The role of wildlife, livestock, and humans in ecosystem restoration

Insights from an African savanna

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The candidate confirms that the work submitted is his own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

Rationale for submitting the PhD thesis in the alternative format:

In this thesis I explore three aspects of ecosystem degradation and restoration in an African savanna: 1) the individual and interactive effects of cattle stocking rate and large wild herbivores on smaller wildlife; 2) whether cattle at different stocking rates functionally replace large wild herbivores in shaping understory vegetation; and 3) the socio-economic factors that influence equity in restoration projects. These three components employ frameworks and methodologies from different disciplines in a mixed methods approach. Compared to a traditional thesis format, the grounding of each component within the relevant literature is more effectively achieved as journal articles, which are presented in:

Chapter 2: Wells HBM, Kimuyu DM, Odadi WO, Dougill AJ, Stringer LC, Young TP (2021) Wild and domestic savanna herbivores increase smaller vertebrate diversity, but less than additively. Journal of Applied Ecology 58:953–963 https://doi.org/10.1111/1365-2664.13843

Chapter 3: Wells HBM, Porensky LM, Veblen KE, Riginos C, Stringer LC, Dougill AJ, Young TP (2021) At high stocking rates, cattle do not functionally replace wild herbivores in shaping understory community composition. Ecological Applications https://doi.org/10.1002/eap.2520

Chapter 4: Wells HBM, Kirobi EH, Chen CL, Winowiecki LA, Vågen T-G, Ahmad MN, Stringer LC, Dougill AJ (2021) Equity in ecosystem restoration. Restoration Ecology 29(5):e133385 https://doi.org/10.1111/rec.13385

For all of the above papers, I conceived the research design, collected the data, analysed the results and wrote the manuscripts. All co-authors contributed critically to manuscript editing and gave final approval for publication. Other supporting first-/co-authored manuscripts are listed in Appendix 1.

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Abstract

Wildlife populations are declining globally and much of the remaining terrestrial wildlife cohabit rangelands alongside humans and their livestock. Over a quarter of the world's land surface is grazed by livestock, which are replacing wildlife, potentially impairing ecosystem structure and function. The aim of this study is to facilitate ecosystem restoration by deepening our understanding of the relationships between wildlife, livestock, humans, and vegetation. Whether livestock can functionally replace wildlife and what factors influence equity in ecosystem restoration, including cost/benefit sharing and involvement in decision-making, remain critical knowledge gaps. I explore three specific aspects through interrelated studies from Laikipia County, Kenya: 1) the individual and interactive effects of cattle at varying stocking rates and large wild herbivores on smaller wildlife; 2) and on understory vegetation; and 3) the influence of socio-economic variables on equity in ecosystem restoration through exotic invasive cactus removal. To address these, I employed a mixed methods approach, incorporating camera trapping and vegetation surveys in a long-term exclosure experiment, together with spatially explicit questionnaires and key-informant interviews. Findings show that smaller wildlife habitat use responds to total herbivory, whether by domestic or wild animals, while understory plant communities are primarily shaped by herbivore identity at high cattle stocking rates. Interactions between cattle and large wild herbivores were evident in their effects on both smaller wildlife and understory vegetation. Employment and distance to restoration site can interact in counterintuitive ways in their influences on perceived equity. Restoration is influenced by different but intimately linked dimensions of equity and incorporating equity into project planning and implementation may improve restoration outcomes. This research is one of the first to experimentally demonstrate interactive effects of cattle stocking rates and large wild herbivores on vegetation and smaller-bodied wildlife and provides novel insights into the factors that influence equity in restoration initiatives.

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Abbreviations

AIC – Akaike Information Criterion

ANOVA – Analysis of variance

CBD – Convention on Biological Diversity

FAO – Food and Agriculture Organisation of the United Nations

GIS – Geographic Information System

GPS – Global Positioning System

HVR – Historical Range of Variability

IPBES – Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

IPCC – Intergovernmental Panel on Climate Change

KLEE – Kenya Long-term Exclosure Experiment

LDN – Land Degradation Neutrality

LMM – Linear mixed model

LTER – Long-Term Ecological Research

LTSER – Long-Term Social-Ecological Research

MA – Millennium Ecosystem Assessment

MRC – Mpala Research Centre

SER – Society for Ecological Restoration

SES – Social-ecological System

SDG – Sustainable Development Goal

UHURU – Ungulate Herbivory Under Rainfall Uncertainty experiment

UN – United Nations

UN-DESA – United Nations Department of Economic and Social Affairs

Chapter 1: Introduction

1.1 Context and rationale

1.1.1 Overview of biodiversity declines and the role of humans and livestock

Wildlife populations are in decline globally (IPBES 2019) and increased domestic livestock grazing is generally considered to be detrimental to biodiversity (Asner et al. 2004; Crego et al. 2020; Kimuyu et al. 2017; Prins 1992; Schieltz & Rubenstein 2016). The 'defaunation' of large wild herbivores in particular is one of the most underestimated drivers of global ecological change (Dirzo et al. 2014; Ripple et al. 2015), and protected areas are proving insufficient to conserve the remaining wildlife globally (Büscher & Fletcher 2020). Alongside rising human populations, domestic animal numbers have increased to an extent that they are replacing wild animals across the world's grazing lands, or 'rangelands' (Ellis et al. 2021; Goldewijk et al. 2011), potentially impairing ecosystem structure and function (du Toit and Cumming 1999; Hempson et al. 2017). Cattle and other livestock now graze more than a quarter of the Earth's land surface (Steinfeld et al. 2006) and are estimated to comprise >90% of the world's non-human mammalian biomass (Bar-On et al. 2018). Much of the remaining wildlife populations cohabit rangeland social-ecological systems, alongside humans and the livestock on which their livelihoods depend (Reid et al. 2008). Rangelands support half of the world's livestock (James et al. 2013) and are the most common land use on the planet, and in drylands more specifically. Inhabited drylands are home to *c*.2.7 billion people, the majority of whom are socio-politically marginalised, and this figure is projected to rise to 4 billion by 2050 (IPBES 2018). Drylands are also major providers of ecosystem services, storing >45% of global terrestrial carbon and hosting over a third of global biodiversity hotspots (James et al. 2013).

These rising global trends in humans and livestock populations, alongside declining wildlife populations, have been associated with dryland degradation, and have led to wide recognition of the need to rehabilitate or restore degraded drylands (ELD 2015; IPBES 2018; Crossman et al. 2016; Verstraete et al. 2011; see Table 1.1 for the definition of 'degradation', 'restoration', and 'rehabilitation'). The importance of ecosystem restoration for a range of dryland ecosystem services including food and water security, climate change adaptation and mitigation, and avoiding conflicts and migration has also been acknowledged (IPBES 2018; McElwee & Nghi 2021). However, ecological restoration success rates in drylands remain alarmingly low (James et al. 2013), due to challenging climatic conditions (Carrick & Krüger 2007) and poor understanding of dryland system dynamics (Bainbridge 2007; Maestre et al. 2016). There is a clear need for a deeper understanding of complex dryland social-ecological systems in order to meet Sustainable Development Goals (SDGs), such as SDG target 15.3 on land degradation neutrality (LDN; Cowie et al. 2018).

LDN aims to achieve zero net degradation (‘no net loss’), or preferably negative degradation at the level of specific land cover types by 2030 (Orr et al. 2017). Pursuing LDN comprises three complementary actions: i) ‘avoid’ new degradation, ii) ‘reduce’ new degradation via sustainable land management in non- or less-degraded areas, and iii) ‘reverse’ past degradation via restoration/rehabilitation in degraded areas. Countries are required to use three LDN indicators to report on progress to the United Nations (UN). The indicators used are land cover (physical land cover class), land productivity (net primary productivity, NPP), and carbon stocks (soil organic carbon, SOC).

However, this approach is not without its limitations. For example, LDN indicators focus on soil and vegetation and regard positive effects on biodiversity simply as co-benefits (Cowie et al. 2018). LDN also proposes the use of current land health status as a baseline, which de-emphasises historical information that may prove valuable in informing restoration (Higgs et al. 2014), while failing to require consideration of the local livelihood context. LDN’s proposal to target restoration in less degraded areas due to cost effectiveness may be in opposition to the priorities of local people (Crossland et al. 2017). Regarding vegetation indices, the lack of correlation or even anticorrelation between a vegetation index proposed for use in LDN monitoring (the normalised difference vegetation index, NDVI) with productivity in certain ecosystems limits the universal utility of this metric (Charles et al. 2017; Qi et al. 1994; Western et al. 2015). LDN’s aspirational goal to ‘sustain and improve the stocks of land-based natural capital and the associated flows of ecosystem services, to support the future prosperity of humankind’ (Cowie et al. 2018) is both strongly anthropocentric and framed within the capitalist paradigm founded on the nature-culture dichotomies that are arguably at the root of degradation processes (Büscher & Fletcher 2020; Kidner 2001; Kimmerer 2015). There are also more ethical or philosophical considerations. For instance, the focus on few indices and the notion of equivalence between land cover types (which they term ‘like for like’) facilitates LDN accounting within and across regions. However, this may lead to perceptions that SOC in one area categorised as the ‘same’ land cover type as another are of equal value – ignoring other values systems such as those of cultural and/or spiritual dimensions (Egan et al. 2011; Berkes 2018). This could be partly addressed by using both ‘science-based’ indices and site-specific indicators identified by local stakeholders (Bautista et al. 2017; Orr et al. 2017; Dallimer & Stringer, 2018).

Within rangelands, soil and vegetation are impacted by both wild and domestic animals via grazing, browsing, trampling, and indirectly via predation. Rangeland soils and vegetation are also impacted by humans through land management practices such as wood harvesting, intentional and unintentional fires, and indirectly via livestock grazing. Therefore, within rangelands, all three LDN actions – ‘avoid’, ‘reduce’, and ‘reverse’ – require an understanding of how humans, livestock and wildlife contribute to degradation and to ecological restoration processes.

When implementing LDN actions within rangelands, the socio-political marginalisation of the economically impoverished communities living in drylands in the Global South needs consideration

(Stringer et al. 2017). These marginalised pastoral regions include north and sub-Saharan Africa, south and central Asia, the middle East, Latin America and the Arctic circle (Blench 2001; Bonfoh et al. 2016). For example, the diverse pastoral systems of south Asia, from the pastoralism of the high-montane ecosystems of Assam, Himachal Pradesh, and Karakorams, to the deserts of Gujarat and Rajasthan are universally marginalised in terms of territory, economic policy, and political status (Scoones 2021). In the Kenyan context that forms the focus of this thesis, marginalisation manifests itself as inequities and social injustices that have been associated with changes in land tenure and land degradation processes that are linked to the region's colonial and precolonial history (Hughes 2006; Letai & Lind 2013; Reid et al. 2008).

Critically, it is widely recognised that ecosystem degradation and poverty are related issues and that equity (defined in Table 1.1) is one of the factors influencing the land degradation-poverty nexus (Adams et al. 2004; Barbier & Hochard 2018). The importance of equity has been recognised across multiple global-scale issues, including climate change (IPCC 2019), biodiversity loss (CBD 2013), land degradation (IPBES 2018; CBD 2013; Crossman et al. 2016), and sustainability more broadly (Leach et al. 2018). The global importance of equity has also been recognised with regards to ecosystem restoration projects (Gann et al. 2019). The Society for Ecological Restoration (SER) includes the promotion of fairness and equity within its code of ethics (SER 2020). This includes honouring local knowledge, addressing structural racism, respecting cultural diversity, and treating people fairly (SER 2020). The UN Decade on Ecosystem Restoration (2021-2030) emphasises the importance of recognition and procedural aspects of equity in particular. The first of nine principles of the UN Decade on Ecosystem Restoration is to promote inclusive and participatory governance, social fairness, and equity from the start and throughout the process (https://www.decadeonrestoration.org/). These aspects include: the participation of relevant stakeholders, inclusion of women, young people, persons with disabilities, indigenous peoples and local communities (UN 2019). Ecosystem restoration is inherently value laden and prone to disagreement and compromise (Egan et al. 2011; Gobster 2007; Jordan 2003). Moreover, ecosystem restoration often involves (in)equity that stems from the structural societal disparities that can underly the ecological degradation that necessitates restoration (IPBES 2018; Schell et al. 2020). Equity issues can also be associated with the process of restoration prioritisation (Crossland et al. 2018; Dallimer & Stringer 2018), as well as during the distribution of the costs and benefits associated with restoration work (Jewitt et al. 2014).

In summary, reducing and reversing the ongoing global biodiversity declines through ecosystem restoration requires a deeper understanding of both the underlying biophysical processes, such as livestock-wildlife interactions, as well as human aspects, such as equity, particularly if SDG aspirations to leave no one behind are to be achieved. This is especially true of drylands that tend to be rich in biodiversity but are home to impoverished human communities (James et al. 2013; IPBES 2018; Stringer et al. 2017). The importance of both biophysical and social dimensions of land degradation and restoration processes in dryland social-ecological systems, as evidenced by this overview, guides the framing of the following sections of the thesis. I start by reviewing the literature on the interactions between livestock, wildlife, humans, and vegetation to provide more detailed background information. I distil the key knowledge gaps from the literature review and define the overarching aim and the objectives that address these knowledge gaps. I then outline the conceptual framework underpinning this thesis, informed by the literature review before describing the research design and methodology. This includes the process of selecting the study site, the ethical considerations of the thesis, an overview of the methods employed (which are further elaborated upon in Chapters 2, 3, and 4), data collection and analysis, and the caveats, limitations, and positionality issues associated with the research. I then highlight the novelty and contributions of the thesis and end by outlining the structure of the thesis and the arrangement of the chapters.

Table 1.1 Key definitions

Term	**Definition**
(Ecosystem) Degradation	A level of deleterious human impact to ecosystems that results in the loss of biodiversity and simplification or disruption of their structure, composition and functionality, and generally leads to reduction in the flow of ecosystem goods and services (MA 2005; Alexander et al. 2011; Gann et al. 2019). It is important to note that ‘degradation’ is notoriously challenging to define and, alternative definitions include the reduction of current and/or future biological productivity and a decrease in capacity of land to produce benefits form a particular land use under a specified form of land management (Okpara et al. 2018; Grainger et al. 2015).
(Ecosystem) Restoration	‘The process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed’ (SER 2004).
Rehabilitation	Management actions that aim to reinstate a level of ecosystem functioning on degraded sites, where the goal is renewed and ongoing provision of ecosystem services rather than the biodiversity and integrity of a designated natural reference ecosystem (Gann et al. 2019).
Equity	Fair or just treatment of individuals or groups (Law et al. 2017). Notably, equity is comparative, principally concerned with relationships between people (McDermott et al. 2013). Equity has many facets, including social (human-centred equity), environmental (equity related to environmental issues), intergenerational (responsibilities to future generations), and the consideration of non-human life (Schlosberg 2013) or entities (e.g. spirits; Martin et al. 2016).

