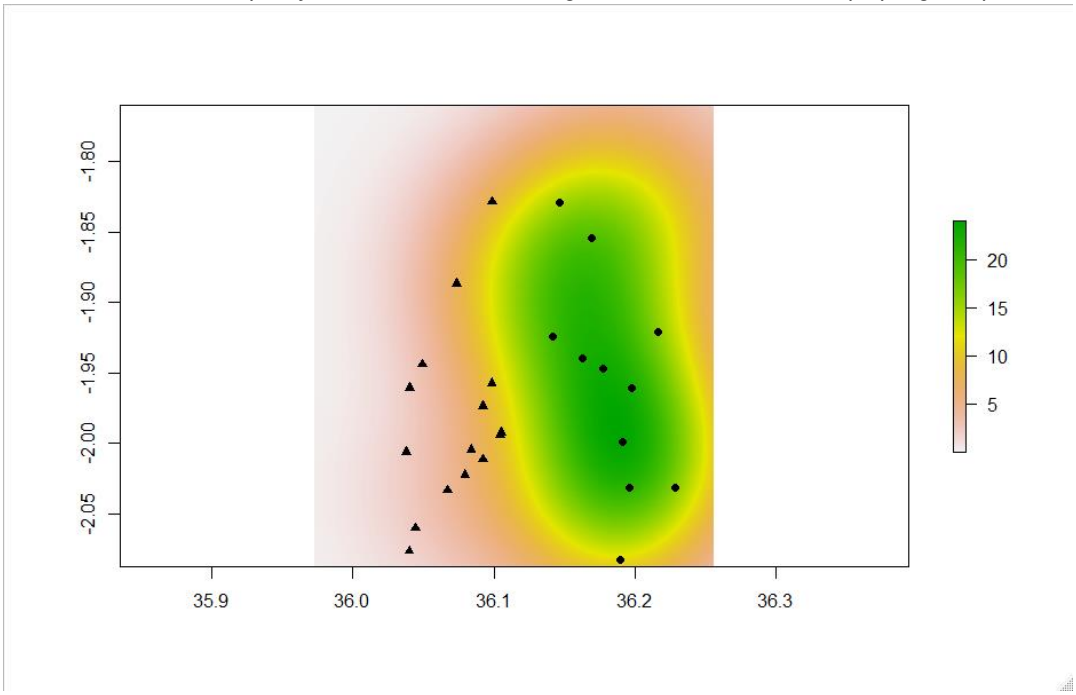
Rainfall

[1] https://www.agrocares.com/media/1703/liab-manual-text-eng.pdf

We extracted monthly rainfall for each plot from the CHIRPS data[13]. At each plot, we calculated the total amount of rain in the preceding three months, six months and two years before the date of data collection.

Livestock Enclosures

The impact of livestock on vegetation is the most pronounced in the proximity of livestock enclosures[14]. In the Shompole and Olkirmatian area (in the South Rift ecosystem), pastoralists still move seasonally with their livestock to effectively manage grazing resources [15,16]. To understand the impact of livestock enclosures on forage collected data on the occupancy of 545 livestock enclosures (Bomas) in the Shompole and Olkiramtian ecosystem on 30 occasions between September 2014 and April 2018. We used the *spatialEco* package to generate a weighted Gaussian Kernel Density estimate for this boma data, with livestock occupancy at each boma as the weight and bandwidth of 0.2[17]. (Sup Figure 1).



Sup Figure 1: The weighted Gaussian Kernel Density from livestock enclosure data. The estimate is weighted by livestock occupancy between September 2014 and April 2018. The bandwidth was set at 0.2. The vegetation plots are displayed as circles (permanent settlement area) and triangles (seasonal settlement area), based on land use.

Drivers of Grass Biomass

We used a Generalised Additive Mixed Model (GAMM) to determine the drivers of log10 transformed grass biomass at the 24 plots across the last 12 years[18]. The GAMM used a negative binomial logit link structure to model univariate and bivariate smooths at the plot level. These smooths included the proportion of grass grazed when samples collected, the mean proportion of grass grazed in the last six months, rainfall within the last three months, rainfall within the last six months, and rainfall within the last two years. To account for soil's influence on grass biomass, we constructed a tensor product interaction of soil clay and silt content and univariate smooths of total nitrogen content and total phosphorus. All smooths used penalised thin plate regression splines[11]. With these splines, the null space is also penalised slightly, and the whole term can therefore be shrunk to zero. To account for temporal autocorrelation, we used an autocorrelation-moving average correlation structure of order three, with the correlation structure nested at the plot level[7]. The smoothing parameters were fit using Restricted Maximum Likelihood (REML). We checked the model for concurvity between smooths, and because of this, we removed total phosphorus and nitrogen and the rainfall in the last six months and repeated the model fitting process. We set the basis size for all smooths to avoid over-fitting.

We performed a random forest analysis to determine the importance of these factors in predicting grass biomass[19]. We used a random forest model because it is insensitive to data distribution, does not assume data independence, can take many potentially collinear variables, and handles higher-order interaction[20]. We set the number of trees to 500 and the number of classification variables used to calculate the split at each node at two determined by a tuning function. All analyses were performed using the package *randomForest*[21].

Drivers of grazing pressure

To understand the drivers of grazing pressure at the ecosystem scale, we compared the mean proportion of grass grazed at each plot to several variables using beta-regression models. These variables were the seasonal abundance of wildebeest, zebra, shoats (sheep and goats), and cattle. These four groups are the ecologically dominant species in the ecosystem[12], and we extracted plot level abundance from the explicit spatial estimates of seasonal abundance for each species from[15]. We also used seasonal livestock enclosure data.

Results

Changes in Rainfall

In systems with low grazing pressure from livestock, rainfall variation is likely the key driver of wildlife abundance[22,23]. In ecosystems with higher grazing pressure, the influence of rainfall on wildlife abundance is reduced[24]. Previous work in Southern Kenya has shown that there have been some changes in annual and seasonal rainfall and drought frequency and intensity. Still, these results are often inconclusive when different spatial and temporal scales are used[10,25].

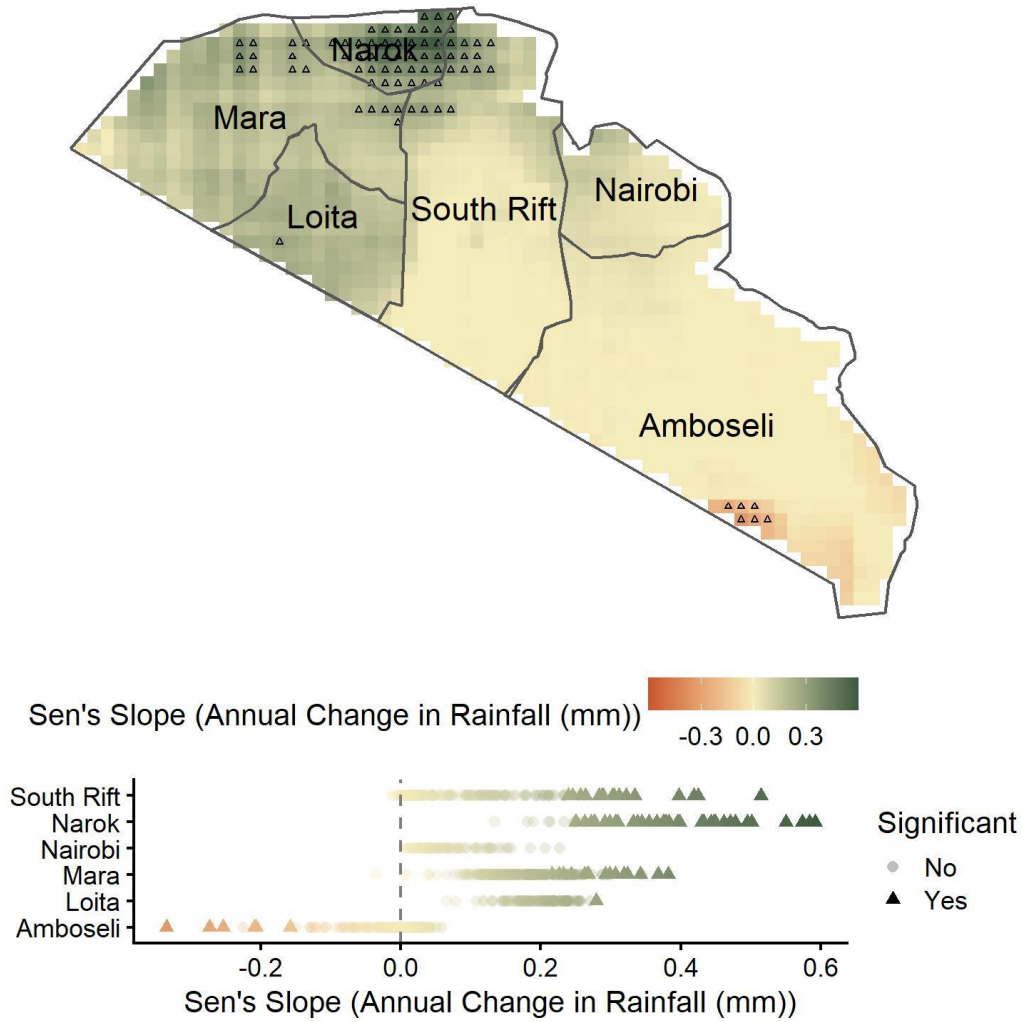
CHIRPS data

Annual Changes

From 1981-2020 most regions had small increases in annual rainfall (Sup Fig. 1). However, this was only significant, using a Sen's Slope, in small areas in the north-west of the study area, particularly in the Narok ecosystem (81% of pixels significant; Sup Table 1). Here rainfall has increased by 5.3mm - 23.5mm per year across the study period (mean - 14.5mm). Small decrease occurred in the Amboseli region (Mean = -0.40mm; 1.5% of pixels significant declines).

Supplementary Table 1. The Sen Slopes test (Theil–Sen) of CHIRPS rainfall data (1981-2020) displayed in Figure x. We provide aggregated summaries for each ecosystem. Significance was assessed at the 95% confidence level.

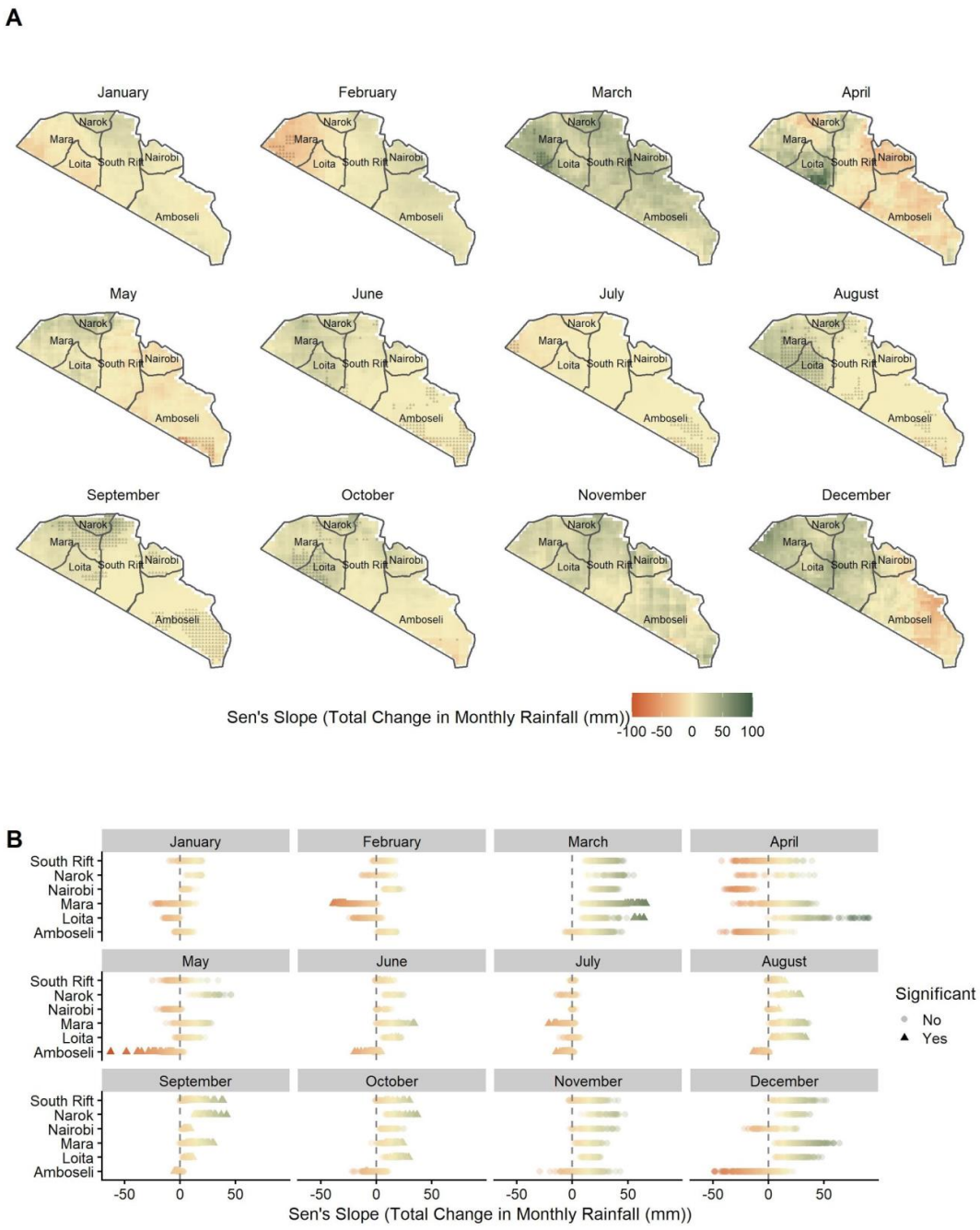
Ecosystem Name	Mean P-Value	Pixels with significant changes	Pixels without significant changes	Mean Sen's Slope	Max Sen's Slope	Min Sen's Slope
Amboseli	0.720	6	405	-0.396	2.357	-13.316
Loita	0.171	1	106	7.865	11.077	2.622
Mara	0.227	15	210	7.111	15.183	-1.424
Nairobi	0.523	0	84	2.646	9.016	0.136
Narok	0.039	39	9	14.528	23.510	5.346
South Rift	0.550	17	260	2.585	20.443	-0.472



Supplementary Figure 1 - Changes in rainfall estimated using Sen's Slope between 1981-2020 in southern Kenya at 0.05° resolution. Significant changes at each pixel are highlighted as triangles in both A) and B). B) shows the changes in rainfall at the pixel level across the six ecosystems, with the majority of pixels seeing small increases in rainfall over time.

Seasonal Changes

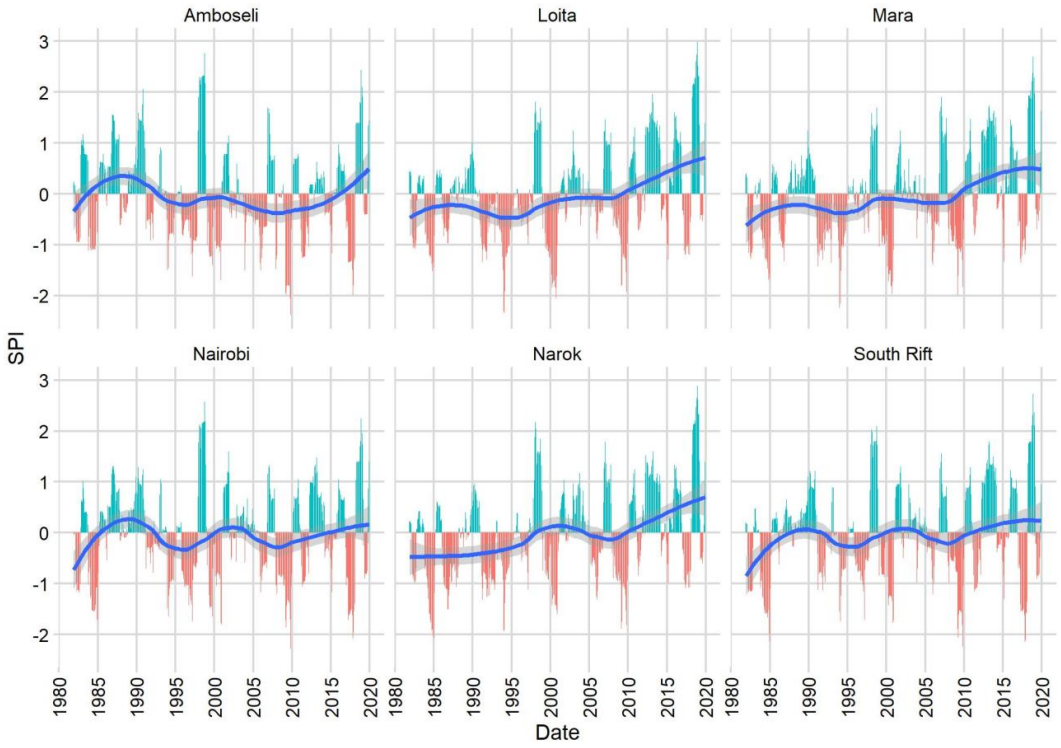
Seasonal Sen's Slope indicates that from May-September, parts of the Amboseli ecosystem are becoming drier. These drops are relatively small across most months. Still, in some areas, these changes are considerable, particularly in May (Sup Fig. 2). In August - October, eastern parts of the Mara, Narok, and Loita ecosystems have seen increases in rainfall, up to 20mm per month in some cases overall (Sup Fig. 2). In February, parts of the Mara ecosystems are significantly drier.



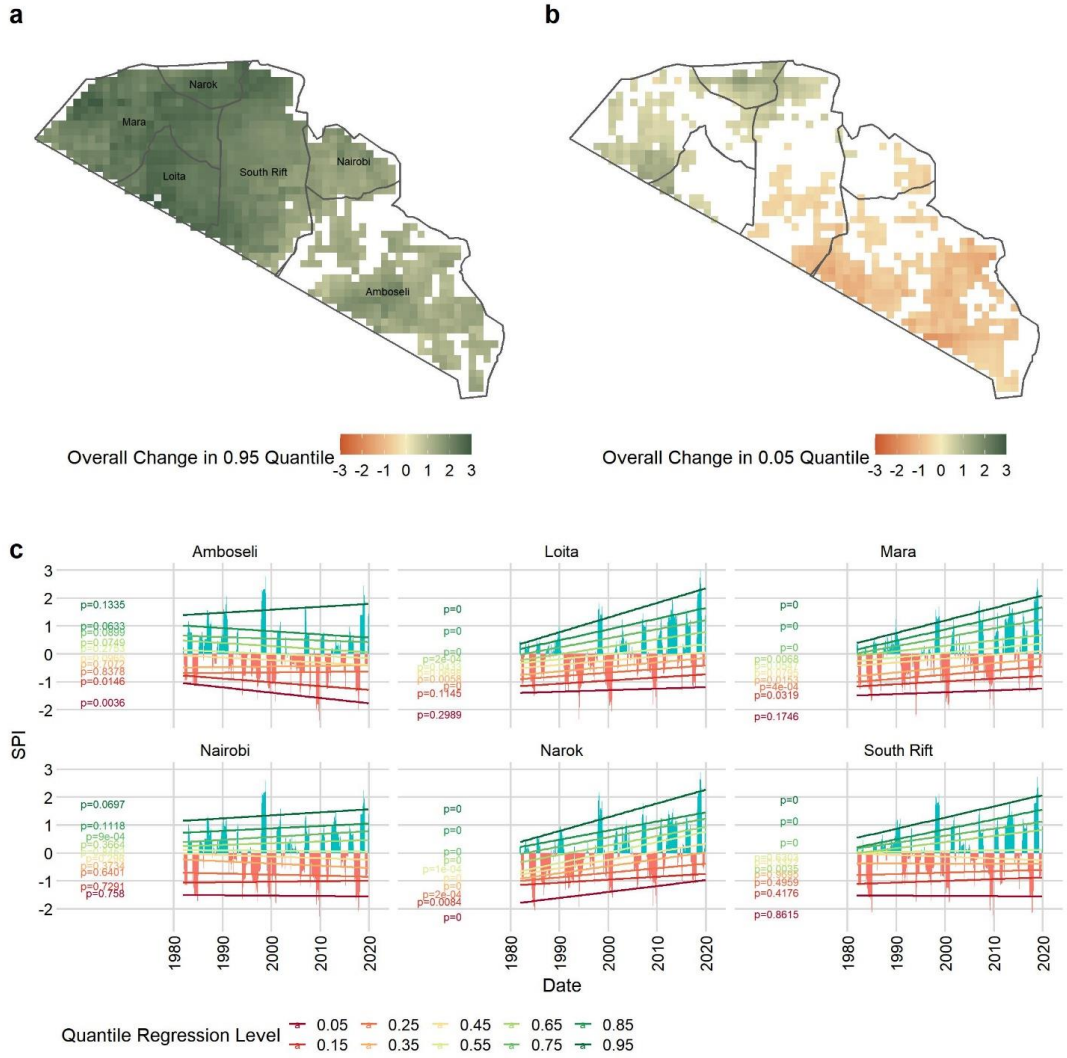
Supplementary Figure 2: Changes in monthly rainfall estimated using Sen's Slope between 1981-2020 in southern Kenya at 0.05° resolution. Significant changes at each pixel are highlighted as triangles in both A) and B). B) shows the changes in rainfall at the pixel level across the six ecosystems.

Changing Drought Frequency and Standardised Precipitation Index

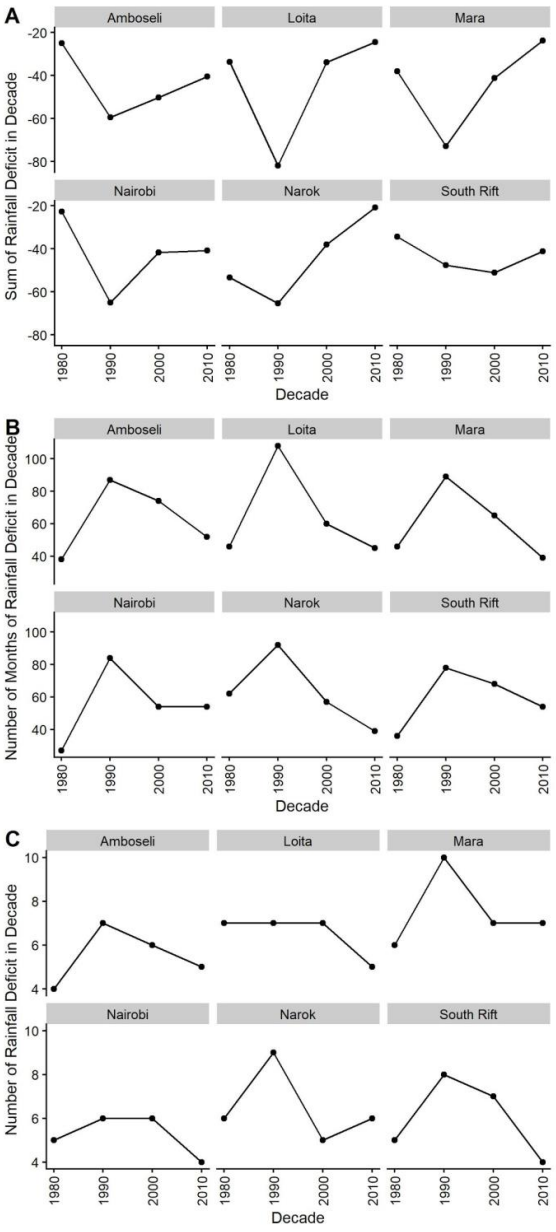
The Mara, Loita, Narok and South Rift ecosystems experienced some periods of rainfall deficit in the 1980s, but most significantly in the 1990s (Sup Fig.3). The intensity, frequency, and total length of rainfall deficits were highest in the 1990s for most ecosystems, with no consistent changes over time (Sup Fig.3; Sup Fig.5). However, quantile analysis suggests extreme high-rainfall events increase in Narok, Loita, Mara and South Rift (Sup Fig.4). Unlike other regions, Amboseli had a period of high rainfall in the 1980s. The 2009 drought can be seen across all ecosystems but is most extensive within the Amboseli ecosystem (where significant declines in wildlife and livestock occured[26]). Loita, Mara, and Narok ecosystems have seen fewer droughts in recent years (since the 2009 drought), and the intensity of these droughts is decreasing (Sup Fig.3). Extreme high rainfall events are most notable across all ecosystems in the 1997/1998 El Nino event and more recently in 2018 and 2019. Quantile regression suggests drought events have increased in severity in Amboseli and parts of the South Rift and decreased in Narok and the Mara (Sup Fig.4)



Supplementary Figure 3: Standardised Precipitation Index (SPI) for the mean monthly rainfall in each of the six ecosystems using the CHIRPS data from 1981-2020. The Mara, Loita, Narok and South Rift experienced major droughts in the 1980s and 1990s. Amboseli had a period of high rainfall in the 1980s. The 2009 drought can be seen across all ecosystems and largest within the Amboseli ecosystem (where significant declines in wildlife and livestock occur). Loita, Mara, and Narok have seen fewer droughts in recent years (since the 2009 drought). Extreme high rainfall events are most notable in the 1997/1998 El Nino event and more recently in 2018 and 2019. A Loess smooth is fit to the SPI data for visualisation only.

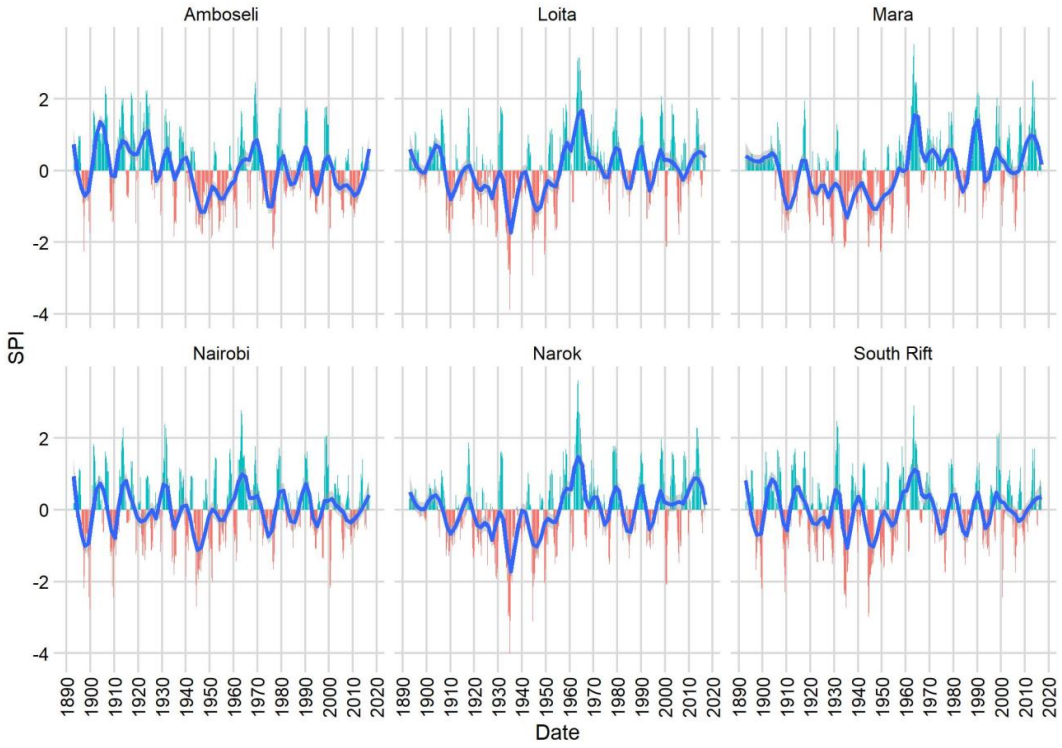


Supplementary Figure 4: Quantile regression of the Standardised Precipitation Index (SPI) of CHIRPS monthly rainfall data (1981-2020) significant changes (p <0.05) at the pixel-level (a,b), and using the mean values per ecosystem (c). a) Displays changes at the 0.95 quantile (extreme high rainfall events) and b) changes at the 0.05 quantile (extreme low rainfall events, i.e. droughts). c) SPI for each ecosystem, and a range of quantile values from 0.05 – 0.95, the regression's p values are shown.

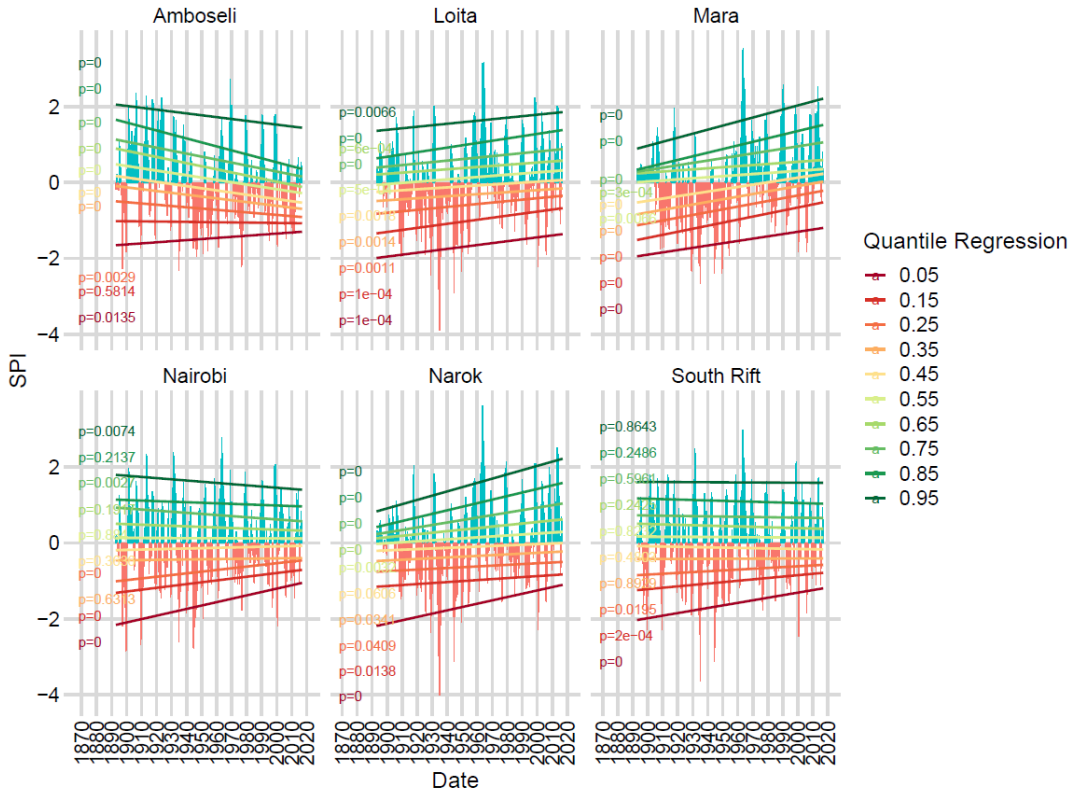


Supplementary Figure 5: Using data from the Standardised Precipitation Index calculated from CHIRPS, we calculate per decade (1980-the 2010s) A)The sum of the SPI in months when SPI is negative; B) The number of months in the decade that had negative values of SPI; and c) The number of times the SPI crossed below 0. The total intensity of periods of rainfall deficit (A) is highest in most ecosystems in the 1990s and improves in the 2010s. The length of periods of rainfall deficit B) and frequency of deficits C) are generally highest in the 1990s and lowest in the 2010s.

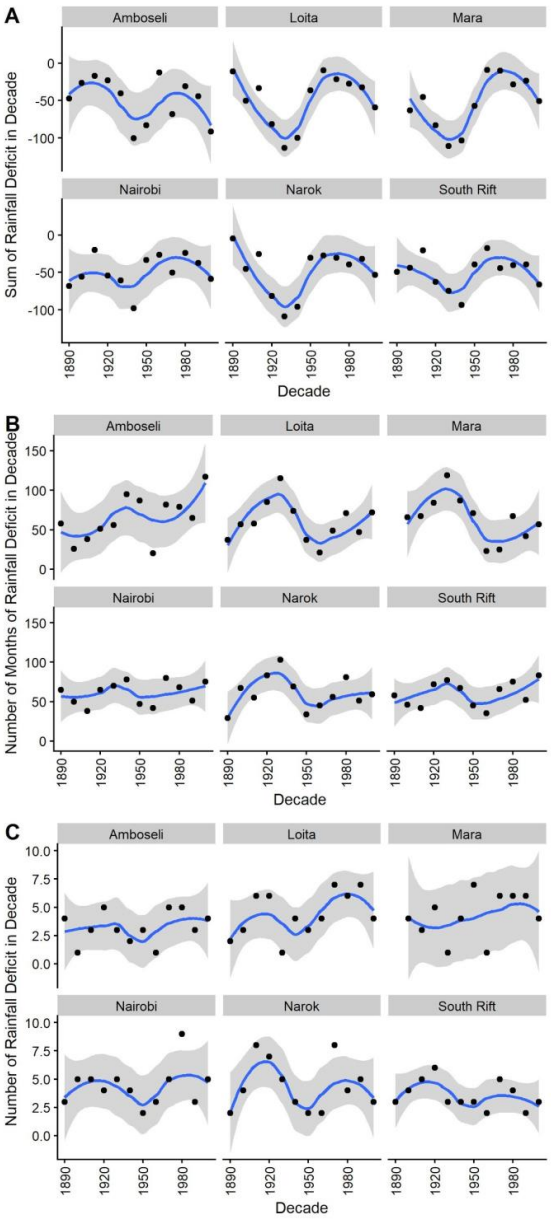
GPCC data



Supplementary Figure 6: Standardised Precipitation Index (SPI) for the mean monthly rainfall in each of the six ecosystems using the GPCC data from 1891-2016. A Loess smooth is fit to the SPI data for visualisation only.



Supplementary Figure 7: Quantile regression of the Standardised Precipitation Index (SPI) of GPPC monthly rainfall data (1891-2016) significant changes (p <0.05) at the pixel-level (a,b), and using the mean values per ecosystem (c). a) Displays changes at the 0.95 quantile (extreme high rainfall events) and b) changes at the 0.05 quantile (extreme low rainfall events, i.e. droughts). c) SPI for each ecosystem, and a range of quantile values from 0.05 – 0.95, the regression's p values are shown.



Supplementary Figure 8: Using data from the Standardised Precipitation Index calculated from GPCC data, we calculate per decade (1890-the 2000s) A) The sum of the SPI in months when SPI is negative; B) The number of months in the decade that had negative values of SPI; and c) The number of times the SPI crossed below 0. The total intensity of rainfall deficit periods (A) is highest in most ecosystems in the 1940s.

Long-term changes in rainfall

The long-term GPCC data allows us to understand these ecosystems' baseline climatic conditions and, therefore, will enable us to reflect on the role of changing climate on ecosystem function and wildlife abundance and composition. There are few long-term monotonic changes in rainfall deficit frequency, intensity, and length over time (Sup Figure 8), with considerable cyclicity in the data. Sup Table 2 breaks down and describes these long-term rainfall trends across regions. Overall quantile regression suggests that drought events reduce severity across all ecosystems, and high rainfall events are increasing in Narok, Mara, and Loita (Sup Figure 7).

Supplementary Table 2

Ecosystem	Description of Long-Term Rainfall Trends
Amboseli	Amboseli was very dry at the turn of the 20th Century. Unlike most ecosystems, until the 1940s, there were exceptionally long wet periods. Amboseli experienced a series of droughts in the 1940-the 50s, a relatively wet 1960s, and an exceptionally large drought during the 1970s. When DRSRS records began in Amboseli in the late 1970s, the wildlife was likely at a lower ebb.
Loita	Loita has a wetter start to the 20th Century, but some large 1930-1940s drought similar to those in the Mara. Very wet during the late '60s, similar to the Mara. Cyclical rainfall events occur, with larger droughts in the mid-1990s, early 2000s, 2005.
Narok	Narok is essentially similar to Loita, although it is getting wetter than the Loita in the 21st Century.
Maasai Mara	The Maasai Mara shows consistently good rainfall at the end of the 19th Century. The ecosystem then experiences large and prolonged repeated droughts until the mid-'60s, with 1918 being the only huge rainfall event. Conversely, the 1960-'70s is very wet in the Mara. This coincides with the highest density of wildebeest ever (and potentially all ungulate concerning the huge amounts of rain). A big drought follows this wet period in the 1980s, with a small drought in the 1990s, a larger one in 2000, and the 2005 drought. This supports the notion from the DRSRR data (alongside the recovery going on in Amboseli' the 70s-'80s) that drought, worsened by density-dependent effects of large herd sizes, may have contributed to the decline in resident ungulates (and migratory usage of the area) from the 1970s-1980s. The recent increase in exceptionally high rainfall in the Mara helps explain why wildebeests have spent less time in Kenya. Coupled with lack of burning, much of the central Mara and Triangle have too much grass for wildebeest. This needs further investigation.
Nairobi	Nairobi seems much more consistently cyclical than the others, with big '40s, '70s droughts. A long wet period during the '60s, similar to all other regions (except Amboseli). There is also a clear spike during the 1998 El Nino event and large deficits during the 2009 drought.
South Rift	The South Rift experience significant droughts in 1900, 1910, and two very large droughts in 1935, 1945. This matches with historical data recorded by Brehony et al., 2020. Like Amboseli, this region experienced large droughts in the mid-1970s, with

larger droughts in the 1983-84 and early 1990s, with a huge drought event in 1999/2000. A large drought event also occurred in 2005.

Previous research has highlighted an increase in droughts across the East Africa region in recent years (2000-2010) and suggests that climate change may be responsible[27]. This leads to the speculation that climate-change-induced drought events are a significant driver of wildlife decline (e.g. Ogutu 2016). Our analysis of the long-term rainfall data demonstrates more nuanced change is present, with more considerable variations in rainfall over the last Century than experienced more recently, and no long-term observable increase in the intensity, length, or frequency of rainfall deficit events.

Changes in NDVI (GIMMS)

Annual Changes

From July 1981-2015, most regions had a decrease in NDVI. Using a Sen's Slope, this was significant in many parts of Amboseli, South Rift, Nairobi, and the edge of the Mara ecosystems. This contrasts with the change in mean rainfall over time, which had small increases in many areas.

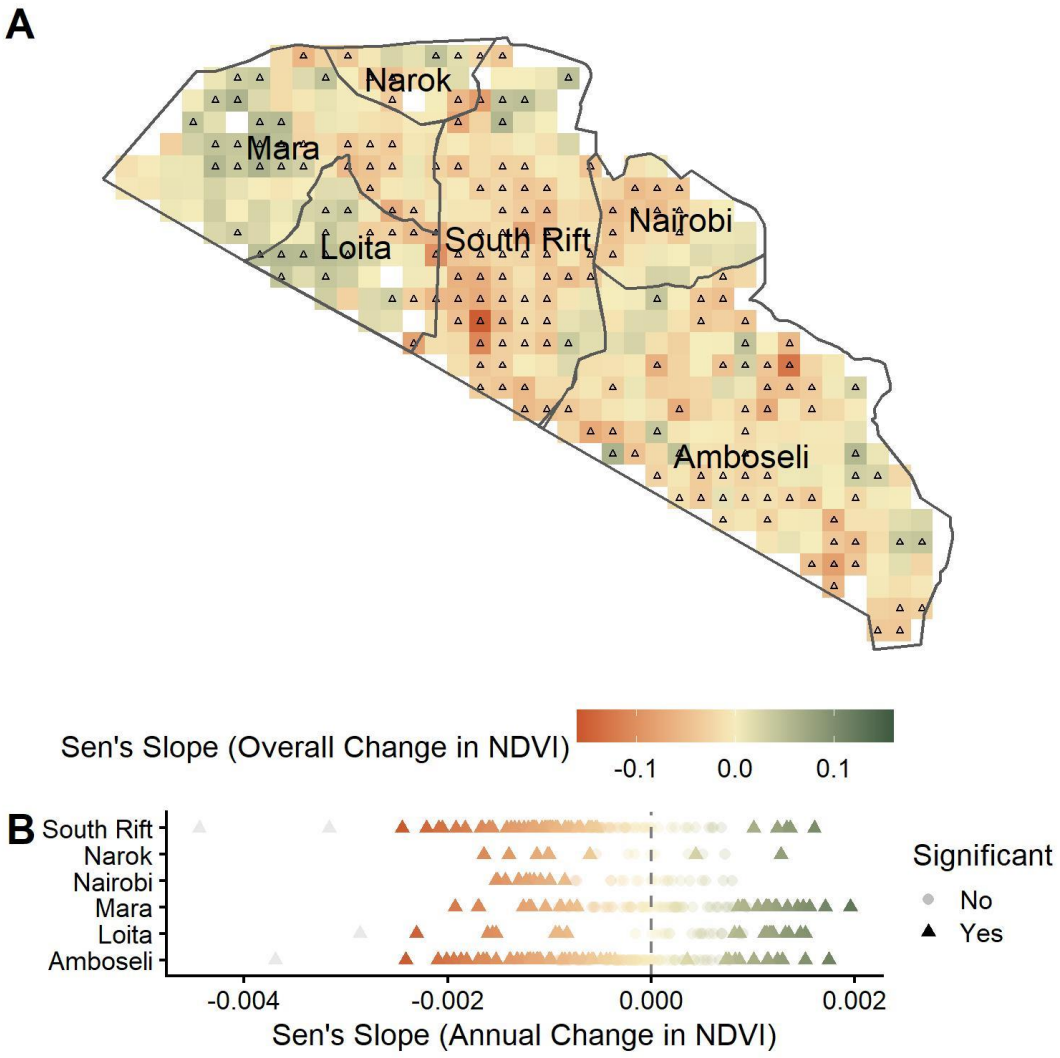
Supplementary Table 3. The Sen Slopes test (Theil–Sen) of GIMMS NDVI data (July 1981-2015) displayed in Sup Fig. 9. We provide aggregated summaries for each ecosystem. Significance was assessed at the 95% confidence level.

Ecosystem Name	Mean P-Value	Pixels with significant changes	Pixels without significant changes	Mean Sen's Slope	Max Sen's Slope	Min Sen's Slope
Amboseli	0.26	62	84	-0.014	0.060	-0.127
Loita	0.18	19	19	0.006	0.052	-0.099
Mara	0.31	29	53	0.004	0.067	-0.067
Nairobi	0.33	11	21	-0.014	0.027	-0.053
Narok	0.25	8	8	-0.009	0.044	-0.057
South Rift	0.17	56	42	-0.023	0.055	-0.153

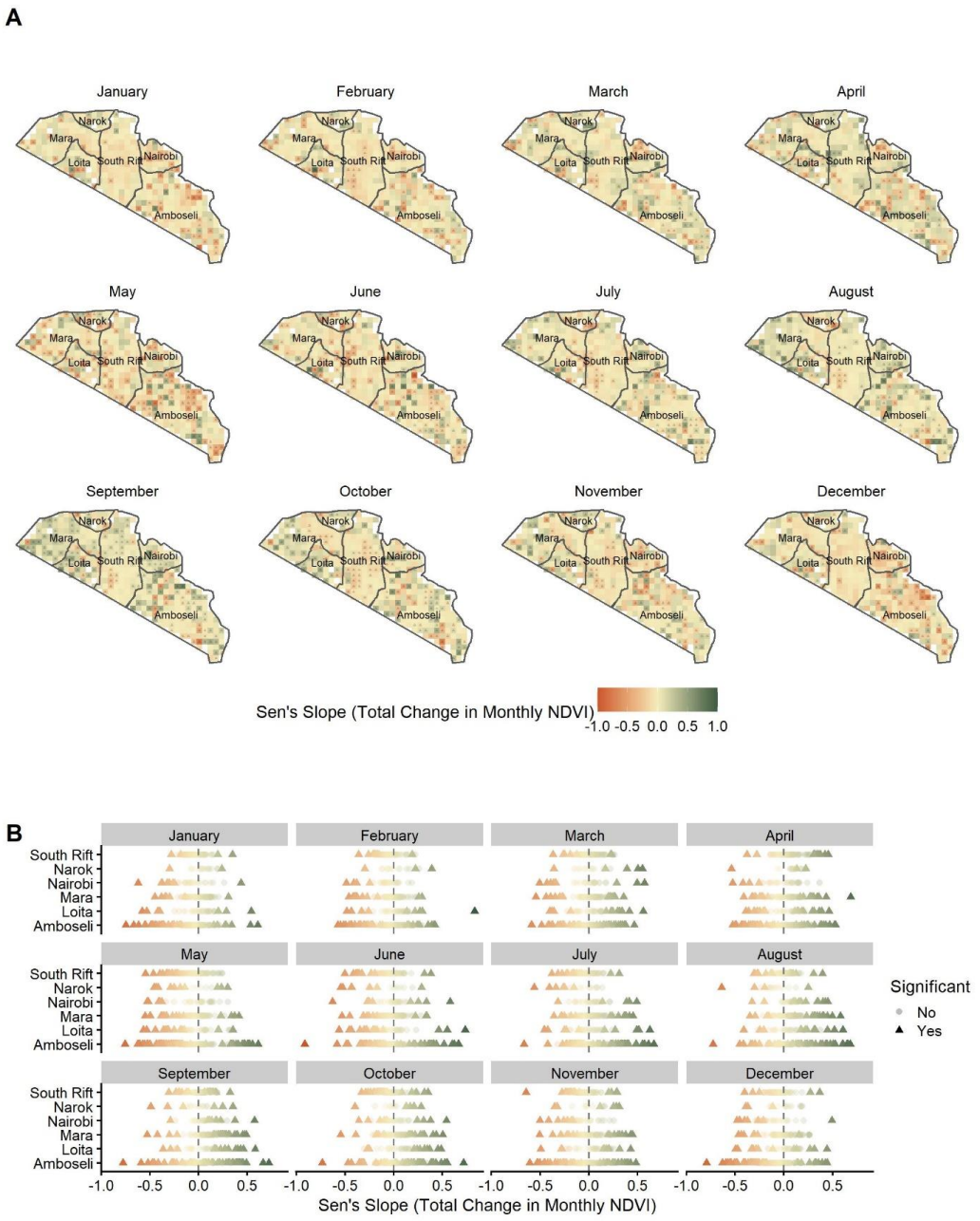
Seasonal Changes

The Sen's Slope estimate for monthly data provided results that were challenging to interpret, and hence we employed the time-series clustering method (Sup Fig. 10,11). These methods show a reduction in the overall predictability of the seasonal cycle from the early (median r-squared = 0.467) to mid-period (median r-squared = 0.365) which stabilises into the late period (median r-squared = 0.398). In particular, parts of the South Rift, Amboseli (towards the western boundary), the Mara (Loita Plains), and the Loita hills have seen reductions in the r-squared value predicting seasonal NDVI. The results show several distinct seasonal time-series of NDVI. In Nairobi, there is a considerable change between the mid and late period from cluster 7 to cluster 5, which indicates a decrease in the peak of NDVI during December and January and a less clear peak in NDVI in May and June (Sup Fig. 11).
Similarly, in Amboseli, there is a considerable drop from cluster 7 to cluster 5 and cluster 5 to cluster 9. This pattern has much deeper drops in NDVI during the long dry season (July-September) and a smaller peak in the long wet season (April-June). In the South Rift, similar patterns occur with changes from cluster 5 to cluster 9, but in addition, there are changes from cluster 9 to cluster 11, indicating even more

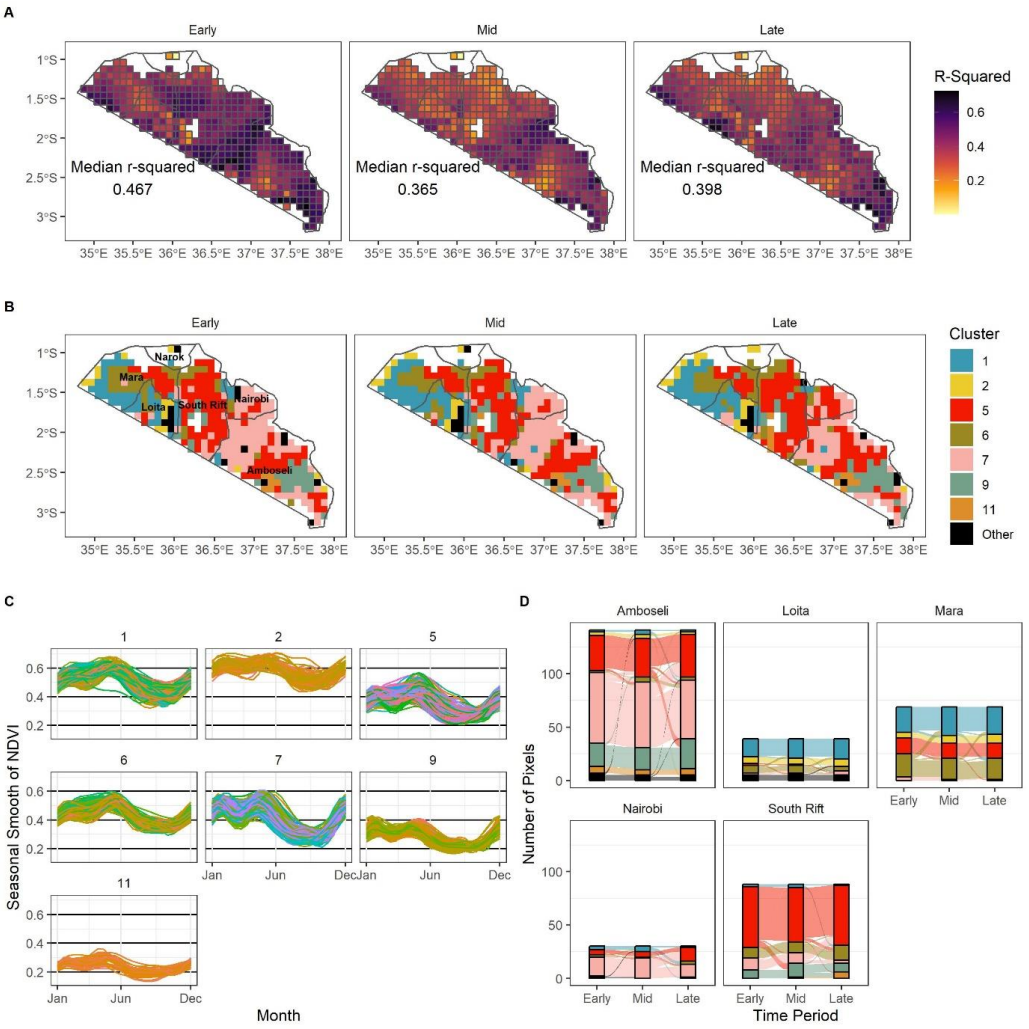
severe reductions in seasonal NDVI peaks, with cluster 11 not showing much recovery from the long rains (October – December). The Mara is one of the only regions where seasonal NDVI appears to have increasing peaks, and shallower seasonal troughs, over the study period. With an increase in pixels from cluster 1 to cluster 2, and cluster 6 to cluster 1.



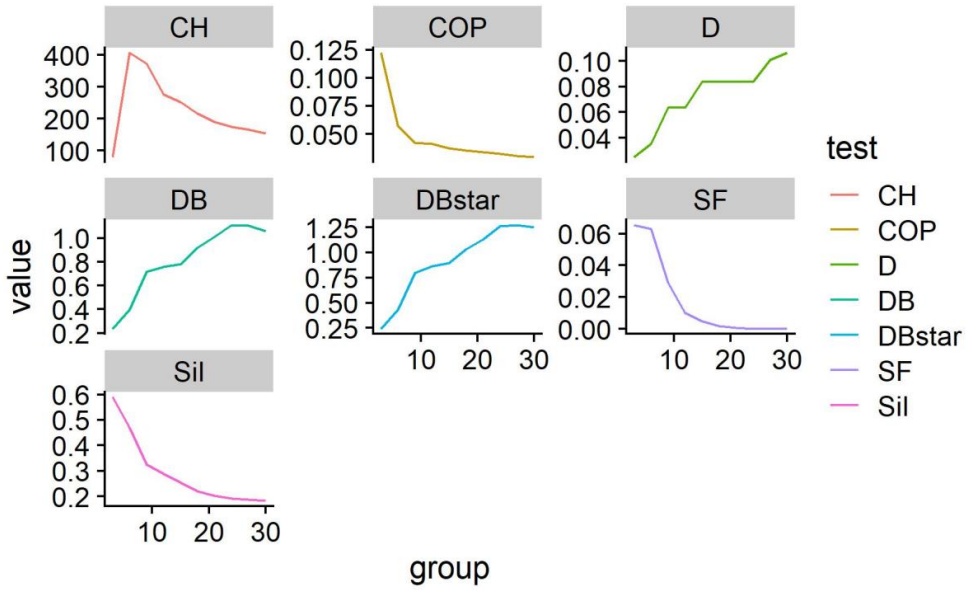
Supplementary Figure 9 - Changes in NDVI estimated using Sen's Slope between July 1981-2015 in southern Kenya at 0.083° resolution. Significant changes at each pixel are highlighted as triangles in both A) and B). B) shows the changes in NDVI at the pixel level across the six ecosystems, with the majority of pixels seeing a decrease in NDVI over time.



Supplementary Figure 10: Changes in NDVI estimated using Sen's Slope between July 1981-2015 in southern Kenya at 0.083° resolution. Significant changes at each pixel are highlighted as triangles in both A) and B). B) shows the changes in rainfall at the pixel level across the six ecosystems. Few clear patterns appear in this data.



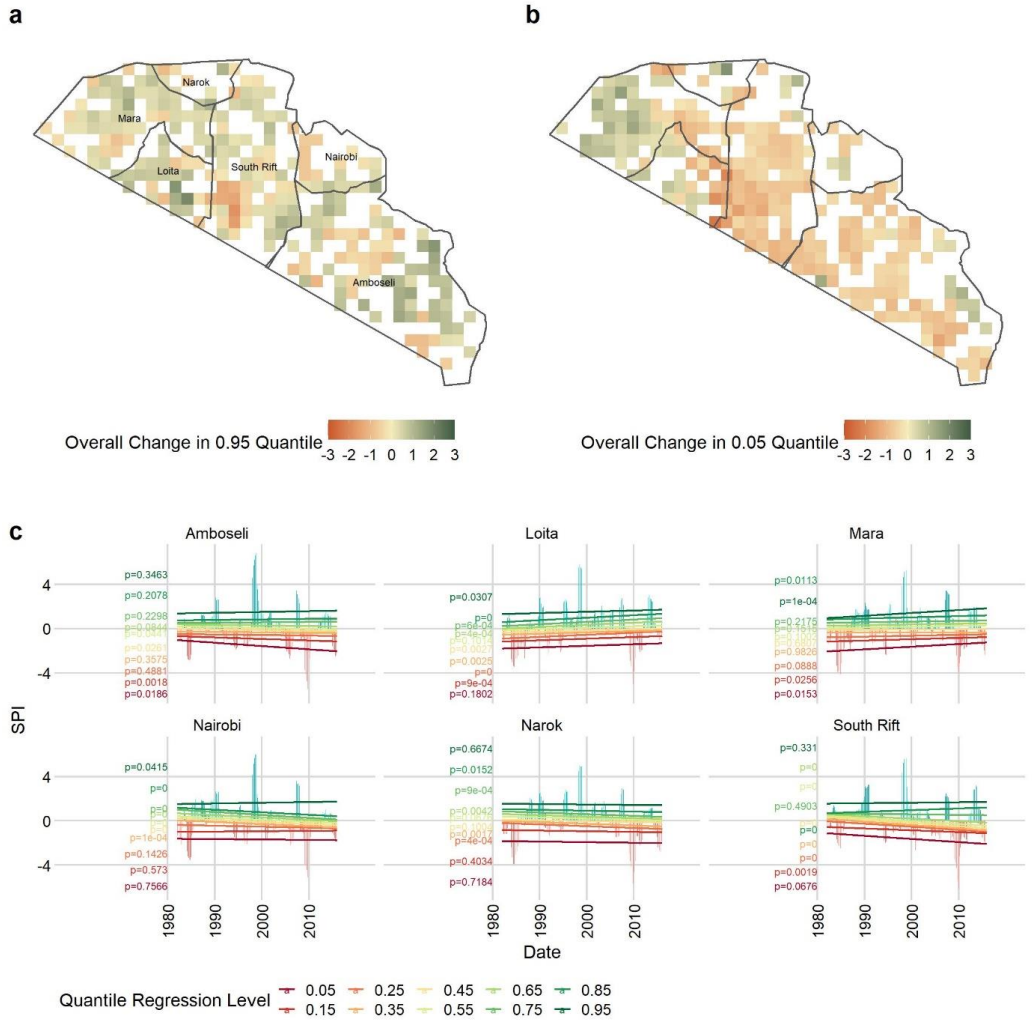
Supplementary Figure 11: Results of the time-series clustering procedure on the GIMMS NDVI data for Southern Kenya from 1981-2015 split into three time periods (Early:1983-1992; Mid: 1992-2004, Late--:2004-2015). A) The r-squared values of the individual generalised additive models (GAMS) for each pixel, with both a trend and a seasonal component. B) The time-series clustering of the seasonal components of the pixel-wise GAMS, we kept only the seven most common clusters and classified the remainder as “others” C) The seven most common clusters and their seasonal pattern of NDVI. D) An alluvial diagram showing the changes in clusters other time per ecosystem. Empty cells either have over 50% agricultural production or permanent water. We excluded Narok from (D) due to the low number of points.



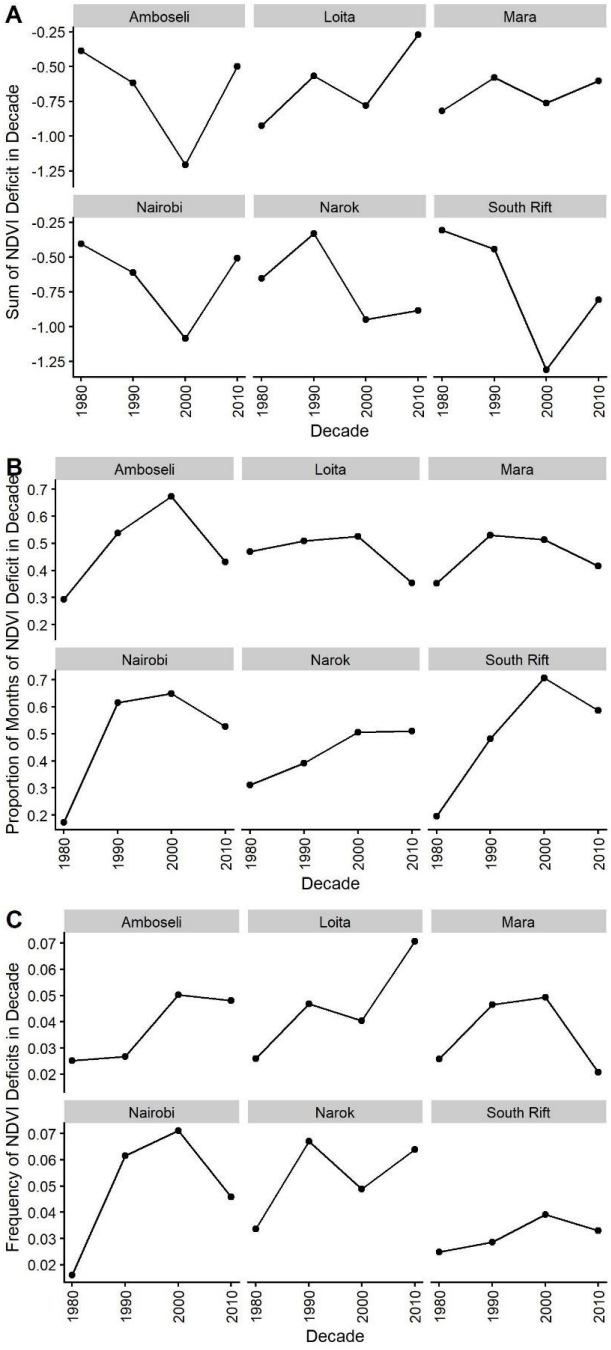
Supplementary Figure 12. Different cluster validity indices used to determine the hierarchal clustering of the seasonal NDVI time-series data. The indexes are CH - Calinski-Harabasz index (to be maximised), COP index (to be minimised); D - Dunn index (to be maximised), DB - Davies-Bouldin index (to be minimised), BDstar - Modified Davies-Bouldin index (to be minimised), SF – score function (to be maximised), Sil – silhouette index (to be maximised).

Changing Drought Frequency and Standardised Precipitation Index

All ecosystems experienced some periods of NDVI deficit in the 1980s (Sup Fig. 13 & 14). The effect of the 1997/8 El Nino event is evident across all ecosystems. The 2009 drought and the general drought conditions in the late 2000s (Sup Fig. 13 & 14). The number of drought months per decade has increased substantially for all ecosystems except the Loita and Mara (Sup Fig. 14). Quantile analysis shows that extreme high NDVI events are both increasing and decreasing across the region. The Mara and Loita ecosystems have seen a decrease in extreme low NDVI events, yet much of the South Rift and Amboseli has seen an increase (Sup Fig. 13).



Supplementary Figure 13: Quantile regression of the Standardised Precipitation Index (SPI) of GIMMS NDVI data (1981-2015) significant changes (p <0.05) at the pixel-level (a,b), and using the mean values per ecosystem (c). a) Displays changes at the 0.95 quantile (extreme high NDVI events) and b) changes at the 0.05 quantile (extreme low NDVI events, i.e., droughts). c) SPI for each ecosystem, and a range of quantile values from 0.05 – 0.95, the regression's p values are shown.



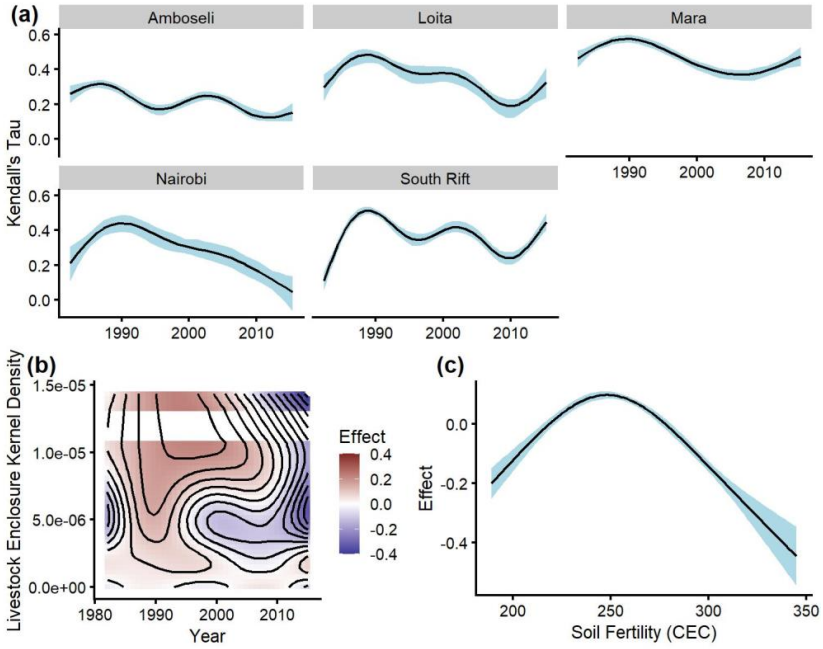
Supplementary Figure 14. Using data from the Standardised Precipitation Index calculated from GIMMS NDVI, we calculate per decade (1980-the 2010s) A)The sum of the SPI in months when SPI is negative; B) The proportion of months in the decade which had negative values of SPI; and c) The frequency of the SPI crossing to become below 0. The total intensity of NDVI deficit periods (A) is highest in most

ecosystems in the 2000s. The proportion of months of rainfall deficit (B) and frequency of droughts (C) are also generally increasing for all ecosystems over time, except the Mara.

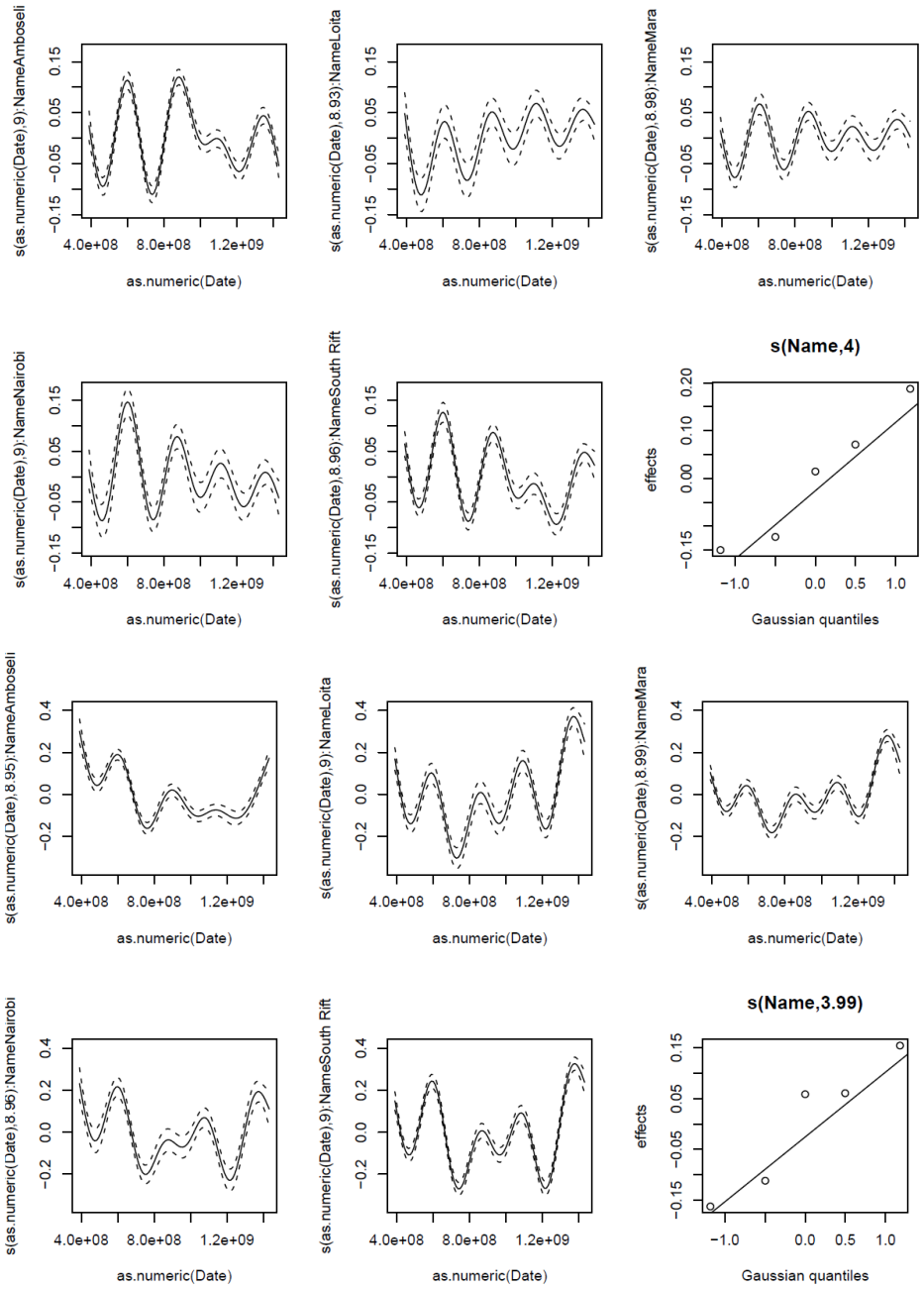
Modelling the effect of NDVI and Rainfall.

Marginal residual plots for the two final bivariate copula GAMs suggest that the choice of distribution for both margins in both examples are sound. In the first model, both rainfall and NDVI scale and location patterns vary considerably over time, matching local climatic variations, with between 8 and 10 basis size used to fit these models. Using Model 1, we created Sup Fig.15a, which demonstrates the correlation between NDVI and rainfall over time during the growing seasons. There are differences between the different ecosystems, and many show a decrease in the correlation over time. Because of the close relationship between NDVI and grass biomass during the growing season[28] this indicates a decrease in the amount of grass biomass per unit of rainfall. Similar trends have been reported in Amboseli from long-term ground-based monitoring (Western in press). Most ecosystems show a strong decline towards the 2009 drought from 1990 peaks. Loita, South Rift and Mara show some recovery of the correlation post-2009. Model details are shown in Sup Fig. 16,17,18,19.

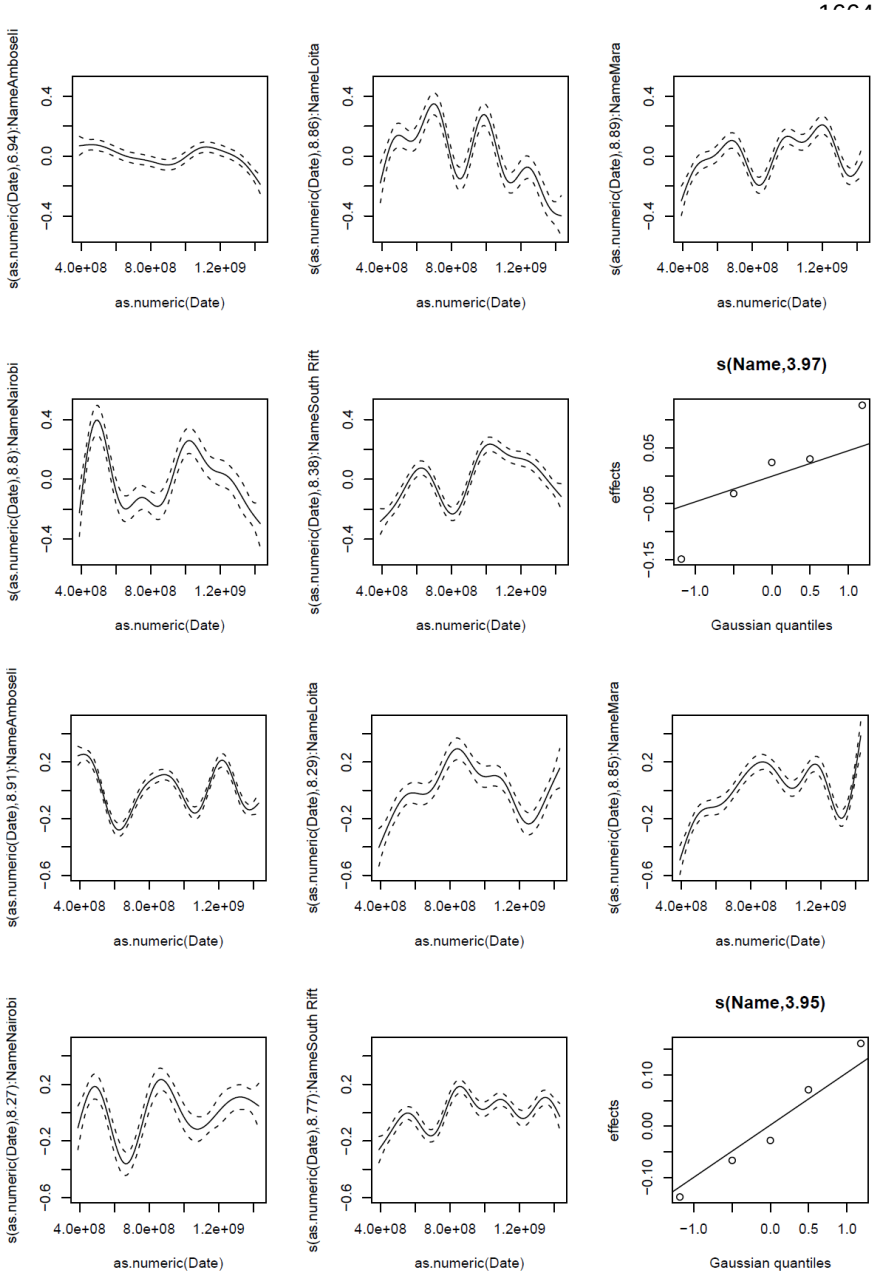
The second model explains the correlation between NDVI and rainfall regarding time, livestock enclosure densities (in 2020) and soil fertility (Supp Fig. 15b). This shows that from 1980 -2010 the correlation is weakening considerably over time, and it decreases the most in areas that will have the higher livestock enclosure density. The areas that now have the highest densities of bomas also tended to be in areas with a higher correlation between rainfall and NDVI, hence likely to be more productive. Areas with the lowest densities of livestock bomas by 2020 tend to have a more stable correlation. In addition, we also show that intermediate soil fertility has the highest correlation with NDVI and rainfall. Areas with higher CEC tend to be ephemeral short grass plains, and those with lower fertility are often more humid forested areas. Model details are shown in Sup Fig. 20,21.



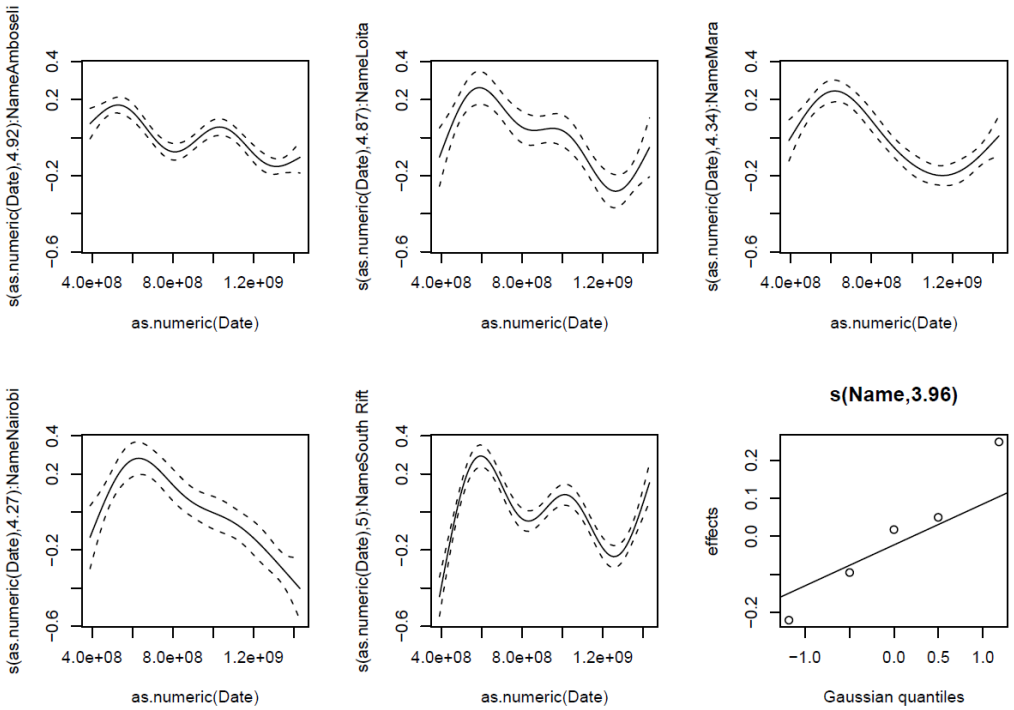
Supplementary Figure 15: (a) Estimates and 95% intervals for Kendall's Tau over time from a Gaussian copula model with gaussian margins fitted to NDVI and rainfall data during the growing season, independently for each ecosystem (Copula Model 1). (b) The estimated smooth effect size of year and livestock enclosure kernel density in 2020, (c) and soil fertility (Cation Exchange Capacity) on the association parameter from a Gaussian copula model with gaussian margins fitted to NDVI and rainfall data during the growing seasons. In (c), the shaded area is 95% confidence intervals.