1.1.2 The interactions between livestock, wildlife, humans, and vegetation

There is a wealth of literature on livestock stocking rate effects on vegetation cover and species composition (e.g. Pakeman et al. 2019; Porensky et al. 2016; Seymour et al. 2010). In grasslands, including African savannas, grazing and/or browsing wild herbivores affect understory plant biomass (Staver et al. 2019), productivity (Frank et al. 2016), diversity (Koerner et al. 2018; Porensky et al. 2013), species composition (Veblen et al. 2016), and plant functional traits (van der Plas et al. 2016). Domestic herbivores also affect understory community composition, diversity, biomass (Pakeman et al. 2019; Seymour et al. 2010; Veblen et al. 2016) and productivity (Charles et al. 2017), and can reduce ecosystem structure and function in ways that are mediated by climate, grazing regime, and herbivore identity (Cingolani et al. 2005, 2014; Eldridge et al. 2016, 2018; Liu et al. 2015; O’Connor et al. 2010). Several recent studies have examined the effects of livestock stocking rates on vegetation diversity and community composition (Pakeman et al. 2019; Porensky et al. 2016; Seymour et al. 2010), but many studies only investigated presence versus absence of livestock (e.g. Borer et al. 2014; Charles et al. 2017; Koerner et al. 2018; Porensky et al. 2013; Veblen et al. 2016). Studying the effects of different livestock stocking rates, as considered in this thesis, better allows us to adjust the management of globally dominant domestic herbivores to balance livelihood aspirations with biodiversity conservation objectives.

Although not as well studied as livestock effects on vegetation, many recent studies have examined the effects of livestock presence on wildlife. A global review revealed that livestock grazing suppresses a broad spectrum of wild mammals and birds (Schieltz & Rubenstein 2016). Despite the paucity of research from the Global South revealed by this review, several notable studies have investigated the impacts of livestock on large wild herbivores. For example, dung surveys in a long term exclosure experiment in a Kenyan savanna showed that the presence of cattle at moderate densities suppress habitat use by several large wild herbivores (Kimuyu et al. 2017). Odadi et al. (2011) showed that cattle gain more weight in the presence of large wild herbivores during the wet season but, during the dry season, cattle gain more weight in the absence of large wild herbivores. However, only very few of the studies reviewed by Schieltz & Rubenstein (2016) considered mammals 1–50 kg, such as primates and suids, despite their conservation importance and potential to harbour zoonotic pathogens (Johnson et al. 2020; Hoffman et al. 2017). Although many studies investigating wildlife responses to livestock grazing have examined birds (e.g. Fletcher et al. 2010; Malm et al. 2020), examples from African ecosystems are rare (Ogada et al. 2008). Crucially, there are few comparisons of multiple livestock stocking rates (Briske et al. 2011) – a knowledge gap which this thesis addresses. Aerial surveys across Kenyan rangelands show that large wild herbivore biomass peaks at intermediate livestock biomass (Ogutu et al. 2016), while similar results were obtained from landscape-scale dung surveys (Keesing et al. 2018). However, because these two studies relied solely on correlations in observational data, the extent to which the observed patterns are due to responses of wild and domestic herbivores to environmental factors as opposed to competition-facilitation dynamics is unclear. Another understudied, but potentially important influence, is that of large wild herbivores in shaping interactions between livestock and smaller-bodied wildlife. This could occur via trophic cascades (the propagation of indirect effects across trophic levels; e.g. rodents & snakes; Keesing & Young 2014), shifts in vegetation structure (e.g. birds; Duchardt et al. 2018), or alteration of plant community composition (van der Plas et al. 2016). The formulation of the thesis was strongly influenced by the dearth of studies investigating the effects of livestock stocking rates on wildlife, in particular smaller-bodied wildlife, and how the impacts of domestic and large wild herbivores may interact in this regard.

Despite the wealth of literature on livestock effects on vegetation (e.g. Pakeman et al. 2019; Seymour et al. 2010; Porensky et al. 2016), we have a poor understanding of the extent to which livestock can functionally replace large wild herbivores in their effects on plant and animal communities (but see Veblen et al. 2016). This knowledge is critical for managing degradation and restoration processes in rangelands and has important implications for both livestock production and biodiversity conservation. In mixed-use rangelands, if livestock can fulfil similar ecological functions to those performed by the wild herbivores that they partially replace, then domestic animals may be grazed alongside wild herbivores without qualitatively impacting native vegetation and wildlife community composition (Veblen et al. 2016). This functional replacement of wild herbivores by livestock could occur if: i) the plant and animal communities are primarily responding to total herbivory as opposed to herbivore identity; ii) the effects of livestock grazing mimic those of the wild herbivore assemblages that they partially replace; and iii) the domestic animal stocking rates do not lead to the local extirpations of any native wild herbivore species. However, if native plant and animal community compositions are qualitatively shifted above a certain livestock stocking rate, then ecosystem restoration measures could involve reducing stocking rates of domestic animals. Reducing livestock stocking rates could slow or reverse land degradation processes, corresponding to ‘reduce’ and ‘reverse’ in the LDN hierarchy, respectively.

Whether livestock can functionally replace wild herbivores in mixed-use systems also depends on whether the effects of livestock and wild herbivores interact and the nature of any identified interactions (Veblen et al. 2016). If the effects of livestock and wildlife are additive (i.e. not interactive), then the net effect of both in mixed-use systems will mirror their summed individual effects. Conversely, if the effects of livestock and wildlife are non-additive (i.e. interactive), then the net effect of both together will either exceed or fall short of their summed individual effects. Determining the existence and nature of these livestock-wildlife interactive effects on vegetation and other wildlife is vital for managing mixed-use rangelands. Moreover, it is important to move beyond simple binary comparisons (e.g. presence-absence of livestock), to test how these interactive effects vary as livestock stocking rates are increased. This thesis takes up this challenge through the specific objectives outlined in section 1.2.

Greater knowledge of the ecological processes that govern degradation and restoration processes is of limited value without a deeper understanding of the human dimensions of social-ecological systems (e.g. Cortina-Segarra et al. 2020). This is particularly true of rangelands due to their rich biodiversity (James et al. 2013) and the often economically impoverished, socio-politically marginalised nature of the human populations (IPBES 2018; Stringer et al. 2017). Recognition of the importance of equity is widespread in the context of conservation outcomes (Halpern et al. 2013), as well as in efforts to address land degradation (IPBES 2018; Crossman et al. 2016) and ecosystem restoration (IPBES 2018; SER 2020; UN 2019). Despite this, the socio-economic factors that influence equity in restoration projects have not previously been explored in depth.

Equity has many facets, including social (human-centred equity), environmental (equity related to environmental issues), intergenerational (responsibilities to future generations), and the consideration of non-human life (Schlosberg 2013) or entities (e.g. spirits; Martin et al. 2016). Inequity may be more important than a society's wealth in predicting a range of societal issues such as literacy, life expectancy, violence, teenage pregnancy, trust, stress, mental illness, and well-being (Pickett & Wilkinson 2009; Wilkinson & Pickett 2019), but this has not gone uncontested (Snowdon 2010). The importance of equity has been discussed in the context of biodiversity conservation and ecosystem governance, often in the form of environmental justice (Sikor et al. 2014; Martin et al. 2013). In conservation research, however, qualitative methods are poorly implemented and reported (Young et al. 2018a), while environmental variables are seldom included in equity studies (Friedman et al. 2018), resulting in many knowledge gaps. Some argue that the inequities created by capitalism as it is currently practiced (Stiglitz 2012) are at the root cause of ecological degradation and the need for restoration (Büscher & Fletcher 2020). However, equity is rarely addressed in ecosystem restoration projects (but see Jewitt et al. 2014), as are social science methods more generally (Wortley et al. 2013; Aronson et al. 2010). A global review of ecological restoration literature between 1984 and 2012 showed that only 3% of studies used social indicators (Wortley et al. 2013). Similarly, a meta-analysis of ecological restoration articles in 13 journals between 2000 and 2008 revealed than only 3% of papers used interviews to evaluate restoration success (Aronson et al. 2010). Interest in social science methods is garnering more attention in more recent times. For example, within social science research more broadly, there is a growing interest in 'pixelizing the social' and mapping social values (Nahuelhual et al. 2016; Liverman 1998). The concept of 'spatial justice' has been applied in urban areas (Soja 2008; Schell et al. 2020), but the use of geographic information systems (GIS) in equity studies remain rare (Friedman et al. 2018; but see Singh et al. 2021).

The importance of integrating perspectives from the social sciences into ecosystem restoration is highlighted by the fact that the major barriers to ecological restoration are mostly social rather than ecological (e.g. Cortina-Segarra et al. 2020). Equity issues are relevant to several aspects of ecosystem restoration, including the process through which restoration activities are conducted and the distribution of the impacts of restoration activities (Crossland et al. 2018; Jewitt et al. 2014; Wells

2019). For example, the process of deciding where to focus restoration activities can have equity implications, which stem from imbalances in decision-making power (Crossland et al. 2018). Similarly, selecting the type of restoration activities to conduct can involve equity issues (Jewitt et al. 2014). Ecological restoration often increases the biological resource base and therefore the way in which these benefits of restoration are shared across communities and landscapes involves equity considerations (Wells 2019a). For example, between 1986 and 2004, over 300,000 ha of Miombo and *Acacia* woodlands in Shinyanga region of Tanzania were restored under the Shinyanga Soil Conservation Programme (Barrow 2014). However, greater accrual of the benefits of restoration by the more powerful community members ('elite capture') exacerbated existing inequalities (Barrow 2014). The ecological dimensions do of course remain a central component of ecosystem restoration. Nevertheless, given the importance of equity in conservation (Halpern et al. 2013; Martin et al. 2013; Sikor et al. 2014) and ecological restoration (IPBES 2018; SER 2020; UN 2019), integration of both equity and ecological dimensions of ecosystem restoration has the potential to benefit restoration efforts. I examine this issue from a spatial perspective in this thesis, within a Kenyan context.

1.1.3 Key knowledge gaps for guiding ecosystem restoration in rangelands

The literature review on the interactions between livestock, wildlife, humans, and vegetation revealed three key knowledge gaps resulting in the following research questions:

1) To what extent can livestock at different stocking rates functionally replace large wild herbivores in their effects on plant and animal communities?
2) Do the effects of livestock at different stocking rates interact non-additively with the effects of large wild herbivores?
3) What socio-economic factors influence the equity of ecosystem restoration efforts?

These research questions were reframed as thesis objectives and are outlined below.

1.2 Aim and objectives

The overarching aim of this thesis is to deepen our understanding of the role of wildlife, livestock, and humans in Kenyan rangeland social-ecological systems, and generate knowledge that can inform ecosystem restoration efforts. The specific objectives are to:

1) Investigate the individual and interactive effects of cattle stocking rate and large wild herbivores on smaller wild vertebrates and the vegetation structural attributes that may be mediating these effects, gleaning insights into whether wild herbivores can be functionally replaced by cattle at different stocking rates;

2) Assess the functional replaceability of large wild herbivores by cattle at different stocking rates by evaluating whether savanna understory vegetation is shaped primarily by total herbivory or herbivore identity, testing for interactive effects between cattle stocking rate and large wild herbivore accessibility; and
3) Examine the socio-economic variables that influence equity in ecosystem restoration projects in Laikipia, Kenya, as well as whether these variables interact.

Addressing these three objectives provides a greater understanding of the roles of livestock (objectives 1 and 2), wildlife (objectives 1 and 2), and humans (objective 3) in ecosystem degradation and restoration processes.

1.2.1 Conceptual framework

The conceptual framework that forms the foundation of this thesis details the relationships between humans, livestock and wildlife, as well as how these three components directly or indirectly influence ecosystem degradation and restoration indicators (Figure 1.1a). Figure 1.1b illustrates the specific relationships within the general conceptual framework investigated in this thesis.