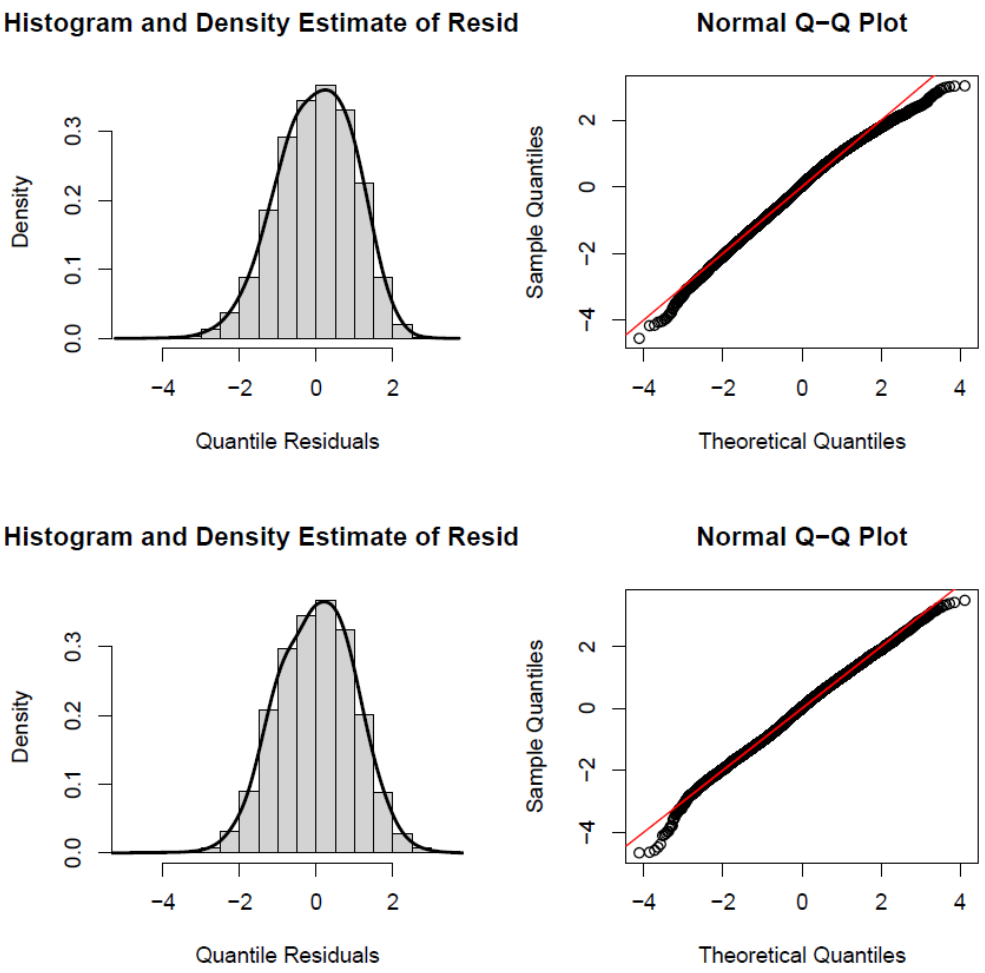
Supplementary Figure 16: The smooth terms for the bivariate copula distribution model for the location equations in NDVI (top) and rainfall (bottom) over the two growing annual growing seasons (April-June; October – December), from 1982 to 2015. Each ecosystem has an independent univariate smooth and a random effect. The effective degrees of freedom are given on the left of each plot.



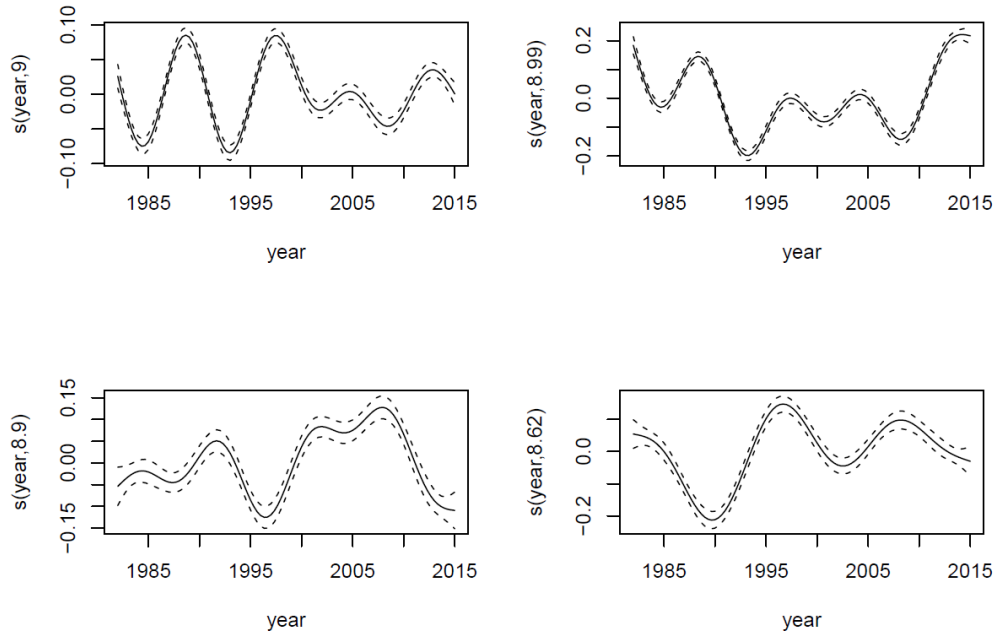
Supplementary Figure 17: Estimated smooth terms and 95% confidence intervals for the copula distribution model for the scale equations in NDVI (top) and rainfall (bottom) over the two growing annual growing seasons (April-June; October – December), from 1982 to 2015. Each ecosystem has an independent univariate smooth and a random effect. The effective degrees of freedom are given on the left of each plot.



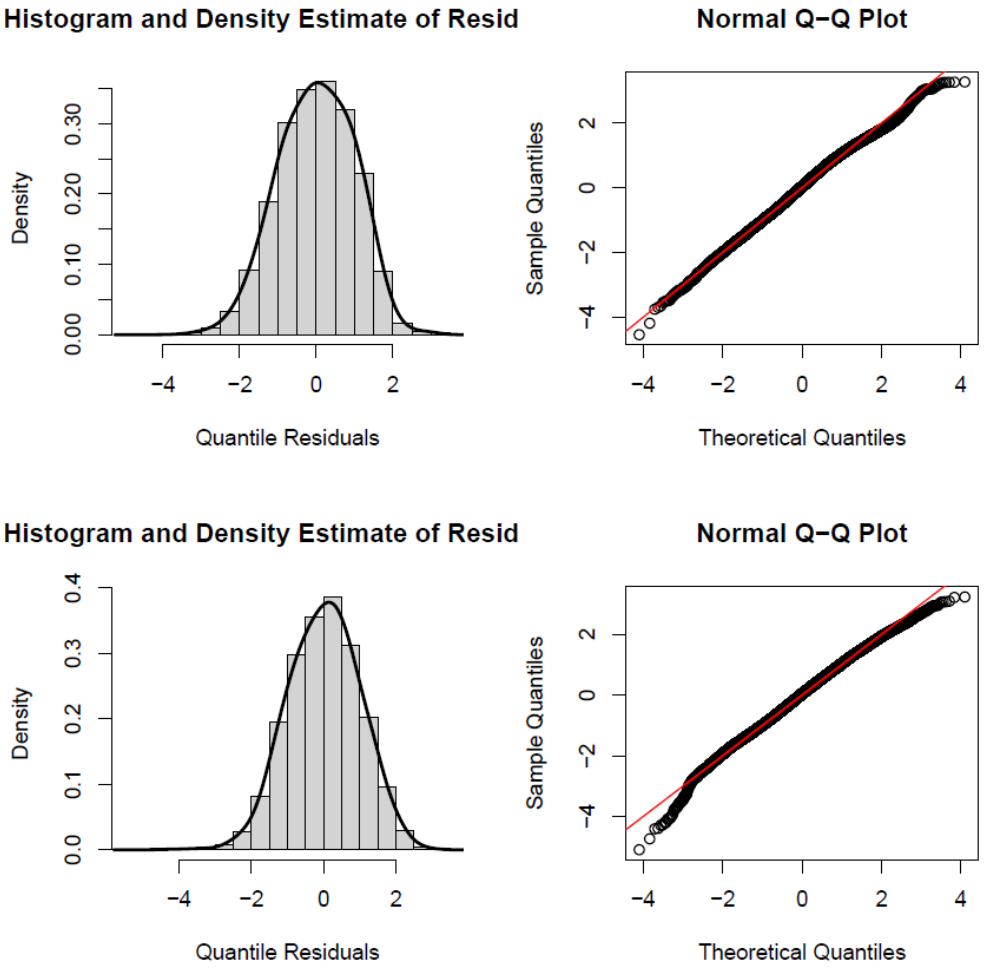
Supplementary Figure 18: Estimated smooth terms and 95% confidence intervals for the bivariate copula distribution model for the association term over the two growing annual growing seasons (April-June; October – December), from 1982 to 2015. Each ecosystem has an independent univariate smooth and a random effect. The effective degrees of freedom are given on the left of each plot.



Supplementary Figure 19: Histograms and normal Q-Q plots of normalised quantile residuals for NDVI (top) and rainfall (bottom) were produced after fitting a Gaussian copula model with gaussian margins to NDVI and rainfall data over-time in the first model.

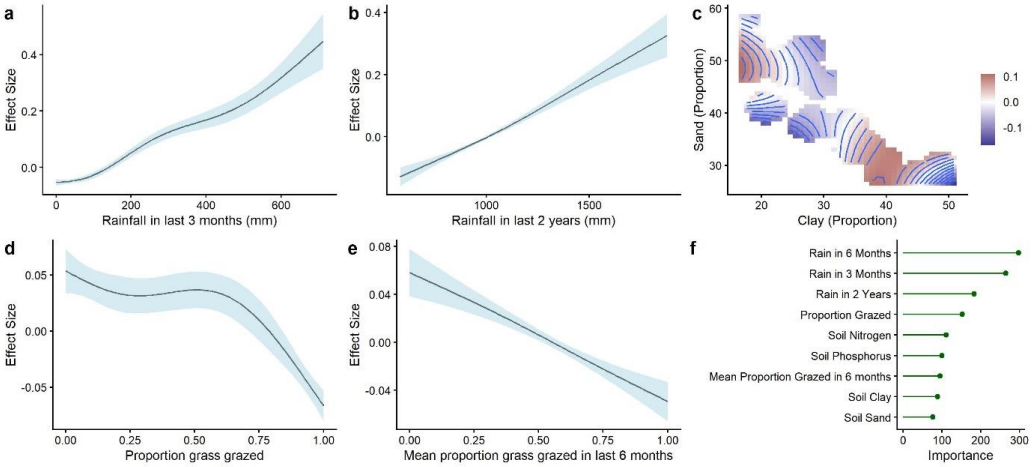


Supplementary Figure 20: Estimated smooth terms and 95% confidence intervals for the bivariate copula distribution model for the NDVI and rainfall location (top-left, top-right) and scale terms (bottom-left, bottom-right) over the two growing annual growing seasons (April-June; October – December), from 1982 to 2015. Each ecosystem has an independent univariate smooth and a random effect. The effective degrees of freedom are given on the left of each plot.



Supplementary Figure 21: Histograms and normal Q-Q plots of normalised quantile residuals for NDVI (top) and rainfall (bottom) produced after fitting a Gaussian copula model with gaussian margins to NDVI and rainfall data over-time in the second model.

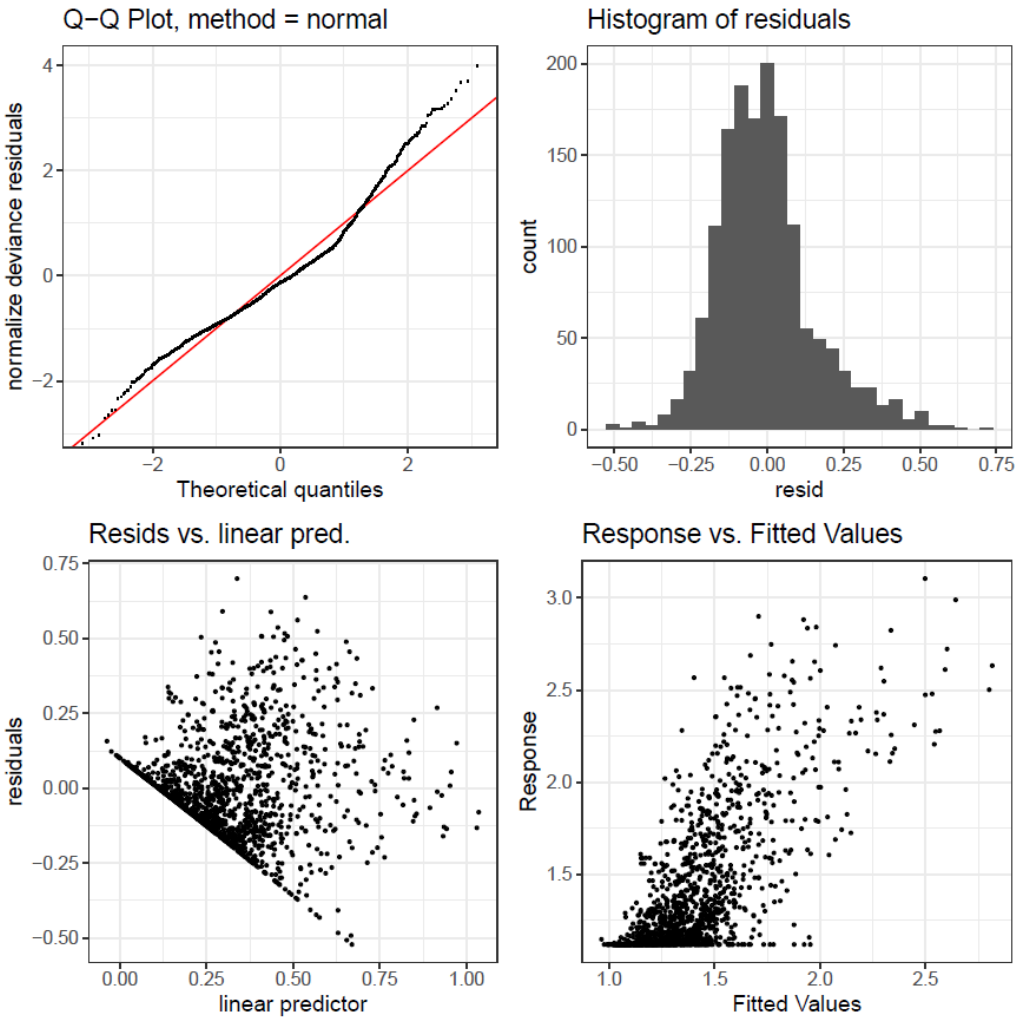
Drivers of Grass Biomass from Shompole and Olkiramatian Data



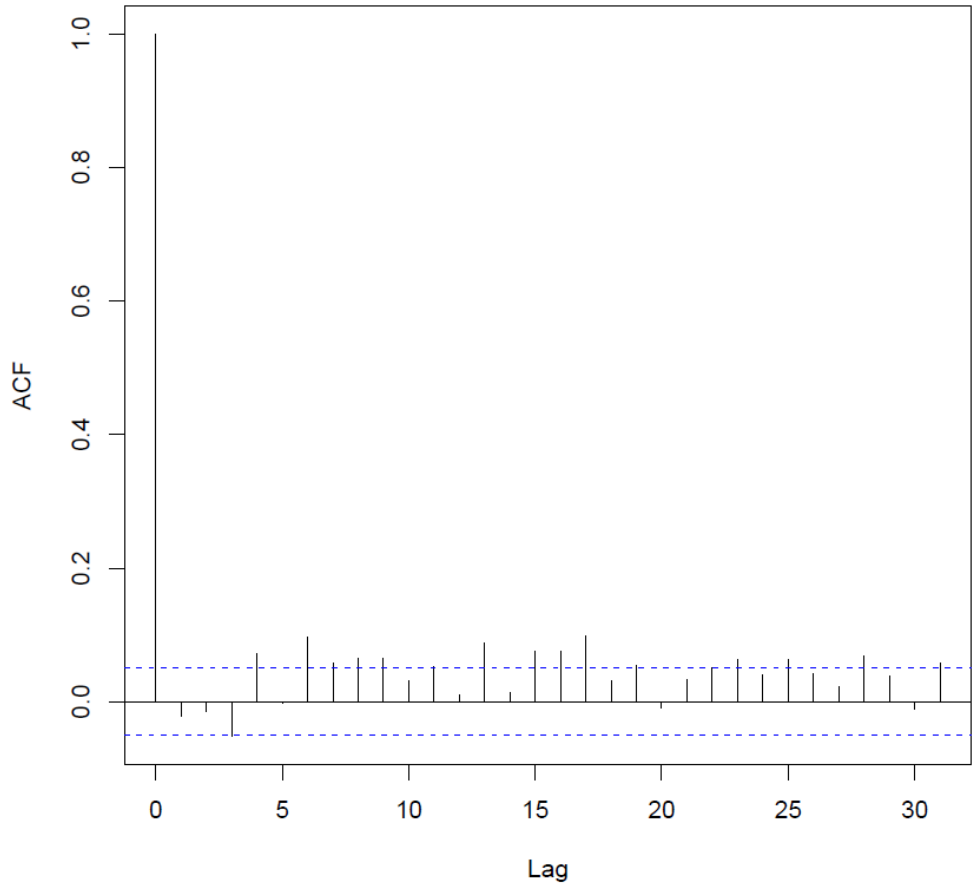
Supplementary Figure 22: The Generalised Additive Mixed Model results with log10-transformed grass biomass as a response variable. Rainfall (a-b); Soil texture (c); and grazing pressure (d-e) all explain standing grass biomass within the Shompole and Olkiramatian region (South Rift Ecosystem). The importance of the different variables used in the random forest models is displayed in (f).

The generalised additive mixed model predicting log10-transformed grass biomass across 24 plots in the South Rift across 12 years had an r-squared value of 0.534. No terms were fully penalised or removed during model fitting (Sup Fig 22a-e). Model fit Sup Fig. 23, and temporal autocorrelation structure Sup Fig. 24 . The GAMM indicates that plot-level biomass is most strongly influenced by (i) rainfall in the last three months (edf = 3.47, $p<0.001$), (ii) and a large impact of rainfall in the previous two years (edf = 1.83, $p<0.001$) with low rainfall periods majorly reducing biomass. Soil texture also impacted grass biomass (edf = 6.70, $p<0.001$), with high clay and low sand proportions having lower grass biomass and areas with soft clay and medium sand having higher biomass. The proportion of grass biomass grazed at the time of data collection (edf =2.96, $p<0.001$) and the mean over the last six months (edf = 1.27, $p<0.001$) both had negative relationships with grass biomass. The random forest model explained 52.8% of the variance in grass biomass. The random forest models most important variables (calculated using node impurity) for predicting grass biomass are rainfall in the last three months, six months, and two years (Sup Fig 22f). Percentage of grass grazed is the next important variable, followed by the soil quality and composition related variables.

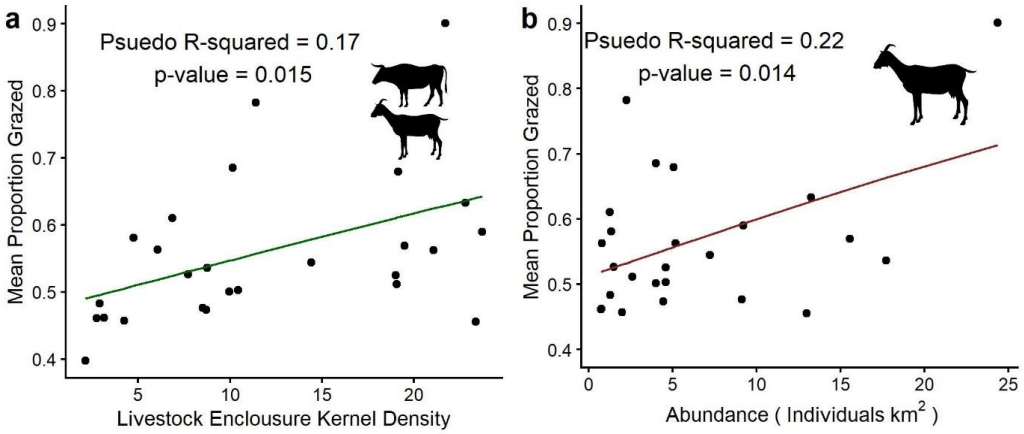
The beta-regression models showed that shoat abundance in the dry season is the only species abundance estimate with a significant correlation to mean proportion grazed at each plot (Sup Fig.25 & 24b, r-squared 0.22, p-value =0.014). Livestock enclosure kernel density is also positively correlated with mean proportion grazed at each plot (Sup Fig. 24a, r-squared 0.17, p-value = 0.015).



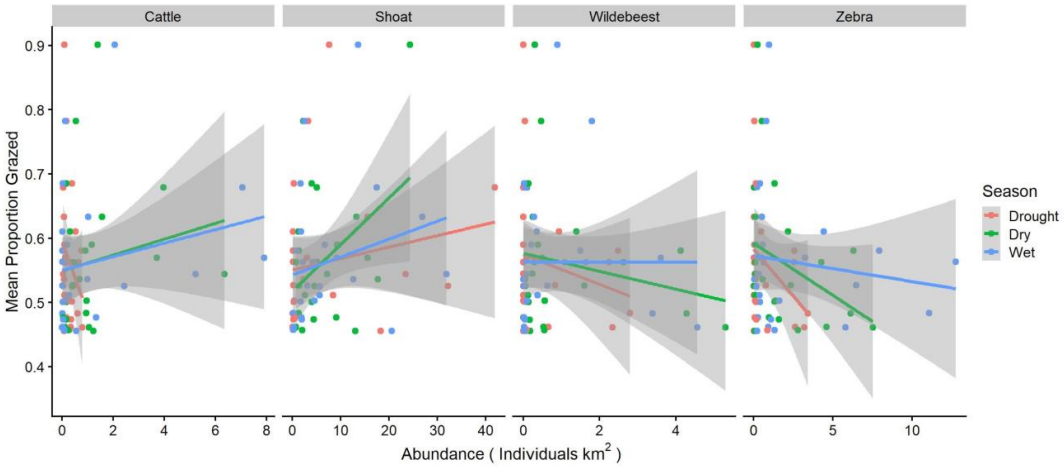
Supplementary Figure 23: Q-Q plots and analysis of the residuals for the generalised additive mixed model explaining grass biomass. This suggested the negative binomial distribution model generally fit the data well, although there is still slight overdispersion at higher densities.



Supplementary Figure 23: The temporal autocorrelation structure of the fitted residuals from the generalised additive mixed model for grass biomass.



Supplementary Figure 24: Beta-regressions explaining the relationship between the mean proportion of grass grazed across 25 plots in Shompole and Olkirimation and A) Livestock enclosure kernel density; B) Shoat abundance in the dry season.



Supplementary Figure 25: Beta-regressions explaining the relationship between the mean proportion of grass grazed across 25 plots in Shompole and Olkirimation and A) Livestock enclosure kernel density; B) Shoat abundance in the dry season.

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Supplementary Text 3 – Connectivity Modelling

We used Circuitscape[1] (http://www.circuitscape.org/) with a moving window analysis, implemented in Omniscape[2] in Julia 1.5, to quantify the changes in connectivity and mobility in Southern Kenya. Our definition of connectivity (modified from McCrae et al. 2016) is the degree to which regional landscapes will sustain ecological processes and are conducive to the movement of many types of organisms. In our case, this is particularly important for both large mammals and livestock.

Circuitscape model's connectivity using electric circuit theory to incorporate all possible pathways between movement sources and destinations and identifies movement via low-resistance routes, i.e., routes presenting relatively low movement difficulty. When two features on the landscape are connected, electrical current flows from one (the source) to the other (the target). Patterns of current flow through intervening areas help identify the ability for movement in the region. Traditionally, conservation planning focuses on using Circuitscape to connect core areas or patches[3,4]. Omnsicape, however, uses a moving-window approach to calculate Omni-directional movement without arbitrary declarations of core areas. This is important in our application, where we are interested in mobility across a range of land tenure systems and understanding the impacts of fragmentation on wildlife and livestock.

The algorithm first requires us to define resistances to different landscape features. We used the study area and added a 10km buffer around the area (which we subsequently clip from the results). We used a resolution of 100m, which we deemed an appropriate trade-off between identifying the impacts of man-made structures on mobility while enabling computational efficiency. Using this resistance map and a source weight raster (calculated from the inverse of the resistance surface in our case) a moving window approach connects a pixel to all other pixels that have a value within a 10-km radius to one another using Circuitscape[2]. We blocked the source data into 3x3 pixels to increase computational efficiencies, with tests suggesting this does not limit our interpretation of the current flow. The results are summed from each moving window into a cumulative current map.

We applied this Omniscape model under two scenarios:

1. **No anthropogenic impact:** the resistance layer was calculated using only slope, a key limitation to movement. We scaled slope using the equation: resistance = 1 + (0.1*slope)^2. Resistance values greater than ten were set to no data values as it was expected that there is generally limited movement across slopes larger than these gradients (~>30 degrees).
2. **Anthropogenic impact:** we used the data from Chapter 5, which provides a database for livestock enclosures, agricultural land use, and fences for over 30,000 km^2 across Southern Kenya to calculate the resistance layer. We supplemented this with a 100m resolution of buildings for Kenya and Tanzania (worldpop.org) and a 30m resolution cropland dataset (www.croplands.org) to ensure complete coverage of our study area. Any pixel containing agricultural land, a fenceline, livestock enclosure or building, was set to a no data value, indicating that no movement is possible across or from this pixel. While strict, we believe this is an accurate representation of humans' impact on mobility within each 100m pixel.

The contrasting models were then compared to calculate a percentage change in cumulative resistance between the two scenarios. We used the ecosystems boundary data to estimate the change in ecosystem size. To do this, we scaled the cumulative current flow for both maps using the *rescale* function in R[5] and excluded any pixels that were greater than 1.5 standard deviations above or below the mean. We excluded any isolated patches that were connected through corridors (areas of high current flow) to the main ecosystem but were less than 100 hectares in size. While arbitrary, this provides a rough assessment of the change in ecosystems' size with and without human-caused limitations to mobility.

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8

New forces influencing savanna conservation: increasing land prices driven by gentrification and speculation at the landscape scale

8. Land price in Southern Kenya

Abstract

Land transformation reduces biodiversity and regional sustainability, with land price being an indicator of the opportunity cost to a landowner of resisting land transformation. However, reliable, spatially explicit databases of current land prices are generally lacking in developing countries. We used tools from data science to scrape 1487 georeferenced land prices for southern Kenya from the internet. We found higher land prices closer to urbanization, in areas of high agricultural productivity, but also around the Maasai Mara National Reserve. Predicted land prices ranged from 662 to 4,618,805 USD per acre. Land speculation from expanding urbanization drives up the opportunity and acquisition costs of maintaining conservation buffer zones, corridors and dispersal areas. However, high land values are also found adjacent to a world-famous tourist destination. Profit-driven turnover of ownership, subdivision, and transformation of land is rapidly underway, to the detriment of savanna biodiversity and the sustainability of the pastoral social-ecological system.

Introduction

Despite global concerns over biodiversity loss and declining environmental sustainability, current conservation expenditures are inadequate (Waldron *et al.* 2013). Strategic prioritization of conservation interventions requires spatially explicit data on economic factors that threaten biodiversity and ecosystem function so that scarce funds can be allocated most efficiently (Naidoo *et al.* 2006; Armsworth 2014). This applies particularly to biodiverse areas where land acquisition costs—the costs of full or partial transfers of land including leases, short term rentals, and management rights—are unknown and land users have freehold or leasehold tenure (Ando *et al.* 1998; Naidoo *et al.* 2006). Dependent on acquisition costs and willing buyers, property sales of undeveloped land often occur, and can result in its transformation into states with lower biodiversity and impaired ecosystem function (Sage 2019). Alternatively, if landowners maintain their land in states that conserve biodiversity and ecosystem services, they might forgo opportunities to adopt alternative and potentially more profitable land uses such as cropping and livestock production (Osano 2005; Norton-Griffiths and Said 2009).

In many important areas for wildlife conservation, net agricultural returns outcompete the current economic or social returns from wildlife, resulting in opportunity costs to landowners that eventually drive a land use change (du Toit *et al.* 2017). Consequently, protected areas (PAs) are mainly situated in regions with the lowest agricultural potential, not the highest biodiversity (Venter *et al.* 2017). Those PAs that do occur in productive regions are increasingly isolated within hard boundaries or eroding buffer areas (Newmark 2008). Outside of PAs, land transformation represents one of the most significant drivers of global biodiversity decline in general (Sage 2019), and local declines in large mammal populations in particular (Newmark 2008). Economic costs are, therefore, increasingly incorporated into conservation planning, and spatially explicit data to estimate these costs are essential for developing a systematic conservation planning framework (Naidoo *et al.* 2006; Adams *et al.* 2019). A key metric is price of land, which not only represents the acquisition cost of the land, but can also indicate the expected discounted future revenues from the land once it has been purchased (although not necessarily the net profit). It, therefore, provides a basis for estimating opportunity costs across alternative land use options (Osano 2005). In some situations, where either the economic or the intrinsic values of wildlife and nature are significant, they could overcome the opportunity costs of conservation even to the extent of inflating local land prices (Gibbons *et al.* 2014).

However, it is challenging to develop spatially explicit estimates of land prices in developing countries, largely due to a lack of reliable databases (Naidoo *et al.* 2006). In the absence of

better data, it is common practice to select proxies of economic forces that affect biodiversity at the landscape scale, and then to extrapolate across a region of interest. However, proxies can be arbitrarily applied and can be at the wrong spatial resolution required for conservation planning, or only weakly supported by comprehensive economic data (Armsworth 2014). A solution is to build a spatially explicit database of actual land prices, thereby providing a reliable basis for mapping spatial heterogeneity in costs and benefits to inform systematic conservation planning, and for providing inference on the drivers of land price (Osano 2005; Naidoo *et al.* 2006). Here, we report on an exercise to achieve this for a region in Africa that is world-renowned for its biodiversity.

Maasai pastoralists, who have always co-existed with diverse wildlife communities, are the traditional land custodians across vast areas of East African savanna. Yet ongoing changes to policy, governance systems, demography, and livelihoods are leading to wide-scale land transformation (Mwangi and Ostrom 2009; Veldhuis *et al.* 2019). A response in Kenya has been the formation of conservancies—areas where landowners set aside their land for the protection of biodiversity—as a mechanism for preventing land transformation and conserving habitats for diverse and abundant wildlife communities (Western *et al.* 2020). These conservancies are often formed through land leasing by ecotourism operators or conservation NGOs, but their long-term sustainability is threatened by mounting opportunity and acquisition costs (Norton-Griffiths and Said 2009). To investigate this threat, we estimated the acquisition costs of land across southern Kenya. We used tools from the field of data science and scraped land asking-prices from internet adverts. We then used a generalized additive model with environmental and anthropogenic covariates to map the spatial variation in land asking-price (from here on referred to as land price). Areas with high predicted land prices are likely to undergo land transformation and be hotspots of future biodiversity losses. We compare predicted land price to the Human Footprint, a cumulative threat map which is indicative of current anthropogenic pressures on biodiversity (Venter *et al.* 2016a; Di Marco *et al.* 2018), to understand where current and future impacts on biodiversity converge or diverge to help prioritise conservation action. Our study reveals profound economic threats to the sustainability of traditional social-ecological systems across African savannas, where wide-scale conservation efforts must address the drivers of land transformation.

Methods

The study focuses on five counties covering 54,471 km^2 in southern Kenya, including six government-protected areas that are supplemented by conservancies (Figure 2). This study area, which includes some of the richest biodiversity in Africa and the highest mammalian

diversity on Earth, also supports the highest abundance of pastoral livestock and wildlife in eastern and southern Africa(Ogutu *et al.* 2016).

Data were scraped from advertisements of plots of land for sale on the website of a major Kenyan newspaper using the package *rvest* in *R version 3.5*(R Core Team 2018). This yielded 4128 potential land sales in the study area, described by location, price, and area of the plot. Each location was then georeferenced (Web Panel 1) and, following cleaning, 1487 land pricings were used in the analysis (Web Figure 1). All prices are presented in U.S Dollars per acre, which is the unit of land area used in the region.

Spatially explicit data were obtained for nine potential predictors of land price, which were chosen for an *a priori* expectation of their effect on land price (Web Table 1 & Web Figure 2). In addition to variables related to the price of land relative to development, the potential yield of maize was used as a proxy for the productivity of agricultural land. Furthermore, distance to the nearest edge of the Maasai Mara National Reserve was included because of its strong tourism industry, which pays lease fees to landowners for exclusive use for ecotourism and conservation, which in turn may inflate land prices.

A generalized additive model (GAM) with a negative binomial logit link structure was used to model univariate smooths of all the predictor variables, with land cover added as a parametric term. Details are given in Web Panel 1. Spatial autocorrelation and concurvity were checked and no issues identified (Web Figure 5&6). The final model was then used to predict land prices across 54,472 cells at a 1km^2 resolution in southern Kenya.

We used a comprehensive cumulative threat map, the recently updated Human Footprint (Venter *et al.* 2016b), to observe current threats to biodiversity (Figure 4; Web Panel 1). To illustrate the costs of implementing large-scale conservation plans we estimated the acquisition costs of land in two separate areas. First, the Shompole-Olkiramatian region in the South Rift Valley which is the only large wildlife refuge in southern Kenya not congruent with a government-protected area (Tyrrell et al. 2017). Second, an area including the Nairobi National Park dispersal area and the remainders of the Athi-Kapiti dispersal areas, which historically supported abundant migratory wildlife, is now highly fragmented (Western and Gichohi 1993; Said et al. 2016) and includes two proposed corridors for wildlife movement (Ojwang' et al. 2017; Web Panel 1; Web Figure 8).

Results

The 1487 georeferenced potential land sales used in our analysis ranged in price per acre from 746 to 7,293,221 USD (Web Figure 1).

Our GAM model fit the data well (Web Figure 5), and explained 75.8% of the deviance (adjusted $R^2 = 0.674$). The full model details are given in Web Table 2 & 3, and Web Figure 4, and the univariate smooths and parametric terms of the models are shown in Figure 1.

The GAM response curves (Figure1) demonstrate several trends: (1) as the distance from Nairobi increases land price reduces dramatically for the first 25km and continues to decline to an asymptote at around 100km; (2) land prices are highest in areas with higher potential maize yields but only after a potential yield of 6 tonnes per hectare; below this threshold land values are suppressed; (3) land prices are higher directly adjacent to the Maasai Mara; (4) land price decreases with distance from major roads; (5) land price increases with increasing herbaceous land cover ($\beta = .652$, $p < 0.001$), cropland ($\beta = .233$, $p = 0.027$), and urbanization ($\beta = .243$, $p = 0.021$) (Web Table 3, and Figure 1).

Government-owned PAs are not on the land market but we predicted their potential land prices as if they were: Nairobi National Park had the highest median of 284,418 USD per acre and Amboseli National Park had the lowest at 2,778 USD per acre. Of the conservancies, the Athi-Kapiti region had the highest median value of 52,481 USD per acre, followed by the Maasai Mara with a median of 10,896 USD per acre, and the South Rift the lowest at 754 USD per acre (Figure 3).

Discussion

The land prices we predicted across 54,471 km^2 of southern Kenya generated one of the few spatially explicit maps of land prices in a developing country. This revealed high spatial heterogeneity in per-acre land price (662 USD in a remote area; 4,618,805 USD in central Nairobi; Figure 2). These prices represent both the acquisition cost of the land and an indicator of the opportunity cost of conservation to landowners. This is because commercial transactions of relatively undisturbed land indicate potential land transformations, and so areas under traditional (pastoral) land use with relatively high or rapidly increasing land prices are where biodiversity losses are likely and environmental sustainability is thus threatened (Figure 4).

Although some caveats to these data exist (Web Panel 1), the overall results, and the method we used to acquire them, have several immediate applications for conservation planning and action. First, the government of Kenya is actively seeking ways to offset the opportunity costs of wildlife to landowners. A task force has been charged with identifying corridors and dispersal areas that should be protected as much as possible from development, as part of a regional conservation master plan. To this end, land price data enable initial assessments of present and future threats to biodiversity through land

transformation. For example, in the direct vicinity of Nairobi there are both high current impacts on biodiversity as indicated by a high human footprint, but also little chance of reversing these trends due to the high opportunity and acquisition costs indicated by the land price (Figure 3&4). Interestingly, our research reveals that land price and current conservation impact do not covary in a simple linear relationship (Figure 4). For example, some areas, such as the Maasai Mara conservancies, have low current threats to biodiversity as indicated by a low human footprint, yet may have a high threat of land conversions as indicated by a higher land price (Figure 3&4). Areas with low current pressure and low land prices may have a high potential for proactive community-based conservation including the South Rift Valley and the Amboseli ecosystem (Figure 3&4). The Shompole-Olkiramatian ecosystem in the South Rift Valley, for example, may require considerably less investment to overcome opportunity costs compared to the Nairobi-Athi-Kapiti ecosystem (Figure 3; Web Figure 8; see below).

Second, this methodology provides a rapid, repeatable, and scalable procedure for collecting land price data where no regional databases exist and allows comparisons with other regions of interest where online data are available. These patterns of changing land price and tenure are not exclusive to Kenya or the African savanna biome. Multiple terrestrial ecosystems, such as the Brazilian cerrado, face similar pressures and would benefit from a similar quantification of land price and its drivers (Reid *et al.* 2014; Rosa 2020).

Third, this method predicts costs at a scale relevant to local systematic conservation planning, rather than at aggregated administrative levels (Armsworth 2014). Finally, none of these estimates rely on data restricted to certain types of land sales but represent the actual asking price on the open market (Naidoo *et al.* 2006; Armsworth 2014). Conservation prioritisation commonly uses arbitrary proxies of acquisition costs, and comparing priority areas identified by different datasets will be important for future efforts to ensure effective and efficient conservation action.