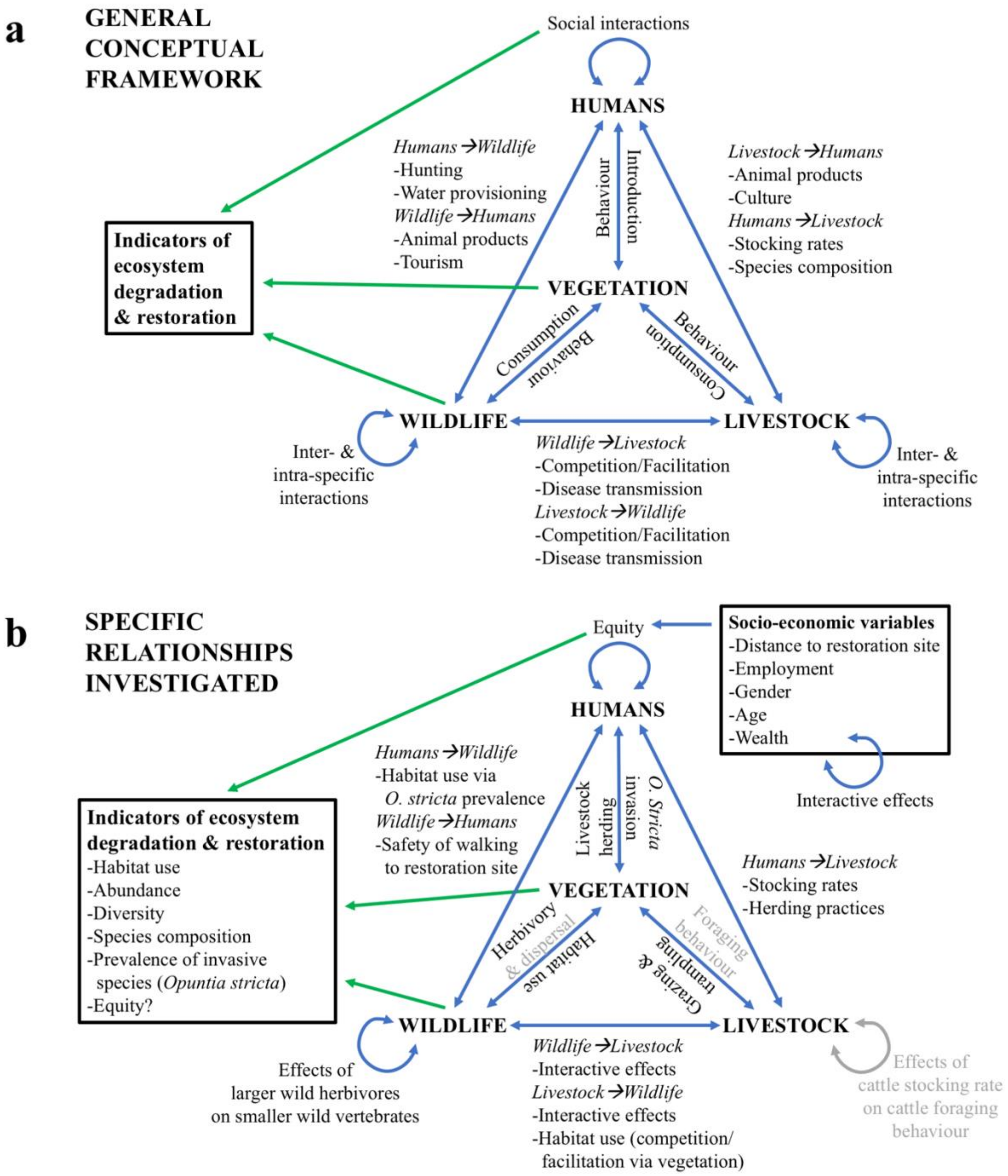

Figure 1.1 Conceptual framework underlying the thesis (**a**) and the specific relationships investigated within the thesis (**b**). Blue arrows show relationships, while green arrows show direct effects on ecosystem degradation and restoration indicators. Grey arrows and text represent processes or relationships that were not investigated within the three core components of the thesis but were addressed in other supporting manuscripts presented as appendices (Appendices 1 & 2). Curved arrows indicate feedback loops.

1.3 Research Design and Methodology

1.3.1 Study site selection

To address the three objectives, I chose a case study site in Laikipia county, central Kenya. I selected this site because Laikipia supports the highest large mammal diversity of any area in East Africa and contains a wide variety of land use and land tenure systems (Sundaresan & Riginos 2010). I also selected Laikipia due to existence of long-term exclosure experiments (Goheen et al. 2018; Riginos et al. 2012; Young et al. 2018b). Through controlled manipulations, these exclosure experiments enable the effects of different herbivore guilds to be teased apart and their interactive effects to be tested. The long duration of the experiments means that we can investigate the treatments in states that are relatively stable compared to the first few years after an exclosure experiment is set up, during which certain treatments are on directional trajectories. Traditional pastoralism is practiced in 10–20% of Laikipia in group ranches designated during the 1970s and abandoned lands, while large-scale private ranching occupies over one third of the county (Georgiadis et al. 2007a, b). Laikipia has a long history of pastoralism beginning around 4,500 years ago (Lane et al. 2011), while Maa-speaking pastoralists arrived around 1750 (Cronk 1989). Livestock-keeping is central to pastoral livelihoods and livestock production accounts for over 12% of Kenya's gross domestic product (Allan et al. 2017). However, the socio-political marginalisation of the indigenous pastoralist communities has been associated with the degradation of both plant and wild animal communities (Crego et al. 2020, 2021; Georgiadis et al. 2007a, b; Hughes 2006; Kinnaird & O'Brien 2012; Letai & Lind 2013; Strum et al. 2015; Unks et al. 2019). Laikipia's rich biodiversity and the importance and prevalence of livestock-keeping make it an ideal study site to address the objectives of this thesis. Lessons from investigating the roles of livestock, wildlife, and humans in land degradation and restoration processes in Laikipia will have applications both within the county and for other similar mixed-use rangeland social-ecological systems globally (Figure 1.2).

The long-term exclosure experiments at Mpala Research Centre (MRC) in Laikipia provide valuable opportunities to address objectives 1 and 2. The importance of long-term ecological research (LTER) has been widely acknowledged (Hughes et al. 2017; Lindenmayer et al. 2012; Müller et al. 2010). There is a LTER site at MRC consisting of selective exclosures that allowed me to address objectives 1 and 2. This was a major motivating factor in selecting Laikipia as a research site. There is also a growing recognition of the need for long-term social-ecological research (LTSER; Dick et al. 2018; Singh et al. 2013; Wells et al. 2019b; Appendix 2). Unfortunately, there are very few LTSER sites globally and there are no existing long-term social research projects in Laikipia. Although I could only conduct a short-duration study, the indigenous pastoral communities of Laikipia, whose land is heavily degraded (Hauck & Rubenstein 2017; King et al. 2008; Letai & Lind 2013; Strum et al. 2015), provide an opportunity to study the socio-economic factors that influence equity in ecosystem restoration projects.

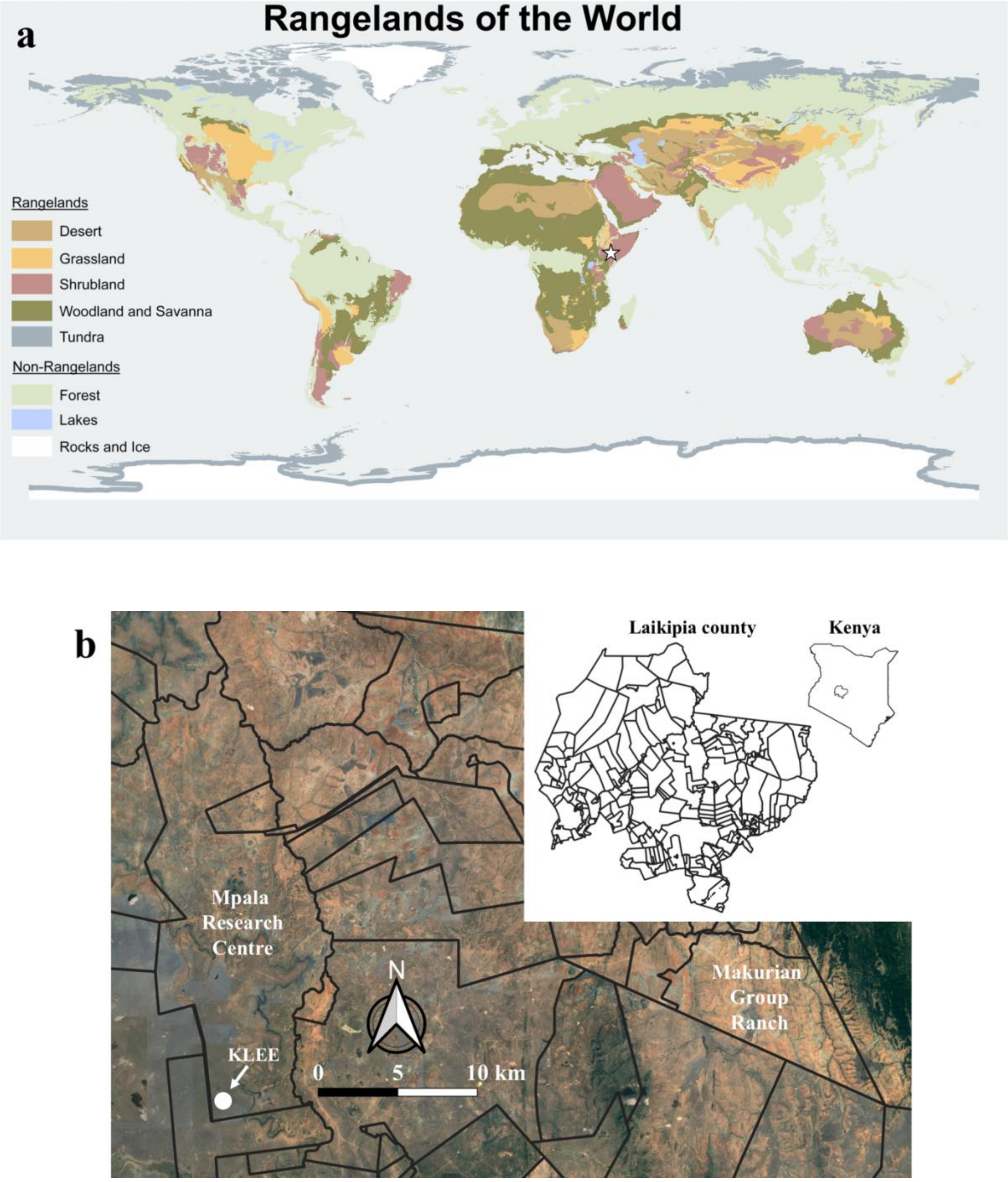

Figure 1.2 The study area situated within global rangelands (**a**–**b**). The global distribution of rangelands (upper panel; available from: https://www.webpages.uidaho.edu/what-is-range/rangelands_map.htm) and the more local context of the study site (lower panel). The star in the upper panel locates Laikipia. The locations of the Kenya Long-term Exclosure Experiment (KLEE) and of Makurian group ranch in relation to Laikipia county and Kenya are illustrated by the inset of the lower panel.

1.3.2 Methodological overview

Addressing the overarching aim of this thesis required the integration of approaches from both ecological and social sciences. More specifically, addressing the objectives relating to interactions between livestock, wildlife, and vegetation, in ecosystem degradation and restoration processes, as well as the objective relating to equity issues associated with restoration projects required the integration of both biophysical and social science methods. To address objectives 1 and 2, I collected data on wildlife and plant communities within the Kenya Long-term Exclosure Experiment (KLEE) plots, located at the Mpala Research Centre (MRC; Figure 1.2). To address objective 3, I worked with the members of a Maasai community managed rangeland called Makurian group ranch, east of the MRC. I facilitated a restoration project in Makurian, which involved employing casual labourers to manual remove an exotic invasive cactus, *Opuntia stricta,* and collecting socio-economic and biophysical data, analysed spatially.

The methodologies that I employed for the ecology-focused components of the thesis at KLEE were developed from the existing methodologies implemented at KLEE, in order to maximise comparability with previous studies in this long-term experiment. For example, I sampled understory vegetation using the same pin frame method as the annual KLEE vegetation surveys. However, this was not the case for surveys that are not conducted regularly at KLEE, such as overstory vegetation surveys. I also employed similar sampling techniques implemented at KLEE for the biophysical aspects of the equity-focused component of the thesis. For example, I conducted dung count belt transects to assess habitat use of the restoration site by wild and domestic animals that follow the KLEE methodology, which is also widely used in other ecosystems (Altendorf et al. 2001; Blake 2002; Daniels 2006; Lunt et al. 2007; Marques et al. 2001; Rasmussen et al. 2005). To evaluate perceptions of equity, I drew from the literature of methodologies appropriate for collecting social data (e.g. Mukherjee et al. 2018; Nyumba et al. 2018; Sutherland et al. 2018; Young et al. 2018a).

1.3.3 Research ethics

The components of the data collection that involved assessing perceptions of equity among community members necessitated an ethical review (ethical review reference: AREA 18-151; Appendix 3). The main ethical concerns related to the engagement of community members during scoping workshops, questionnaires, and in-depth interviews. It is important for participants of social studies to be clearly informed about the purpose of the study, to provide consent, and for the implications of participation to be mutually agreed by both researchers and participants. Prior to each workshop, questionnaire, or interview, I communicated clearly to the participants the purpose of the study, the data anonymisation process, data storage protocol, the process of sharing data with third parties (e.g. other researchers) and the ability of participants to withdraw at any stage during data collection. I informed participants of their rights under the ‘Data Protection Agreement’, which consists of: the right to: 1) access data, 2) rectify data, 3) erase data, 4) restrict how data are processed, 5) to object to data processing and 6) to receive data in a commonly used format. As some participants were illiterate or semi-literate, I undertook this consent process using a ‘verbal informed consent protocol’ (Appendix 4). As it was impractical for a witness to be present at all times, I verified the verbal informed consent by recording it in writing and including it in the research transcript.

There are also ethical considerations associated with my positionality in relation to, as well as power dynamics among, me as the researcher and project leader, my research assistants, and participants and respondents in the equity component of this thesis. I attempted to address these reflexively as much as possible. I elaborate on these issues in further detail in section 1.3.6.

1.3.4 Data collection

To assess habitat use by wild and domestic animals, I used dung surveys along belt transects (detailed in section 4.4.4) and camera traps (detailed in section 2.3.3). I used quadrats and pin frames along line transects to monitor understory vegetation (detailed in section 3.3.3) and belt transects to monitor overstory vegetation (detailed in section 2.3.3). I also quantified densities of the invasive cactus, *Opuntia stricta*, using belt transects (detailed in section 4.4.4). I collected social data through focus group discussions, questionnaires, key informant interviews, and participant observation (detailed in section 4.4.4). By recording the Global Positioning System (GPS) location of the households of the respondents, I was able to map the social data collected and assess the effect of distance to the restoration site on perceived equity.

1.3.5 Data analysis

I performed all statistical analysis in R version 3.6.2 (R Core Team 2019) and managed spatial data in QGIS version 3.4.8 (QGIS 2019) and R version 3.6.2. The free and open source nature of R and QGIS make them ideal for replicability, particularly for poorly resourced researchers. To compare the effects of total herbivory versus herbivore identity, I used the Akaike Information Criterion (AIC). I used linear mixed models (LMMs) to test for statistical differences between treatments while accounting for random effects. I applied LMMs to test the individual and interactive effects of cattle and large wild herbivores on smaller-bodied wildlife and understory vegetation. When random effects were not an issue, I employed analysis of variance (ANOVA). I applied ANOVA to test for the influence socio-economic factors on perceived equity and the responses of domestic and wild herbivores to the densities of an invasive cactus, *Opuntia stricta*. I used QGIS version 3.4.8 to visualise the results of the spatially explicit questionnaire responses. To characterise plant community composition, I employed multi-species hierarchical models implemented under a Bayesian framework.