Previous work on opportunity and acquisition costs in savanna ecosystems has focused on the forgone profit from agriculture as the main competing costs to wildlife-friendly land use (Norton-Griffiths and Said 2009; du Toit *et al.* 2017). We found that agricultural potential was indeed a factor in our analysis, but it had a much smaller effect on the price of land in southern Kenya than did urban expansion and infrastructure development (Figure 1 and Web Figure 7). Historically, most of the wildlife-rich areas of southern Kenya have been used by pastoral Maasai people for their livestock, with land held under communal tenure. Facing economic and political pressures, most of these areas have now been privatized and subdivided (Mwangi and Ostrom 2009). The new landowners, who accrue few economic

benefits from wildlife and have dwindling profits from livestock, have typically sold at least part of their land to partake in the cash economy (Rutten 1992). Subsequently, much of this land has been fenced, with the woody vegetation removed and sold as charcoal and the land converted into agriculture or urban development, or held by speculators hoping for increasing land prices (Rutten 1992; Kimani and Pickard 1998; Said *et al.* 2016). This trend of land subdivision and subsequent sale is ongoing across the region, and the price of land is likely to continue to increase as the human population and national economy both grow. Economic drivers are thus shrinking the remaining areas of habitat for wildlife and rangeland for livestock, severing connectivity between wildlife subpopulations, and thereby threatening one of the most diverse assemblages of large mammal species in existence (Ogutu *et al.* 2016; Said *et al.* 2016; Web Figure 9).

In the case of land close to Nairobi, where there is a high demand for housing estates and industrial parks, the outlook for biodiversity conservation is poor. In the last 30 years, the Athi–Kapiti plains adjacent to Nairobi National Park have been subdivided into individual plots. Now, despite efforts to establish payments for ecosystem services within conservancies, wildlife populations have plummeted and the National Park has become an island in a sea of development (Figure 4)(Said *et al.* 2016). The surrounding land now has a median sale value of 51,264 USD per acre, offering a return on investment well above that received from wildlife conservation (Figure 3). Additionally, the land inside the national park is potentially worth 282,961 USD per acre; keeping it as a national park represents a considerable commitment by the Kenyan government to protect wildlife habitat. To conserve the remaining dispersal areas adjacent to the National Park and in the Athi-Kapiti plains is now virtually impossible through financial reasoning alone. Our data show that the market-value purchase of dispersal areas and corridors laid out in government plans for this area could cost 40 billion USD (Web Figure 8). We accept that some individual landowners might resist selling their land due to the traditionally high social and cultural values they attach to their land and wildlife. However, from present trends, the scale and rate of industrial and urban development (Said *et al.* 2016) make it unlikely that traditional values are sufficient to maintain connectivity between the Athi-Kapiti plains and Nairobi National Park.

Interestingly, our research shows that land prices also increase with proximity to Maasai Mara National Reserve. Land for sale in this region is advertised for the development of tourism facilities, private holiday homes, and to protect and appreciate wildlife. The target market is non-local investors and wealthy individuals, thus introducing the process of gentrification (Web Panel 2; Web Figure 9). Whether or not this will facilitate biodiversity conservation remains to be seen, and conservancies in this region, funded by tourism and philanthropy, currently provide landowners with an average annual income of ~15 USD per

acre (MMWCA 2019). These payments come with the condition of maintaining the land in a state fit for wildlife conservation, preventing land transformation. Yet, with a median land value of 10,895 USD per acre (Figure 2&3), there is a strong financial incentive for landowners to sell. Even with the added income accrued from tourism-based employment and livestock grazing schemes within conservancies. Proximity to a rich wildlife resource is inflating local land prices, similar to patterns seen in other parts of the world (Gibbons *et al.* 2014), which could increase adjacent development and speculation, and make future investments in land and leases for conservancies more expensive (Armsworth *et al.* 2006).

Conclusions

Displacements of traditional subsistence pastoralists from land sold to wealthier investors from elsewhere (gentrification), and land transactions motivated by potential resale profits (speculation), are rapidly underway in southern Kenya. There are profound implications for the traditional Maasai social-ecological system and the conservation of a global biodiversity treasure. We urge that land price trends be monitored across rangeland ecosystems and that bold and creative policies be introduced to enable landowners within these “working landscapes” to offset the opportunity costs of resisting land transformation (Norton-Griffiths and Said 2009; Kremen and Merenlender 2018). In particular, our findings underscore the urgency of finding economic solutions to ensure the long-term sustainability of African wildlife, wildlands, and traditional pastoral systems (Western et al. 2020). Options include targeted government subsidies to private landowners, payments for ecosystem services, improved livestock management, restructured tourism revenue flows, incentives for domestic tourism, and innovative financial structures to enhance wildlife-based revenues to local households (Lindsey *et al.* 2020). Meanwhile, extensive land-price mapping should be used to inform regional land-use planning, such as that already underway across Kenyan rangelands from both the bottom up (communities and conservancies) and top down (national and regional governments).

Under sustained population and economic growth, urbanization and land speculation will continue across African savannas—where most of the planet’s remaining megafauna occur—and may influence the economic viability of wildlife-friendly landscapes (Newbold *et al.* 2015). Understanding these drivers of land transformation, and using this knowledge in a systematic conservation planning framework that optimises conservation expenditure, will be vital for conserving biodiversity on enough land to achieve globally agreed conservation targets (Allan *et al.* 2019).

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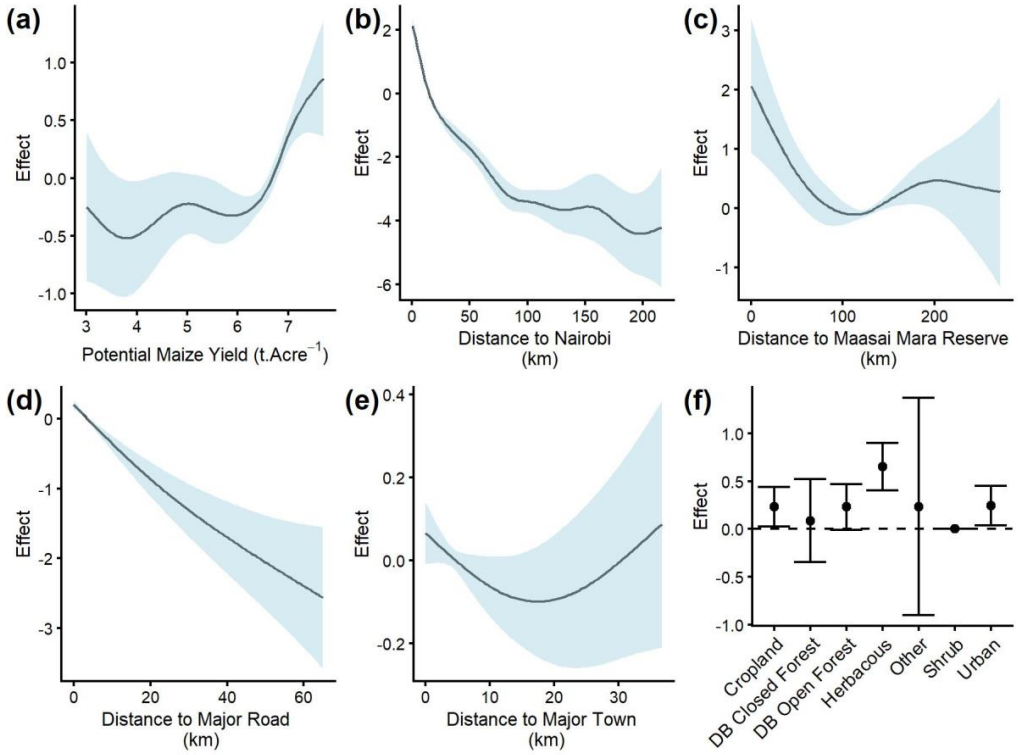


Figure 1 a-e Generalised additive model smooths for the non-parametric terms included in the final model explaining land price in southern Kenya. The price of land per acre (effect size) was influenced by a) the potential yield of maize (tonnes/acre); b) the distance to Nairobi (Kenya's capital and largest commercial hub); c) distance to the Maasai Mara (a world-famous tourist destination, and a significant contributor to the local and national economy); d) the distance to main roads; e) distance to major towns; and f) land cover – the shrub parametric term is used as the intercept (reference land cover with zero effect) for the model. DB is an abbreviation of Deciduous Broadleaf. Blue shading on a-e indicates 95% confidence intervals. Error bars on f represent the 95% confidence intervals for the parametric land cover terms. The probability of future urban expansion and population density were removed during penalization.

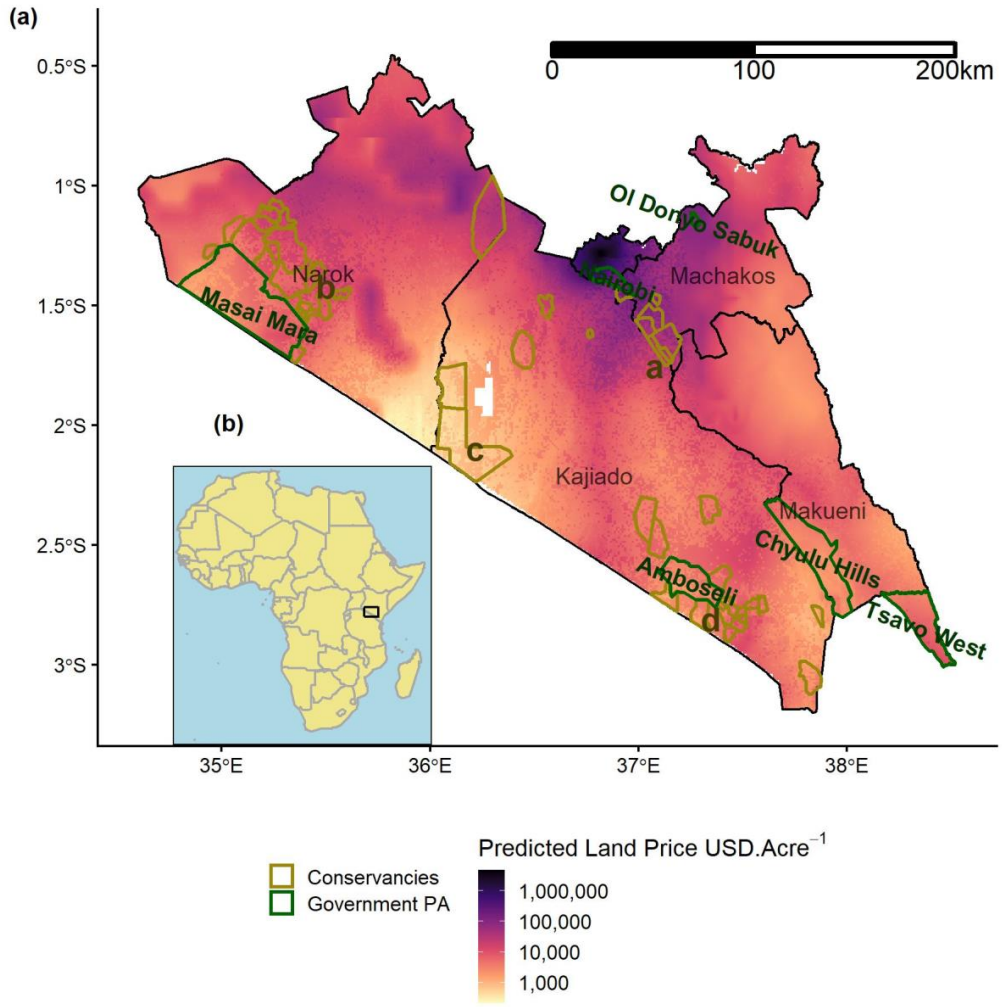


Figure 2 a) Map of the predicted price of land (USD per acre) for the southern Kenyan counties of Kajiado, Narok, Makueni, Machakos, and Nairobi (covering 54,471 km^2). The land price color scale has been log-transformed. Kenya's government-protected areas are shown in dark green (Tsavo West National Park, Ol Donyo Sabuk National Park, Nairobi National Park, Maasai Mara National Reserve, Chyulu Hills National Park, and Amboseli National Park), and the operational private and community conservancies in khaki (conservancies are areas where landowners have agreed to use their land for wildlife conservation). The conservancies are grouped into four administrative regions labeled as a) Athi-Kapiti; b) Maasai Mara; c) South Rift; d) Amboseli. Predicted land price is several orders of magnitude higher in central Nairobi than the surrounding region. b) An inset displaying the study region in southern Kenya (rectangle) within the African continent.

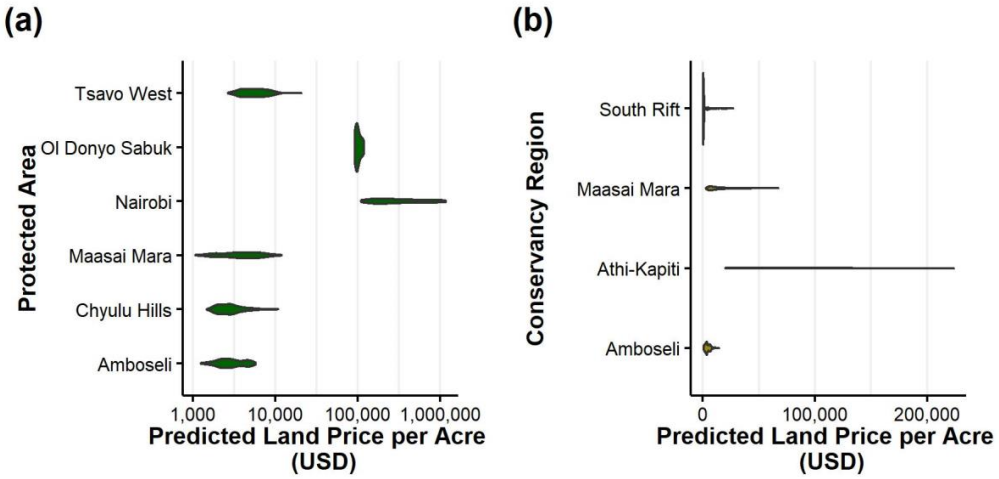


Figure 3. Violin plots showing the distributions of (a) predicted land price per acre for each of the government-run protected areas and (b) predicted price per acre for each conservancy region. The violin plots outlines illustrate kernel probability density, i.e. the width of the shaded area represents the proportion of the data located there. Note the difference in scale on the x-axis. The x-axis scale in (a) has been log-transformed to accommodate the higher land prices in Nairobi National Park and Ol Donyo Sabuk National Park.

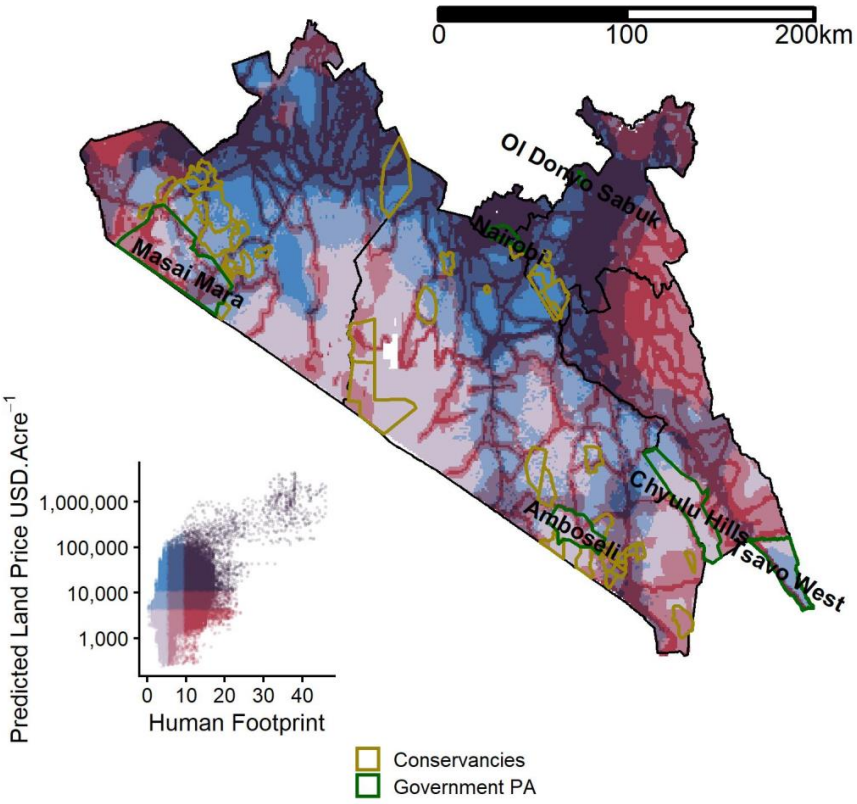
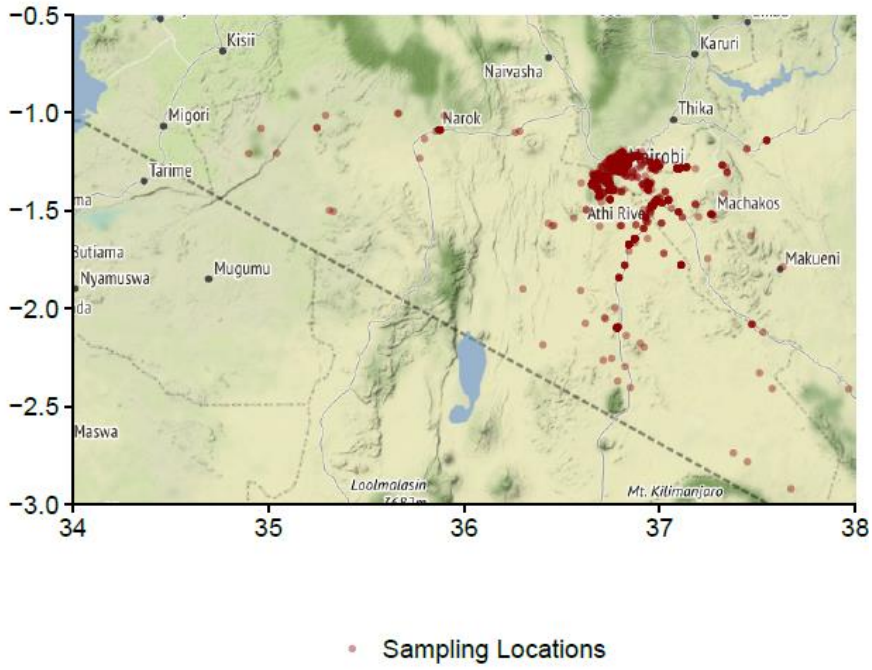


Figure 4 - A bivariate plot of predicted land price (USD per acre) against the Human Footprint (Venter et al., 2016). This compares the current impacts of development, infrastructure, and land-use as indicated by the Human Footprint (a scaled level of threat from 0 – no impact to 50 – completely human-dominated urban systems), against the potential impacts as suggested by land price and its link to land sale and conversion. Note the low current impacts but high land prices (red), in the Maasai Mara region, around Nairobi, and along the main roads. Low impacts and low land prices (light blue) indicate areas with potential for community-based conservation, such as the South Rift Valley and the Amboseli region.



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375 **Web Figure 3** - Locations of georeferenced price per acre data points used in the generalized
376 additive model. The breakdown of locations by county was 741 in Nairobi, 498 in Kajiado, 213 in
377 Machakos, 27 in Narok, and 8 in Makueni

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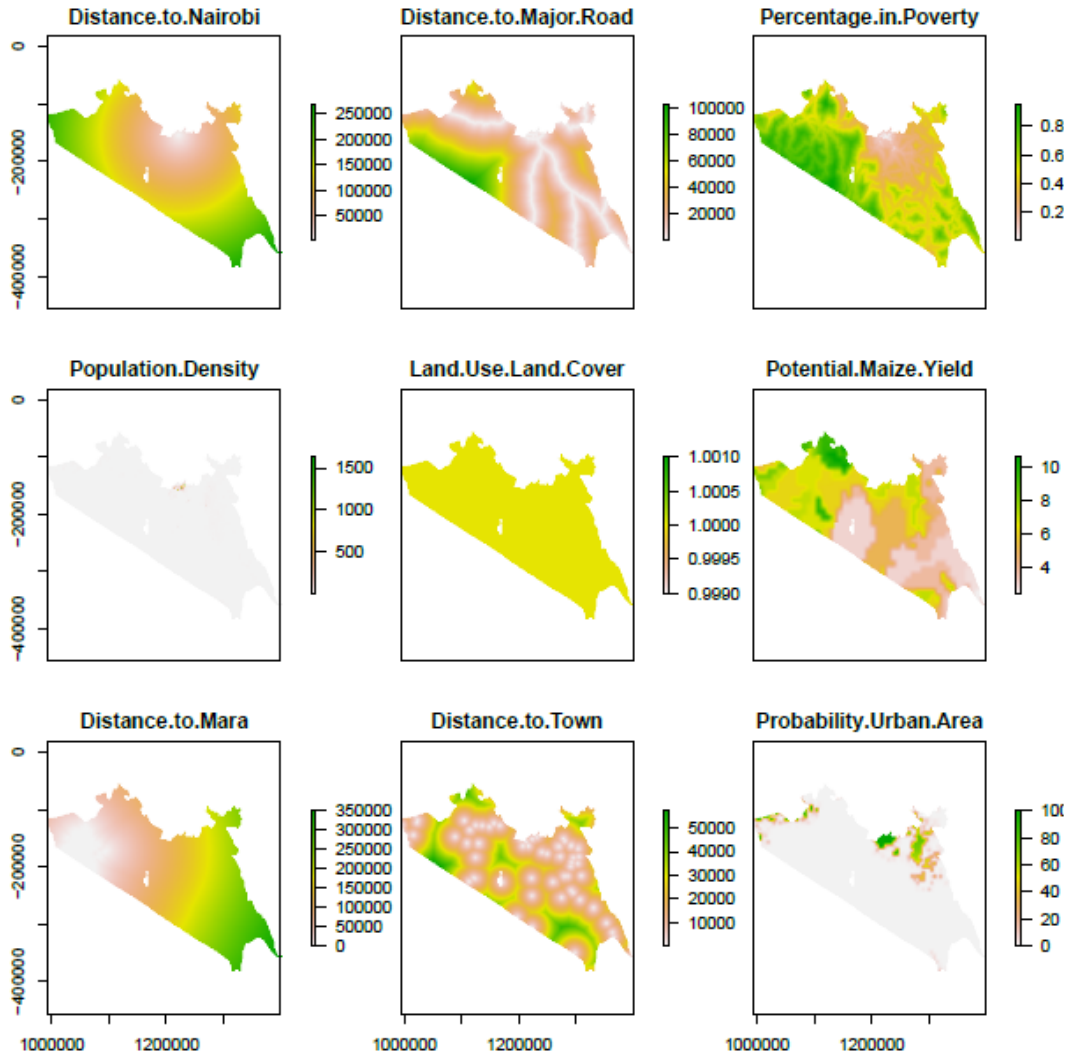
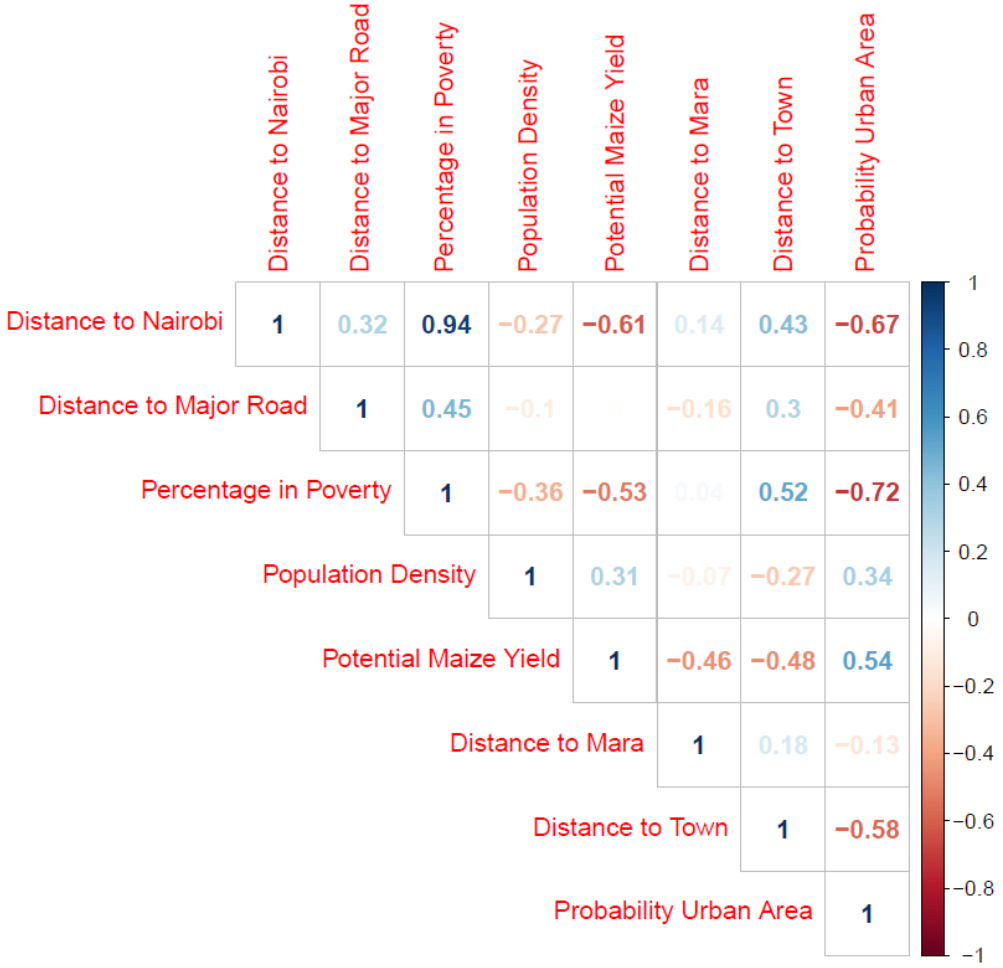


Web Figure 4 - Predictor variables used in the generalized additive model process for Southern Kenya. These variables are also used to generate a predicted surface of land price.



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386 **Web Figure 5** Correlation plot of the proposed covariates in the model. The spearman's rank
387 correlation coefficient is provided for each combination. The percentage of poverty was removed
388 because it was correlated with the probability of future urban areas (>0.7).

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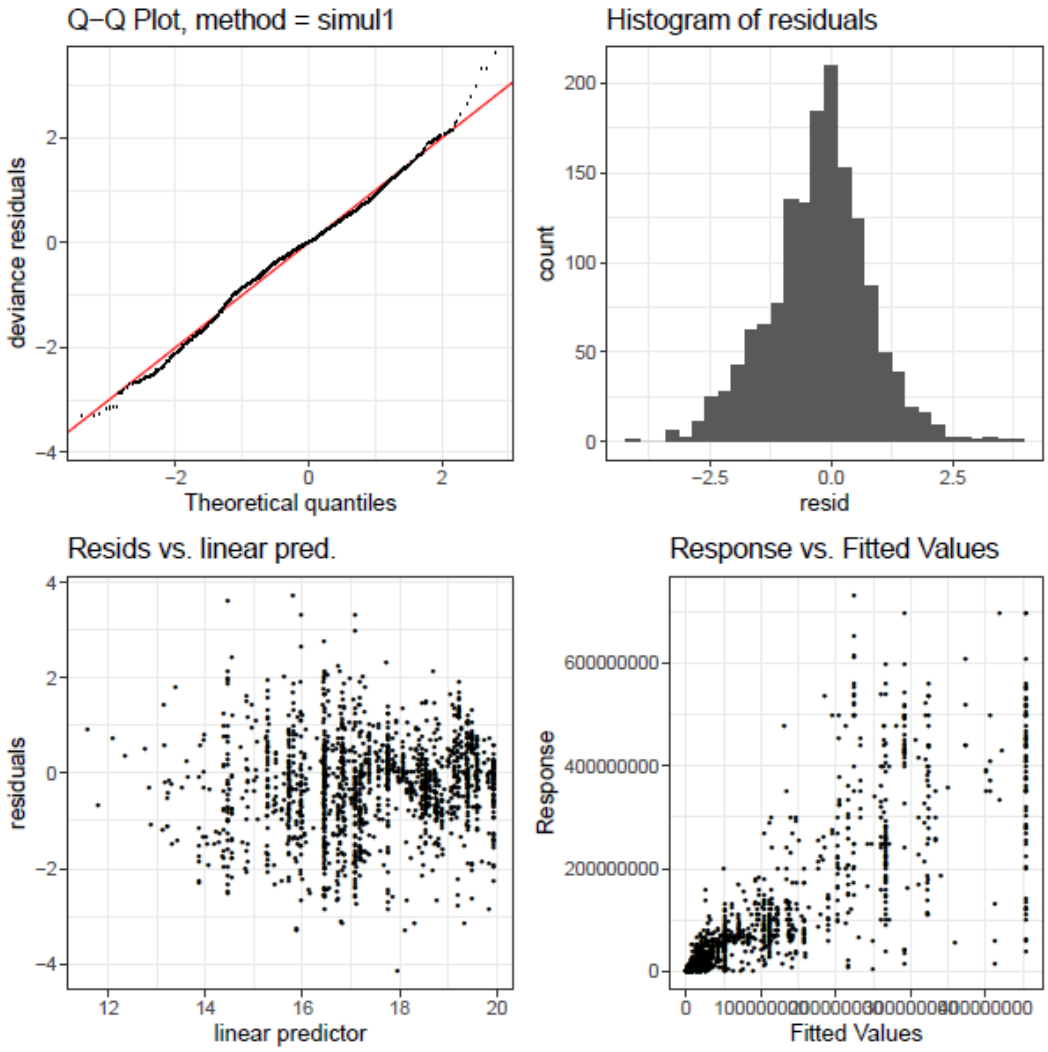

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391 **Web Figure 6 –** Final generalised additive model residuals plotted to assess model fit.

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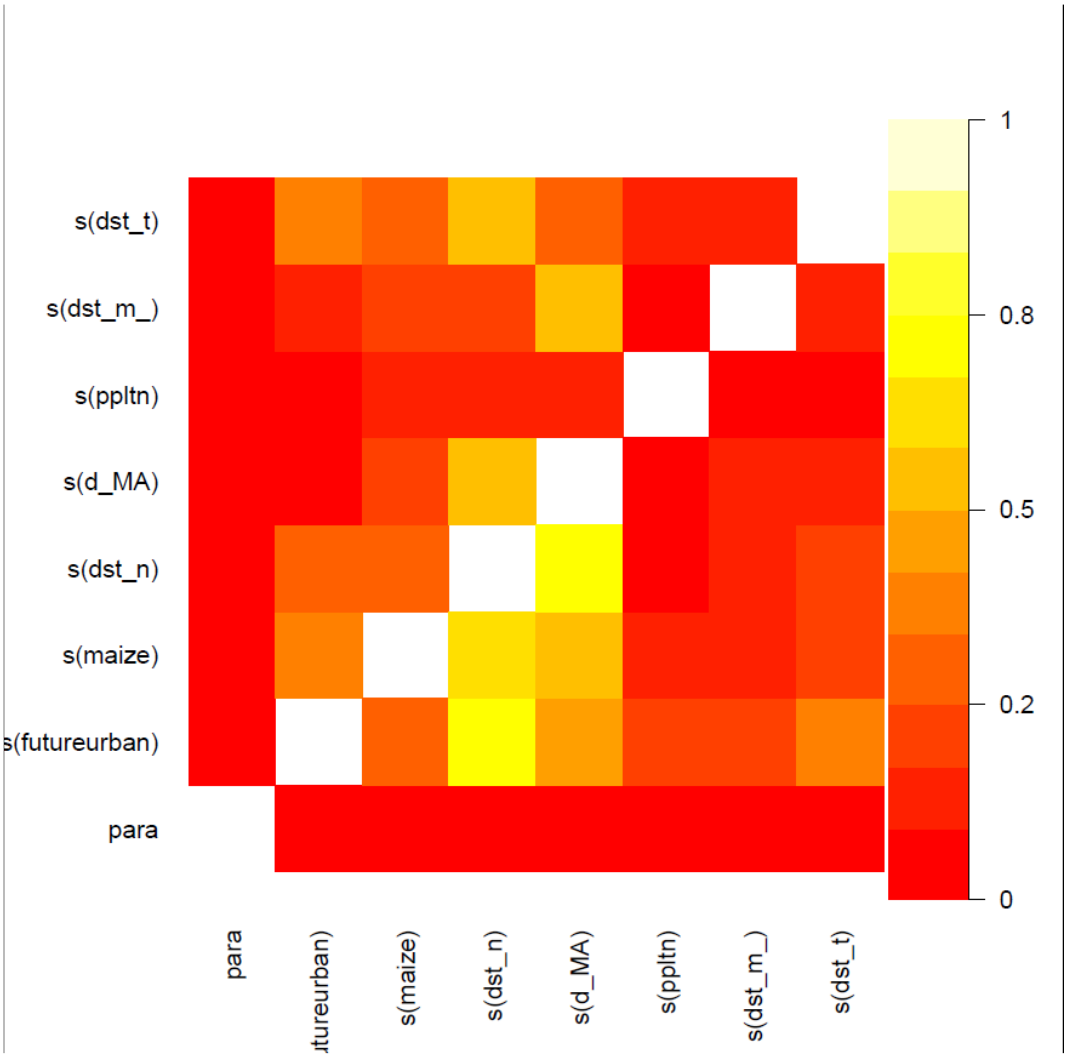
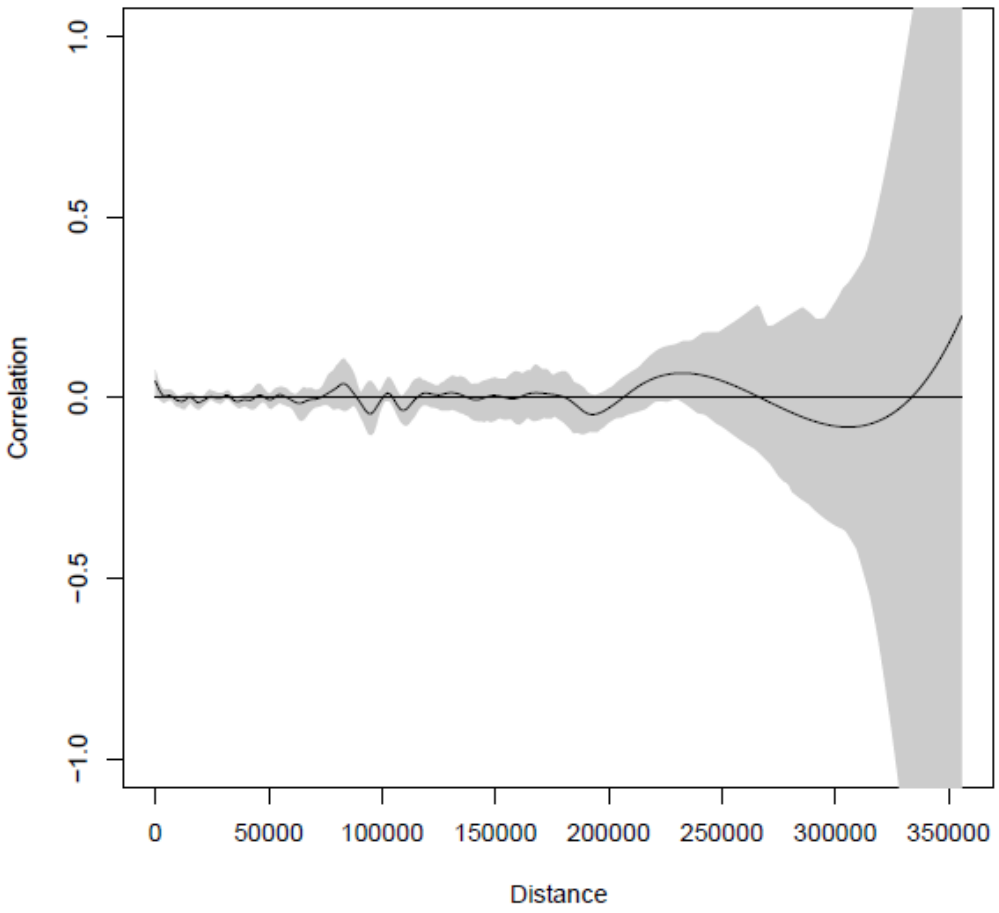


Web Figure 7 – Plot of concurvity between different terms in the model. Concurvity occurs when some smooth term in a model could be approximated by one or more of the other smooth terms in the model. Concurvity can be viewed as a generalization of co-linearity, and causes similar problems of interpretation 7. No issues in concurvity where identified between variables. s(dst_t) – Distance to Major Town; s(dst_m_) – Distance to Major Roads; s(ppltn) – Population Density; s(d_MA)- Distance to Maasai Mara; s(maize) – Potential Maize Yields; s(futureurban) – Probability of Urban Expansion.



Web Figure 8 – Spatial -autocorrelation plot of the final GAM model residuals suggests that there is little spatial-autocorrelation. We used the package ncf (Bjornstad 2019).

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413 **Web Figure 7** Predicted effect size for each term from the Generalised Additive Model for the study
414 area in southern Kenya. The large decrease in land value with increasing distance from Nairobi and
415 Main roads are evident. The potential yield of maize also increases the value of land in the fertile and
416 high rainfall Mau Forest in the Northwest of the study region (which is under heavy encroachment
417 from agricultural expansion). Distance to Major Town and Land use have small effects on predicted
418 land price. Proximity to the Maasai Mara in the west of the study-region increases predicted land
419 price.