1.3.6 Limitations and positionality

Despite the unique opportunities afforded by well-controlled manipulative experiments such as KLEE, there are several important limitations to consider. Firstly, it is unclear to what extent the findings of such localised experiments can be extrapolated to other climates and habitat types (Young et al. 2013). This is because herbivore effects can vary with environmental factors such as climate (Bakker et al. 2006; Eldridge et al. 2016; Goheen et al. 2013) and vegetation productivity (Daskin & Pringle 2016). Secondly, although three cattle stocking rates, as used in this thesis, is an improvement on simple presence-absence comparisons, these three cattle treatments are not able to represent the wide range of cattle grazing regimes practiced, which can vary not only in stocking rate, but also in timing, intensity, and duration of grazing (Briske et al. 2011; Schieltz & Rubenstein 2016). The identity of the domestic animal (e.g. cattle versus sheep versus goats versus camels) is also likely to be important (Tóth et al. 2016), as well as herd species compositions and herd demographics (Fraser et al. 2014; Jerrentrup et al. 2015; Liu et al. 2015). Finally, there are spatio-temporal scale issues stemming from the short duration of the research and the small size of the study sites. For example, some of the patterns observed in the exclosure plots may be due to contrasts with surrounding habitat rather than the treatments *per se* (Bergstrom et al. 2018).

All of the ecological limitations mentioned here would be addressed, at least in part, by landscape-scale analyses spanning gradients of vegetation productivity and habitat types that also include different species of domestic and wild species. One such analysis is listed in Appendix 1. Landscape-scale analyses have their own limitations, chiefly, the challenges associated with assessing causal relationships from observational data. However, these types of analyses are useful for hypothesis generation as well as valuable complements to localised, well-controlled manipulative experiments, such as those presented in Chapters 2 and 3.

One of the main caveats associated with any social study relates to positionality (England 1994; Rose 1997). I am a young, ethnically Asian-European man educated in Kenya, Japan and the United Kingdom, and am a descendant of a colonial white Kenyan family. Personality may be an important aspect of positionality (Moser 2008). In this regard, I have a quiet, reserved, and introverted personality. There are also positionality issues associated with simultaneously acting as a project leader, employer, and researcher. All of these aspects of positionality are important to consider in relation to the positionalities of the community members with whom I interacted, as well as the positionality of my research assistant and Maa-English interpreter (McIntosh 2016). These positionality issues and how they may influence the interpretation of the results of the paper presented in Chapter 4 are expanded on in more detail in section 4.3.4, as well as in the accompanying positionality statements attached in Appendix 7.

1.4 Novelty and contribution of the thesis

To my knowledge, Chapters 2 and 3 of this thesis provide the first studies to experimentally test whether cattle at more than two stocking rates can functionally replace large wild herbivores in their effects on plant and smaller wildlife communities, as well as how these cattle stocking rate effects interact with the presence of large wild herbivores. Most research on the impacts of livestock on wildlife only compare livestock presence versus absence (Briske et al. 2011), while few studies consider mammals between 1–50 kg (Schieltz & Rubenstein 2016). The general paucity of ecological research in the Global South means that the studies presented in Chapters 2 and 3 contribute valuable information to the global scientific knowledgebase of livestock-wildlife interactions.

The paper presented in Chapter 4 of this thesis offers novelty in exploring the socio-economic factors that influence equity in ecosystem restoration. Ecosystem restoration research has largely focused on ecology (but see Egan et al. 2011), so Chapter 4 provides a valuable contribution to assessing the human dimensions of restoration that have received considerably less attention (Aronson et al. 2010; Wortley et al. 2013). Moreover, the study presented in Chapter 4 provides a rare spatially explicit analysis of perceived equity (Friedman et al. 2018), building on the growing spatial-social analysis literature (Liverman 1998; Nahuelhual et al. 2016; Soja 2008; Schell et al. 2020). Chapter 4 also addressed broader calls to make restoration 'people-centric' (van Noordwijk et al. 2020) but highlights the importance of going beyond simply 're-peopling' restoration (Elias et al. 2021).

All three papers (Chapters 2, 3, and 4) revealed interactive effects between explanatory covariates. In Chapters 2 and 3 non-additive effects were found to occur between ecological factors (in this case, cattle stocking rate and the accessibility to large wild herbivores). Meanwhile, Chapter 4 showed that non-additive effects can occur between socio-economic factors (in this case, employment by the ecosystem restoration project and the distance to the restoration site). In addition, the integration of social and biophysical methods in Chapter 4 allowed more robust evaluation of the outcomes of restoration activities (in this case, the use of the restoration site by herders and their livestock following restoration activities). The integrated nature of this thesis adds value by providing both biophysical and socio-economic perspectives on land degradation and restoration processes, which are typically explored in isolation (Aronson et al. 2010; Wortley et al. 2013), but which need to be examined together in order to support restoration activities and achieve LDN goals.

Critically, the integrated approach provides novel insights that would not have been gleaned from either purely biophysical or social methods alone. Chapter 5 provides a guide for how similar integrated studies can add value to global debates relating to ecosystem degradation and restoration research and how the results of such studies can be communicated effectively to land managers and local communities (see Appendices 9 and 10 for communicating the findings of this thesis to relevant stakeholders).

1.5 Thesis structure

This thesis is composed of five chapters in compliance with the alternative thesis format established by the University of Leeds:

- Chapter 1 is an introductory chapter that provides context and rationale, defines the aims and objectives, and outlines the methodology employed for this thesis, as well as highlighting the novelty and contributions of the thesis.
- Chapter 2 presents the manuscript focussing on the individual and interactive effects of cattle stocking rate and large wild herbivores on smaller wild vertebrates. This manuscript was published in the Journal of Applied Ecology.
- Chapter 3 presents the manuscript evaluating whether savanna understory vegetation responds primarily to total herbivory or herbivore identity, as well as exploring interactive effects between cattle at various stocking rates and large wild herbivores. This manuscript was published in the journal Ecological Applications.
- Chapter 4 presents the manuscript examining the socio-economic factors that influence equity in ecosystem restoration, using invasive cactus removal in a communally managed rangeland as a case study. This manuscript was published in the journal Restoration Ecology.
- Chapter 5 provides a synthesis of the findings of the thesis and discusses its implications, suggesting directions for future research and drawing out the main conclusions in relation to the overall aim and objectives.

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Chapter 2: Wild and domestic savanna herbivores increase smaller vertebrate diversity, but less than additively (published in Journal of Applied Ecology)

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2.1 Abstract

Cattle and other livestock graze more than a quarter of the world's terrestrial area and are widely regarded to be drivers of global biodiversity declines. Studies often compare the effects of livestock presence/absence but, to our knowledge, no studies have tested for interactive effects between large wild herbivores and livestock at varying stocking rates on small-bodied wild vertebrates. We investigated the effects of cattle stocking rates (none/moderate/high) on the diversity of wildlife 0.05–1,000 kg using camera traps at a long-term exclosure experiment within a semi-arid savanna ecosystem in central Kenya. In addition, by selectively excluding wild ‘mesoherbivores’ (50–1,000 kg) and ‘megaherbivores’ (> 1,000 kg; elephant and giraffe), we tested whether the presence of these two wild herbivore guilds (collectively, ‘larger wild herbivores’) mediates the effect of cattle stocking rate on habitat use and diversity of ‘smaller wildlife’ (mammals ranging between 10 and 70 cm shoulder height and birds). Our results show that cattle enhance alpha diversity of smaller wildlife (with or without larger wild herbivore presence) and of all wildlife 0.05–1,000 kg (with or without megaherbivore presence), by altering vegetation structure. However, for smaller wildlife, this effect is less pronounced in the presence of larger wild herbivores, which also shorten grass. In the absence of cattle, mesoherbivore-accessible sites showed higher alpha diversity of smaller wildlife than sites excluding mesoherbivores. Smaller wildlife habitat use was increased by high cattle stocking rates and wild mesoherbivores more in the presence of the other. Our findings imply that grazing, whether by livestock or wildlife, can enhance local savanna wildlife diversity. The biodiversity benefits of localised increases in herbivory are likely to be due to shortened grass and associated visibility improvements (for predator avoidance/foraging). This suggests that land managers can increase local biodiversity by shortening grass, with wild or domestic herbivores (or both), at least in patches within a taller grass matrix.

2.2 Introduction

Over a quarter of the Earth's land surface is grazed by cattle and/or other domestic animals (Steinfeld et al. 2006). Livestock comprise > 90% of the planet's non-human mammalian biomass (Bar-On et al. 2018). Wildlife populations are declining globally (Brondízio et al. 2019) and livestock grazing is generally considered to be detrimental to biodiversity (Asner et al. 2004; Crego et al. 2020). Across the world's rangelands, including African savannas, livestock continue to replace wildlife, potentially with negative impacts on ecosystem structure and function (du Toit & Cumming 1999; Hempson et al. 2017). A global review showed that livestock grazing suppresses a broad spectrum of wild mammals and birds (Schieltz & Rubenstein 2016). However, few of these studies considered mammals 1–50 kg, such as primates and suids, despite their conservation importance and potential to harbour zoonotic pathogens (Hoffman et al. 2017; Johnson et al. 2020). Although many studies investigating wildlife responses to livestock grazing have examined birds (e.g. Fletcher et al. 2010; Malm et al. 2020), examples from African ecosystems are uncommon (Ogada et al. 2008) – a general symptom of the paucity of research from the Global South. Crucially, there are few comparisons of multiple livestock stocking rates (Briske et al. 2011).

Another understudied but potentially important influence is that of large wild herbivores in shaping interactions between livestock and small-bodied wildlife. This could occur via trophic cascades, for example, the shortening of herbaceous vegetation by livestock can reduce prey species densities, resulting in suppression of predators (e.g. rodents and snakes; Keesing & Young 2014). Wild herbivores of different sizes have distinctive effects on plant functional composition in savannas (van der Plas et al. 2016), and vegetation consumption by large wild herbivores can affect densities or habitat use of small-bodied wildlife (e.g. white rhinoceroses *Ceratotherium simum* benefitting impalas *Aepyceros melampus*, Cromsigt & te Beest 2014). Small-bodied wildlife also respond to vegetation structure (e.g. birds; Duchardt et al. 2018), which is shaped by both domestic and large wild herbivores in mixed-use rangelands. In mixed-use systems, additive effects may occur where grazing by large wild herbivores amplifies the cattle grazing effect, as both herbivore types reduce the height and shift the composition of herbaceous vegetation (Veblen et al. 2016). In the case of small mammals that are suppressed by cattle grazing via herbaceous cover reduction, the effect of cattle stocking rates on small mammal habitat use would be dampened if large wild herbivores and cattle supress each other to such an extent that herbaceous cover is unchanged.

Alternatively, if wildlife responds to changes in tree density, the presence of ecosystem-engineering megaherbivores may mediate (enhance/buffer) the effect of cattle stocking rate by thinning the overstory. Megaherbivores (e.g. elephant *Loxodonta africana*) can also buffer the negative impacts of cattle on wild ungulates (Kimuyu et al. 2017; Young et al. 2005), likely by altering cattle grazing behaviour (Odadi et al. 2011), which in turn impacts herbaceous vegetation, because cattle forage less when elephant are present (Veblen et al. 2016).

Our objectives were to investigate: (a) how cattle stocking rate affects alpha (local) diversity of wildlife 0.05–1,000 kg, and (b) whether cattle stocking rate effects on diversity and habitat use by smaller wild vertebrates (mammal and bird species 10–70 cm shoulder height [s.h.]) are mediated by the presence of ‘mesoherbivores’ (50–1,000 kg) and ‘megaherbivores’ (elephant and giraffe *Giraffa camelopardalis*) – collectively termed ‘larger wild herbivores’. Such information can guide land management decisions that promote biodiversity in mixed-use rangelands, while maintaining productive and economically viable livestock systems to feed a growing human population.

2.3 Methodology

2.3.1 Study area

We conducted this study in the Kenya Long-term Exclosure Experiment (KLEE) plots at Mpala Research Centre (0°17′N, 36°52′E, 1,800 m a.s.l.) in Laikipia, Kenya, where livestock-keeping has long played an important role for livelihoods and culture. Rainfall at KLEE is weakly trimodal with a pronounced dry season December–March. Between 2001 and 2019, annual rainfall averaged 613 mm year^{-1} (range: 421–1,009 mm year^{-1}, inter-annual coefficient of variation: 27%). Soils are poorly drained vertisols with high clay content (> 40%) known as ‘black cotton’. Black cotton soils are widespread across Africa and, with other vertisols, cover > 100 million hectares across the continent (Ahmad 1996). The overstory of this savanna ecosystem is dominated by *Acacia drepanolobium* (syn. *Vachellia drepanolobium*, 97% of the canopy; Young et al. 1998), while five perennial grass species comprise 85% of the herbaceous understorey (Porensky et al. 2013). Mpala Research Centre is managed for both wildlife conservation and livestock production. Cattle are the main domestic animal, stocked at moderate densities of 10–15 cattle km^{-2} (Veblen et al. 2016). Livestock grazing lands cover 80% of Kenya's area and account for > 12% of gross domestic product (Allan et al. 2017).

2.3.2 Experimental Design

The KLEE plots, established in 1995, use fences to control access to 200 × 200 m (4-ha) treatment plots by three herbivore types – wild mesoherbivores (50–1,000 kg, ‘W’), megaherbivores (elephant and giraffe, ‘M’) and cattle (‘C’) – in different combinations. There are three replicate blocks, each consisting of six treatments (18 plots in total): (a) ‘MWC’ (accessed by megaherbivores, mesoherbivores and cattle), (b) ‘MW’ (accessed by megaherbivores and mesoherbivores), (c) ‘WC’ (accessed by mesoherbivores and cattle), (d) ‘W’ (accessed by mesoherbivores only), (e) ‘C’ (accessed by cattle only), (f) ‘O’ (excludes megaherbivores, mesoherbivores and cattle). Mesoherbivores are excluded from O and C plots by a 2.3-m tall 11-strand fence of alternating live and ground wires, the lowest (ground) wire being at ground level. This fence is easily permeable to species < 70 cm s.h., but excludes ostriches *Struthio camelus,* and may partially exclude spotted hyaenas *Crocuta crocuta* and striped hyaenas *Hyaena hyaena* (both ≥ 70 cm s.h., but both caught on camera traps in O and C plots on few occasions). All species mass and height categories are based on mean adult body mass and shoulder heights, respectively, from Kingdon et al. (2013).