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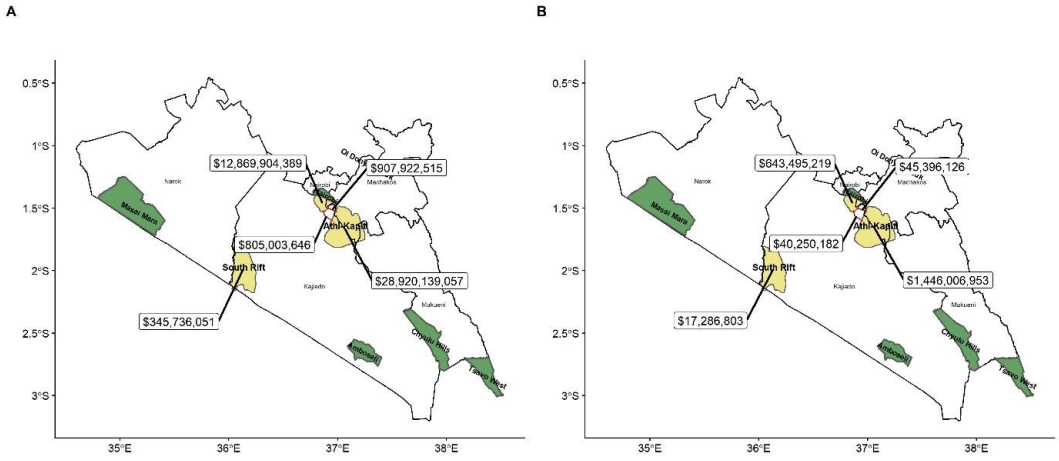

Web Figure 8: A map of the study area in southern Kenya displaying: A) total land price in U.S dollars; and B) potential annual lease fees per year in U.S dollars, calculated as 5% of the total land value. These lease fees are poor estimators of the actual value required to run community conservation programs, as they ignore other societal benefits such as job creation and development programs, as well as revenue generation from community livestock co-existing with wildlife. However, they give a generalisation of the cost of conservation if the land was to be leased as an exclusive use area. These estimates are calculated for two areas of conservation importance (khaki), and two corridors (red lines near Nairobi). The key areas are (i) the South Rift Valley (Shompole-Olkiramatian; bottom-left), the only large wildlife population in Southern Kenya not associated with a government protected area(Tyrrell *et al.* 2017); (ii) The fragmented Nairobi National Park ecosystem (top-right) and the remainders of the Athi-Kapiti dispersal areas(Said *et al.* 2016), including two proposed corridors. Government protected areas are shown in green. County boundaries used in this study are shown in black.

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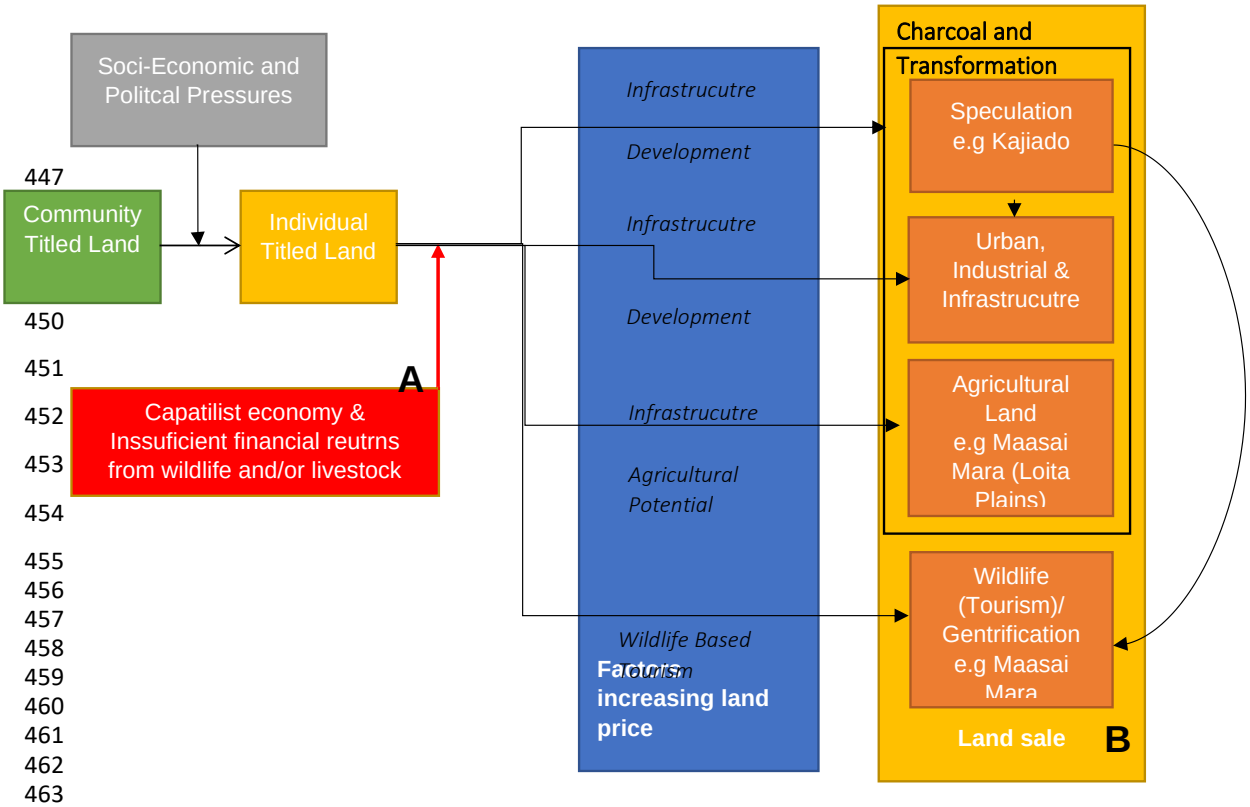

Web Figure 9: Relationship between the price of land and land use change in southern Kenyan rangelands.

Historically, most of the wildlife-rich areas of southern Kenya have been used by pastoral Maasai people for their livestock, with land held under communal tenure. Facing economic and political pressures, most of these areas have now been privatized and subdivided (Mwangi and Ostrom 2009). The new landowners, who accrue few economic benefits from wildlife and have dwindling profits from livestock, which become less resilient under smaller parcels sizes, have typically sold at least part of their land to partake in the cash economy (Rutten 1992). Subsequently, much of this land has been fenced, with the woody vegetation removed and sold as charcoal and the land converted into agriculture or urban development, or held by speculators hoping for persistently increasing land prices which they can subsequently sell as urban development increase (Rutten 1992; Said *et al.* 2016). Land speculation has been ongoing in Kenya for several decades and is widespread in the Southern Kenyan rangelands(Kimani and Pickard 1998). This trend of land subdivision and subsequent sale is ongoing across the region, and the price of land is likely to continue to increase as the human population and national economy both grow. Economic drivers are thus shrinking the remaining areas of habitat for wildlife and rangeland for livestock, severing connectivity between wildlife subpopulations, and thereby threatening one of the most diverse assemblages of large mammal species in existence (Ogutu *et al.* 2016; Said *et al.* 2016). In the Mara, we also see that the proximity to a rich wildlife resource is inflating local land prices, similar to patterns seen in other parts of the world (Gibbons *et al.* 2014). Land for sale in this region is advertised for the development of tourism facilities, private holiday homes, and to protect and appreciate wildlife, with the target audience of these adverts being non-local wealthy investors and individuals. These individuals, often outsiders can make substantial money. This is what we term “gentrification”,by which the character of a neighborhood changes through the influx of more affluent residents or businesses, which can lead to displacement of previous residents. In some conservancies, dividends from these tourism facilities are used to reduce the opportunity costs of living with wildlife **(A)**. However, this amount paid to landowners is often too low compared to the total revenue generated by tourism. Many investors do not provide dividends to wildlife owners. Hence, it does not reduce the desire to sell land for agricultural, urban, or other developments. To overcome these negative trends, policies can be

enacted to prevent land use change **(B)** through spatial planning frameworks, or **(A**) by increasing the value of wildlife and wildlands through payments for ecosystem services, tourism revenue to landowners, and other consumptive and non-consumptive uses of wildlife.

Web Panel 1

The package *rvest* in R version 3.5.2 (R Core Team 2018; Wickham 2019a) was used to scrape The Star (a Kenyan daily newspaper) classifieds section of its website specifically searching for advertisements for lands sale (www.the-star.co.ke/land-plots). These are land parcels without buildings. Data were accessed for Kajaido, Nairobi, Narok, Makueni, and Machakos counties. We downloaded the following information from each advert: price, title, description, location, and size. The size, location, and price fields were often blank or provided incorrect information.

The title field was searched for words following "in" or "at", up to the word "for", to identify locations. If the title contained none of these phrases, we retained the first word of the title as a potential proxy for location (filtering out many common starting words and any title starting with a number). The description field was then searched for the words "in", "for", and "near", and the following 15 characters were selected. This was conducted using the package *stringr* (Wickham 2019b). The package *googleway* (Cooley 2018) was used to access the google geocoding API

to georeference these locations. First, we used the first word extracted from the location field to search for a geocoded address. If the API returned no result, we geocoded the full location field. We also extracted a potential location from the title and subsequently cleaned and then georeferenced. Those entries which had no results returned by the API were subsequently checked for a comma, and if commas where present, the first two elements in the field were used, and "-", "<e4><ec>", and "NA" were removed, and then geocoding was repeated using these updated potential locations. This process aided the geocoding API in finding locations.

We then used information extracted from the sales description field, looking for the keywords "in", "at", and "near" and the subsequent 15 characters, which was then combined with the information extracted from the title field, to provide a potentially more accurate address. Such as "[near] total petrol station, [in] Narok".

Geocoding was repeated using this address. The final latitude and longitude for each advert were used from this combined location, or if this was blank, then the results from the title field or location field were used.

The size of the plot was determined by extracting any string before the word acre (and variations), or by searching for a plot size (e.g. 100ft by 100ft), in both the title field and description field. These strings were then filtered by searching for any digits before the word acre, or any regular expression of the size found in these adverts (e.g., eight, ¾ etc.) When the lengths or area were in feet, they were converted into acres.

The price for each plot was usually given in the downloaded price field. However, the price given is often either an asking price per acre or a price for the entire plot. To try and minimize this error, we searched in the description field for any phrase relating to the price per acre, including common expressions of cost, such as "million", "m (short for million)", "k" (short for thousand). Price per acre can then be calculated for those plots with a size and price successfully extracted. Any price less than 70,000 shillings per acre was checked, and if the price per acre was greater than 40,000, it was included. We then filtered the data to remove data points in each government ward that were outside the 97.5% and 2.5% quantiles; we also filtered duplicates and those outside the geographic range of the model. This process resulted in a total of 1487 georeferenced points per acre (Web Fig 1). We converted the land price in Kenya shillings into U.S dollars using a rate of 101.62 Kenyan Shillings to 1 USD.

To improve the geographic spread of data points, we also gathered data for several areas known to the authors as having land for sale, but not represented in our database, by manually searching another website (www.olk.co.ke). This website could not be scrape using the same method due to technical limitations. Instead, we manually searched for four locations: "Maasai Mara", "Maji Moto", "Bisil", "Kimana", all four areas are known to have land for sale, but were not recorded in our previous database. This provided an additional 31 locations with price per acre. Removing these data points from the analysis provided little difference in conclusions, but decreased precision in model accuracy.

Caveats

We captured advertised asking prices, which are likely somewhat higher than negotiated sale prices, but the two prices track one another, and asking price is a generally robust index of land value. In addition, purchases or leases of large areas may not necessarily be reflected by these predicted open-market prices, as actual transactions this big may distort the market, and the data collected are from smaller, potentially higher-value transactions.

Generalized Additive Model

A generalized additive model (GAM) with a negative binomial logit link structure was used to explain land price using univariate smooths of all the predictor variables (Web Table 1), with land cover added as a parametric term. The smoothing parameters were selected using restricted maximum likelihood. We allowed the model to add an extra penalty to each term so that it could be penalized to zero to remove variables from the model, and this was used for model fitting using mgcv (Wood 2006; Marra and Wood 2011). Spatial autocorrelation and concurvity were checked and no issues identified (Web Figure 5&6). We used the package ncf (Bjornstad 2019), with spatial correlograms indicating no spatial autocorrelation present. The final model was then used to predict land prices across 54,472 cells at a 1km2 resolution in southern Kenya.

Current and future threats

Following the prediction of land price across the region, we used a comprehensive cumulative threat map, the recently updated Human Footprint map of eight anthropogenic pressures on the terrestrial environment (Venter *et al.* 2016), to observe current threats to biodiversity. Human Footprint is measured using eight variables including built-up environments, population density, electric power infrastructure, croplands, pasture lands, roads, railways, and navigable waterways. We plotted this against land price to observe immediate threats posed by development, land transformation, and human population pressures, against land price and the potential threat posed by land purchase and conversion of use.

Costs of conserving ecosystems

To demonstrate the utility of the land price data for conservation planning and prioritization, we used the predicted land price data to calculate the potential acquisition (and lease) costs associated with protecting functional ecosystems. We used the Kenya governments report on “Wildlife Migratory Corridors and Dispersal Areas”(Ojwang’ *et al.* 2017), with additional data to digitize; (i) the South Rift Valley (Shompole-Olkiramatian)(Tyrrell *et al.* 2017); and (iii) Nairobi National Park and the Athi-Kapiti dispersal areas(Western and Gichohi 1993; Said *et al.* 2016), including two proposed corridors (which we estimated to be 1km wide)(Ojwang’ *et al.* 2017). These ecosystem boundaries and corridors are rough, but we believe reasonably represent the boundaries as laid out by the government and conservation practitioners in the region. We used the package *exactextractr*(Daniel Baston 2019) to extract a land price for each area, and calculate an annual lease price as 5% of this value, this is assuming that the land is leased in its entirety for wildlife conservation. We present the results in Web Figure 8.

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Web Panel 2: Quotes from adverts selling land surrounding the Maasai Mara Reserve

"The Naretoi estate, set on the banks of the Mara River, used to be an intensive farm (previously called Olerai Mara Farm, owned by the Wood family from 2000-2013)under pivot irrigation. The founders of Naretoi bought the farm in 2013 and have returned the farm back into its natural state, restoring habitats and enhancing biodiversity. The Naretoi project is essential for the sustainability of the Enonkishu Conservancy, and will secure the wildlife grazing land in the surrounding 10,000 acres, as well as working with the community to broaden livelihood opportunities.

Naretoi presents an opportunity to own a piece of the legendary Maasai Mara and build your dream home in a safe, managed and beautiful part of the Northern Mara ecosystem" - Advert 1

"105 acres land near Musiara Airstrip gate and Governor camp.The land has a permanent river. There murram access road. The land has trees and wild animals.
It very ideal for hotel and camp.Already change of user to hotel and camp done.The land is gentle slopping" – Advert 2

"This property is ideally situated in Ol Choro Oiroua Conservancy and touches the Mara River. The plot is also surrounded by an abundance of wildlife and would be ideal for a lodge or tented camp.

SUMMARY
• 48 acres (19.42 Ha)
• Set on the banks of the Mara River
• In Ol Choro Oiroua Conservancy, bordering the Maasai Mara Reserve
• Freehold title" – Advert 3

Web Table 1 – Predictor variables use in the model

Variable Name	Type	Source	Reason for inclusion
Population	Continuous (100 m res)	Worldpop.org.uk (Stevens *et al.* 2015)	Population density influences the available land for development.
Poverty	Continuous (1km res)	Worldpop.org.uk (Stevens *et al.* 2015)	Areas of higher poverty levels may be less desirable and cheaper.
Probability of Urban Expansion in 2030	Continuous (0-1 at a 2.5 arc-minute resolution)	Sedac.ciesin.columbia.edu (Seto *et al.* 2012)	Land speculation and purchasing in future zones of development.
Distance to major roads	Continuous distance derived from shapefiles	Primary, Trunk or Motorways classification. data.humdata.org (exported from Open Street Map)	Land closer to roads has a higher demand .
Distance to Nairobi	Continuous distance derived from shapefiles	Location of Nairobi City Centre	Nairobi is the major economic hub in the region and serves as the center for development.
Land Use and Land Cover	Categorical (100m)	Copernicus land.copernicus.eu/global	Different land use types and land cover types will have different values. We classified any landcover categories at less than 1% frequency of the samples as "other", remaining with six classes.
Potential Maize Yields	Five-minute by five-minute resolution (~10km x 10km at the equator)	http://www.earthstat.org/ (Mueller *et al.* 2012)	Maize is a valuable crop in Kenya, and high-quality agricultural land could be worth more.
Distance to Maasai Mara Protected Areas	Continuous distance derived from shapefiles	Kenya Wildlife Service and Kenya Wildlife Conservancies Association	Private land adjacent to protected areas can be more valuable.

All spatial data were projected into the Albers equal-area projection at a resolution of 1km x 1km and cropped to the extent of the study area (Sup Figure 2). We acquired county boundaries from the GADM (Database of Global Administrative Areas) database (GADM 2019).

When potential predictor variables were correlated by 0.7 or more (Spearman rank correlation coefficient), just one was used in the modeling process (Sup Figure 3). Therefore, we removed the percentage in poverty before model fitting, retaining population density.

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660 **Web Table 2 – The non-parametric smooth terms from the final generalized additive model of**
661 **land price. EDF is the estimated degrees of freedom for each term.**

Term	EDF	p.value
Probability of Urban Expansion	0.0034	0.5639
Potential Yield of Maize	3.9302	0.0000
Distance to Nairobi	8.3678	0.0000
Distance to Maasai Mara Protected Areas	4.0060	0.0000
Population Density	0.0028	1.0000
Distance to Major Roads	1.7386	0.0000
Distance to Major Towns	1.1769	0.0502

662

663 **Web Table 3 - Parametric terms, the parameter estimates, their standard errors, and the p-**
664 **value from the generalized additive model.**

Term	estimate	std.error	p.value
(Intercept)	17.1583	0.0959	0.0000
Herbacous	0.6524	0.1278	0.0000
Cropland	0.2327	0.1049	0.0265
Urban	0.2425	0.1052	0.0211
Decidious Broadleaf Closed Forest	0.0862	0.2220	0.6978
Decidious Broadleaf Open Forest	0.2298	0.1222	0.0600
Other	0.2343	0.5799	0.6862

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Incorporating social-ecological complexities into conservation policy

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Incorporating social-ecological complexities into conservation policy

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ABSTRACT

In the process of developing new conservation policies, policymakers must have access to information which will inform their decisions. Evidence rarely considers the complexities of social-ecological systems. The Social-Ecological Systems Framework (SESF) is an adaptable yet structured approach for understanding the processes that lead to changes in natural resources, using a systems-based approach that aims to treat ecological and social components equally. Few conservation planning and policy initiatives have implemented the SESF to assess the interlinked social and ecological consequences of conservation policies. We apply the SESF to explore the barriers to the potential implementation of a policy of consumptive utilisation of wildlife in Kenya, a policy regarded as successful in several southern African countries. Using secondary data and expert review we developed a conceptual model of the social-ecological system associated with consumptive utilisation of wildlife in Kenya. We then analysed how different combinations of first and second-tier variables interacted to create focal action situations, and subsequently identified seven barriers to this policy. Our analysis revealed that game ranching would require large-scale investment in effective monitoring systems, new regulations, training, market development and research, considerations about equity, and devolved ownership of wildlife. The least barriers existed for game farming. The SESF appears to be a useful framework for this purpose. In particular, it can help to reveal potential social and ecological barriers which conservation policies might face in attempting to meet intended goals. The information required to implement the SESF are necessarily cross-disciplinary, which can make it challenging to synthesise.

1. Introduction

Conservation policymaking should be evidence-informed (Adams and Sandbrook, 2013; Sutherland et al., 2004). When developing a new conservation policy, information from a range of sources can be integrated to improve the quality of evidence provided for policy decisions, including quantitative and qualitative data; local and indigenous knowledge; and local and international perceptions (Adams and Sandbrook, 2013; Bennett, 2016). Evidence can also be collated from the successes or failures of previous and current policies both within the administrative regions of interest (state, country, etc.) and regions external to the process. However, when implementing or importing new conservation policies, it is vital to acknowledge that regional heterogeneity exists in both the ecological and social realms, with differences across space, time and organisational units all influencing the potential for social-ecological sustainability (Liu et al., 2007). The evidence used to enlighten policymaking should, therefore, be relevant to the context in which it will be applied rather than assuming that 'one-size-fits-all' (Adams et al., 2019; Dressel et al., 2018).

Frameworks for analysing policies, such as the "Eightfold Path to Policy Analysis" (Bardach, 2000) provide useful ways to think systematically about how to achieve the intended policy objective. However, when policies pertain to conservation, it is critical to acknowledge that natural resources, including wildlife, are part of multi-faceted and complex social-ecological systems (SES; Ostrom, 2007). Failing to explore the full suite of social and ecological factors determining the success or failure of conservation policies (Brehony et al., 2018), and preparing for unexpected interactions between factors, and their associated challenges can result in failure to achieve the intended conservation goals (Liu et al., 2007).

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9. Incorporating social-ecological complexities into conservation policy

1.1 Social-Ecological Systems Framework for conservation policy analysis

Ostrom's (2009) Social-Ecological Systems Framework (SESF) is an adaptable yet structured approach to understanding the processes that lead to the deterioration or improvement of natural resources, using a systems-based approach that aims to treat ecological and social components equally. SESF originates in the discipline of political science (social science) and is based on theories such as collective choice, common-pool resources, and natural resource management (Binder et al., 2013). It aims to move beyond simple panaceas, and towards a diagnosis of "the source, and possible amelioration, of poor outcomes for ecological and human systems" (Ostrom and Cox, 2010).

Establishing a diagnosis when faced with a problem in an SES requires careful study of complex, multi-variable, non-linear, and cross-scale interactions, and how these are changing through time (Liu et al., 2007). The SESF achieves this by analysing the attributes and interactions of four main subsystems: resource users, governance system, resource system, resource units (McGinnis and Ostrom, 2014; Fig. 2). The crucial part of this analysis is in the "Focal Action Situations", where interactions between the subsystems lead to outcomes and feedback to each core subsystem. While examples primarily at the local scale were used to develop the SESF, its design ensures it is applicable at regional, national, and international scales, and importantly, it incorporates interactions across these scales (Cumming et al., 2015). Based on these criteria, the SESF facilitates the selection of variables in relation to case studies and can be used to understand changes in interactions and outcomes when the system changes.

Despite the growing frequency of use of SES language within conservation planning and policy initiatives, and continued calls for further integration of the social sciences into conservation science (Bennett, 2016), few examples exist where the SESF has been implemented to enlighten the development of conservation policies (Ban et al., 2015; Bennett et al., 2018; Guerrero and Wilson, 2017). Importantly the SESF explicitly accounts for the influence of social factors on the system, including individuals, institutions, governance structures and existing policy, which many conservation planning processes inadequately address (Ban et al., 2015). In this paper, we show how the SESF can be used to enlighten conservation decision making, by applying it to a multifaceted conservation policy option, which has been implemented in other, apparently similar SES.

1.2 Implementing the Social-Ecological Systems Framework in context

Conservation of savannah ecosystems in Africa often encourages the sharing of practices and policies adopted in southern Africa countries with countries in East Africa. For instance, Beale et al. (2013) provided a set of ten valuable lessons for conservation in East Africa from experiences over the last few decades in southern Africa. Beale et al.'s (2013) lessons are ranked without consideration to local variations in social and ecological systems, and as the authors acknowledge, these local conditions are important considerations when implementing new policies or interventions.

The trade of wildlife and the cropping of wildlife for sale as game meat is common in southern Africa, and both are cited as ecologically and economically successful strategies for conservation (Lindsey, 2011). It is perhaps unsurprising, therefore, that there have been public, governmental, and academic calls to implement a policy of consumptive use of wildlife in Kenya (Norton-Griffiths, 2007).

In Kenya, 60% of wildlife exists outside protected areas (Western et al., 2009). Overcoming opportunity costs to landowners, which are created by forgoing land options which are not compatible with wildlife conservation, and incurring costs from wildlife - such as competition for grazing, human-wildlife conflict, and disease transmission - are major challenges to conservation sustainability (du Toit et al., 2017). In recent years, Kenya has developed policies and legislation which, under the mandate of Kenya's 2010 constitution, aim to increase the economic value of wildlife across the country, accrued at multiple levels including landowners, county government, and the national treasury (Government of Kenya, 2013). The resulting revenue generation has primarily occurred through ecotourism, but there are concerns that this is not enough to counter the continued widespread losses of wildlife (Ogutu et al., 2016).

In April 2018, Kenya's Ministry of Tourism and Wildlife launched a task force to investigate the potential for the sustainable consumptive utilisation of wildlife, through the cropping of wildlife for the sale of game meat, and the trade of live wildlife. The notice also explicitly stated that Kenya has banned sport hunting and has no intention of opening this debate. Both were to be examined through extensive "game ranching" and intensive "game farming" frameworks. Kenya's Wildlife Act (2013) describes "game farming" as the rearing of wildlife in an enclosed and controlled environment for wildlife conservation, trade and recreation; and "game ranching" as the keeping of wildlife under extensive natural conditions with the intention of engaging in wildlife conservation, recreation and trade. In addition to the appointed task force, there was a request for expert and public participation to provide evidence on the potential implementation and impact of this policy for consideration by the Ministry. We, the authors of this paper, used this opportunity to investigate how the SESF can be used as a tool to provide evidence to policy-makers (Toomey et al., 2017), by highlighting potential barriers to achieving intended policy outcomes. Two pieces of Kenyan policy defined the outcomes: firstly, the 2013 Wildlife Act, which includes a provision for a wide range of both consumptive and non-consumptive wildlife users' rights devolved to landowners (Government of Kenya, 2013); secondly, the National Wildlife Strategy which sets a clear vision for the conservation of wildlife in Kenya over the next decade, namely, that "Kenya's wildlife is healthy, resilient and valued by Kenyans" (Ministry of Tourism and Wildlife 2018). We used the SESF to explore the impact that potential policy changes might have on social and ecological subsystems when aggregated in different ways (Bodin and Tengö, 2012) through the following two guiding research questions:

1. Will the consumptive utilisation of wildlife in Kenya lead to improved benefits for landowners with wildlife, all Kenyans (including through increased food security), and the national government? (O1)
2. Will the consumptive utilisation of wildlife in Kenya lead to the sustainable conservation of wildlife and ecosystems? (O2)

This allowed us to then ask:

3. What are potential ecological, social, and economic barriers to implementing a policy of sustainable consumptive utilisation of wildlife in Kenya?

The outcomes of this investigation were subsequently submitted as a report to the task force (Tyrrell et al., 2018).

2. Methods

The framework for our analysis is laid out in Fig. 1, and was guided by the updated SESF described in McGinnis and Ostrom, 2014 (Fig. 2) and the diagnostic framework of Hinkel et al. (2015). The under-recognized potential to contribute to the understanding of conservation problems through the integrated experience of individuals, or what Sanderson et al. (2002, p. 71) calls 'practical wisdom', guided the composition of this authorship team. We, the authors of this paper, have knowledge and experience from a variety of backgrounds, namely: conservation policymaking at a national level; representation of community landowners at a sub-national level; representation of private and community landowners at a national scale; rangeland and wildlife

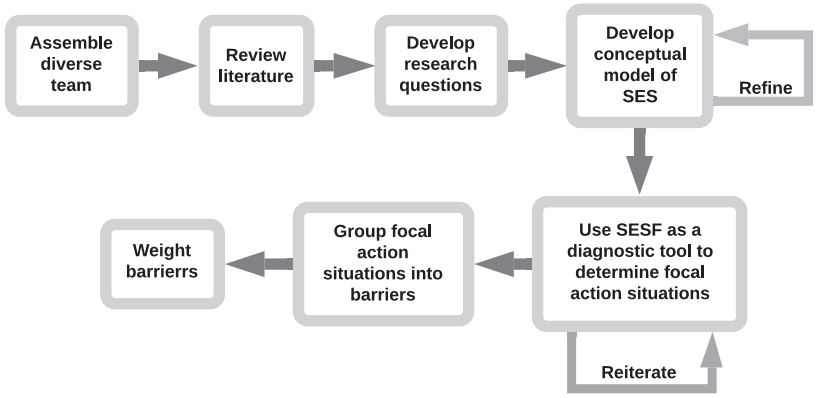

Fig. 1. The methodological framework used to develop the list of barriers to achieving desired outcomes from the implementation of the conservation policy.

ecology; geography. Importantly, the team included people with the insights and perspectives of key stakeholders (Bennett et al., 2018) and incorporated knowledge and experience from different academic disciplines.

2.1. Constructing a conceptual model

Our analysis began with a literature review on the consumptive use of wildlife in Kenya, East Africa, Southern Africa, and globally, conducted by PT and PB (Fig. 1). We then held a workshop with all the authors to feedback the findings from the literature review, and to develop our understanding of the SESF in this context, including the social, economic, and political setting. All our explorations were guided by the recommendations from McGinnis and Ostrom, 2014 (Fig. 2) and the diagnostic framework of Hinkel et al. (2015; Fig. 4, Supplementary Table 1) and were based on our research questions, which were determined by the scope of the task force, as laid out by the Ministry of Tourism and Wildlife. We discussed and defined the first-tier subsystems; the resource system, resource units, actors and governance systems (Fig. 2). We listed all the pertinent second-tier variables which were relevant to our research questions and the aforementioned policy objectives (Fig. 2). These are given in Fig. 2, where they have been assigned a code, which we refer to, in brackets, in our results. Although we do not report third-tier variables, we used Vogt et al.'s (2015) framework to improve our deductive inquiry by ensuring that ecological attributes in the resource system and resource units were explicitly incorporated into the SESF. The transdisciplinary composition of our authorship team was critical to identifying the non-exhaustive list of focal action situations that would result in this SES.

The resultant conceptual model includes the possibilities of both extensive game ranching and intensive game farming as resource systems (Figs. 3 & 4). In our analysis, we assumed these are the two types of resource systems (RS) that "create the conditions for the existence of a stock of resource units" (Ostrom et al., 1994). Our conceptual models also included cropping and live trade of wildlife as different types of consumptive use (Fig. 4).

Wildlife is a public resource in Kenya (ROK, 2010) but user rights of wildlife (both consumptive and non-consumptive) can be granted by the County Wildlife Conservation and Compensation Committees (Government of Kenya, 2013). In its current form, the 2013 Wildlife Conservation and Management Act (ROK 2013) allows for the keeping of some species on game farms (see Tenth Schedule for full list). Therefore, in our conceptual model, wildlife is defined as the resource unit (RU), separated into large mammals (e.g. zebra, kudu, eland etc.) and other wildlife (those listed in the Tenth Schedule of ROK 2013; Fig. 4). Wildlife is a public resource in Kenya; therefore, all wildlife is treated like a collective good in all focal action situations (Hinkel et al., 2015).

Land in Kenya is considered to be either public, private, or community land (ROK 2010), and conservation as a land use may happen under all of these land tenure options. Our conceptual model assumes that private landowners (an individual, family or body corporate) and community landowners (defined by Kenya's 2016 Community Land Act as a group of individuals) will be the primary actors (and beneficiaries). Their income benefits would be from the sale of wildlife and their products, alive or dead (Figs. 3 & 4). The intensive nature of game farming makes it akin to agricultural production, even within areas of community land tenure, and the management of this resource system may act as if it has de facto private ownership.

2.2. Using the SESF as a diagnostic tool

Following this process of producing our conceptual model, in two subsequent meetings, the authors used the SESF as a diagnostic tool (Ostrom, 2007; Ostrom, 2009; McGinnis and Ostrom, 2014; Hinkel et al., 2015) to analyse how the interactions, outcomes, and feedbacks of the variables defined in the conceptual model, revealed focal action situations (when interactions become outcomes with feedback; this is the basis of Fig. 2). We specifically analysed how different resource systems, resource units, actors, governance systems, and types of consumptive use affected the focal action situations, and how this, in turn, affected the first tier variables (Fig. 4).

These focal action situations were subsequently compiled and analysed by PT and PB, who organised them into groups of focal action situations, based on similarity. This initial set of barriers was then presented back to all the authors over another meeting, where they were refined, based on our knowledge, experience, and collective understanding of the SES. These represented the barriers to the sustainability and positive social-ecological outcomes of consumptive utilisation of wildlife in Kenya (Nagendra and Ostrom, 2014). Finally, through consensus, we assigned a weight to each barrier– low, medium or high – for each combination of primary actor, benefit, type of consumptive use, resource unit, and resource system. We did not explicitly operationalise the SESF with quantitative and qualitative data in a spatially explicit manner (Leslie et al., 2015) as these data were not available within the time frame required for policy action. This entire process took 3 months.

3. Results

3.1. Barriers to effective outcomes

Using the SESF and our conceptual model, we have identified seven barriers to the successful implementation of consumptive wildlife

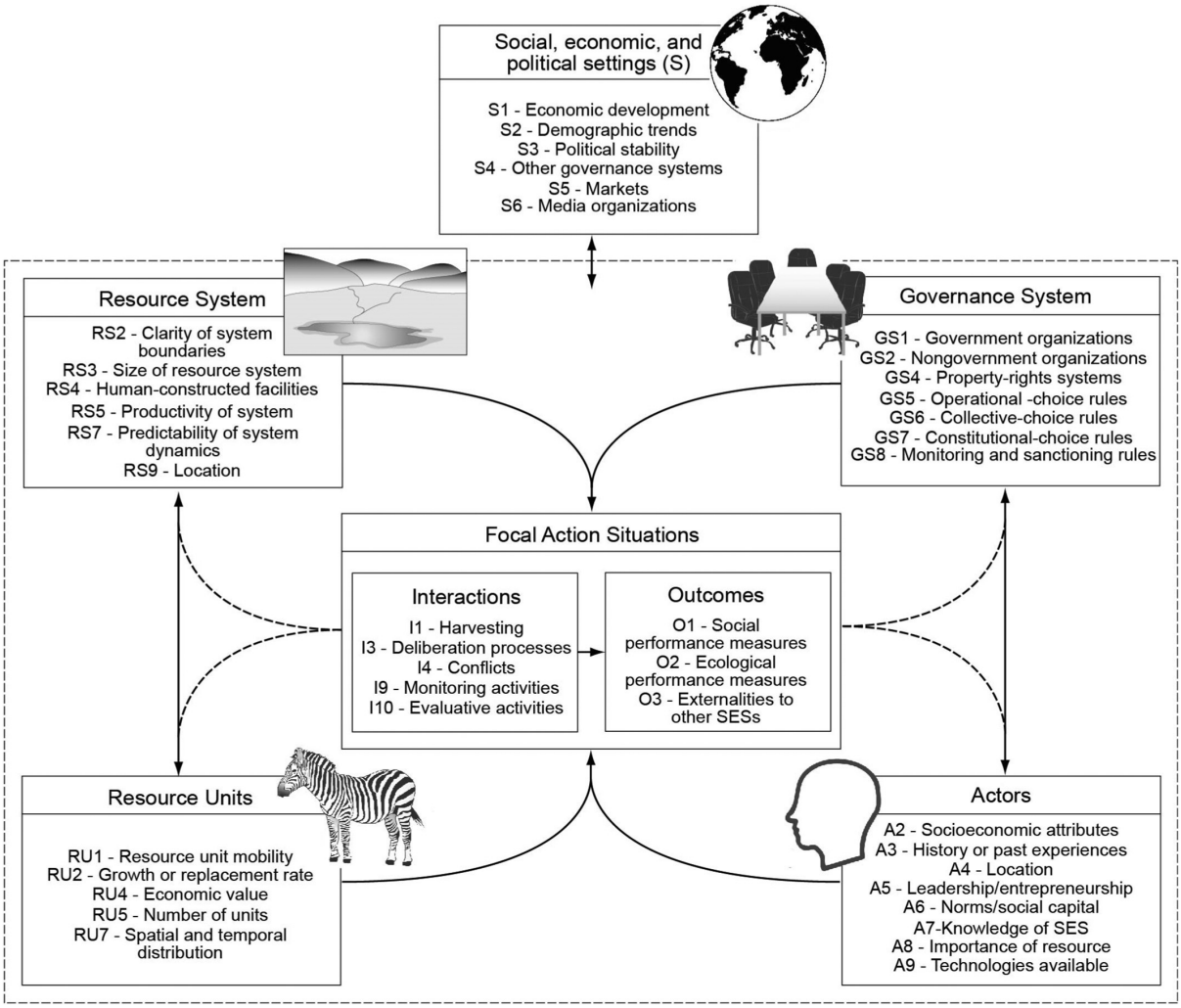

Fig. 2. Social-ecological system framework (SESF) with first-tier subsystems adapted from McGinnis and Ostrom (2014). Solid boxes denote first-tier subsystems: Resource System, Resource Units, Governance Systems, and Actors. Each subsystem contains the second-tier variables which were identified in our analysis. Focal Action Situations are where interactions between the subsystems are transformed into outcomes. Solid arrows denote direct connections. Dashed arrows denote feedback from action situations to each of the subsystems. The dotted-and-dashed line that surrounds the interior elements of the figure indicates that the focal SES can be considered as a logical whole, but that exogenous influences from related ecological or social-economic-political settings at larger or smaller scales, can affect any subsystem of the SES.

utilisation in Kenya. We present each of these barriers and elaborate on how the SESF and our conceptual model aided our analysis. Throughout our results, we refer to the relevant second-tier variables in brackets, based on the codes given in Fig. 2.

3.1.1. Ownership and wildlife movement

The ownership and mobility of wildlife pose a significant barrier to the successful implementation of consumptive utilisation of wildlife for game ranching, particularly on community-owned land. The semi-arid and arid nature of most of Kenya's wildlife areas lead to high spatial and temporal variability in rainfall and, therefore, pasture quality and quantity (Fynn et al., 2014; RS7, RS5). Consequently, wildlife moves to capitalise on this underlying functional heterogeneity (RU1, RU7; Tyrrell et al., 2017). The scale of movement can be orders of magnitude larger than individual land parcels, representing a mismatch between ecological and anthropogenic boundaries of resource systems (Hobbs et al., 2008; RS3). The movement of wildlife across landscapes blurs the lines over wildlife user rights, whether for trade or cropping. In fenced, private lands, the mobility of wildlife is restricted (RU1), the resource system is bounded (RS2), and the landowner becomes the de facto 'owner' of wildlife (GS4). In many landscapes without fencing, primarily community areas, but also private land in some regions, wildlife ownership is less clear. Considerable consensus-building between landowners (I3) will be required to ensure equitable sharing of resources to avoid conflict (I4). A lack of consensus could potentially lead to an increase in fencing (RS4) to claim resource ownership (Løvschal et al., 2017). Restrictions on mobility by fencing dryland ecosystems can result in: a reduction in the size of the resource system (RS3); a mismatch between the ecological and the user-defined boundaries of the resource system (RS2; Western and Gichohi, 1993); limited access to spatial and temporal heterogeneity for people and wildlife (RS7, Western et al., 2020); lower productivity and carrying capacity for

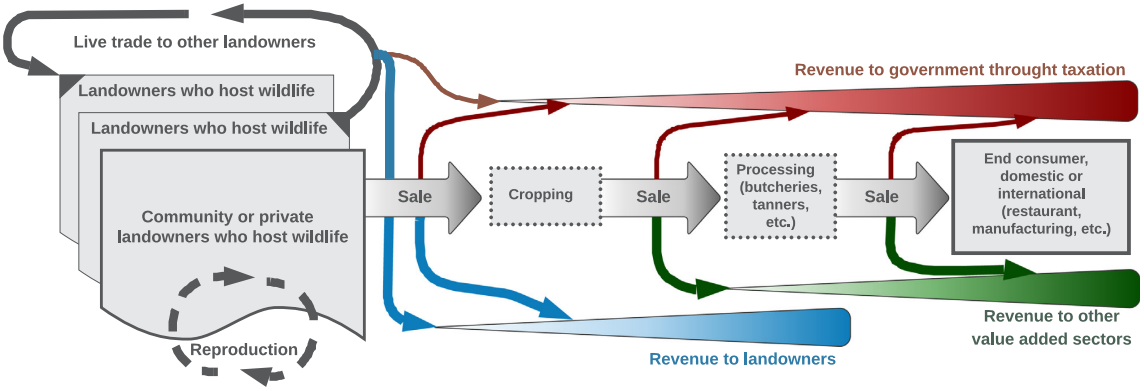

Fig. 3. Simple conceptual model and value chain of potential game ranching and game farming operations in Kenya. This value chain does not include non-consumptive values of wildlife, including, and not limited to cultural, ecotourism, or research (Western et al., 2019).

livestock and wildlife (RS5; Fynn et al., 2014). This conflicts with wildlife and other national policies that aim to maintain mobility (O1, O2, O3).

In South Africa and Namibia, wildlife ownership rights are devolved to landowners. This clarifies resource ownership, and theoretically, provides incentives for improved management. Such a solution could reduce conflict between landowners, and between landowners and the government (I4), especially regarding the setting of harvesting quotas (I1). In such a system, landowners decide which species they will manage, and these decisions are often driven by market forces (S5). Landowners may also choose to work collectively to manage larger ecosystems, thereby overcoming constraints to wildlife mobility (Lindsey, 2011). However, this is no panacea, as similar situations can exacerbate the fencing of rangelands and encourage the removal of non-profitable wildlife (Pitman et al., 2017; O2). Furthermore, devolved ownership could create confusion (I4) over who is responsible for human-wildlife conflicts, such as crop-raiding and predation (O2).

In Kenya, game farming is already based on an intensively managed system, with user rights and ownership devolved to the landowner.

At present, when considering live national trade, the low economic value of the majority of live wildlife (RU4) and the lower frequency of trade (RU5; I1) means that there is less likely to be significant conflict (I4) between resources users with unclear ownership.

3.1.2. Market-based challenges

The consumptive use of wildlife results in different wildlife products that can be sold to consumers. These products include primary products, such as game meat, horns, skin, and bone, but further processing can also provide secondary products such as treated hides and ornaments (Fig. 3).

A successful economic model of the consumptive use of wildlife relies on the assumption that there exists a large market that values these products (S5, RU4; Department of Environmental Affairs 2018). Without this economic value passed on to landowners, the consumptive utilisation of wildlife might not be viable (O1), opportunity costs of living with wildlife would not be met, and when landowners are solely dependent on consumptive utilisation (A8), this can result in land conversion to alternative non-wildlife uses (Cousins et al., 2008; O2). The lack of economic value was a significant issue in the previous wildlife cropping program in Kenya (Kock, 1995; Tasha Bioservices, 2001). For both game ranching and game farming, considerable thought, investment, and research are required to ensure a sustainable and profitable game meat market (A7, A4) with input required from nongovernment (GS2) and government agencies (e.g. Ministry of Agriculture, GS1).

To find a market (S5) the game meat industry could target a) the 1.4 million tourists arriving in Kenya each year (Turner, 2017); b) the broader Kenyan population; or c) an international market. In South Africa, for instance, revenue is generated from tourists in the domestic market, and international export sales, with over 160,000 carcasses sold to Europe in 2005 (Hoffman and Wiklund, 2006). However, Kenya cannot assume that these same markets will exist as, for example, Kenyan game meat may not be accepted in the European market due to disease control regulations (Naziri et al., 2015). Other markets might be found, for example by targeting legal game meat markets in the Middle and the Far East, and by promoting the potential health benefits of some types of game meat (Hoffman and Wiklund, 2006). However, following the outbreak of SARS-CoV-2, these markets are likely to be very carefully controlled and regulated, thereby increasing costs all along the value chain (Fig. 3) and decreasing economic value to the

Primary Actors (A)	Benefit	Type of consumptive use	Stock of Resource Units (RU)	Resource Systems (RS)
Private landowners or Community landowners	Income from consumptive wildlife utilization	Sell wildlife products through cropping	Large mammals*	Extensive game ranch
		Sell wildlife through live trade	Other wildlife**	Intensive game farm

* Large mammals include zebra, kudu, eland, etc.
** Other wildilfe are listed in the Tenth Schedule of the 2013 Wildlife Conservation and Management Act: reptiles, snails, frogs, butterflies, ostrich, pigeons, doves, ducks, guinea fowl, quelea (for all animals groups, those listed in the Sixth Schedule are excluded).

Fig. 4. Appropriating action situations for the system studied (adapted from Hinkel et al., 2015).

producers. A longer-term problem is presented by the changing values of some global (and local) consumers, who are increasingly averse to the consumption of any animal products, including wildlife (O1), perhaps increasingly so after the SARS-CoV-2 outbreak. The market for secondary products also needs consideration. Previously in Kenya, due to a lack of infrastructure (RS4), animal hides were sent to South Africa for processing, significantly reducing the value of the product to both the landowner and harvesters (RU4; Tasha Bioservices, 2001). Increasing the economic value of these products, for the benefit of the landowners and the government, requires significant infrastructural development and improved knowledge of landowners (RS4, A7, A9; Department of Environmental Affairs 2018). The trade of wildlife raises similar concerns.

Finally, as long as wildlife is a common (GS4), ungoverned resource without monitoring (I9, GS5), legal markets (RU4) could make wildlife protection on game farms and game ranches increasingly difficult, and rather than decreasing poaching, consumptive utilisation could encourage poaching syndicates to form and exploit this resource (I4, A8; Schneider, 1990; Macnab, 1991).

3.1.3. Unintended conservation consequences

Game ranching can potentially ensure that landscapes remain in a state which benefits conservation (Cousins et al., 2008). However, there may be uneven importance assigned to some species with greater market value (Cousins et al., 2008; Pitman et al., 2017). As the market for wildlife products grows (S5), there could be a drive to decrease the number of species that serve no economic purpose as cropped wildlife and are instead seen as an additional 'economic cost' due to competition or predation (RU4; Geist and Veleius, 1988; Macnab, 1991; Cousins et al., 2008). For instance, carnivores, many of which are of high conservation concern, may be eradicated or removed from game ranching operations if they are seen as an economic threat (Cousins et al., 2008; Geist and Veleius, 1988). There could also be incentives to introduce non-native herbivores with a greater economic value (RU4) as has happened in South Africa (Castley et al., 2001). Furthermore, market incentives could result in the intensification of even extensive ranching, through hormones, sterilization, and breeding (S5, RU2, RU5; Knox et al., 1991; Mulley et al., 1996). All of these would have widespread impacts on ecosystem functionality and biodiversity conservation (O2; Richardson, 1998; van Kooten et al., 1997). These focal action situations do not necessarily fit the ecosystem-based approach to conservation that Kenya currently aspires to in the Wildlife Act. 2013 (O1, O2).

The intensive nature of game farming, with single species and high productivity, makes it unclear how this would contribute to broader conservation goals (Macnab, 1991). Game farms could cause a decrease in non-farmed wildlife without regulatory frameworks (GS8), devolved property rights (GS4), and enforcement (I9,I10; Brooks et al., 2010; Lyons, 2012; Tensen, 2016). In Vietnam, for example, commercial farming of the Southeast Asian porcupine (Hystrix brachyura) lead to the exploitation of wild porcupines, caused by high demand from farms and consumers. This may be the cause of the massive decline in wild populations across the region (Brooks et al., 2010). Game farming will likely require a species by species approach, with appropriate regulation and monitoring of both wild and farmed stock (GS8, I9), to ensure the sustainability of wild populations (O2).

Cultural perceptions of wildlife may change when they are given an instrumental monetary value. Changing wildlife to a consumable commodity, like livestock, could alter the care that humans provide wildlife when the economic value of wildlife is emphasized over other, non-monetary values (Pitman et al., 2017). This is of particular importance in community land, where cultural values that allowed for coexistence between wildlife and livestock are rapidly being eroded (A6), and with it reduced tolerance for wildlife, including carnivores (Western et al., 2019). Nevertheless, for landowners where wildlife does not have an intrinsic or cultural value, their instrumental value may be necessary for continued conservation (A3, A4, A2, A6).

3.1.4. Equity and conflict between actors

The previous wildlife cropping program was seen to only really benefit large-scale private landowners (Tasha Bioservices, 2001). Private landowners are likely to benefit more from consumptive utilisation, due to higher productivity lands (RS5, see below); established knowledge of requirements and regulations (A7, GS8; Norton-Griffiths, 2007); demarcated land, often fenced, to effectively own wildlife (GS4); infrastructure for wildlife cropping (A9); closer proximity (in general) to established markets and transport (A4); and greater financial capital to successfully implement and market wildlife products (A2). Additionally, without regulation and support (GS8), many communal lands have historically been susceptible to poor governance (A3, A5) and elite capture of resources, which can result in unscrupulous practices and exploitation by harvesters (A7; Bond and Mkutu, 2018; Tasha Bioservices, 2001). Models such as the Kenya Wildlife Conservancies Association and the new Community Land Act (2016) can play an important role in supporting devolved management and equitable revenue sharing (A5, A6, I3, GS6, GS5, O2).

In Kenya, the largest and most stable remaining wildlife populations (RU2, RU5) are in areas of high rainfall and forage productivity with low variability (RS7, RS5). These areas are generally under private ownership and would likely have the largest quotas (I4) and potentially the most profitable wildlife cropping business. However, much of Kenya is semi-arid and arid, and these areas are generally under community ownership. They have much lower wildlife densities, with populations that move across large landscapes (RU1, RU2, RU5; Ogutu et al., 2016). This reality could limit the scope for financially and ecologically sustainable wildlife cropping in community lands.

Differences in historical perceptions between actors (A3), are also likely to have an impact on the support for the consumptive utilisation of wildlife in Kenya. Private landowners saw the greatest benefit under the previous wildlife cropping program (Tasha Bioservices, 2001), and many are in favour of the return of wildlife cropping and trade (Kaelo, pers. coms.). Many community landowners, however, report that they saw little benefit from the program, and are averse to the re-adoption of a system that has historical failures, and that can clash with cultural values attached to wildlife (RU4, O2; Tasha Bioservices, 2001; Western et al., 2019).

Tourists are an additional important actor in this SESF who must be considered in this context. Tourism is a major revenue earner for Kenya, contributing 9–11% of the total gross domestic product (Turner, 2017). In particular, tourism plays an essential role in wildlife conservation by giving wildlife additional economic value (RU4). The greater Maasai Mara ecosystem is the best example of this in Kenya, where tourism generates revenue for 106,102 households, covering 170,131 Ha of land, and hosting 25% of Kenya's wildlife (KWCA, 2016). In areas like this, where non-consumptive ecotourism is profitable, consumptive utilisation of wildlife could be a competing interest. For instance, in the greater Maasai Mara, community and private land surround the National Reserve and wildlife utilizes public, private and community land (RU7, RU1 I4; Ogutu et al., 2016). Conflicts may arise between actors, including landowners, protected area authorities, and tourism operators regarding wildlife ownership, cropping, and trade. Such conflicts may restrict the potential of wildlife cropping to areas away from National Parks and Reserves, and into private, and community lands far from government-protected areas (O1).

Equality between actors is also an important consideration where tensions might arise between community landowners (I4) who are directly dependent on their land and also wildlife, for their income (A8), and the more productive land of large scale private ranchers with often more profitable ecotourism, livestock, and agricultural businesses. Failing to consider such tensions will ultimately hinder success (O1; Pasmans and Hebinck, 2017), and could result in reduced tolerance or even resentment towards wildlife in community land (O2; Josefsson,

2014). On the other hand, due to their higher productivity, private lands are also the most vulnerable to conversion to other non-wildlife compatible land use options (S1, RS5, O3). Therefore, denying the opportunity to offset wildlife-related costs by allowing consumptive utilisation may hinder broader conservation goals in some of these areas (du Toit et al., 2017). Careful prioritization and evaluations of these trade-offs are, therefore, a significant consideration.

Game farming typically induces fewer conflicts between actors because of its large production yields, similar to those of agricultural, and because they are managed and owned by individuals in much smaller areas where perceived ownership of the resource unit is clearer.

Many of the same equity issues apply to the trade in wildlife. Unlike wildlife cropping, however, the high infrastructural costs related to meat and wildlife products which may act as a barrier for community landowners, are not required, which lowers the barriers to wildlife trade (RS4, A2).

3.1.5. Contribution towards national goals

3.1.5.1. Food security. The argument that wildlife cropping could be adopted in Africa to increase food security goes back to the 1960s and 1970s (Macnab, 1991). Much of the argument for wildlife cropping as a form of food security emphasizes the economic and ecological viability of wildlife over livestock in semi-arid and arid areas (RU2, RU5). However, livestock systems are much more efficient for meat production for a variety of ecological and economic reasons (RU2; RU5; see Macnab, 1991).

Additionally, the scope of game ranching may be limited spatially across the country, due to many of the reasons discussed in this article. In Kenya, where livestock already represent the vast majority of rangeland biomass (Ogutu et al., 2016), food security would be better addressed through provisions to increase the efficiencies of livestock systems, rather than the exploitation of game meat. Furthermore, for Kenyans to eat game meat, they would have to want to eat it (many traditions in Kenya forbid this, A6), and it would have to be affordable, which would drive down the economic value of wildlife to landowners (RU4), potentially resulting in land conversion to more profitable alternatives (see Section 3.1.2; O1, O2).

It is possible that game farms, with their focus on intensive production, could potentially support goals of food security and economic development (O1; Macnab, 1991). These would be input-heavy industries with other potentially harmful ecological impacts, in the same vein as intensive livestock production.

3.1.5.2. National economy. If implemented successfully and monitored effectively, wildlife cropping and/or trading would result in increased revenue generation to landowners who host wildlife, other sectors which generate value from this sector, and the national government (Fig. 2; GS1, RU4, O1). However, evidence suggests that returns on consumptive utilisation can be highly variable (Barnes, 1998). Revenue generation would depend on taxation structures, legislation, markets for game products, and the scale of production available for consumptive wildlife utilisation systems (RU5; see above).

If consumptive utilisation of wildlife does not provide financial revenue to the national treasury (either through taxation, employment etc.; O1), it will likely be side-lined in national development plans (S1), impacting the long-term sustainability of these systems (O2).

3.1.6. Logistical, infrastructural, and regulatory sustainability

3.1.6.1. Setting offtake quotas. A critical tenet of the wildlife cropping model on game ranches and game farms is that wildlife will be sustainably harvested (I1), to ensure the long-term viability of wildlife populations (O2). Despite evidence for sustainable harvesting of wildlife in other regions (such as South Africa), determining levels of wildlife offtake, and setting operational (GS5), and monitoring and sanctioning (GS8) rules is a contentious issue within game farming (Georgiadis et al., 2003). Long-term population monitoring programs are one of the most informative approaches to provide baseline information against which any harvesting effects on game ranches and farms can be monitored, and quotas decided (Weinbaum et al., 2013). High-quality data are needed to inform quotas (GS8), which requires expertise and financial capital (A2, A7, A9, I9, I10). The closest equivalent is the Department for Resource Surveys and Remote Sensing (DRSRS) who have conducted aerial counts across Kenya for the last 50 years (see Ogutu et al., 2016). However, these data are patchy in both time and space; they are poor for monitoring smaller-bodied species (Buckland et al., 2001); they do not account for demographic parameters needed to set quotas (Ginsberg and Milner-Gulland, 1994); and their outputs do not always reflect the relevant spatial and temporal variation in wildlife abundance needed for quota setting (see below; O2).

During the previous wildlife cropping program in Kenya, quota setting was a major problem. Several methods were used to count wildlife; there were disputes about who should conduct the censuses (I4); there was a lack of scientific basis for setting and allocating quotas (I1); there was little enforcement of quotas (see below, van Kooten et al., 1997; Tasha Bioservices, 2001). Subsequent evaluations of the previous wildlife cropping program found that in Laikipia County, when incorporating environmental variability (RS7), wildlife counts (RU5) and demographic parameters (RU2), the approved quota (I1) of 15% of the population was not sustainable (Georgiadis et al., 2003).

Any quota setting should be based on rigorous and species-specific scientific data, build in uncertainty, allow for adaptive management capacity (GS5; Ling and Milner-Gulland, 2006), and acknowledge the complex dynamics of wildlife populations (Weinbaum et al., 2013).

Given the Kenyan context, implementing harvest quotas would be easiest on some private ranches with high-quality wildlife count data (e.g. Ogutu et al., 2017; A7) and with the financial resources to continue monitoring and quota setting (A2). This would be made easier by the fact that many private ranches are fenced, with clear boundaries (RS2).

Similar consideration has to be given to the trade of wildlife between areas in a game ranching context. However, the lower volume of live trade between landowners (RU5) over cropping, could ensure its sustainability.

Intensive game farming could be sustainable on a smaller scale, where wildlife effectively becomes a private good, with easier monitoring, management, and regulation. Such game farms effectively function in a similar way to commercial livestock farms (Bulte and Damania, 2005; Mockrin et al., 2005).

In Kenya's current policies, it is not clear which government institution should have the mandate to set quotas on wildlife cropping and regulate trade, both issues where clarity and consent need to be clear (GS1, GS2, GS8, I9, I10).

3.1.6.2. Harvesting process. The previous attempt at wildlife cropping on game ranches in Kenya faced several harvesting issues which continue to act as barriers (Tasha Bioservices, 2001). First, harvesters cropped beyond quota (I1) to increase short-term gains for themselves (A7), leading to decreasing ecological sustainability in the long term (O2). This was due to a lack of oversight (GS8) or incorrect perceptions of sustainable levels of harvest without adequate knowledge of the SES (A7), as discussed above. Second, a lack of monitoring and oversight (GS8) meant that benefits accrued by the harvester were not always passed on to the landowners (mainly in community land; Fig. 3; O1). Third, the inefficient use of wildlife products meant that the full economic values of wildlife (RU4) were not realised by landowners (O1). Finally, abuse of user rights and unethical culling practices undermined the legitimacy of the process, primarily due to a lack of governance (GS8).

These barriers might be overcome with clear harvesting rules, regulations, and governance structures (GS5, GS6, GS8). In South Africa, practical harvesting techniques have been developed, which both

minimise stress to the animal without compromising efficiency (Hoffman and Wiklund, 2006; Lewis et al., 1997). These techniques could increase the economic return for landowners while improving the legitimacy of the process (O1). Certain species such as zebra, eland, impala, and kudu, are more costly to crop, often involving helicopters (A9), which can significantly increase costs for harvesters (A2), and decrease the economic gain from wildlife for landowners (O1; Hoffman and Wiklund, 2006).

Importantly, in addition to the harvesting procedures, careful thought must be given to the control of wildlife disease (Kock, 1995). Diseases that are not controlled and not monitored may have negative consequences for the health of other animals and humans, and knock-on effects to other SESs (O3). If this happens, the potential loss in the market value of meat could undermine its long-term sustainability (see Section 3.1.2 above). A key mechanism to prevent the spread of disease in South Africa is the requirement that all animals are chilled < 2 h after slaughter (Hoffman and Wiklund, 2006). In many areas of Kenya, especially those far from urban centres (RS9, A4), this would require significant investment in cold storage and transport facilities (RS4), increasing the cost of wildlife cropping for harvesters and landowners. Monitoring and harvesting rules (GS5, GS8) will also require conformity with several different legislations.

Overall, regulation of every step in the process (Fig. 3) will require resources, workforce, and processes. In South Africa, for example, each farm is registered, each harvester is licensed and regulated, the game depot is licensed, and each carcass is traced from the moment of cropping to its sale (Hoffman and Wiklund, 2006). Harvesters, farmers, and distributors are inspected for conformity with the rules and regulations. To ensure this level of conformity, and to ensure positive conservation outcomes, Kenya will require new or adapted legislation (GS6, GS7, GS8), new or modified government agencies (GS1), and finance and expertise to conduct these activities (I9, I10; Cousins et al., 2010). Even in the productive game ranches of South Africa, the regulatory environment is plagued with uncertainty (Kamuti, 2014).

Achieving this kind of systemic change is likely to be difficult under the current economic and political setting. In particular, corruption could hinder transparency at multiple points in the process and prevent the equitable sharing of revenue (S1, S4, S3).

3.1.7. Economic and demographic development

Kenya is in a stage of both rapid economic (S1) and demographic (S2) growth. Policy directives and decisions made now must be viewed in the light of future developments. Geographic areas with the highest opportunity cost of conservation to game farmers and game ranchers are usually those with the highest cultivation and development potential (du Toit et al., 2017). The potential for cultivation coincides with high rainfall and high ecosystem productivity (RS5, RS7). With increasing demands for food production, the cost of forgoing development may not outweigh the costs of utilizing wildlife (O1). Even if wildlife cropping and trade could increase the return on investment to landowners, landowners may not be able to generate enough revenue in the long run to offset the total opportunity costs without other social-cultural or financial incentives (RU4). On the other-hand, game farming is a more intensive land use, with potentially higher financial returns per unit area, which lowers the cost of foregoing other development and land use options.

4. Discussion

Our analysis used the SESF to identify seven overarching barriers to the successful implementation of consumptive wildlife utilisation in Kenya. These barriers, unless appropriately addressed, could limit the ability for the consumptive wildlife utilisation to achieve its desired ecological and socio-economic goals (Fig. 5). Our analysis also revealed that of all the options that have been suggested, the option with the lowest barriers to implementation is game farming on private or community land (Fig. 5). Although this option might contribute to national goals of economic development and food security, our results show that it is unlikely to offset opportunity costs to landowners who host wildlife and does little to contribute towards Kenya's conservation goals of protecting wildlife populations and ecosystem services. More importantly, it is not clear how game farming's focus on high productivity of a single or few species can contribute to broader conservation goals (Macnab, 1991). Cropping of wildlife in game ranching, on both community and private lands, has a broad range of barriers to overcome if it is to be successful (Fig. 5). Overcoming these would require large scale investment in effective monitoring systems, new regulations, training, market development and research, considerations about equity, and devolved ownership of wildlife.

Although we focus on Kenya, this approach can be applied in many other areas. In this article, we have shown its value when assessing the potential impacts of conservation policies pertaining to wildlife utilisation and the wildlife commons (Smith et al., 2019). The SESF can be useful when developing strategies for the implementation of conservation plans (Ban et al., 2015; Guerrero and Wilson, 2017), but as we have shown here, it also represents an important tool for untangling the complex impacts of conservation policy decisions on social and ecological components of these systems, and how these can ultimately impact intended goals. In so doing, the SESF allows conservation policymakers to avoid some of the pitfalls of using a one-size-fits-all approach to conservation policy formation and implementation.

Furthermore, it allows for a focus beyond the social *or* ecological component – such as the potential economic gain or ecological viability of offtake – which, when considered alone, would do not allow for a comprehensive understanding of more complex systems with feedbacks (Brehony et al., 2018). The SESF allows conservation policymakers to conceptualise the interactions between subsystems at and across multiple scales, where markedly different factors can influence the sustainability of conservation actions (Cumming et al., 2015). For example, we demonstrate that for some private landowners the barriers to implementing consumptive utilisation may be low, yet at the scale of a national SES, cross-scale feedbacks between subsystems (such as market constraints and equity) may limit the success of this policy in fulfilling national goals. Indeed, previous attempts at wildlife cropping in Kenya were found to only really benefit large-scale private landowners, whereas most community landowners saw little benefit (Tasha Bioservices, 2001). Such inequality between actors have to be seriously considered as they can result in tensions which could ultimately lead to resentment towards wildlife in community land, and hinder overall success of the policy (Josefsson, 2014; Pasmans and Hebinck, 2017; Martin, 2017).

The SESF also allows conservation policymakers to consider variations between different resource systems and the type of consumptive use, which can help in identifying the factors which are key for a policy to achieve intended goals.

Policymakers are routinely faced with tight deadlines to make important decisions. In our analysis, our transdisciplinary team used evidence and information from numerous sources, interpreted through the SESF, to understand multiple focal action situations resulting from the suggested policy intervention, all under a tight deadline. As discussed, this process revealed important barriers to achieving intended goals, but it was also challenging and time-consuming. Transdisciplinary teams, as in the case of this paper, can help to provide high-quality information, knowledge from a broad set of scientific disciplines, and importantly, perspectives from stakeholder representatives (Bennett et al., 2018). Without this diversity and wealth of experience, the process of utilizing the SESF requires even greater effort (Leslie et al., 2015). However, incorporating more quantitative data relevant to our research questions, such as market surveys, wildlife numbers, and spatially explicit data would have enriched our analyses (Dressel et al., 2018). We suggest that further research is required to explore these individual barriers in greater depth and determine if these

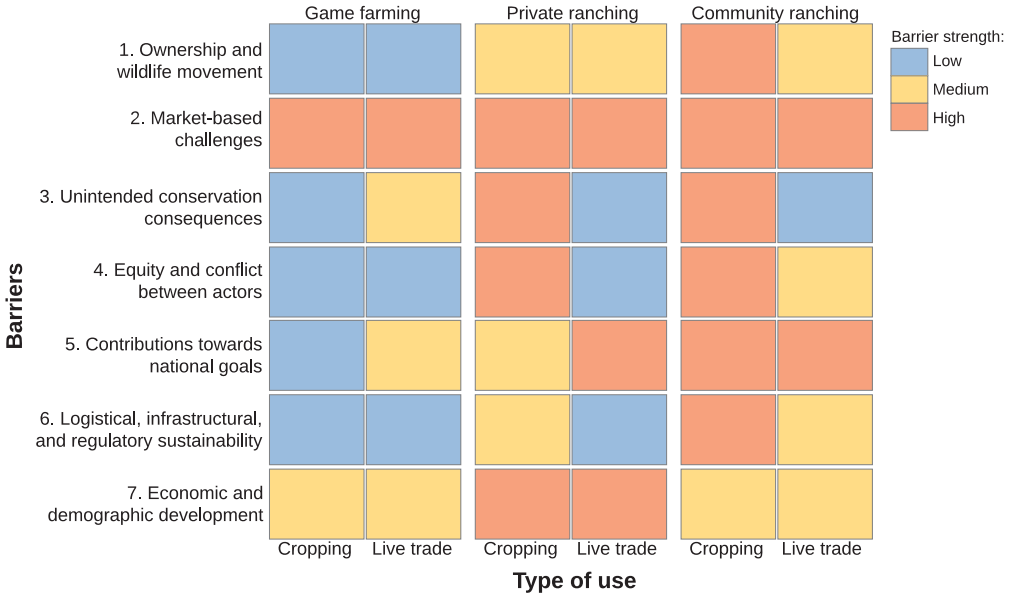

Fig. 5. Summary of the relative strengths of the barriers to consumptive use of wildlife, either trade or cropping, under different land-tenure arrangements.

barriers to sustainability can be overcome.

SES are complex, and our analysis focused on the system and scale that was most relevant to our research questions. However, as Larrosa and Carrasco (2016) point out, even considering a new conservation policy is a process embedded in the SES. The moment the policy is discussed, it becomes part of the SES, redefining it, and therefore affecting all four subsystems, with feedback loops (Fig. 2). Such complexity continues to be a challenge to understand, but building on approaches like ours will help us to untangle the complexity.

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CRediT authorship contribution statement

Peadar Brehony:Conceptualization, Methodology, Formal analysis, Investigation, Writing - review & editing. **Peter Tyrrell**:Conceptualization, Formal analysis, Investigation, Writing - original draft. **John Kamanga**: Conceptualization, Formal analysis, Writing - review & editing.**Lucy Waruingi**:Conceptualization, Formal analysis, Writing - review & editing.**Dickson Kaelo**:Conceptualization, Formal analysis, Writing - review & editing.

Declaration of competing interest

PT, JK, LW, and DK are engaged in conservation in the region. However, the authors have no affiliation with any organization with a direct or indirect financial interest in the subject matter discussed in the manuscript.

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10
Discussion

The profit-driven turnover of ownership, subdivision and transformation of land in southern Kenya is rapidly underway, fragmenting ecosystems, changing governance structures, and degrading rangelands (Chapter 4,5,6,7). This process is causing widespread detrimental impacts to savanna biodiversity and the sustainability of the pastoral social-ecological system (Chapter 7). In the face of global change, it is evident that economic incentives, supported by the devolved management and governance of rangelands and wildlife, will be vital for conservation in this region (Chapter 5,9, Appendix B). Ensuring there is an instrumental value of wildlife for landowners and national governments is critical, allowing landholders to convert wildlife and biodiversity from a short-term liability into a long-term asset (Norton-Griffiths et al. 2009). In these rapidly changing landscapes, we cannot rely on the intrinsic value of wildlife alone to carry their conservation. This southern Kenya example serves as a case study of broad relevance to other areas of the African savannas where the same processes are underway.

In the following sections, I will detail this trajectory of change in southern Kenya. I will use evidence from my chapters to document the status of biodiversity and the large mammal community, explain the main ecological and socio-economic drivers causing these changes, place these drivers of change in the regional perspective,

and highlight the required interventions to mitigate large-scale biodiversity loss. I will also draw attention to existing gaps in knowledge, where more research may be necessary.

10.1 Government-led protected areas are inadequate to address biodiversity loss

The extreme economic pressure driving land transformation and habitat loss in Kenya are concerning for biodiversity. In Kenya, similar to global conservation efforts, Protected Areas (PAs) have been the focal response to biodiversity loss (Watson, Dudley, et al. 2014). However, they have generally failed to halt overall biodiversity declines and habitat loss. From 2001 to 2020, for example, Kenya lost 361,000 hectares of tree cover, equivalent to an 11% decrease in tree cover since 2000[1]. This is concerning because the countries' conservation efforts do not cover biodiversity outside PAs adequately (Chapter 2), with only 16% of amphibians, 45% of birds, and 41% of mammals well represented by the PA network. 5.2% of species have no range overlap with national PAs at all. The lack of adequate conservation attention has led to rapid declines of biodiversity outside PAs across unprotected rangelands, and urban and agricultural landscapes. For example, Augur buzzards (Buteo augur), a raptor thought to be of low conservation concern, has lost nearly 50% of its territories over nearly two decades around the horticultural areas of Lake Naivasha (Eichenwald et al. 2021). These findings are similar to global and regional analyses that demonstrate that PAs cover only a tiny fraction of biodiversity (Larsen et al. 2014).

In addition, the distribution of current PAs, and the focus of Kenya's wildlife policy in general, is in areas of lowest human pressure, often with the highest large mammal densities (Chapter 2). However, despite most conservation attention directed towards large mammal communities, they too have experienced widespread and rapid detrimental changes across Kenya. In the six ecosystems we focus on in

[1] www.globalforestwatch.org

southern Kenya there have been major changes in large-herbivore community composition over the last 40 years, with large decreases in all wild-herbivore functional types except for non-ruminant grazers (Chapter 7). Two ecosystems, Maasai Mara and Nairobi, both with government-led PAs, show the greatest declines in wild herbivores. Across all ecosystems (covering >35,000km^2), the wild-herbivore community has undergone downsizing, reductions in diversity, and homogenisation within and across ecosystems. These changes in southern Kenya are not unique, with the majority of Kenyan ecosystems experiences significant declines in wildlife. Some estimates indicate that Kenya-wide, wildlife abundance has dropped by 70% since the 1970s (Ogutu, Piepho, et al. 2016). This evidence suggests that PAs are not adequate to protect large mammal communities for three reasons. First, most of Kenya's wildlife exists outside of government-led PAs (Western, Russell, et al. 2009). Second, PAs were not designed around optimised ecological functionally for wild herbivores. Even the largest PAs do not encompass the functional heterogeneity[2] required to maintain large, diverse and resilient herbivore communities (Western and Gichohi 1993; Newmark 2008; Fynn and Bonyongo 2011). Three, PAs alone are not addressing the complex set of drivers causing biodiversity loss, even inside their boundaries.

Simultaneously, government-led PAs are under extreme pressure, with many PAs now isolated in a sea of human pressures. We found that at least 38% of all PA boundaries in eastern and southern Africa are 'hard' and thus transformed by human pressures (Chapter 2). Only half of all buffer areas surrounding PAs remain intact for wildlife. These edge effects impact biodiversity and wildlife through factors such as human-wildlife conflict, pollution, genetic isolation, and over-exploitation, and by altering ecosystem function through changes to fire, migrations, forage production and habitat degradation (Newmark 2008; Fynn and Bonyongo 2011; Mose and Western 2015; Thuo 2020; Western, Mose, Maitumo, et al. 2021; Western,

[2]Fynn et al. (2016) define functional heterogeneity as *"...spatial and temporal variation in the grass height (structure), productivity, phenology, composition and chemical attributes of grassland and savanna plant communities, which determine the abundance, stability, diversity and spatial distribution of large mammalian herbivores in African savannas"*.

Mose, Worden, et al. 2015; Veldhuis, Ritchie, et al. 2019). This intense pressure threatens the utility of PAs as a tool for conserving biodiversity. In particular, many of Kenya's PAs had hard boundaries, reducing their effectiveness. Nairobi National Park has one of the hardest boundaries of any PA in Africa, which has caused the loss of access for wildlife to the Athi-Kapiti wet season dispersal area due to urban and agricultural development. This, in turn, led to a reduction in wildlife mobility and a subsequent collapse of the Nairobi National Park's gazelle populations, and then wildebeest and topi populations (Western and Gichohi 1993; Sitati et al. 2014) (Chapter 7), and with it, an increase in conflict between lions and humans as they search for prey during the wet season (Gichohi 2003).

Our analysis has revealed some important patterns and highlighted the inadequate distribution of, and the pressure on, the current PA network. Given that vast area of the region are likely to be converted to agricultural production (Williams et al. 2020) and urban areas (Seto et al. 2012; Güneralp et al. 2018) to cater for rising populations and consumption, strategic planning and economic incentives must be put in place to ensure adequate production of biodiversity and ecosystem services. There is little scope for expanding government-administered PAs across Kenya to protect biodiversity due to limited funding opportunities and pressure for competing land-use options. This limitation applies throughout eastern and southern Africa. Therefore, strategic prioritisation and investment, which cut across species and land use boundaries, will be vital given the already underfunded nature of conservation (Lindsey, Miller, et al. 2018). In Kenya, the first step is to conduct priority setting to identify the minimal viable ecosystems required for large mammals (Western and Gichohi 1993). The second step requires the spatial prioritisation of conservation action using higher-quality data on biodiversity, ecosystem services, and conservation costs (Xu et al. 2017). Finally, priority setting and policy decisions must provide solutions to address the drivers of biodiversity loss.

10.2 Drivers of change in the southern Kenya large herbivore community

To adequately address the drivers of biodiversity loss in southern Kenya, and in particular the large herbivore community, we must understand the key social and ecological dynamics of rangeland social-ecological systems (SES). Here we synthesise our knowledge documented in this thesis regarding the ecological and social forces driving changes in southern Kenya. These results show that proximate anthropogenic stressors are overwhelmingly strong drivers of ecosystem-level change.

10.2.1 East African 'droughts' are driven by livestock, not climate change

Increased aridity and drought intensity due to climate change has been proposed as a reason for the changing composition of mixed wildlife-livestock assemblages in Kenya (Ogutu, Piepho, et al. 2016), and elsewhere in the region (Veldhuis, Kihwele, et al. 2019). However, in East Africa, it is unclear what impact climate change may have on wildlife. Modelling the Amboseli ecosystem dynamics, for example, suggests that climate change is a minor threat to elephants' survival compared to rampant habitat loss (Boult et al. 2019). In southern Kenya, changes to the broader wild-herbivore community have been driven, in part, by the severity of drought events (Chapter 7) (Dublin and Ogutu 2015). Therefore, increasing drought intensity and frequency resulting from climate change is potentially a wide-scale driver of change in wild-herbivore communities across ecosystems. Indeed, some evidence from southern Kenya suggests changes in annual and seasonal rainfall and drought frequency and intensity, but the combined evidence is inconclusive when different spatial and temporal scales are used (Lyon and Dewitt 2012; Western, Mose, Worden, et al. 2015; Bartzke et al. 2018)(Chapter 7). However, it is difficult as yet–at least for southern Kenya–to identify a consistent trend attributable to global climate change and thus identify the impacts of climate change on the large-herbivore community (Chapter 7). This mirrors the global deficiency of data

on the impacts of climate change on large mammals (Paniw et al. 2021). More research and information are needed on both the trajectory of climate change and its potential impacts on the large herbivore community.