The treatment plots accessible to cattle are typically grazed by 100–120 mature Boran cows *Bos indicus* (sometimes with calves and/or bulls) for 2–3 days (2 hr day^{-1}) within a 2-week period, three to four times per year. The timing and number of grazing days depends on forage availability and reflects typical grazing regimes of ranches in the region, wherein cattle graze in an area for several days before being moved to allow that area to recover. For these six treatments, we selected one of four 50 × 50 m (0.25-ha or 1/16 of the plot) subplots within the central hectare of each of the eighteen 4-ha treatment plots for wildlife and vegetation monitoring. In cattle-accessible plots, the subplot closest to the higher-cattle-stocking-rate subplots (described below) was selected to maximise comparability with moderate-cattle-stocking-rate plots, while subplots were randomly selected in plots excluding cattle (the experimental layout is illustrated in Appendix 5: Figure S5.1).

Each of the treatment plots accessible to cattle (MWC, WC, C) contains a 50 × 50 m subplot at a corner/edge established in 2008. Here, the same cattle herd is grazed for a further 30 min following the initial 2-hr grazing period in the wider plot, to achieve an approximately fourfold increase in cattle stocking rate compared to the wider plot (Appendix 5: Figure S5.2). These three additional treatments are named: (a) MWCh, (b) WCh and (c) Ch, where ‘h’ denotes high cattle stocking rate. We note that ‘grazing’ also involves trampling, which is a considerable cause of disturbance. Grazing behaviour can also be altered by time of day and the presence of other herbivores (Odadi et al. 2017). Because cattle only access individual plots a few times per year, responses of most wildlife are unlikely to be due to direct interaction with cattle or herders. Fire has not been used as a management tool in this ecosystem for over 50 years and is rarely used by other ranches in the region. Natural-ignition fires have not occurred in decades, if at all. See Young et al. (1998) and Young et al. (2018) for further details of the experimental design.

2.3.3 Data collection

To assess wildlife habitat use, between 23 May 2019 and 26 May 2020, we deployed one camera trap (Browning Strike Force HD Pro X) in each of the twenty-seven 50 × 50 m subplots (three replicates of nine treatments). Cameras were secured to a tree 80 cm above the ground, avoiding glades, and ensuring a view unobstructed by woody vegetation within the detection zone to eliminate detectability issues due to trees and shrubs. To avoid bias towards any particular species, we did not specifically target animal trails. Cameras were programmed to take three images per trigger (1 s apart) with a 1-min delay between triggers. Cameras were checked every 2–3 weeks to download images, replace batteries and ensure cameras were operational. Camera traps were operational for an average of 364 (± 2 SE, range: 340–374) trap nights. Vegetation in the cameras’ detection zones was not cleared. Although this increased false trigger rates, potential biases due to animals’ attraction/repulsion towards clearing-induced shorter vegetation were avoided. Each camera's detection area is 275 m^2 (11% of the subplot area), calculated as: $(\mathit{detection\ angle} \times 360 - 1) \times \pi \times (\mathit{detection\ range})^2$, where *detection angle* is in degrees and *detection range* in metres.

We measured two covariates that could affect wildlife habitat use: grass height and tree density (Riginos & Grace 2008; Soto-Shoender et al. 2018). Grass height was measured every 2–3 weeks in three locations within each camera's detection zone (2 m in front of the camera) using a Robel pole – the resulting metric correlates with grass biomass (Robel et al. 1970). The density of *A. drepanolobium* trees taller than 2 m was assessed in each of the 27 subplots using four 10 × 40 m belt transects. Because fence maintenance can influence tree density, we excluded a 10-m wide buffer on the two sides of subplots located in a corner of the 4-ha main plots and excluded an identical buffer in all other subplots. Images were managed using the *camtrapR* package version 2.0.3 (Niedballa et al. 2016) in R version 3.6.2 (R Core Team 2019).

2.3.4 Data analyses

All statistical analyses were performed in R. We excluded all domestic species and all wild species that comprised fewer than five detections per 100 trap nights, to avoid biases induced by very rare species. This left 27 species, of which 25 (93%) were 0.05–1,000 kg (i.e. excluding elephant and giraffe; Table 2.1; Appendix 5: Figure S5.3). We used the *vegan* package version 2.5-6 (Oksanen et al. 2019) to calculate Shannon–Wiener diversity (H'), which we converted to 'effective number of species' by taking exp (H') (Jost 2007). Treatment effects on the effective number of species were investigated for these 25 species 0.05–1,000 kg (only for the six treatments accessible to wild mesoherbivores) and for 16 species whose access to O, C and Ch subplots appears unaffected by the 11-strand fence that excludes larger wild herbivores. We term these 16 species (all 10–70 cm s.h.) 'smaller wildlife'. We use shoulder height to define smaller wildlife because warthogs *Phacochoerus africanus* (65 cm s.h., 70 kg) have a larger body mass than taller species excluded by the 11-strand fence (e.g. Grant's gazelle *Nanger (Gazella) granti*, 85 cm s.h., 52 kg). Habitat use by larger mammals (> 50 kg; zebra *Equus quagga*, eland *Taurotragus oryx*, oryx *Oryx beisa*, hartebeest *Alcelaphus buselaphus*, Grant's gazelle, elephant, giraffe) has already been investigated at this site using dung surveys (Kimuyu et al. 2017). Therefore, we focussed particularly on two groups of wildlife whose responses to herbivore treatments are difficult to capture using dung surveys: (a) 'smaller mammals' (defined here as species 10–70 cm s.h.; distinguished from small mammals, because some species are relatively large e.g. warthogs), (b) 'birds' (bird species < 50 kg living/foraging primarily on the ground that trigger camera traps). A third group, 'larger carnivores' (spotted and striped hyaena), was excluded from analyses due to potential fence permeability effects.

Images taken 1 hr apart were treated as independent detections (Soto-Shoender et al. 2018). To evaluate the effects of treatments and environmental covariates (grass height and *A. drepanolobium* density) on wildlife habitat use, we employed beta-distributed generalised linear mixed models using the *glmmTMB* package version 1.0.1 (Brooks et al. 2017). Prior to modelling, habitat use was standardised and rescaled by converting independent detections per trap night, first to an open unit interval (0,1) by taking $y' = (y - a) \times (b - a) - 1$, where a and b are the minima and maxima, respectively, from the data, then compressing to remove 0s and 1s by taking $y'' =$

$[y'(N-1)+0.5] \times N^{-1}$, where N is the sample size (Smithson & Vercuilen 2006). We examined proportional effects in the rescaled standardised data, which do equal the proportional effect in the unscaled values.

To separate the individual and interactive effects of herbivore types, we coded the interaction terms mesoherbivores(yes/no) × cattle(none/moderate/high) and megaherbivores(yes/no) × cattle(none/moderate/high) as fixed effects. In order to assess intra-annual dynamics (i.e. month effects), we coded grass height × month as fixed effect and plot as a random effect to account for temporal non-independence. When analysing treatment effects on all species groups combined, species-nested-within-plot (to account for repeated measures when averaging monthly) or block (to account for spatial block effects when averaging annually) were coded as random effects. A Gaussian linear mixed model was employed to test treatment effects on grass height, crossing treatment effects with month and coding plot as a random factor to account for temporal non-independence. Analysis of variance (ANOVA) was used to test treatment effects on *A. drepanolobium* density. When using Gaussian models, we visually checked normality and homoscedasticity of residuals. We did not perform model selection. Herbaceous vegetation can influence detectability, so we also ran the diversity and habitat use analyses on a subset of the data (December 2019 to January 2020) when grass height was not significantly affected by treatments (cattle, moderate, $Z = -1.5$, $p = 0.14$, high, $Z = -0.33$, $p = 0.74$; mesoherbivores, $Z = -0.65$, $p = 0.52$; megaherbivores, $Z = -1.5$, $p = 0.12$). We also analysed smaller mammal habitat use and responses to vegetation after excluding carnivores (servals *Leptailurus serval*, jackals *Canis mesomelas*) to assess their influence (Appendix 5: Table S5.1).

Table 2.1 Phylogenetic and dietary characteristics of wildlife species recorded in this study in sufficient numbers for analysis (for a full list, see Appendix 5: Figure S5.3)

Type	**Common name**	**Scientific name**	**Order**	**Family**	**Diet**
Megaherbivores	African elephant	*Loxodonta africana*	Proboscidea	Elephantidae	Mixed feeder
(*n* = 2)	giraffe	*Giraffa camelopardalis*	Artiodactyla	Giraffidae	Browser
Mesoherbivores	plains zebra	*Equus quagga*	Perissodactyla	Equidae	Grazer
(*n* = 6)	common eland	*Taurotragus oryx*	Artiodactyla	Bovidae	Mixed feeder
	beisa oryx	*Oryx beisa*	Artiodactyla	Bovidae	Grazer
	hartebeest	*Alcelaphus buselaphus*	Artiodactyla	Bovidae	Grazer
	Grant's gazelle	*Nanger granti*	Artiodactyla	Bovidae	Mixed feeder
	African buffalo	*Sycerus caffer*	Artiodactyla	Bovidae	Grazer
	common ostrich	*Struthio camelus*	Struthioniformes	Struthonidae	Omnivore
Smaller mammals	common duiker*	*Sylvicapra grimmia*	Artiodactyla	Bovidae	Browser
(*n* = 9)	steenbok*	*Raphicerus campestris*	Artiodactyla	Bovidae	Browser
	common warthog*	*Phacochoerus africanus*	Artiodactyla	Bovidae	Grazer
	hare*	*Lepus* spp.	Lagomorpha	Leporidae	Grazer
	olive baboon*	*Papio anubis*	Primate	Cercopithecidae	Omnivore
	northern lesser galago (bushbaby)*	*Galago senegalensis*	Primate	Galagidae	Omnivore
	serval*	*Leptailurus serval*	Carnivora	Felidae	Carnivore
	black-backed jackal*	*Canis mesomelas*	Carnivora	Canidae	Omnivore
Birds	helmeted guineafowl*	*Numida meleagris*	Galliformes	Numididae	Omnivore
(*n* = 9)	crested francolin*	*Dendroperdix sephaena*	Galliformes	Phasianidae	Omnivore
	yellow-necked francolin*	*Pternistis leucoscepus*	Galliformes	Phasianidae	Omnivore

	cattle egret*	*Bubulcus ibis*	Pelicaniformes	Areidae	Insectivore
	black-bellied bustard*	*Lissotis melanogaster*	Oditiformes	Otididae	Omnivore
	buff-crested bustard*	*Lophotis gindiana*	Oditiformes	Otididae	Omnivore
	superb starling*	*Lamprotornis superbus*	Passeriformes	Sturnidae	Insectivore
	northern white-crowned shrike*	*Eurocephalus ruppelli*	Passeriformes	Laniidae	Insectivore
Larger carnivores	spotted hyaena	*Crocuta crocuta*	Carnivora	Felidae	Carnivore
(*n* = 2)	striped hyaena	*Hyaena hyaena*	Carnivora	Felidae	Omnivore

2.4 Results

We recorded a total of 6,672 independent detections of 49 mammal and bird species (45 wild and four domestic) over 9,841 trap nights. Among the 27 wildlife species that each accounted for greater than five detections per 100 trap nights, 25 species (0.05–1,000 kg; 75% of total detections; *n* = 4,972) remained after excluding megaherbivores. The 16 smaller wildlife species (53% of total detections; *n* = 3,527) represented a wide range of phylogenetic and dietary characteristics (Table 2.1).

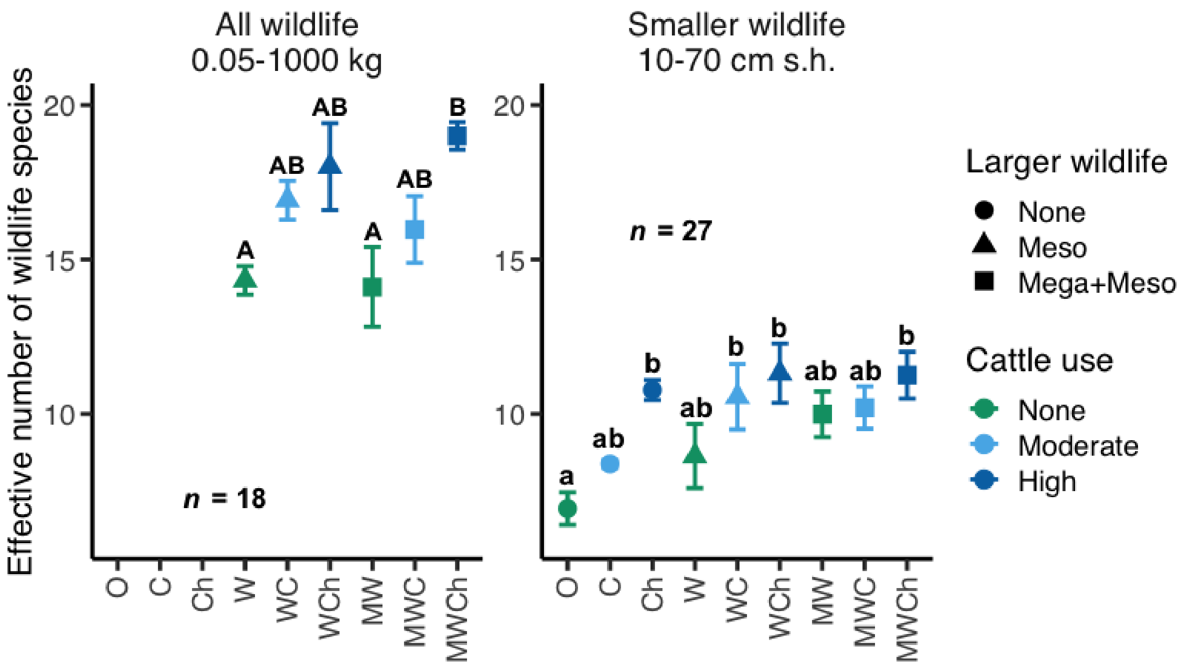

Figure 2.1 Diversity (effective number of species) responses to treatments for all wildlife 0.05–1000 kg and smaller wildlife (10–70 cm shoulder height [s.h.]) able to access all treatments unimpeded (means ± 1 SE). 'C' = only cattle allowed (moderate); 'Ch' = only cattle allowed (high); 'W' = wild mesoherbivores allowed; 'M' = megaherbivores (elephant, giraffe) allowed; 'O' = cattle, mesoherbivores and megaherbivores excluded. Beta-distributed linear mixed models (species groups modelled separately): *habitat use ~ M * C + W * C + (1|Block)*. Treatments sharing letters are not significantly different ($p > 0.05$) based on Tukey post hoc tests. The Tukey results indicate that significant pairwise differences in smaller wildlife diversity were not detected between the eight treatments accessible to cattle and/or larger wild herbivores.

2.4.1 Species diversity

Considering all 25 wildlife species 0.05–1,000 kg, alpha diversity (effective number of species) increased by 18% (equivalent to more than two species, $Z = 2.31$, $p = 0.02$) and 26% (more than three species, $Z = 3.26$, $p = 0.001$) in moderate- and high cattle stocking rate plots respectively (Figure 2.1). Compared to plots excluding cattle and larger wild herbivores, diversity of the 16 small-bodied wild species 10–70 cm s.h. (i.e. excluding ostrich, striped hyaena and spotted hyaena) was 55% higher (almost four species, $Z = 4.49$, $p < 0.001$) in plots with high cattle stocking rates, but not significantly higher in plots with moderate cattle stocking rates ($Z = 1.69$, $p = 0.09$). Compared to plots excluding cattle and larger wild herbivores, plots accessible to wild mesoherbivores had 25% (equivalent to at least one species, $Z = 1.99$, $p = 0.05$) more diverse communities of smaller wildlife, but the effect of megaherbivores was not significant ($Z = 1.58$, $p = 0.11$). For the December–January subset (which accounts for grass-induced detectability issues), the effects of moderate cattle stocking rates ($Z = 0.06$, $p = 0.95$) and mesoherbivores ($Z = 0.26$, $p = 0.79$) were not significant, but high cattle stocking rates still increased smaller wildlife diversity (effective number of species) by 60% (three species, $Z = 2.62$, $p = 0.01$; Appendix 5: Table S5.2).

Alpha diversity was negatively correlated with grass height (wildlife 0.05–1,000 kg, $Z = -4.41$, $p < 0.001$; wildlife 10–70 cm s.h., $Z = -3.12$, $p = 0.002$; Figure 2.2) but not significantly correlated with *A. drepanolobium* density (wildlife 0.05–1,000 kg, $Z = 1.59$, $p = 0.11$; wildlife 10–70 cm s.h., $Z = -0.58$, $p = 0.56$).

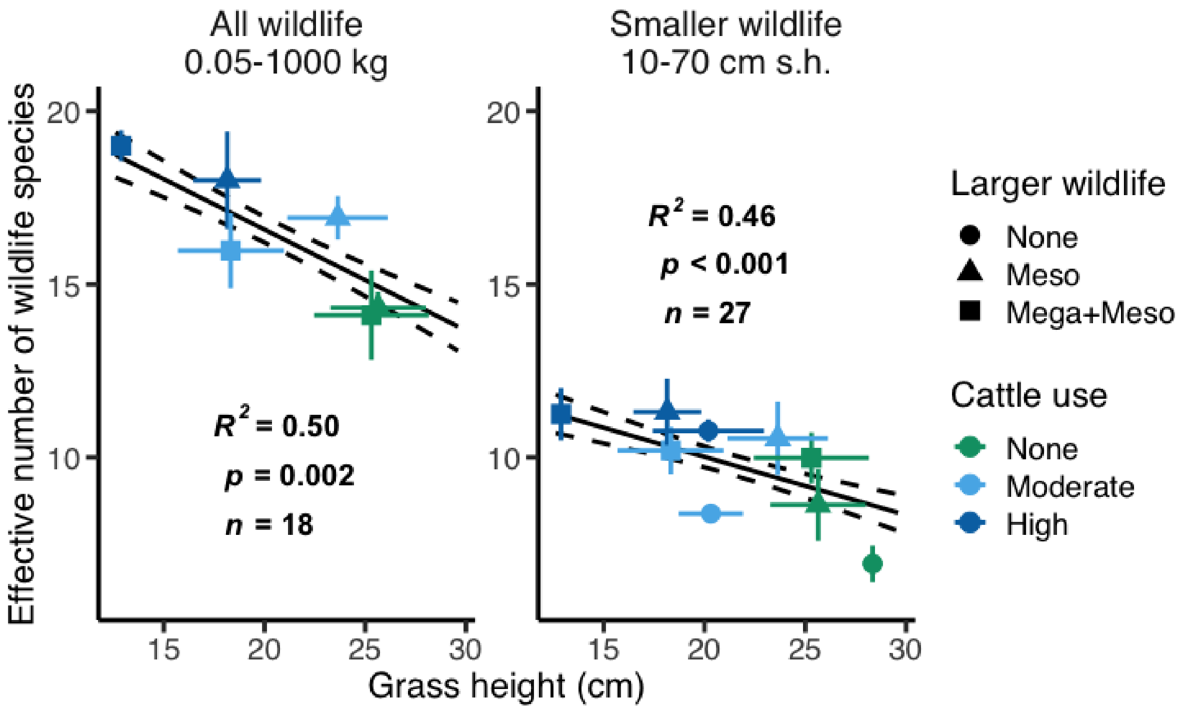

Figure 2.2 Diversity (effective number of species) correlations with annually-averaged grass height for all wildlife 0.05−1000 kg and smaller wildlife (10−70 cm shoulder height [s.h.]) able to access all treatments unimpeded (means ± 1 SE). Fitted means (solid lines) and standard errors (dashed lines) of gaussian linear mixed models (species groups modelled separately): *diversity ~ grass height + (1|Block)*. R^2 = marginal R^2. ‘Meso’ = accessible to wild mesoherbivores (50−1000 kg); ‘Mega’ = accessible to megaherbivores (elephant, giraffe); ‘None’ = no wild mesoherbivores/megaherbivores.

2.4.2 Wildlife habitat use

Habitat use of smaller wildlife (smaller mammals and birds) was not significantly affected by cattle alone (moderate, $Z = 1.53$, $p = 0.13$; high, $Z = -0.32$, $p = 0.75$) or wild mesoherbivores alone ($Z = 0.36$, $p = 0.72$), but was increased 60% more in plots accessible to both mesoherbivores and cattle (high) than expected by summing their individual effects (mesoherbivores × cattle, high, $Z = 2.36$, $p = 0.02$; Figure 2.3). There were no significant treatment effects for December–January (Appendix 5: Table S5.2).

Similarly, smaller mammal habitat use was not significantly affected by cattle (moderate, $Z = 1.53$, $p = 0.13$; high, $Z = -0.32$, $p = 0.75$), wild mesoherbivores ($Z = 0.36$, $p = 0.72$) or megaherbivores ($Z = -1.90$, $p = 0.06$) but, during December–January, was significantly reduced by megaherbivores ($Z = -4.34$, $p < 0.001$) and cattle at high stocking rates ($Z = -3.66$, $p < 0.001$). Smaller mammal habitat use was impacted more positively in plots accessible to both wild mesoherbivores and cattle (high) than expected by summing their individual effects (mesoherbivores × cattle, high, overall, 298%, $Z = 2.20$, $p = 0.03$; December–January, 155%, $Z = 0.81$, $p = 0.001$). The effect of high cattle stocking rates on ground bird habitat use was not significant overall ($Z = 1.84$, $p = 0.06$) or during December–January ($Z = 0.67$, $p = 0.50$). Habitat use by birds peaked over the 2 months following cattle use (Figure 2.4).

Species-specific treatment responses are illustrated in Appendix 5: Figure S5.4 & Table S5.3.

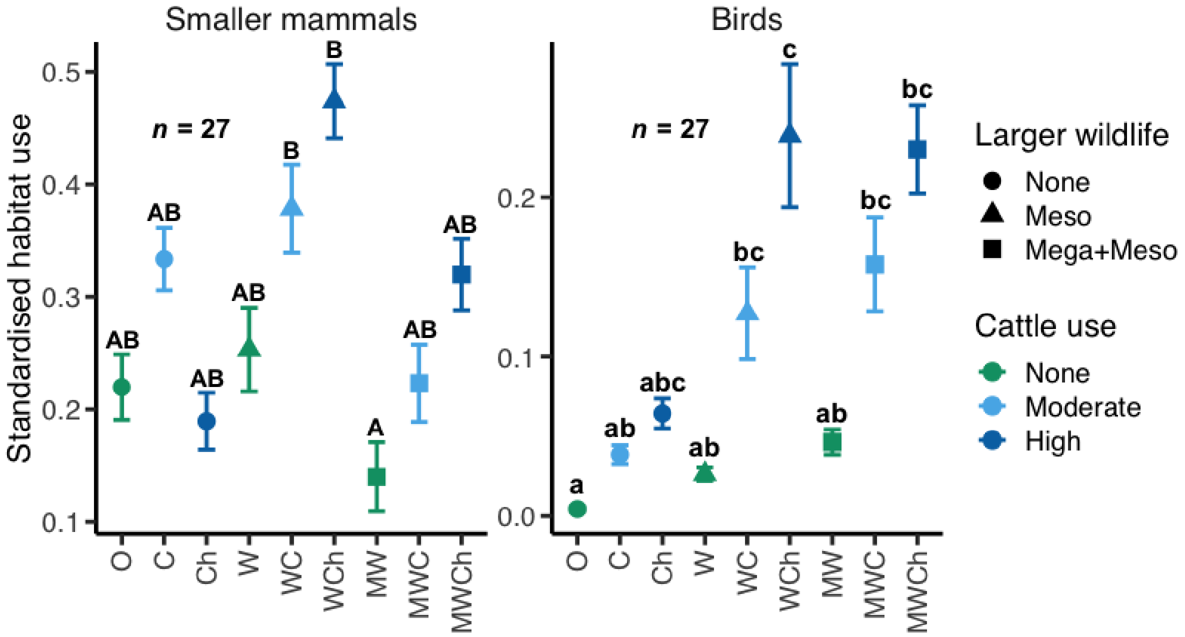

Figure 2.3 Treatment effects on species group habitat use (means ± 1 SE; scales differ). Habitat use is standardised and rescaled by converting images per trap night to an open unit interval (0,1) then compressing to remove 0s and 1s. ‘C’ = only cattle allowed (moderate); ‘Ch’ = only cattle allowed (high); ‘W’ = wild mesoherbivores allowed; ‘M’ = megaherbivores (elephant, giraffe) allowed; ‘O’ = cattle, mesoherbivores and megaherbivores excluded. Beta-distributed linear mixed models (species groups modelled separately): $habitat\ use \sim M * C + W * C + (1|Block)$. Treatments sharing letters are not significantly different ($p > 0.05$) based on Tukey post hoc tests.

2.4.3 Vegetation

Grass was significantly shorter in plots grazed by cattle at different time-scales at moderate stocking rates (averaged monthly, 33% or 11 cm, $Z = -3.10$, $p = 0.002$; averaged annually, 28% or 8 cm, $Z = -3.39$, $p < 0.001$) and high stocking rates (averaged monthly, 54% or 18 cm, $Z = -5.14$, $p < 0.001$; averaged annually, 30% or 9 cm, $Z = -3.65$, $p < 0.001$). Similarly, grass was significantly shorter in plots accessible to wild mesoherbivores when averaged monthly (23% or 8 cm, $Z = -2.18$, $p = 0.03$) but not annually (10% or 3 cm, $Z = -2.18$, $p = 0.21$). Monthly averaged grass height was reduced in plots accessible to cattle and megaherbivores more than expected based on summing their individual effects, at both moderate and high cattle stocking rates (megaherbivores × cattle, moderate, 46% or 15 cm, $Z = -3.07$, $p = 0.03$; high, 35% or 12 cm, $Z = -2.35$, $p = 0.02$). These relationships were not significant when averaging annually (megaherbivores × cattle, moderate, 20% or 6 cm, $Z = -1.68$, $p = 0.09$; high, 18% or 5 cm, $Z = -1.56$, $p = 0.12$).

Acacia drepanolobium density was reduced 29% by megaherbivores ($F = 9.06$, $p = 0.008$), but not significantly affected by cattle ($F = 0.18$, $p = 0.83$) or wild mesoherbivores ($F = 0.02$, $p =$

0.88). Only 19% of the variation in tree density was related to treatments, while over 60% of the variation in grass height was explained by treatments.

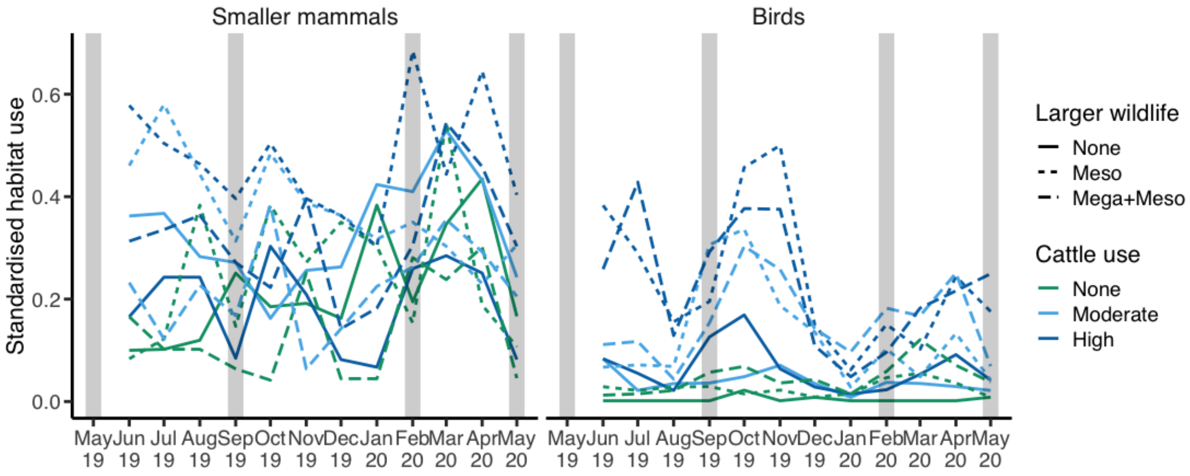

Figure 2.4 Monthly mean habitat use by treatment for four species groups. Habitat use is standardised and rescaled by converting images per trap night to an open unit interval (0,1) then compressing to remove 0s and 1s. Grey bars indicate cattle grazing events. 'Meso' = accessible to wild mesoherbivores (50−1000 kg); 'Mega' = accessible to megaherbivores (elephant, giraffe); 'None' = no wild mesoherbivores/megaherbivores.