While little evidence exists in East Africa for increasing frequency of climate-change-induced drought events, the frequency of drought events, measured by forage deficits, has increased in areas where the sedentarisation and fragmentation of pastoral commons restrict livestock mobility and increase local livestock densities and grazing pressures (Western, Mose, Worden, et al. 2015; Western, Mose, Maitumo, et al. 2021) (Chapter 7). The effect of increased livestock herbivory on wildlife community composition operates through two main processes. First, livestock and their associated human presence may directly cause spatial and temporal displacement of wildlife, especially at key grazing and water points (Carter et al. 2012; Valls-Fox et al. 2018). Second, when competition occurs between wildlife and livestock for forage resources, supplementary feeding and livestock watering typically result in wildlife being out-competed (Hempson et al. 2017; Ogutu, Piepho, et al. 2016; Veldhuis, Ritchie, et al. 2019). Increasing livestock herbivory intensity, and increased forage deficits is a key determinant of changes to the wildlife community in southern Kenya (Chapter 7). Increased local stocking rates reduce the grass biomass per unit rainfall and create deeper annual and seasonal deficits in grass biomass than from rainfall-induced droughts alone, the frequency of which is increasing in some areas (Western, Mose, Worden, et al. 2015; Western, Mose, Maitumo, et al. 2021) (Chapter 7). These local changes are in turn driven by larger-scale changes affecting the pastoral social-ecological system, influencing the mobility of wildlife and livestock populations.

10.2.2 Widespread ecosystem fragmentation is driven by policy and market forces

Changes to livestock and wildlife mobility are among the most significant forces driving changes in eastern and southern Africa. Fragmentation from land-use change and fencing and sedenterisation in rangelands lead to the loss of mobility

and compressions of pastoralists and wildlife, increasing local herbivore grazing intensity (Butt 2010; Groom and Western 2013; Mose and Western 2015; Western, Mose, Maitumo, et al. 2021) (Chapter 7). In addition, fragmentation prevents seasonal movements of both wildlife and livestock to key resource areas – such as drought refuges - which are critical for survival (Hobbs et al. 2008a; Fynn, Augustine, et al. 2016). Across southern Kenya, these changes have been driven by pre-and post-colonial government policies continually encouraging the privatisation and subdivision of unfenced communally-owned land and the sedenterisation of pastoralists (Mwangi and Ostrom 2009). When coupled with Kenya's fast-growing economy and population, land commodification and demands for land, shrinking space for pastoralism, and expansion of government-protected areas and conservancies, fencing on private land has rapidly increased to protect individual property rights and resources (including forage for livestock) and to avoid human-wildlife conflict (Said et al. 2016; Løvschal et al. 2017; Rutten 1992; Mwangi and Ostrom 2009; Weldemichel and Lein 2019). This has led to the mobility of wildlife and livestock being curtailed in southern Kenyan rangelands due to over 40,000 km of fencing, primarily in private land-holdings with the highest land prices (Chapter 5, 6), 1500 km^2 of agricultural land, and 35,000 livestock enclosures tightly packed in private, subdivided land (Chapter 6). This widespread fragmentation will continue to negatively impact wildlife assemblages and pastoral livelihoods (Chapter 7).

The principal drivers of rangeland fragmentation lie in national and global market forces and the national policies supporting economic expansion. The national and global need to increase food production (Foley, Ramankutty, et al. 2011) leads to the wide-scale conversion of rangelands into croplands, especially in areas of the highest agricultural potential (Lambin and Meyfroidt 2011). Additionally, rapid urbanisation and development occur across much of the developing world, with rangelands being rapidly converted to meet the demands of a growing global population (Foley, Defries, et al. 2005; Newbold 2018; Güneralp et al. 2018) and their infrastructural requirements (Laurance 2018; Damania et al. 2019). These economic and policy forces are pushing landowners in southern Kenya to accept

land transformation, land sale, and infrastructure development at the expense of fragmenting ecosystems (Chapter 4,5,6,8).

Therefore, a major challenge for conservation is to overcome the economic costs to landowners for forgoing these economic options (Norton-Griffiths & Said 2009; du Toit et al. 2017). In southern Kenya, these opportunity costs are rapidly increasing with land speculation and associated urbanisation (Tyrrell, Naidoo, et al. n.d.) (Chapter 8). This massively drives up the costs of maintaining conservation buffer zones, corridors, and dispersal areas (Chapter 8), with costs to conserve even small areas now far higher than can be earned from wildlife-based income alone. Because of these economic forces, the Nairobi National Park and Athi-Kapiti ecosystem, adjacent to Nairobi, is now almost entirely fragmented with a collapse of the previously rich migratory system of wildlife and pastoralism (Said et al. 2016; Nkedianye et al. 2020). Addressing these economic forces is a crucial conservation concern in southern Kenya.

Sound governance systems are required to ensure the equitability and effectiveness of using economic incentives (such as ecotourism revenue) to overcome these conservation challenges (Chapter 4). Also, poor governance and management of livestock further accelerate the negative impacts of fragmentation on rangeland productivity (Chapter 4, 7). Governance and the institutions made available to communities by government policy (centralised, top-down or localised, bottom-up) affects the ownership of resources, decision-making ability, access to resources, benefits and livelihoods, and the sustainability of resource use (Ostrom 2009; Ostrom 2007; Sayer et al. 2013; Berkes 2007). Multiple governance models exist across the southern Kenyan rangelands, with varying degrees of success to devolve benefits and improve the management of natural resources (Chapter 4)(Bedelian and Ogutu 2017; Tyrrell, Russell, et al. 2017; Brehony 2020). Broader details on the complexities of the governance of wildlife and livestock in southern Kenya are provided by Brehony (2020), Western (2019), and Cockerill and Hagerman (2020).

While we have documented the main drivers of change to the wildlife-livestock interface in southern Kenya, other factors may play an essential role in the future.

Fragmentation, for example, has also negatively impacted fire regimes and nutrient dispersal across landscapes, which may have large-scale ecological impacts in the future (Western and Gichohi 1993; Veldhuis, Ritchie, et al. 2019; Hempson et al. 2017; Probert et al. 2019; Morrison et al. 2018; Doughty 2017). Other costs associated with wildlife-livestock interactions may also impact the long-term viability of coexistence. Diseases in wildlife populations have high coexistence costs, but we have struggled to curtail their impact because of a lack of understanding of the disease process itself and limited collaboration between livestock and wildlife agencies (Kock et al. 2009). The scale of human-wildlife conflict also dictates local communities' tolerance to wildlife (Western 2019), and widescale mitigation is required. All these impacts require further investigation.

10.2.3 Conservation in eastern and southern Africa must address socio-economic and political drivers

Our comprehensive analysis and review exposes proximate anthropogenic stressors as overwhelmingly strong drivers of ecosystem-level change and confirms their importance for conservation within the rangelands of eastern and southern Africa. While the ultimate driver of rangeland ecosystem change is rainfall, and with frequencies and intensities of meteorological droughts expected to increase with ongoing global climate change, their effects will be additive to those of proximate drivers operating at a shorter time scale (Sankaran et al. 2005; Platts et al. 2015). The lesson from southern Kenya is that African savannas can quickly flip from rain-driven to human-driven ecosystems. Thus, conservation solutions must focus on local drivers of change, which must be traced back to the higher-level socio-economic and political developments to which they are responding.

Wildlife and biodiversity trends across eastern and southern Africa have mirrored Kenya's losses with rapid declines due to human pressures (Daskin and Pringle 2018; Craigie et al. 2010a; Estes et al. 2006). Across the region, the pressures on natural resources will continue to increase in the next 50 years. Africa's human population is projected to double by 2050 to 2.5 billion people and almost double

again by 2100 (Sanderson et al. 2018). This rapid expansion, coupled with economic growth, spurring on increasing consumption and infrastructure development, will further exacerbate pressures (Williams et al. 2020; Newbold et al. 2015; Laurance 2018). Also, similar to Kenya, rangelands in eastern and southern Africa are dominated by livestock (Du Toit and Cumming 1999; Hempson et al. 2017) and are experiencing fragmentation at different rates because of land use and land tenure changes impacting rangeland productivity and wildlife populations (Hobbs et al. 2008a; Reid et al. 2014; Elliot, Cushman, et al. 2014).

Bearing these factors in mind, it is likely that these large anthropogenic pressures will dominate the future trajectory of much of the livestock-wildlife interface in eastern and southern Africa for the foreseeable future. However, the uniqueness of each social-ecological system at any given time, ranging from its ecological properties, response to climate change, and social structures, will dictate the essential drivers shaping the large herbivore community (Brehony 2020).

10.3 Moving conservation towards a working landscape approach

I have so far documented: (i) the need to increase the area of land under conservation in eastern and southern Africa to prevent continued biodiversity loss and to maintain, restore, and improve ecosystem function; and (ii) the need for conservation interventions in rangelands to address the economic, political, cultural, and individual well-being elements of the system.

Therefore, in addition to the historical focus on prioritising PAs' protection in eastern and southern Africa (Adams and McShane 1992; Brockington 2002; Lindsey, Allan, et al. 2020), approaches that include communities outside PAs that align human livelihood activities with conservation objectives will be increasingly essential to meet both conservation and development goals (Beale et al. 2013; Western and Pearl 1989). These approaches are also likely to improve social and political will for conservation when local community aspirations are met, the lack of

which could pose an even more significant long-term threat to PAs. In particular, this calls for a "working landscape approach", where landscapes are managed to complement biodiversity conservation goals while they contribute to producing food, materials, clean water, and healthy soils and provide vital ecosystems services such as carbon storage (Kremen and Merenlender 2018). These approaches aim to tackle nations joint commitments to both global biodiversity targets and the sustainable development goals (SDGs). Working landscapes approaches are part of broader landscape-based approaches (Arts et al. 2017), which will be particularly important for the sustainability of the rangelands of eastern and southern Africa, where livestock-wildlife interactions and the complex SESs they are embedded in dictate the future of biodiversity. Using these approaches, it is vital that we re-define what we typically understand as "conservation success" (Appendix A), broadening our goals to include multiple aspects of the SES, not just the ecological ones.

Policy reforms, changes to conservation practice, and economic incentives will be required in rangelands and PAs to overcome the barriers leading to continued biodiversity and ecosystem function losses (Chapter 4)(Western, Tyrrell, et al. 2020). In the South Rift Valley in southern Kenya, we demonstrate how a landscape approach ("inside-out conservation"), that incorporates a broad suite of actors at multiple scales allows for the conservation of large open landscapes, biodiversity, and the coexistence between wildlife and livestock. This is achieved indirectly by reinforcing pastoral practices that depend on open space, mobility, social networks and institutional arrangements governing common-pool resources. This conservation approach starts from community aspirations that emphasise the links between livelihoods, productivity, efficiency, and resilience in pastoral economies but is assisted by wildlife enterprises' secondary benefits. While chapter 4 demonstrates one instance of this, multiple examples exist to demonstrate the ecological and social sustainability of mixed livestock-wildlife landscapes (Keesing et al. 2018; Allan, Tallis, et al. 2017; Bedelian and Ogutu 2017).

These new landscape-based approaches, incorporating livestock and wildlife and multiple sectors and stakeholders, present a unique set of challenges for the

conservation community. Below we build on work in chapter 4 to demonstrate a framework that helps to overcome these.

10.4 A framework for addressing anthropogenic drivers and creating working landscapes.

To achieve a working landscape approach, the critical challenge is to understand how governance impacts the conservation of biodiversity and natural resources (Brockington et al. 2019). Conceptualising landscape governance as a capacity is a valuable mechanism to identify actions that will address governance issues, and overcome the anthropogenic threats to biodiversity (Sayer et al. 2013; Arts et al. 2017; Sayer 2009). In short, the five specific landscape capacities can be summarised as follows:

1. the capacity to "think" landscape, not only to understand the natural-ecological characteristics of a landscape but also its socio-cultural identity and sense of place;

2. the capacity to achieve internal coherence by embracing a landscape's diversity of stakeholders and facilitating multistakeholder collaboration across levels and scales;

3. the capacity to make institutions work for landscapes, by recognising and capitalising on endogenous landscape institutions and building new institutions connected to broader policy frames and markets;

4. the capacity to create marketable landscape values by nurturing entrepreneurship, creating sustainable landscape business models, and attracting landscape finance;

5. the capacity to manage resources by understanding endogenous management systems and identifying options for more scientifically based resource management systems, participatory spatial planning, and decision making.

I briefly break down these capacities below with examples of how organisations, communities, and governments are overcoming barriers to conservation at the livestock-wildlife interface.

10.4.1 Thinking and acting from a landscape perspective

Thinking from a landscape perspective requires two important elements when approached from the conservation realm. First, there is a need to acknowledge the entire ecological characteristics and extent of a landscape. For example, recent concerns around the Mara River's over-utilisation have broadened the scope of conservation in the region from focusing on the Mara-Serengeti Ecosystem to the broader Mara-Mau-Serengeti ecosystem to protect the Mara rivers headwaters in the Mau escarpment (Mnaya et al. 2017). Second, there is a better need for managers and actors to understand and cultivate peoples' relationships with landscapes. In doing so, managers will be better equipped to develop management activities that will avoid conflict and gain public support (Hausmann et al. 2016). For example, the strong cultural identity and social bonds of Maasai pastoralists in southern Kenya aids decision making at a landscape level due to a shared identity centred around cattle, which need wide, open landscapes (Chapter 4). On the other hand, resistance to conservation in some Tanzanian Wildlife Management Areas and Kenyan conservancies can be linked to local communities desires to make decisions about their landscapes without top-down control (Weldemichel 2020).

10.4.2 Achieving coherence through the empowered institutions

The correct governance structures and institutions are vital for generating consensus and coherence between multiple stakeholders and facilitating collaboration across levels and scales. Community-based conservation (Western 1982; Western and Pearl 1989) and community-based natural resource management (Songorwa et al. 2000) have developed in the last thirty years to overcome these challenges. In Kenya, for example, to protect wildlife and improve local livelihoods outside of PAs, the number

of conservancies (CBC) in Kenya has proliferated, from less than 5 in the early 1990s to over 140 in 2016, now covering over 30,000km^2 (KWCA 2016). Importantly for these institutions' success, national policies and legislation have devolved the right to manage and benefit from their wildlife resources to conservancies and landowners, in cooperation with national and regional government (Western, Waithaka, et al. 2015; Cockerill and Hagerman 2020). Conservancies are now an essential component for the long term viability of wildlife populations both outside and inside protected areas (Dolrenry et al. 2014b; Western, Waithaka, et al. 2015; Ihwagi et al. 2015; Ojwang' et al. 2017), and for improving the capacity of communities for sustainable rangeland management (Glew 2012; Brehony 2020). Multi-scale collaboration is now widespread in Kenya with "umbrella" bodies for conservancies at the landscape/ecosystem scale (Chapter 4).

However, coherence and consensus-building between multiple stakeholders remain one of the largest challenges in conservation (Cockerill and Hagerman 2020). For example, the problem with many community conservation projects is that the objective is still solely to preserve wildlife, and they tend to ignore the objectives and aspirations of local people (Berkes 2007). Large-scale infrastructural development and the conflict generated between national governments, development groups, and conservation groups (Holdo et al. 2011; Laurance 2018; Lesutis 2019) represent another example of failure to build the correct institutions to allow for multiple objectives to be reached. In Kenya, steps still need to be taken to ensure cross-sector collaboration to ensure competing objectives for landscapes are debated and met (Chapter 2). Multiple objectives can only be achieved under more complex multi-level governance approaches, often outside of the wildlife conservation sector (Chapter 4).

10.4.3 Multiple management principles needed for sustainability at the livestock-wildlife interface

Sustainable and successful management of the livestock-wildlife interface relies on several knowledge bases and principles. In general, multiple knowledge streams need to be used collectively to inform conservation management, yet management

approaches in conservation that explicitly have more than one objective are rare (Berkes 2007). Rethinking management objectives from a holistic, multistakeholder viewpoint is vital. This includes the ecological knowledge to ensure livestock-wildlife coexistence, the social tolerance to allow this to happen, and the broader strategic planning and management of natural resources in the face of global change.

There are wide-scale efforts across the region to develop institutions and management practices that improve rangeland health. In general, a robust theoretical basis exists around functional heterogeneity theory as a basis for management (Fynn, Kirkman, et al. 2017; Fynn, Augustine, et al. 2016; Russell et al. 2018; Tyrrell, Russell, et al. 2017; Odadi et al. 2017), and much of this knowledge was already present within traditional pastoral societies (Tyrrell, Russell, et al. 2017; Brehony 2020). Sustainable livestock management, when implemented correctly, may also create ecological space for wildlife (Tyrrell, Russell, et al. 2017). These management principles are being rapidly adopted across the region. As discussed above, this relies on the correct institutions and social structures to be in place (Brehony 2020). However, it also requires a desire from local communities to coexist with wildlife. This may arise from tangible economic benefits, cultures of coexistence and tolerance, conservation education, and socio-political context (Western 2019). Finally, with the extensive demographic and economic transition ongoing on the continent, it will be necessary to incorporate multiple stakeholders into forward-thinking strategic planning to achieve conservation goals. Generating collaborative scenarios that galvanise transformative change at the landscape level will be critical to ensure that competing objectives for food security, wildlife conservation, and economic development are achieved sustainably (Sayer 2009; Swetnam et al. 2011; Butler et al. 2016).

10.4.4 Creating marketable landscape values

There is a considerable need to develop both policies and economic opportunities that will allow for sustainable and competitive returns for land use options that are compatible with wildlife conservation (Norton-Griffiths et al. 2009; du Toit et al.

2017). Across the region, there is a severe lack of funding to cover opportunity costs and management costs for PAs, and the current funding models lack long-term resilience to global shocks (Waldron et al. 2013; Lindsey, Miller, et al. 2018; Lindsey, Allan, et al. 2020) (Appendix B). At the moment, the primary mechanism for generating income from wildlife are either consumptive use (e.g. trophy hunting, game meat), and non-consumptive use (e.g. ecotourism). In Kenya, for example, many of the community and private conservancies have focused on ecotourism as a primary financial mechanism to incentivise conservation (Western, Waithaka, et al. 2015). In southern Africa, consumptive use of wildlife, through trophy hunting and game meat, has proven a viable and sustainable economic option to support wildlife as a land-use (Richardson 1998). While in areas of lower agricultural potential, with lower opportunity costs, mixed livestock-wildlife ecosystems can be economically viable and successful when the cost of living with wildlife is mitigated (du Toit et al. 2017). Solutions such as compensation for losses to carnivores (Dickman et al. 2011), or payment for ecosystem services, represent other emerging options for landowners (Appendix B).

These economic options for conservation are vital for the long-term sustainability of conservation. However, rarely do policymakers, practitioners, or academics address the social-ecological complexities of these economic policies (Macdonald 2019). Few are silver bullets. Any economic solutions must be crafted for the SES in question, and we cannot assume that one funding solutions will work in different SES with different economic values, policies, governance, and cultures (Chapter 9). Using the Social-Ecological Systems Framework (SESF) is one method to ensure the impacts of policy changes are accounted for (McGinnis and Ostrom 2014; Ostrom 2009). The SESF is an adaptable yet structured approach for understanding the processes that lead to changes in natural resources, using a systems-based approach that aims to treat ecological and social components equally. Few conservation planning and policy initiatives have implemented the SESF to assess the interlinked social and ecological consequences of conservation policies. The SESF appears to be a useful framework for this purpose. In particular, it can help to reveal

potential social and ecological barriers which conservation policies might face in attempting to meet intended goals (Chapter 9).

10.5 In closing

As we enter the UN Decade of Ecosystem Restoration, a global call for "Preventing, halting and reversing the degradation of ecosystems worldwide", we must acknowledge that nowhere on the planet is more at risk of wide-scale degradation than the rangelands of eastern and southern Africa (Newbold 2018; Williams et al. 2020). However, as we show, these areas are vital to achieve broader conservation and sustainable development goals. It is evident that proximate anthropogenic stressors are the overwhelmingly strong drivers of ecosystem-level change. These demographic, economic, and global market forces driving change are likely to increase in magnitude across the region in the coming years. A business-as-usual trajectory will fail to protect livelihoods, biodiversity, and ecosystem services now and into the future. A landscape-based approach working across scales and sectors while incorporating and reacting to these SES's complexities is a critical step. Ultimately, conservation priorities should be defined with local communities and with a broad lens. This broader perspective improves the chances that global biodiversity targets and SDGs are aligned and that resources are used to benefit both people and wildlife through PAs and in the larger, more functional landscapes in which they are embedded.

Appendices

A

Bringing back complex socio-ecological realities to the study of CBNRM impacts: a response to Lee and Bond (2018)

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Bringing back complex socio-ecological realities to the study of CBNRM impacts: a response to Lee and Bond (2018)

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Lee and Bond (2018) claim to quantify the ecological success of a community-based wildlife conservation intervention in Tanzania. In this reply to their article, we take issue with 3 aspects of their study. First, the study inadequately equates ecological success with increased wildlife and reduced livestock densities. Second, the study fails to adequately account for causality between the Wildlife Management Area (WMA) policy and the observed changes in wildlife and livestock densities. Third, the study misrepresents the reality of community-based conservation in Randilen WMA. Researchers seeking to further our understanding of community-based natural resource management by evaluating its impacts must proceed with careful attention to the complex and dynamic socio-ecologies of the environments they study.

Watafiti Lee na Bond (2018) walichapisha andiko lao la kitafiti ambapo wanadai kwamba walipima mafanikio ya kiikolojia yaliyotokana na mpango wa ushirikishaji jamii katika uhifadhi wa wanyamapori nchini Tanzania. Katika utafiti wao, walitumia Eneo la Jumuiya la Hifadhi ya Wanyamapori Randileni (Randileni WMA) lililopo Wilayani Monduli kama mfano. Kuna mambo matatu ambayo tungependa kuyatolea ufafanuzi ikiwa ni sehemu ya majibu yetu kwa andiko lao. Kwanza, utafiti wao umefanya kosa la kutumia ongezeko wa idadi la wanyamapori na kupungua kwa wastani wa idadi ya mifugo kama kiashiria cha matokeo chanya ya kiikolojia. Pili, utafiti wao haujaweza kuonesha ipasavyo uhusiano kati ya sera ya ushirikishwaji (WMA) na mabadiliko waliyoripoti ya kuongezeka kwa idadi ya wanyamapori na kupungua kwa idadi ya mifugo kwenye eneo. Tatu, utafiti wao umeshindwa kuakisi hali halisi ya mpango wa ushirikishaji jamii katika uhifadhi ilivyo huko Randilen WMA. Tunapendekeza kwamba, kwa watafiti wanaolenga kupima matokeo ya mpango wa ushirikishwaji jamii katika usimamizi wa maliasili ili kuongeza uelewa, ni muhimu kuzingatia uchangamano na hali halisi ya muingiliano wa masuala ya kijamii na kiikolojia katika mazingira na maeneo wanayofanyia tafiti zao.

Key words: community-based natural resource management, conservation, semi-arid environment, wildlife livestock coexistence, Wildlife Management Area

In their paper "Quantifying the ecological success of a community-based wildlife conservation area in Tanzania," Lee and Bond (2018) aim to address an important and understudied aspect of community-based wildlife management: its ecological outcomes. They do so on the basis of a study of Randilen Wildlife Management Area (WMA). WMAs represent a key community-based natural resource management (CBNRM) strategy of Tanzania, already covering around 3% of the country and aiming to cover an additional 12% in the future (Bluwstein et al. 2018). Research on the ecological outcomes of WMAs is, therefore, warranted.

While we agree with Lee and Bond (2018:459) that "the ecological success or failure of CBNRM projects is rarely rigorously assessed," we contend that their study, too, does not

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meet this salient criterion. Specifically, we are concerned by 3 problematic aspects of their study: 1) their concept of ecology fails to account for the underlying ecosystem processes and the inherent temporal and spatial variability of the socio-ecological system under study; 2) their methods cannot substantiate their claim to causality as they do not account for rival explanations and their data are collected across a time period that is too short to be meaningful for ecological studies in the context of semi-arid environments; and 3) we believe that the characterization of community-based conservation in this study site is inaccurate, and thus misrepresents the claimed success of CBNRM. We unfold these 3 critiques in more detail and conclude by urging future research to carefully consider the complex ecologies of people and wildlife in a dynamic environment in order to produce accurate insights.

Equating Ecological Outcomes With Livestock and Wildlife Densities

In seeking to assess the ecological success of CBNRM, Lee and Bond (2018) equate more wildlife and less livestock with better ecological outcomes, and vice versa. In doing so, they build on a reductionist and static concept of ecology that is at odds with a large literature on rangeland ecology (Sprugel 1991; Brockington and Homewood 2001; Fynn et al. 2016). Lee and Bond's (2018) study area is part of northern Tanzania's semi-arid rangelands, the ecological conditions of which are governed primarily by stochastic and highly variable dynamics of rainfall and drought (Homewood et al. 2009). Pastoral livestock mobility as a strategy to access seasonally available pasture and water resources across large landscapes has proven to be a sustainable strategy in adapting to these highly uncertain environments (Western 1982; Müller et al. 2007; Freier et al. 2014). This mobility shapes livestock density across time and space, and it responds to and, in turn, shapes the underlying productivity and resilience of semi-arid environments (Illius and O'Connor 1999; Boone et al. 2008).

Although wildlife and livestock do sometimes compete for the same resource, this relationship is complex, varies by guild, and can be synergistic (Odadi et al. 2011; Charles et al. 2017). However, especially when poorly governed, livestock grazing may lead to detrimental impacts on wildlife populations. Yet, livestock management can be used as a tool to increase functional heterogeneity and provide both high-quality grazing and dry season reserves for wildlife, while generating income to communities (Butt and Turner 2012; Fynn et al. 2016; du Toit et al. 2017). When managed for heterogeneity, East African rangelands can support high densities and diverse communities of both livestock and wildlife (Tyrrell et al. 2017).

Studies on the health of ecological systems must take long- and short-term variation in rainfall and other bio-climatic factors into account. Furthermore, by focusing only on the density of a few large mammal species and livestock, Lee and Bond (2018) fail to adequately describe the state of the environment and the spatially and temporally variable ecological processes that sustain wildlife or livestock, or both (Bennett et al. 2009).

Methodological Conundrums in Attributing Change in Semi-Arid Environments

The positive ecological impacts claimed by Lee and Bond (2018) do not withstand the scrutiny required in impact evaluation studies (Ferraro and Pressey 2015). A rigorous study of ecological impacts in the context of semi-arid environments requires a significantly longer study period than that of Lee and Bond (2018). This is due to the highly variable spatial and temporal distribution of rainfall, which can mask the ecological impact of conservation interventions.

Impact evaluation also requires attention to causality (showing correlation is not enough) through exploring possible alternative explanations. Lee and Bond (2018) rely on comparing the WMA to a similar (matched) site to bolster their claim to causality. Although the matched approach compares treatment and control sites that appeared similar at a point in time before the intervention, matching is only as good as the data informing it. Factors that are not taken into account during matching may have dissimilar effects on treatment and control sites over the observation period. Only very rarely do matching approaches generate sets of control and treatment units so similar that differences, other than the intervention, can be disregarded entirely (Rubin 2006). In the case of Lee and Bond (2018), given a fluctuating environment and the many possible confounding variables, the observed differences in wildlife and livestock densities may be caused by a host of factors other than the "treatment." For instance, the authors suggest that "Giraffes may have shifted their distribution into the WMA as a result of lower relative density of humans and livestock inside the WMA" (Lee and Bond 2018:463). While this may be true, this spatial-temporal relationship has not been tested (a novel methodology using the same method of data collection can be found in Miller et al. 2013), and no alternative explanations beyond the focus on livestock and poaching have been explored. The same goes for conclusions pertaining to Kirk's dik-dik (*Madoqua kirkii*), whose population decline outside of the WMA is attributed to a potential loss of vegetation cover, again attributed to cattle or poaching, but without supporting information.

Lee and Bond's (2018) claim to causality is thus poorly substantiated as they do not account for rival and potentially important explanations for the changes in densities that they observe.

Characterizing Community-Based Conservation

Our third and final point of contention pertains to how Lee and Bond (2018) have characterized community-based conservation. The authors have framed their research of a community-based wildlife conservation area as *if* it is taking place in the context of a conservation management intervention that operates according to CBRNM principles with agreed-upon rules and regulations. Loveless (2014) shows us that this is simply not the case with Randilen WMA, where WMA implementation was imposed against a backdrop of community frustrations (see Igoe and Croucher 2007 for similar findings in the neighboring Burunge WMA). Lee and Bond (2018), therefore, have

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studied a conservation intervention that is only in rhetoric participatory and community-based, while in reality, coercive (see Bluwstein et al. 2016).

Why does this distinction between the rhetoric and reality of community-based conservation matter for a study of ecological outcomes? First, by failing to critically assess the specific nature of the policy they study, Lee and Bond (2018) attribute "success" to CBNRM, when, in fact, governance processes on the ground would align better with a label such as "fortress conservation" (Brockington 2002). Second, a growing body of research illustrates how restrictive community conservation interventions that do not genuinely include local people in decision making, may, in fact, undermine conservation objectives and *ecological* outcomes (Duffy et al. 2014; Oldekop et al. 2016). We are thus left with unconvincing claims of short-term positive ecological outcomes, when, in reality, the lack of genuine community participation and inclusion in decision making could undermine actual long-term positive ecological outcomes.

Discussion

Lee and Bond (2018) fail to provide compelling evidence for the ecological success of community-based conservation in Randilen WMA. They employ an inappropriate concept of ecology by using higher wildlife and lower livestock densities as a proxy for ecological success, without taking into consideration rangeland health and processes, or the temporal and spatial variability of the socio-ecological system under study. By doing so, they ignore a large body of scholarship on the ecology of rangelands and livestock–wildlife interactions in semi-arid environments.

The methods to evaluate ecological impacts that Lee and Bond (2018) employ require a significantly longer study period between baseline, intervention, and outcome in the context of semi-arid environments, where highly variable spatial and temporal distribution of rainfall can mask other ecological interventions. Furthermore, evaluations of ecological impacts must explore and account for rival explanations when aiming to demonstrate causality.

Finally, Lee and Bond's (2018) characterization of community-based conservation misrepresents the reality of Randilen WMA, conflating coercive conservation interventions with genuine community-based conservation, which can undermine long-term positive ecological outcomes.

Lee and Bond (2018) have not quantified ecological success, but instead have demonstrated what conservation success can look like. Indeed, conservation intervention objectives are not necessarily the same as ecologically sound objectives (Adams and McShane 1992; Bennett et al. 2009; Fynn and Bonyongo 2011). If Randilen managers aimed to reduce the livestock density in the WMA, such a reduction—if realized—could qualify as a successful conservation initiative regardless of the ecological state of the environment.

While we agree that large numbers of poorly managed livestock may result in negative ecological outcomes, the continued vilification of livestock and pastoral livelihoods, based on an inappropriate concept of ecology and weak empirical evidence, sustains the false notion that wildlife and livestock must be managed separately. It perpetuates a century-old myth (Adams and McShane 1992) built on confounding actively managed rangelands with natural ecosystems that conservation scientists would like to protect from the very pastoral interventions that have co-produced these ecosystems together with wildlife. Future research on the ecological outcomes of community-based conservation must carefully consider the complex ecologies of people and wildlife in a dynamic environment.

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Conserving Africa's wildlife and wildlands through the COVID-19 crisis and beyond

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Conserving Africa's wildlife and wildlands through the COVID-19 crisis and beyond

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The SARS-CoV-2 virus and COVID-19 illness are driving a global crisis. Governments have responded by restricting human movement, which has reduced economic activity. These changes may benefit biodiversity conservation in some ways, but in Africa, we contend that the net conservation impacts of COVID-19 will be strongly negative. Here, we describe how the crisis creates a perfect storm of reduced funding, restrictions on the operations of conservation agencies, and elevated human threats to nature. We identify the immediate steps necessary to address these challenges and support ongoing conservation efforts. We then highlight systemic flaws in contemporary conservation and identify opportunities to restructure for greater resilience. Finally, we emphasize the critical importance of conserving habitat and regulating unsafe wildlife trade practices to reduce the risk of future pandemics.

The world is currently facing a major disease pandemic due to SARS-CoV-2 and its associated illness, COVID-19[1]. Governments are taking drastic steps to stem disease spread, including international travel restrictions and lockdowns of hundreds of millions of people. These measures are having massive socioeconomic impacts, as businesses and industries halt or scale back operations. The world's stock markets have become volatile, and a global recession is imminent. Virtually all sectors of life are affected and will likely remain so for at least 6–12 months[2]. Africa's economy could suffer from reductions in foreign investment, reduced inflows of remittances and foreign aid, and lower overall earnings[3]. Gross domestic products (GDPs) may contract by 4%, and governments face reduced tax revenues and devalued currencies, resulting in severe budget deficits and knock-on effects on African livelihoods[4]. Lockdown restrictions and economic turmoil could also compromise conservation of Africa's immensely valuable wildlife and wildlands, and the people who benefit from them.

Africa has nearly 2,000 Key Biodiversity Areas and supports the world's most diverse and abundant large mammal populations[5,6]. Financially, the most apparent value of Africa's wildlife and wildlands stems from wildlife-based tourism, which generates over US$29 billion annually and employs 3.6 million people[7]. Trophy hunting, a subset of the tourism industry, generates an estimated ~US$217 million annually over >1 million km^2 (refs. [8,9]). Tourism helps governments justify protecting wildlife habitat. It creates revenue for state wildlife authorities, generates foreign exchange earnings, diversifies and strengthens local economies, and contributes to food security and poverty alleviation (Table 1). Tourism generates 40% more full-time jobs per unit investment than agriculture, has twice the job creation power of the automotive, telecommunications and financial industries, and employs proportionally more women than other sectors[10].

Africa's wildlife also attracts considerable foreign investment via funding for conservation efforts (Table 1). Contributors range from multilateral institutions and bilateral funding agencies to private foundations, philanthropists, zoos and non-governmental organizations (NGOs). Reliable data on the scale and composition of donor funding are scarce, but external support makes up a substantial proportion of the total funding for wildlife conservation (Table 1). For example, donor contributions account for 32% of protected area (PA) funding in Africa, reaching 70–90% in some countries[11].

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Table 1 | Impacts and examples of conservation funding sources in Africa

Funding sources for conservation	Regional impact and funding	Examples of funding supporting government wildlife authorities, NGOs and community-based conservation	COVID-19-related threats to funding
Photographic tourism	• ~70 million visits per year to protected areas in Africa worth US$10–50 billion[68] • ~8.5% of continent's GDP[7] • 3.6 million direct jobs on the continent[7] • ~24 million indirect jobs	• ~50% (US$30 million) of Kenya Wildlife Service's annual budget from tourism, supporting management in 39 national parks and reserves[69] • ~80% of Zimbabwe Parks and Wildlife Management Authority's budget derived from tourism (including trophy hunting) (ZimParks, personal communication) • ~80% of Kenya community and private conservancies' operating budget from tourism, covering >60,000km^2, supporting >3,000 rangers and >700,000 households[70] (D.K., personal communication) • ~50% of Uganda Wildlife Authority's budget from gorilla-based tourism[71] • ~80% (US$52 million) of South African National Parks' annual budget from tourism, supporting 19 national parks[72]	• Closure of international travel, which could extend for months, reduces tourism • Closure of domestic travel reduces tourism • Economic recession reduces future international travel • Fear of travel during COVID-19 pandemic reduces arrivals
Trophy hunting	• ~US$200 million annually, practised over an area of >1 million km^2 (refs. [8,9]) • ~552,000 km^2 (43%) of PA extent in lion range dependent trophy hunting (R. Feber, personal communication)	• Supports budgets of 82 conservancies in Namibia covering ~20% of the country (162,000 km^2), encompassing ~189,000 community members (9% of Namibia's population)[73] • ~68% of Tanzanian PAs rely on income from trophy hunting, covering 250,000 km^2 • ~38% of Zimbabwe's state-owned PAs are designated as hunting areas, as are large areas of community and private land (ZimParks, personal communication)	• Closure of international travel, which could extend for months, reduces hunting • Economic recession reduces hunting • Fear of travel during COVID-19 pandemic reduces arrivals • Increase in blanket opposition to all wildlife trade
International aid	• ~US$833 million from 2010–2016 to combat illegal wildlife trade, of which ~US$609 million to PA management estimated for the period 2000–2009 for the whole continent[74] • Makes up an average of 32% of the management budget of PAs in Africa, up to 70–90% in some countries[11]. • >US$6 million from the Association of Zoos and Aquariums members to African species in 2018[75]	• ~90% (~US$3 million) of Northern Rangelands Trust's budget supporting 39 community conservancies across 42,000 km^2 (ref. [76]) • ~25% (US$3.35 million) of Gorongosa National Park's 2019 budget from bi- and multilateral cooperation partners[77]	• Economic recession reduces aid budgets • Focus shifts to humanitarian and financial crisis relief
Philanthropy • Individuals • Corporations • Foundations • Zoos		• 40% (US$120 million) of World Wildlife Fund's global budget from individual donors[78] • ~35% (US$12 million) of African Wildlife Foundation's 2019 budget from individual donors, ~30% (US$10 million) from public sector donors[79] • ~32%, 25% and 23% of Africa Parks' 2018 budget of US$50 million donated by public institutions, individuals and foundations, respectively, supporting 15 parks across 105,000 km^2 in 9 countries[80] • 58% (~US$8 million) of Gorongosa National Park's 2019 budget from foundations, philanthropy and donations[77] • >US$11 million for Sheldrick Wildlife Trust in 2018–2019[81], donated by individuals, corporations, private foundations and public charities, supporting PA management, lease fees, community education and outreach, and veterinary assistance across Kenya	• Economic recession reduces philanthropic spending[38] • Focus shifts to humanitarian and financial crisis relief • Zoo closures limit income and conservation spending (215 of 238 American zoos and aquariums closed as of 23 March 2020[82]; US museum and zoo community requesting US$4 billion support[83])
Domestic expenditure	• Variable, but often low	• ~50% (US$30 million) of Kenya Wildlife Service's budget from national government[69] • Only 3% of African Parks' 2018 operational budgets from national governments[80]	• Local economic recessions reduce national budgets • Governments shift focus to humanitarian and financial crisis response and healthcare infrastructure

Funding from international aid is higher than estimated because spending has increased since previous estimates[11,74] and estimates are not exhaustive. No comprehensive estimate for domestic governmental expenditure exists.