2.4.4 Vegetation correlates of wildlife habitat use

Across all smaller wildlife (smaller mammals and birds), habitat use declined with increasing grass height when averaged monthly ($Z = -3.58$, $p < 0.001$) or over the entire year ($Z = -6.60$, $p < 0.001$). The statistical significance of this relationship depended on temporal scale in smaller mammals (monthly: $Z = -2.81$, $p = 0.01$, annual: $Z = -1.76$, $p = 0.08$) and birds (monthly: $Z = -5.10$, $p < 0.001$, annual: $Z = -4.93$, $p < 0.001$; Figure 2.5a).

Habitat use across all smaller wildlife was positively correlated with *A. drepanolobium* density ($Z = 2.13$, $p = 0.03$). *Acacia drepanolobium* density was positively correlated with smaller mammal habitat use ($Z = 3.98$, $p < 0.001$), but did not significantly correlate with ground bird habitat use ($Z = 0.24$, $p = 0.81$; Figure 2.5b).

Species-specific responses to vegetation are illustrated in Appendix 5: Figure 5.5 & Table S5.4.

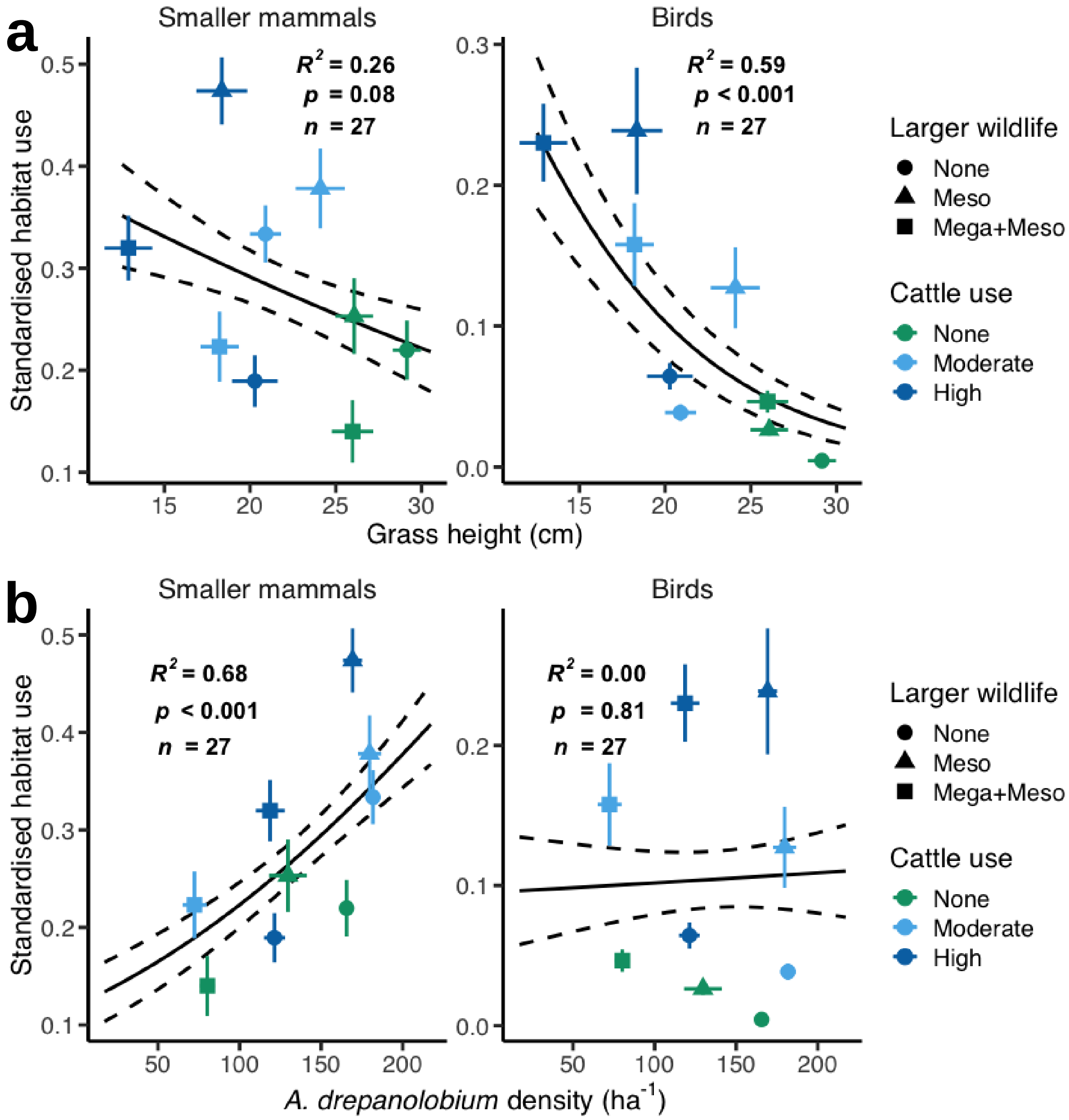

Figure 2.5 Species group habitat use correlations with annually-averaged grass height (**a**) and *Acacia drepanolobium* density (**b**) (means ± 1 SE; scales differ). Habitat use is standardised and rescaled by converting images per trap night to an open unit interval (0,1) then compressing to remove 0s and 1s. Fitted means (solid lines) and standard errors (dashed lines) of beta-distributed linear mixed models (species groups modelled separately): *habitat use ~ grass height + (1|Block)*. R^2 = marginal R^2. 'Meso' = accessible to wild mesoherbivores (50–1000 kg); 'Mega' = accessible to megaherbivores (elephant, giraffe); 'None' = no wild mesoherbivores/megaherbivores.

2.5 Discussion

We present experimental evidence that cattle at moderate and high stocking rates increase alpha diversity of wildlife 0.05–1,000 kg. Both cattle (at high and, to a lesser extent, moderate stocking rates) and larger wild mammalian herbivores (mesoherbivores and, to a lesser extent, megaherbivores) increase diversity and, in some cases, habitat use of smaller wildlife (10–70 cm s.h.). These effects on smaller wildlife may be due to factors such as increased visibility and predator avoidance (due to altered vegetation structure) and/or trophic cascades.

A trade-off exists between predation risk and food availability in savannas. Larger bodied species are less vulnerable to predation (Hopcraft et al. 2012) and, for smaller species, shorter grass can lower predation risk by increasing visibility (Riginos 2015). This may explain the preference for more heavily grazed plots by smaller mammals and birds. Similarly, preference by ostriches for treatments with megaherbivore-induced tree density loss may also reflect predation avoidance (we assume that the effects of megaherbivores are primarily due to elephant because giraffe do not feed on the herbaceous layer and have a comparatively minor effect on tree density).

Trophic cascades may also be responsible for the preference of cattle treatments by birds (Dennis et al. 2008), particularly cattle egrets *Bubulcus ibis*, galliforms and passerines. Birds' responses to grazing are well known to be species- and site-specific, often mimicking that of small mammals but, contrary to our findings, most studies show that grazing suppresses gallinaceous birds (Briske et al. 2011). The preference by omnivorous/insectivorous bird species for higher-cattle-stocking-rate plots in this study may be due to greater success catching invertebrates due to visibility or more abundant invertebrates attracted by increased cattle dung. Cattle egrets' habitat use unsurprisingly coincided with cattle (and buffalo *Syncerus caffer*) presence. By contrast, habitat use by galliforms (helmeted guineafowl *Numida meleagris,* crested francolin *Dendroperdix sephaena*, yellow-necked francolin *Pternistis leucoscepus*) peaked over the 2 months following cattle use (Figure 2.4), when herbaceous vegetation is beginning to respond to October rainfall, but before grass height peaks in December–January (Appendix 5: Figure S5.6). As their activity peak does not coincide with the months of shortest grass, our results suggest that galliforms are tracking seeds or invertebrates proliferating in cattle plots in response to vegetation growth. A global review suggests that grazing tends to reduce arthropod diversity (due to unintentional predation/disturbance, reduced resource base and changes in vegetation), but can increase arthropod diversity if benefits of grazing-induced heterogeneity compensate for the overall decrease in resources (van Klink et al. 2015). The high cattle stocking rate effect on diversity and habitat use of smaller wildlife persisted during December–January, suggesting that the positive effects of grazing are not solely due to detectability effects of grass height, but also suggests that diversity and habitat use are responding in a lagged way to short grass in preceding months.

Our results also show that the effects of cattle and wild mesoherbivores on smaller wildlife diversity are less than additive, so the impacts of each are less in the presence of the other. Wild mesoherbivores (and to a lesser extent megaherbivores) increase alpha diversity of smaller mammals, but less so where cattle are present, particularly at high cattle stocking rates. Similarly, cattle increase smaller mammal diversity, but less so in the presence of wild mesoherbivores (and megaherbivores). The general pattern of wildlife dampening the effects of cattle mirrors the trend of elephant mitigating the effects of cattle in this system (Kimuyu et al. 2017; Sitters et al. 2020).

Correlations between grass height/tree density and diversity/habitat use suggest that vegetation structure plays an important role in mediating treatment effects on smaller vertebrates. The importance of vegetation structure has also been demonstrated for small-bodied wildlife elsewhere (e.g. birds; Duchardt et al. 2018). The observed contrasting responses of steenboks *Raphicerus campestris* and duikers *Sylvicapra grimmia* (also black-bellied bustard *Lissotis melanogaster* and buff-crested bustard *Lophotis gindiana*) to grass height and tree density, demonstrate that even sympatric morphologically and functionally similar species can show differing responses to the same environmental variables.

Other factors can influence wildlife habitat use in savannas, including soil and foliar nutrient content. Cattle grazing can reduce soil carbon/nitrogen and grass nitrogen – effects that are reversed by megaherbivore presence over the long term (Sitters et al. 2020). Soil and foliar nutrients are also well known to be influenced by tree canopies (Sitters et al. 2020), but we were not able to test the influence of soil/foliar nutrients as we did not measure these variables. There are several other limitations of the experiment, such as restricted range of soil, vegetation and cattle stocking rate gradients, as well as grass-induced detectability issues. We attempted to address detectability issues by analysing the December–January subset, which gave similar results in general for diversity. The negative effects of high cattle stocking rates and megaherbivores on smaller mammal habitat use during December–January suggest that these two effects may be masked by grass-induced detectability effects. The degree of influence of other biases, such as observed patterns being restricted to this particular time of year, is unclear.

While the KLEE has demonstrated that cattle generally suppress other large herbivores via forage reduction (Kimuyu et al. 2017), our results suggest that smaller vertebrates may be more sensitive to structural differences in vegetation induced by wild and domestic herbivores. The effects of grazing may also depend on whether it enhances spatio-temporal heterogeneity, the importance of which has been recognised in rangelands (Fynn et al. 2016). The study design generates heterogeneity at different scales by creating areas of taller/shorter grass and higher tree density than the surrounding matrix, while creating smaller shorter grass areas within the main 4-ha plots through high cattle use. More heavily grazed patches may offer better foraging opportunities, refugia from predators and ease of locomotion, only within a matrix of taller grass habitat with higher prey abundance.

To our knowledge, this study provides the first experimental evidence that larger wild herbivores (mesoherbivores and megaherbivores) mediate the effects of cattle stocking rate on alpha diversity and habitat use of smaller wild vertebrates. Our results demonstrate that grazing, whether by cattle (at both moderate and high stocking rates) or larger wild herbivores, can increase alpha diversity of smaller wildlife (10–70 cm s.h.) in savannas, at least at small spatial scales. Consequently, savanna rangeland managers may be able to increase the diversity of wildlife (particularly smaller vertebrates) through grazing by domestic or wild herbivores. The positive effects of grazing on local wildlife diversity may depend on the state of the surrounding habitat. This work also has implications beyond tropical savannas. The role of larger wild herbivores in mediating livestock grazing effects will be an important consideration in rewilding efforts globally, where livestock cohabit with reintroduced wildlife.

2.6 Supporting information

Appendix 5. Supporting data

2.7 References

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Chapter 3: At high stocking rates, cattle do not functionally replace wild herbivores in shaping understory community composition (published in Ecological Applications)

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3.1 Abstract

Over a quarter of the world's land surface is grazed by cattle and other livestock, which are replacing wild herbivores, potentially impairing ecosystem structure and functions. Previous research suggests that cattle at moderate stocking rates can functionally replace wild herbivores in shaping understory communities, but it is unclear whether this is also true under high stocking rates. It is also unclear whether wild herbivore effects on plant communities moderate, enhance, or are simply additive to the effects of cattle at high stocking rates. To evaluate the influence of cattle stocking rates on the ability of cattle to functionally replace wild herbivores and test for interactive effects between cattle and wild herbivores in shaping understory vegetation, we assessed herbaceous vegetation in a long-term exclosure experiment in a semi-arid savanna in central Kenya that selectively excludes wild mesoherbivores (50–1000 kg) and megaherbivores (elephant and giraffe). We tested the effects of cattle stocking rate (zero/moderate/high) on herbaceous vegetation (diversity, composition, leafiness) and how those effects depend on the presence of wild mesoherbivores and megaherbivores. We found that herbaceous community composition (primary ordination axis) was better explained by the presence/absence of herbivore types than by total herbivory, suggesting that herbivore identity is a more important determinant of community composition than total herbivory at high cattle stocking rates. The combination of wild mesoherbivores and cattle stocked at high rates led to increased bare ground and annual grass cover, reduced perennial grass cover, reduced understory leafiness, and enhanced understory diversity. These shifts were weaker or absent when cattle were stocked at high stocking rates in the absence of wild mesoherbivores. Megaherbivores tempered the effects of cattle stocked at high rates on herbaceous community composition but amplified the effects of high cattle stocking rate on bare ground and understory diversity. Our results show that, contrary to previous findings at moderate stocking rates, cattle at high stocking rates do not functionally replace wild herbivores in shaping savanna herbaceous communities. In mixed-use rangelands, interactions between cattle stocking rate and wild herbivore presence can lead to non-additive vegetation responses with important implications for both wildlife conservation and livestock production.

3.2 Introduction

Cattle and other livestock graze more than a quarter of the Earth's land surface (Steinfeld et al. 2006) and are estimated to comprise > 90% of the world's non-human mammalian biomass (Bar-On et al. 2018). Across the world's rangelands, including African savannas, livestock continue to replace large wild herbivores (> 50 kg), potentially with negative impacts on ecosystem structure and function (du Toit and Cumming 1999; Hempson et al. 2017). Understanding how plant communities respond to partial or complete replacement of large wild herbivores by livestock requires knowledge of i) the extent to which and at what stocking rates livestock can functionally replace large wild herbivores and, ii) in mixed-use rangelands, whether the effects of wild and domestic herbivores are simply additive to those of livestock grazing, or whether large wild herbivores moderate or amplify the effects of livestock on vegetation. This understanding is critical in rangeland management for maintaining plant diversity and predicting plant community responses to ecological restoration and herbivore reintroductions. Shifts in rangeland plant communities are also important because associated changes in forage quality and quantity can impact large wild herbivore abundance and diversity (Olff et al. 2002), as well as livestock grazing (Odadi et al. 2011).