Wildlands and conservation areas provide critical resources for local people who benefit from using wildlife, grass, water, firewood and non-timber forest products. During times of distress such as economic downturns, people rely more heavily on such resources[12]. In addition, Africa's wildlife provides important cultural and heritage values for multiple ethnic groups, and charismatic species have extensive symbolic value internationally[13]. Africa's wildlife also holds considerable 'existence' value—the value people derive from simply knowing it exists[14].

The state of African conservation

The backbone of African conservation efforts is made up of 7,800 terrestrial PAs covering 5.3 million km^2, ~17% of the continent's land area[15]. PA coverage in some countries (notably in southern and East Africa) far exceeds the global average. In parts of Africa, vast transfrontier conservation areas transcend national borders, creating protected landscapes spanning hundreds of thousands of square kilometres. Most PAs are state-owned and managed by government wildlife authorities, often with substantial support from tourism and

hunting operators[16]. Increasingly, conservation NGOs and private sector entities cooperate with governments to manage state-owned PAs through collaborative management partnerships (CMPs)[17]. In addition, conservation efforts on private and community lands have grown in recent years[18,19], expanding wildlife habitat, buffering PAs, reducing edge-effects, improving ecosystem representation, securing seasonal migration areas, and meaningfully engaging and benefiting rural communities that live with wildlife[20–22]. In Namibia, community conservancies account for 170,000 km², and in South Africa, game ranches cover 205,000 km², both exceeding the land area encompassed by state PAs[19,23]. Community-based conservation (CBC) programmes have grown in the last 20 years, supporting millions of rural African livelihoods[22,24].

Despite impressive political commitment to conservation in Africa, the continent suffers severe and persistent funding shortages that hinder management effectiveness. Africa's state-owned savannah PAs with lions face recurrent budget deficits of US$1.2 billion per annum, rendering wildlife susceptible to threats, while forest PAs are likely no better protected[11]. Key threats include habitat loss, degradation, fragmentation, encroachment, poaching and climate change[25–27]. These factors, combined with poor governance, poverty, increasing human populations and illegal wildlife trade, continue to drive wildlife declines across the continent[11,28–30]. In particular, the loss of large mammals compromises ecosystem function[31,32]. Thus, with few localized exceptions, African conservation was in crisis even before COVID-19 hit. The pandemic could amplify the crisis to catastrophic effect.

Environmental impacts of the COVID-19 crisis

Researchers have documented some positive environmental outcomes of the COVID-19 pandemic. For example, reduced industrial activity and mechanized transport have lowered emissions and air pollution worldwide[33]. Some Asian countries (notably China and Vietnam) have taken steps to restrict trade that threatens wildlife. If regulated and enforced over the long term, such restrictions could reduce poaching in Africa for illegally sourced products that supply Asian markets. Gabon has banned consumption of bats and pangolins following the COVID-19 crisis[34]. Transport restrictions due to lockdowns may curb trade in wildlife products and provide respite for PAs that suffer negative impacts of tourist congestion.

These positive environmental outcomes are likely temporary and prone to reversal when travel restrictions ease and countries return to business as usual. We argue that the net environmental impact of the COVID-19 crisis in Africa will be strongly negative because the crisis creates a 'perfect storm' of reduced funding, lower conservation capacity, and increased threats to wildlife and ecosystems (Fig. 1). Wildlife conservation arguably faces its most serious challenge in decades.

Reduced conservation funding

Governments face severe budget crises driven by the economic fallout of the COVID-19 pandemic and the cost of relief measures. Shortages will compel policymakers to cut anything perceived as 'non-essential'[4]. African wildlife authority budgets, already grossly inadequate, risk being slashed further, jeopardizing wildlife and wildlands.

Compounding these effects is the continent-wide collapse of wildlife-based tourism due to travel restrictions and traveller concerns (Fig. 2; Table 1). While previous shocks, for example, the 2014 Ebola epidemic and the 2008 financial crisis, markedly reduced tourism in some African countries, the negative, continent-wide impacts of COVID-19 on the industry are unprecedented in scale and severity[35]. Some 90% of African tour operators have experienced >75% declines in bookings[36]. Because tourism is the largest contributor to PA financing in some countries, lost revenues have major ramifications for state wildlife authorities, private concessionaires and landowners, and community conservation programmes (Figs. 1 and 2)[37]. Decreasing tourism revenue threatens millions of jobs and peripheral industries, severely impacting the livelihoods of some of the continent's poorest people (Box 1). For nations less reliant on wildlife tourism for conservation (for example, in the forest biome), the impact will be lower. However, if the industry is slow to bounce back, under-visited PAs developing nascent tourism products may be the last to see visitors.

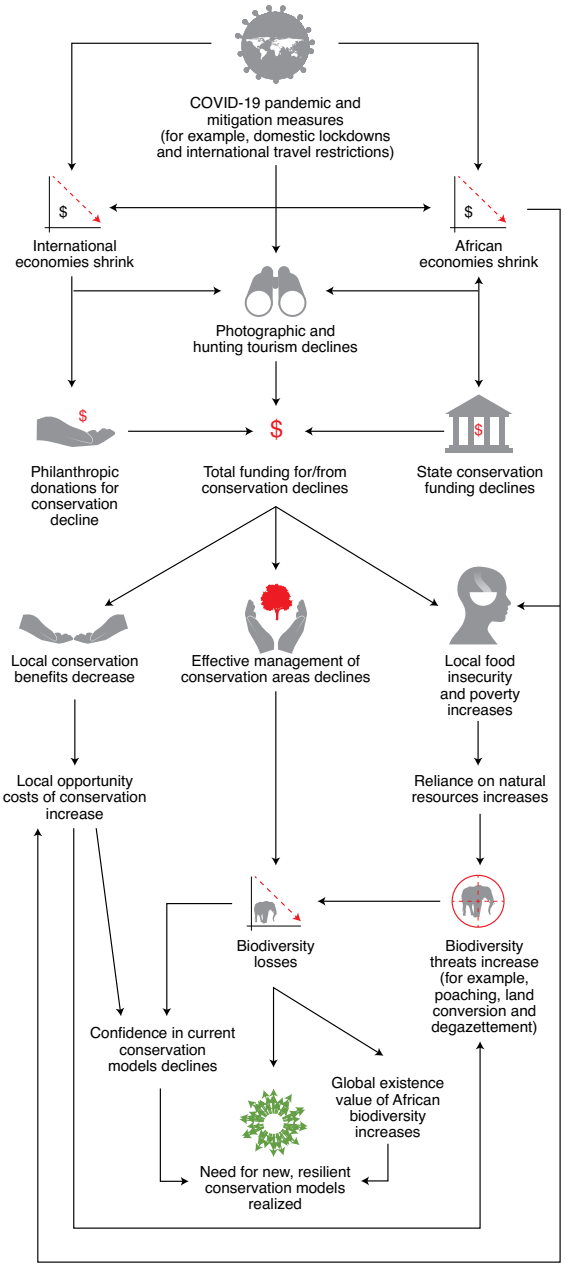

Fig. 1 | Schematic of the potential cascading impacts of COVID-19 on conservation in Africa. Arrows indicate the directionality of potential impacts among different elements in Africa's conservation framework.

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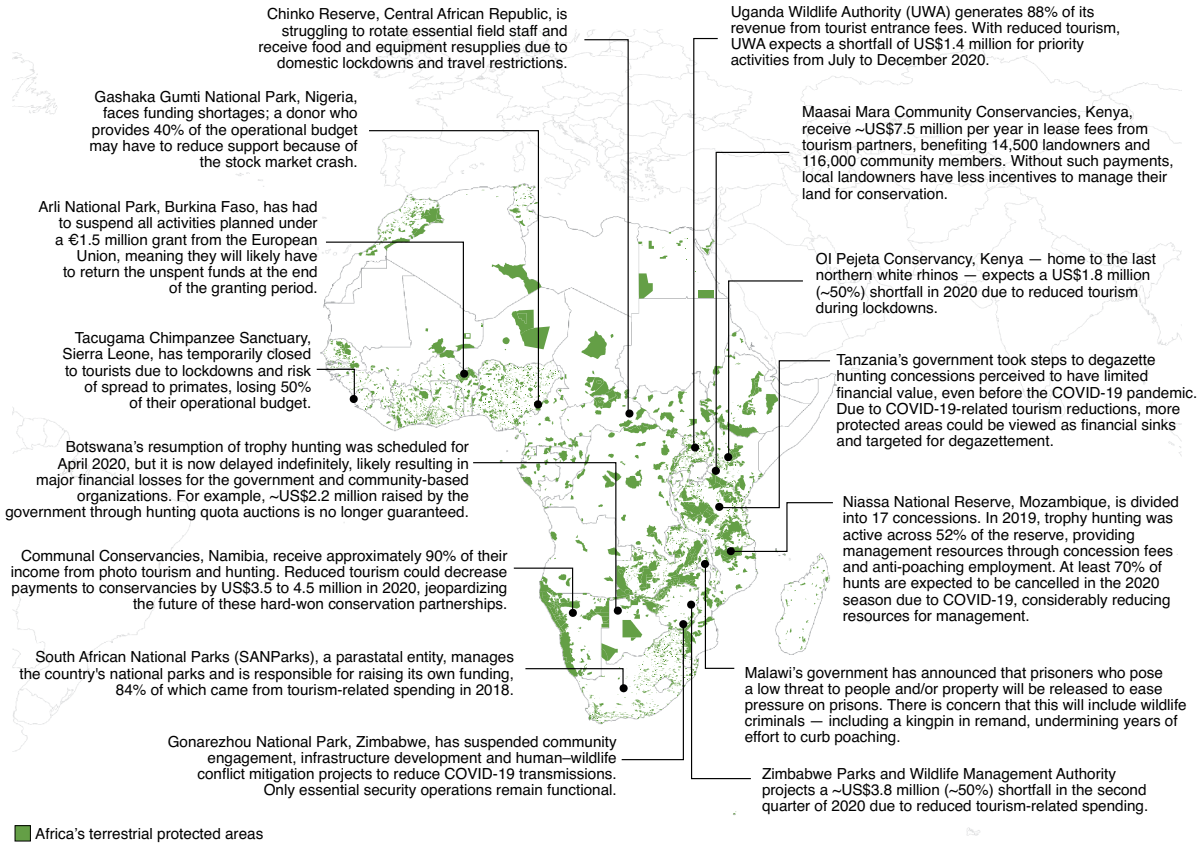

Fig. 2 | Examples of realized and potential impacts of COVID-19 on conservation in Africa, as of April 2020. 'Africa's terrestrial protected areas' refers to all nationally gazetted, terrestrial protected areas in Africa[15]. The source of each example is shown in Supplementary Table 1.

Beyond tourism revenue losses, we expect reduced donor funding for African conservation over the next 1–2 years and possibly longer due to flagging economies and shifting priorities. During the previous global financial crisis, total charitable giving in the United States dropped by 7% in 2008 and 6.2% in 2009[38], and conservation endowments declined in value by 40%[39]. The current economic downturn and stock market volatility, to an even greater degree, may reduce capacity of private donors, corporations and foundations to give philanthropically. Restrictions on travel and gatherings have caused cancellation and postponement of key conferences and conservation fund-raising events. Many zoos are closed, and reduced revenues will likely limit support for in situ conservation efforts. The pandemic will also shift focus from conservation towards humanitarian causes. Some bi- and multilateral donor agencies increased funding to developing countries in response to the 2008 financial crisis[40], but the extent of the current economic and humanitarian challenges is such that any additional funding would likely be directed at those realms. Some emergency conservation funding is being organized in response to the crisis[36], though it will likely fall far short of offsetting losses.

Impaired conservation operations

Reduced funding is likely to constrain the ability of conservation practitioners to manage PAs and other conservation landscapes, force lay-offs of key staff, and prevent purchase of critical supplies[35] (Figs. 1 and 2, Box 1). In addition, COVID-related restrictions on people's movements undermine the ability of practitioner agencies to undertake their conservation work, as reported by the author group's extended network of field colleagues (Figs. 1 and 2). Some lockdown policies in African countries prevent all but 'essential services'. Generally, anti-poaching seems to be permitted, but rotating staff and supplying field rangers with essential consumables may be disrupted, resulting in exhaustion and reduced morale of rangers (Figs. 1 and 2). Policies that prevent operations and activities deemed non-essential could have considerable impacts on community conservation, which often relies on regular meetings, interactions and collaboration among a variety of actors, often without access to remote communication technology (Box 1).

Increased conservation threats

Natural resources and the ecosystems that produce them face heightened pressure due to the COVID-19 pandemic. Plummeting tourism revenue and negative economic impacts of the pandemic will likely increase rural poverty. Simultaneously, COVID-19-related restrictions and budget constraints will impair conservation operations. Consequently, as detailed in Fig. 1 and Box 1, we expect increased poaching, tree cutting, artisanal mining, PA encroachment, agricultural conversion and possibly the ultimate degazettement of the most-affected PAs. With many ecosystems and wildlife populations already near tipping points, the current crisis may result in population declines, local extinctions of some species, and intensified disruptions of ecological processes[6].

Box 1 | Impact of COVID-19 on local communities and conservation threats

People living on the periphery of PAs are often food-insecure, neglected by governments and heavily dependent on natural resources[96]. However, they are the users of and potential custodians of natural resources. They bear costs of conservation (for example, through human–wildlife conflict, exclusion from natural resources, and, in some cases, loss of land), often without receiving commensurate benefits. For several decades, community-based conservationists have tested economic and engagement models to empower local communities to own and manage natural resources in the ecosystems where they live[97].

The COVID-19 crisis challenges these models. Impacts on community-based conservation and the tourism industry have massive economic implications for communities[3]. Loss of tourism and trophy hunting revenue can increase opportunity costs of conservation and the risk of land conversion. The sudden loss of wildlife-based revenue could erode communities', private landowners', and even governments' confidence in wildlife conservation as a reliable land-use option. Movement restrictions and social-distancing rules curtail engagement between conservation groups and communities, compromising hard-won trust with local people[98].

Besides the loss of tourism revenue, rural communities face financial hardship from the wider economic turmoil wrought by the COVID-19 pandemic and governmental responses. In some areas, livestock markets have closed, cutting off revenue streams for rural communities. Nearly 20 million jobs are at risk on the continent if the crisis continues[3]. Following lockdown-driven unemployment, people may return to rural homes, as has been observed for transnational labourers, many of whom returned to communities next to PAs near international borders[99].

Increased poverty and food insecurity will likely increase conservation threats. In the absence of financial capital reserves, food-insecure rural Africans could be attracted to the periphery of PAs to draw upon natural resources[100]. Anticipated effects include increased poaching, tree cutting for timber and charcoal, artisanal mining, PA encroachment by people and livestock, and conversion of natural habitat[101]. We expect the threat posed by the increase in consumption of bushmeat to be particularly severe, with anecdotal evidence reported from Tsavo East National Park (https://go.nature.com/32rNQYH). These threats will coincide with reduced funding, operational ability, and field presence of community conservancies, state wildlife authorities, private landowners, conservation NGOs, and tourism and hunting companies.



Homesteads at the periphery of the unfenced Gonarezhou National Park, Zimbabwe, Great Limpopo Transfrontier Conservation Area; 2009. Credit: Alexandre Caron

Following the emergency response to the crisis in the periphery of PAs, new models linking conservation and local development will be needed.

Risk of future outbreaks due to human impacts on nature

The COVID-19 pandemic, like the SARS-CoV 1 and Ebola epidemics, likely originated from human consumption of wild animals. Live wildlife markets create opportunities for pathogens to infect naïve domestic species or humans and trigger new diseases[41,42]. In Africa, particularly in the tropical forest biome, bushmeat markets expose human populations to species identified as high risk for pathogen spillover, such as primates, bats and rodents[43]. The combined effects of reduced conservation efforts and increased poverty could create a positive feedback loop where intensified reliance on natural resources spurs human encroachment into natural habitats, increases exposure to and consumption of wild animals, and amplifies future pandemic risks[44]. Conversely, effective conservation of species and habitats has been directly linked to decreases in the number of viruses that animals share with humans[45]. Adapted disease surveillance systems, especially for the wildlife–domestic–human interface, need to be developed and supported in emergence hotspots[46].

How can the world mitigate these risks?

The conservation crisis facing Africa must not be overlooked, even as governments and NGOs respond to the health and humanitarian crisis. While the current focus on health and the economy is critical, a longer-term perspective is vital. Supporting conservation efforts will help national and local African economies recover from the devastating impacts of COVID-19 by diversifying and bolstering economies, creating employment for rural citizens, and protecting ecosystem services. Safeguarding wild habitats against encroachment can also help tackle a key root cause of emerging zoonotic diseases, lessening future pandemic risks. Reducing support for African conservation at this critical juncture could undo decades of progress. Here, we describe steps necessary to safeguard African wildlife and landscapes and associated rural populations during and beyond the COVID-19 crisis. We outline actions needed to (1) manage the immediate crisis; (2) tackle environmental destruction and address the ongoing threats of habitat destruction and illegal, unsustainable and/or unsafe wildlife trade; and (3) address systemic flaws in the current conservation model.

1. Manage the immediate crisis. African conservation will flounder unless the international community intervenes to provide crisis funding, recognizing conservation as an essential service and PAs as global public goods. The developed world is rapidly implementing mechanisms to bail out impacted businesses and industries, which in the United States runs into trillions of dollars. However, cash-strapped governments in developing countries lack such potential. Furthermore, no such mechanisms exist for supporting conservation specifically. Donors could unite to create an emergency fund for struggling wildlife authorities, communities, private landowners and conservation NGOs. In addition, key industries underpinning conservation efforts, such as tourism, need support, both via tax breaks and direct financial assistance, provided they can demonstrate ongoing investment into protection of the wildlands on which they depend. Realistically, the developed world

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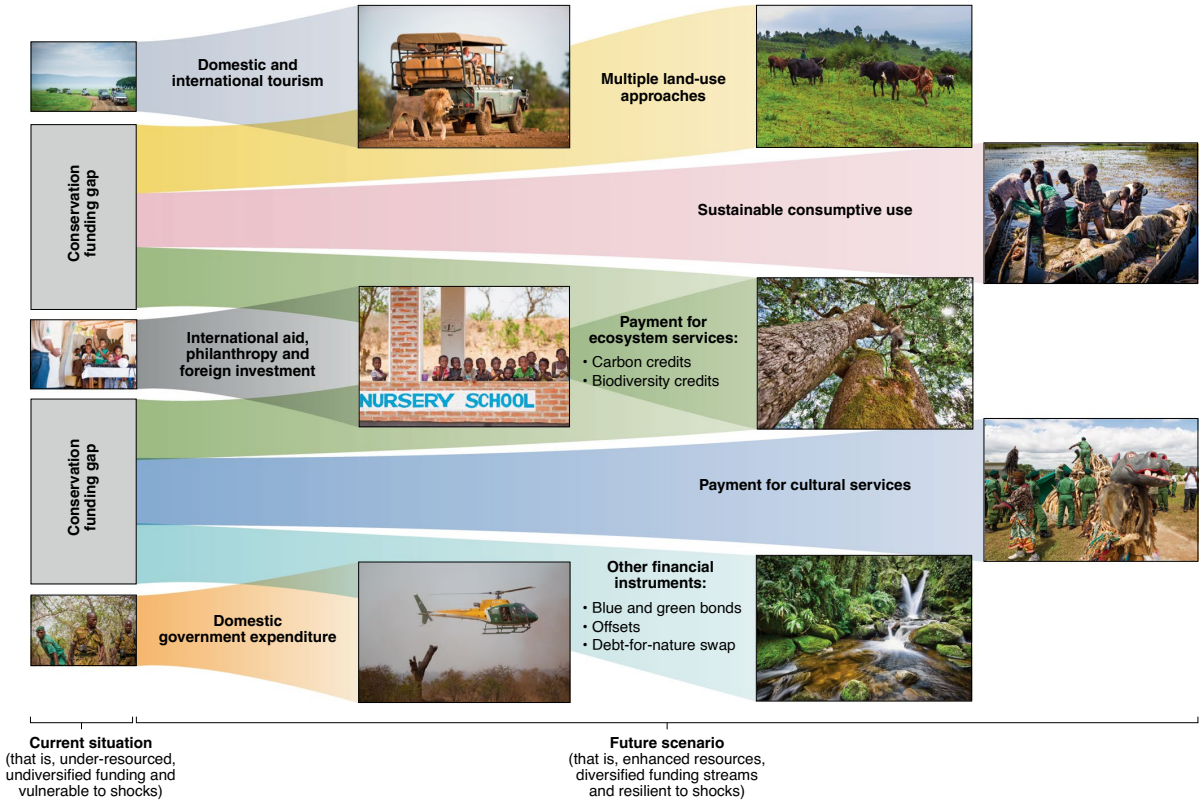

Fig. 3 | Conservation funding in Africa is insufficient, lacking diversity and vulnerable to shocks like the COVID-19 pandemic. Enhancing the magnitude and diversity of funding could increase resilience and efficacy. For more detail, see Table 2. Photograph credit: Morgan Trimble.

would have to be the primary source of such funding, from multi- and bilateral institutions, corporations and the public. International philanthropic foundations have an opportunity to intervene, make a transformational difference to conservation in Africa and help avert disaster.

Business as usual will not be possible for most conservation practitioners during the crisis. They will require strategic planning to prioritize critical activities and minimize risks of 'overstretching'. They should emphasize maintaining crucial operations and retaining as many members of staff as possible, such that they can expand again when the crisis abates. Conservation practitioners and large NGOs in particular must cut wastage and excesses. NGOs should prioritize salaries for staff in Africa where possible, noting that salary protection schemes do not generally exist on the continent.

2. Defend against future disease outbreaks by regulating wildlife trade and minimizing habitat loss. China and Vietnam have taken steps to restrict trade and consumption of wildlife in response to the COVID-19 outbreak. Worldwide, governments and organizations should improve regulations and enforce existing laws to clamp down on unsafe wildlife trade practices that jeopardize human health or conservation objectives. Trade restrictions should be appropriate, proportionate and enacted with local buy-in and political commitment. Otherwise, unsustainable or dangerous trade may resume as soon as the immediate crisis abates. Efforts to stamp out unsafe and unsustainable practices should not, however, undermine legal components of the wildlife trade industry that are or could be well regulated, pose a controlled disease-transmission risk and support millions of livelihoods[47].

In addition to addressing the disease-transmission risk of the wildlife trade, governments and organizations should tackle the other critical drivers of infectious disease emergence including habitat destruction, which can be driven by industrial livestock production[44,48]. In forest regions of the continent, logging and mining are encroaching into remote areas[49,50], likely facilitating disease spread into and amongst human populations, as seen in the Amazon[51]. Forest regions urgently require flexible funding mechanisms to prevent the sale of forest concessions and construction of development corridors through and unsustainable resource extraction from natural habitats. Such steps could also help protect Indigenous peoples from disease and from losing ancestral lands.

3. Address systemic flaws in the structure and function of conservation in Africa. The COVID-19 crisis has highlighted the fragility of conservation efforts in Africa and has exposed fundamental shortcomings (Fig. 3).

Baseline funding for conservation from African governments is simply inadequate. Many nations struggle with high poverty rates and do not have the luxury and the wealth to conserve African wildlife and wildlands alone. Currently, overreliance on short term, ad hoc external funding streams (including philanthropy) is unsustainable and insecure. Many PAs rely on a single, inadequate funding source. Tourism is a promising but insufficient source of conservation funding. Some African countries' overreliance on international tourism to support conservation creates vulnerability to stochastic events. Few hold sufficient funds in reserve to finance conservation operations through hard times. Other countries do not benefit substantially from wildlife-based tourism at all (Fig. 4). Where tourism

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Table 2 | Mechanisms to generate funding for conservation in Africa

	Funding source	Rationale	Steps to unlock or improve revenue stream	Examples
Diversify revenue streams from wildlife-friendly land use	Multiple land-use approaches (for example, livestock co-management)	When managed correctly, livestock can create resilient income for private and community landowners, while achieving ecological goals[22,61].	Encourage and support competent governance systems and institutions working at appropriate spatial scales to ensure sustainable rangeland management in and around PAs, where applicable	Ol Pejeta Conservancy, Kenya
	Sustainable consumptive use of wildlife	Revenue gained from sustainable consumptive use of wildlife (for example, game meat and trophy hunting) can provide income for local communities and wildlife authorities.	Where appropriate, devolve rights over wildlife to the lowest possible level, incentivizing landowners to sustainably manage their wildlife resources; ensure accountability, good management and transparency	Conservancies in Zimbabwe, Namibia's community conservancies, and well-managed state-owned concessions across multiple countries (noting that by no means all concessions are well managed)
	International tourism	Only a handful of African countries earn substantial tourism revenue to fund conservation, but many have potential.	Invest in infrastructure and protect wildlife assets, while developing enabling environments for tourism[55,73]	Botswana, Rwanda and others
	Domestic tourism	Domestic tourism may be less susceptible to global economic shocks and travel restrictions; growth could increase local and regional support for conservation efforts[58].	Increase domestic marketing, reduce barriers to access, offer prices and packages tailored to locals.	Nairobi National Park, Kenya
Increase domestic expenditure	Domestic government expenditure	Few nations invest in their PAs, yet PAs can contribute considerably towards national GDP and employment and provide ecosystem services.	Consider identifying a set budgetary allocation for the protection of nature, similar to the 2003 Maputo Declaration on Agriculture and Food Security; support alignment between development and conservation expenditure	In northern Kenya, research suggests economic returns from investment in conservation could exceed those from road construction[84]
	Endowments	Endowments can help buffer the risk of critical losses of operating revenue during financial crises and provide budget stability and continuity	Encourage governments, particularly those in the developed world, to help establish and fund national endowments to manage natural assets	~100 conservation endowments across 60 countries globally and at least 14 in southern and 93 in East Africa
	Financial instruments (offsets, blue and green bonds)	Rapid development in Africa risks widespread environmental degradation, but infrastructure- and resource extraction- offsets present enormous financial opportunities for conservation.	Consider mandating and improving mechanisms for offset payments to generate sustainable revenue to fund PA networks.	Construction of South African United Pulp Mill, and land set aside for new PAs
Increase international funding	Foreign investments and partnerships for PA management	Investments and collaborative management partnerships in PAs have increased in recent years, driven by substantial foreign investment and vastly improving conservation performance of some PAs[17,24]	Create enabling political and regulatory environments to attract investors and partners to help manage and support PAs and community lands	African Parks' network of PAs; Gorongosa National Park, Mozambique; Gonarezhou National Park, Zimbabwe
	Payments for ecosystem services	Carbon credits, one example of payments for ecosystem services, can help tackle both the climate and biodiversity crises[85], especially efforts focused on securing critical wilderness areas, including PAs[86]	Formalize, scale up, and require mechanisms for such payments for carbon emitters and adapt to include payment for standing carbon as well as avoided losses	Wildlife Works, Tsavo, Kenya (www.wildlifeworks.com)
	Payment for cultural services	Globally, branding, advertising, television, film and products make wide use of wildlife, including many endangered African species; corporations that derive profit from wildlife could contribute to ensure their persistence in the wild[87]	Encourage industry and business to contribute each time an animal appears in their adverts or media to raise money for wildlife conservation, habitats and animal welfare	Lion's Share Fund (www.thelionssharefund.com)
	Debt-for-nature swaps	Many countries are highly indebted with debt repayments consuming 22% of the continent's budgets[4], and a comprehensive debt moratorium could release up to US$50 billion[88]; Debt-for-nature swaps could forgive debt while mandating local investment in natural assets.	Adapt support for debt forgiveness[89] to include directives to invest in conserving natural assets	Trialled in the Seychelles[90]

None of these funding sources are panaceas, and for many, logistical, ethical, social and ecological constraints may limit broad-scale application.

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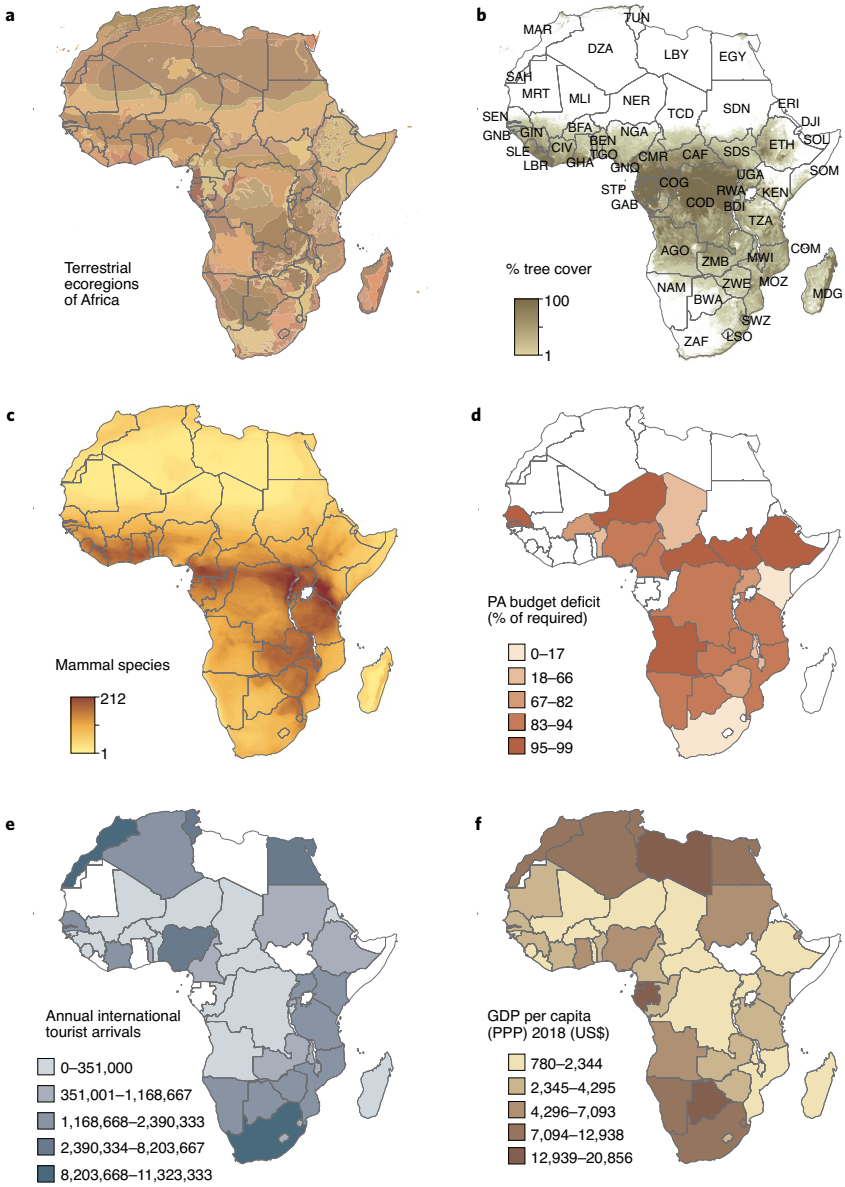

Fig. 4 | Heterogeneity of the African continent will shape the socioeconomic and environmental impacts of the COVID-19 pandemic and the appropriate response from conservation stakeholders. a, The terrestrial ecoregions of Africa[91]. **b**, Percentage tree cover with >10% canopy density in 2000[92] (source: Hansen/UMD/Google/USGS/NASA). Countries are labelled with their ISO-3 codes. **c**, Mammal species richness[93]. **d**, Funding deficits of national protected area networks in African lion range states[11]. **e**, The average number of annual international tourist arrivals to African countries from 2016–2018[94]. **f**, The GDP per capita (corrected for purchasing power parity (PPP)) in current US dollars of African countries in 2018[95]. In **d**–**f**, countries are filled white where data were unavailable, and values were classified using the Jenks natural breaks method.

does flourish, the communities bearing the costs of wildlife often receive negligible benefits, disincentivizing conservation.

There is also a lack of sufficient, long-term, systematic support for African conservation from the Global North, who benefit considerably from Africa's wildlife and lands, without contributing sufficiently towards its costs. Relative to their wealth, some African countries carry a disproportionately high burden from their conservation efforts and so, the international community should provide support at commensurate levels, recognizing that Africa's natural treasures are global assets; environmental services from Africa benefit the world through carbon sequestration; and African ecosystems play a critical role in safeguarding human mental and physical health[11–13,52].

Most fundamentally, there is insufficient alignment between conservation and human-development agendas. Here, we outline emerging opportunities to rethink and restructure conservation funding in Africa to improve long-term resilience (Fig. 3).

B. Conserving Africa's wildlife and wildlands through the COVID-19 crisis and beyond

Increase the resilience of conservation. Africa is diverse, presenting an array of contexts in which conservation must be practised. Thus, the solutions we suggest must be tailored appropriately (Fig. 4).

3a. Recognize the reliance of development on natural assets. Effective long-term conservation in Africa depends on finding sufficient funding and building political and public will. Aligning conservation and development interests could help on both fronts. African economies depend considerably on ecosystem services, so this alignment can be supported in several ways, for example:

(i) Quantify the value of natural assets and ecosystem services and incorporate those values into national budgets, balance sheets, and planning for natural resource use to reinforce the value of conservation.
(ii) Position PAs in their broader landscapes as hubs for local development, service provision and even disaster relief. This has been achieved via collaborative management partnerships for some African PAs[17,24].
(iii) Properly engage local people as stakeholders in conservation. Inside PAs, create forums that enable communities to participate in PA governance and ensure communities benefit from tourism to strengthen engagement. Outside PAs, promote policies that devolve resource and wildlife utilization rights to communities to support sustainable management and strengthen institutions that allow communities to optimize their economic opportunities[53].
(iv) Encourage conservation organizations to work with development specialists on visible support for core community livelihoods, such as livestock and crop production, thereby earning public backing and increasing resilience of local communities to shocks such as the COVID-19 pandemic[22]. For example, if conservation organizations provide security or markets for livestock, local people would link those benefits to conservation; the 'herding for health' programme is testing this approach in northern Kenya and southern Africa[54].

3b. Support African civil society conservation efforts. With international conservation organizations limited by travel restrictions, there is an opportunity for national conservation organizations and civil society efforts to fill gaps. International partners should support local people and services by providing funding and sharing expertise remotely. Once the crisis has subsided, local conservation capacity will have increased and could continue to be supported, together with revived efforts by international NGOs.

3c. Diversify revenue-generating options from wildlife areas. The volatility of international tourism and decline in trophy hunting demonstrate the need to create local revenue streams that are resilient to global shocks (Fig. 3, Table 2). Only a handful of African countries earn substantial wildlife tourism revenue[16]. Others need to unlock tourism potential by investing in infrastructure and wildlife protection and creating an enabling environment for tourism[55,56] (Fig. 3, Table 2). Conversely, some southern and East African nations heavily reliant on international tourism should foster domestic tourism to increase resilience to global shocks and build longer-term public support for conservation[57,58]. With the trophy hunting industry apparently waning, due in part to pressure from Western anti-hunting advocates, PAs that currently depend on trophy hunting revenue should seek alternative income streams[59]. Given the existing serious funding deficits for conservation in Africa (Fig. 4), collapse of the trophy hunting industry in the absence of alternatives carries grave ramifications for conservation across vast areas[16,59]. Wealthier countries must contribute towards alternative and improved revenue-generating mechanisms to help pay for the management and opportunity costs of Africa's vast network of semi-protected areas. In some contexts, livestock or sustainable use of wildlife can be compatible with conservation[60,61]. In South Africa, a biodiversity economy strategy promotes bioprospecting and game ranching for hunting and meat-, skin- and leather exports as key revenue streams complementing eco-tourism[62]. Africa is developing at a rapid pace, and governments should use the 'biodiversity mitigation hierarchy' to diminish ecological damage and mandate offset payments to generate sustainable revenue for conservation[63].

3d. Increase domestic expenditure. Ultimately, for wildlife and wildlands to deliver on their economic potential, African governments must invest sufficiently to protect their own assets. After the crisis subsides, African nations could identify a set budgetary allocation for the protection of nature, similar to the 2003 Maputo Declaration on Agriculture and Food Security. National governments could also establish endowment funds with the help of foreign investment, mandate a biodiversity mitigation hierarchy, and develop green and blue bonds.

3e. Increase international funding. While greater domestic investment is desirable, substantially more financial support is needed beyond this. Emerging mechanisms for international governments, corporations, individuals and NGOs to provide funding include investments in PAs and community land, payments for ecosystem and cultural services, and debt-for-nature swaps (Table 2).

3f. Improve revenue distribution mechanisms. Africa needs improved mechanisms to effectively generate and disburse wildlife-related revenue and offset the opportunity, indirect and direct costs of wildlife. Such mechanisms need to recognize the role of governments, private landowners, and communities in Africa as custodians of global wildlife assets. Examples include: (1) direct payments by wealthy countries to African nations for setting aside wilderness, such as the payments made by Norway to Gabon[64]; (2) land leases, whereby land is leased from owners and set aside for conservation to prevent conversion to less biodiversity friendly land use, as occurs, for example, in conservancies around the Maasai Mara[65]; (3) biodiversity stewardship programmes that pay or incentivize landowners to practice conservation-friendly land management; (4) performance payment schemes that reward local people for conserving wildlife (as is being trialled in Mozambique, Namibia and Tanzania, for example, http://wildlifecredits.com); (5) 'conservation basic incomes' that compensate communities who protect nature[66]; and (6) schemes and actions that reduce the cost of coexisting with wildlife[67].

Conclusions

The COVID-19 crisis threatens conservation efforts in Africa with a 'perfect storm' of reduced conservation funding, depleted management capacity, collapse of community-based natural resource management enterprises, and elevated threats. The crisis demands a concerted international effort to protect and support Africa's wildlife and wildlands and people that are dependent on them. African governments, the international community, donors and conservation practitioners should collaborate through decisive effort and adaptive management to minimize negative impacts. At this critical juncture, business as usual could be catastrophic, but decisive and collaborative action can ensure that Africa's wildlife survives COVID-19 and that more resilient conservation models benefit humans and wildlife for generations.

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The authors declare no competing interests.

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