In grasslands, including African savannas, grazing and/or browsing wild herbivores affect understory plant biomass (Staver et al. 2019), productivity (Frank et al. 2016), diversity (Koerner et al. 2018; Porensky et al. 2013), species composition (Veblen et al. 2016) and plant functional traits (van der Plas et al. 2016). The consequences of wildlife extirpation for understory vegetation may be dependent on climate and the identity of the species lost or the species remaining, either wild or domestic (Burkepile et al. 2017; Burns et al. 2009; Goheen et al. 2013; Staver & Bond 2014; van der Plas et al. 2016). Domestic herbivores also affect understory community composition, diversity, biomass (e.g. Pakeman et al. 2019; Seymour et al. 2010; Veblen et al. 2016) and productivity (Charles et al. 2017), and can reduce ecosystem structure and function in ways that are mediated by climate, grazing regime, and herbivore identity (Cingolani et al. 2005; Eldridge et al. 2016, 2018; Liu et al. 2015; O'Connor et al. 2010; Young et al. 2013). Several studies have examined the effects of livestock stocking rates on vegetation diversity and community composition (e.g. Pakeman et al. 2019; Porensky et al. 2016; Seymour et al. 2010). In contrast to only investigating presence versus absence of livestock (e.g. Charles et al. 2017; Koerner et al. 2018; Porensky et al. 2013; Veblen et al. 2016), studying the effects of different livestock stocking rates better allows us to understand and adjust the management of globally dominant domestic herbivores to meet biodiversity conservation objectives.

Livestock at a particular stocking rate could functionally compensate for wild herbivore losses in shaping plant communities if: i) livestock diets mirror the collective diets of the assemblage of wild herbivores lost (Cingolani et al. 2014); ii) plant communities respond primarily to total herbivory (not herbivore identity), which remains comparable following replacement of wild herbivores by livestock (Perevolotsky & Seligman 1998; Veblen et al. 2016); and/or iii) domestic and wild herbivores have similar non-consumptive effects on vegetation (e.g. trampling or nutrient addition via defecation) and these effects overpower consumptive effects. However, if criteria such as these are not met, replacement of wild herbivores by livestock would lead to plant community shifts. For example, if livestock stocking rates are increased to the point that the total herbivory by domestic and wild herbivores exceeds the herbivore pressure with which the ecosystem coevolved, plant communities can cross thresholds to assume functionally different states. There is ample evidence that rangeland vegetation can be characterised by threshold dynamics and that herbivory – by livestock, wild herbivores, or both – can drive shifts among states (Bestelmeyer et al. 2015; Briske et al. 2003; Vetter 2005).

We generally lack studies that experimentally tested the effects of large wild herbivores in the context of more than two livestock stocking rates (i.e. presence versus absence) on understory vegetation. Previous work from our study system in central Kenya identified strong impacts of cattle presence on understory plant successional dynamics, diversity, and community stability (Veblen & Young 2010; Porensky et al. 2013; Riginos et al. 2018). Veblen et al. (2016) showed that savanna understory plant community composition (measured using primary ordination axis scores) was explained more by total herbivory than herbivore identity, and cattle at moderate densities appeared to functionally replace the resident large wild herbivore assemblage in shaping understory vegetation. However, whether this pattern persists at higher cattle stocking rates is unknown, as is how the effects of high cattle stocking rates interact with native herbivore presence. Investigating the effects of increasing cattle stocking rates is important because rangelands in this region, particularly those that are communally managed, are stocked at higher rates than the moderate stocking rates evaluated by Veblen et al. (2016) (Crego et al. 2020; Wells et al. 2021a).

To test this experimentally, we assessed herbaceous vegetation in the Kenya Long-term (25-year) Exclosure Experiment, which enabled us to test the individual and interactive effects of wild mesoherbivores (50–1000 kg), megaherbivores (elephant and giraffe), and cattle at three stocking rates (zero/moderate/high). Our objectives were to investigate: 1) the extent to which cattle at high stocking rates functionally replace the loss of large wild herbivores (wild mesoherbivores and megaherbivores), and 2) whether the effects of large wild herbivores on savanna vegetation moderate, enhance, or are simply additive to the effects of cattle at moderate and high stocking rates.

3.3 Methodology

3.3.1 Study site

We conducted this study in the Kenya Long-term Exclosure Experiment (KLEE) plots at Mpala Research Centre (0°17’N, 36°52’E, 1800 masl) in Laikipia, Kenya. Kenya is a biodiversity hotspot in which livestock-keeping plays an important role for livelihoods and culture (Sundaresan & Riginos

2010). Rainfall at the site is weakly trimodal with a pronounced dry season December-March. From 2001 to 2019, annual rainfall averaged 613 mm yr^{-1} (range: 421-1009 mm yr^{-1}, annual coefficient of variation: 27%). Rainfall totals over the March-May ‘wet season’ prior to sampling were 393, 210 and 204 mm in 2018, 2019 and 2020 respectively (2001-2019 mean: 225 mm; Appendix 6: Figure S6.1). Soils are poorly drained vertisols with high clay content (> 40%) known as ‘black cotton’. Black cotton soils are widespread across Africa and with other vertisols cover > 100 million hectares across the continent (Ahmad 1996). The overstory of this savanna ecosystem is dominated by *Acacia drepanolobium* (syn. *Vachellia drepanolobium*, 97% of the canopy; Young et al. 1997), while five perennial grass species comprise 85% of herbaceous understory cover (Porensky et al. 2013). Mpala Research Centre is managed for both wildlife conservation and livestock production, where cattle are the main domestic animal. Livestock grazing lands cover 80% of Kenya’s area and account for > 12% of gross domestic product (Allan et al. 2017).

3.3.2 Experimental design

The KLEE plots, established in 1995, use barriers to control access to 200 × 200 m (4-ha) treatment plots by three herbivore guilds – wild megaherbivores (‘M’, elephant and giraffe), wild mesoherbivores (‘W’, 50–1000 kg) and cattle (‘C’) – in different combinations. There are three replicate blocks, each consisting of six treatments (18 plots in total): 1) ‘MWC’ (accessed by megaherbivores, wild mesoherbivores and cattle), 2) ‘MW’ (accessed by megaherbivores and wild mesoherbivores), 3) ‘WC’ (accessed by wild mesoherbivores and cattle), 4) ‘W’ (accessed by wild mesoherbivores only), 5) ‘C’ (accessed by cattle only), 6) ‘O’ (excludes cattle, wild mesoherbivores and megaherbivores). The treatment plots accessible to cattle are typically grazed by 100–120 mature Boran cows *Bos indicus* (sometimes with calves and/or bulls) for 2–3 days (2 hrs day^{-1}) within a 2-week period, 3–4 times per year. The timing and number of grazing days depends on forage availability and reflects typical grazing regimes of ranches in the region, wherein cattle graze in an area for several days before being moved to allow that area to recover.

Each of the treatment plots accessible to cattle (MWC, WC, C) contains a 50 × 50 m (0.25-ha, or 1/16 of the plot) subplot (established in 2008), in which the same cattle herd is grazed for a further 30 mins following the initial 2-hr grazing period in the wider plot, to achieve an approximately four-fold increase in cattle stocking rate compared to the wider plot (Appendix 6: Figs. S6.2–6.3). These three additional treatments are named: 1) MWCh, 2) WCh, and 3) Ch, where ‘h’ denotes high cattle stocking rate. We note that ‘grazing’ also involves trampling and nutrient cycling effects (Sitters et al. 2020). Grazing behaviour can also be affected by time of day and the presence of other herbivores (Odadi et al. 2017). Because cattle only access individual plots a few times per year, responses of most large wild herbivores are unlikely to be due to direct interaction with cattle or herders. Fire has not been used as a management tool in this ecosystem for over 50 years and is rarely used by other ranches in the region. Natural-ignition fires have not occurred in decades. See Young et al. (1997) and Young et al. (2018) for further details of the experimental design.

3.3.3 Data collection

To assess understory vegetation, we sampled herbaceous plants during May-August in 2018, 2019, and 2020. We measured aerial cover every 10 m by counting the number of pins of a 10-point pin frame (vertical pins separated by 5 cm) hit by each species (maximum one hit per pin per species). For the main six treatments (O, C, W, WC, MW, MWC), we sampled 10 100-m transects within the central hectare of the 18 4-ha treatment plots, recording pin hits every 20 m for a total of 50 sites. We further subsampled pin hits and leaf verses stem hits for the five dominant species (*Brachiaria lachnantha, Themeda triandra, Pennisetum stramineum, P. mezianum, Lintonia nutans*) by sampling four of 10 transects (second, fourth, sixth and eighth transects) totalling 20 sites. For the 50 × 50 m high cattle stocking rate subplots (Ch, WCh, MWCh), we ran four 40-m transects (leaving a 10-m buffer along two sides to minimize edge effects of the 4-ha plot), recording pin hits every 10 m for a total of 16 sites. Leaf versus stem pin hits were only recorded at eight sites (second and fourth transects).

To estimate total herbivory, we used camera traps. We deployed one Browning Strike Force HD Pro X camera in each of the 27 plots (three replicates of nine treatments) between 23 May 2019 and 26 May 2020. Cameras were secured to a tree 80 cm above the ground, avoiding treeless glades that occur throughout the landscape, and ensuring a view unobstructed by woody vegetation within the detection zone. Cameras were programmed to take three images per trigger (1 second apart) with a 1-min delay between triggers. Cameras were checked every 2–3 weeks to download images, replace batteries and ensure cameras were operational. Camera traps were operational for an average of 364 (± 2 SE, range: 340–374) trap nights. Each camera's detection area is 275 m^2 calculated as: $(detection\ angle \times 360^{-1}) \times \pi \times detection\ range^2$, where detection angle is in degrees and detection range in metres. For further details of the camera trap methodology see Wells et al. (2021b). We calculated total annual herbivory as $\sum body\ mass \times number\ of\ individuals \times duration \times detection\ area^{-1} \times trap\ night^{-1} \times 365.25$, for each species where the duration is in hours (each image corresponds to one minute). We included the sixteen herbivore species > 2 kg: elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, plains zebra *Equus quagga*, Grevy's zebra *Equus grevyi*, eland *Taurotragus oryx*, buffalo *Syncerus caffer*, hartebeest *Alcelaphus buselaphus*, oryx *Oryx beisa*, Grant's gazelle *Nanger granti*, impala *Aepyceros melampus*, ostrich *Struthio camelus*, duiker *Sylvicapra grimmia*, steenbok *Raphicerus campestris*, warthog *Phacochoerus africanus*, hare *Lepus* spp., and cattle. Although the total herbivory metric was calculated for a single 12-month period, this period was representative of average annual rainfall at the site (Appendix 6: Figure S6.1).

3.3.4 Statistical analysis

All statistical analyses were performed in R version 3.6.2 (R Core Team 2019). To test how the understory plant community was responding to treatments and total herbivory, we assessed community composition and quantified plant diversity metrics (effective number of species, evenness, and dominance).

To assess herbaceous community composition, we performed an unconstrained ordination in the *boral* package version 1.9 (Hui 2016) on relative abundance data by fitting a latent variable model (negative binomial with log-link, no fixed effects, and random effect of year), using Bayesian Markov chain Monte Carlo (MCMC) parameter estimation. Model-based methods have several advantages over, and have been shown to outperform, distance-based approaches to ordination such as non-metric multidimensional scaling (Warton et al. 2015). We ran one MCMC chain for 10^5 iterations, discarded the first 10^4 as burn-in and thinned by one in 90 iterations for a total of 1,000 posterior samples. We used very weakly informative priors with normal distributions, mean zero and variance 10. We assessed model convergence by visualising MCMC chain traces and using Geweke diagnostics (Hui 2016) and ensured that residuals met model assumptions (Appendix 6: Figure S6.4). Prior to diversity and ordination analyses, species observed in < 5% of samples (plots within years) were excluded (*c.f.*, Veblen et al. 2016), leaving 51 taxa (48 species and three multi-species genera) of the original 81 taxa (78 species and three multi-species genera).

We used the *vegan* package version 2.5-6 (Oksanen et al. 2019) to calculate Shannon-Wiener diversity, H', which we converted to 'effective number of species' (the number of equally likely elements needed to produce the diversity value, H') by taking exp (H'), to facilitate interpretation (Jost 2007). We calculated evenness by taking H'/H'_{max}, and assessed dominance using the Berger-Parker dominance index, D (relative cover of the most abundant species; Berger & Parker 1970).

To evaluate the individual and interactive effects of wild mesoherbivore presence, megaherbivore presence and cattle stocking rate on understory vegetation, we employed linear mixed-effects models (LMMs) to model herbivore treatment effects on 1) primary and secondary community ordination axes (latent variables 1 and 2); 2) absolute cover of species groups (life forms: grass, forb; life histories: annual, perennial); 3) species-specific relative cover; 4) species-specific and across-species leaf-to-stem ratio (leaf:stem); and 5) diversity metrics (effective number of species, evenness, and dominance). We implemented LMMs in the *glmmTMB* package version 1.0.1 (Brooks et al. 2017). To distinguish between individual and interactive effects of herbivore types we coded cattle (none/moderate/high), wild mesoherbivores (presence/absence), megaherbivores (presence/absence), and interactive terms cattle × mesoherbivores and cattle × megaherbivores as fixed effects. Metrics derived from pin hits (absolute/relative cover) were scaled to correct for unbalanced sampling effort – i) 16 versus 50 sampling locations in high-cattle-stocking-rate and all other treatments respectively, and ii) subsampling of dominant species – and square-root-transformed to normalise.

To evaluate the effects of total herbivory on understory vegetation we used LMMs to test the relationship between total pin hits and the five sets of herbaceous plant response variables listed above. Second-order polynomial functions were implemented when their fit had $p < 0.05$.

To directly compare herbivore-identity and total-herbivory approaches to modelling herbaceous plant responses, we performed model selection using Akaike's information criterion (AIC). We compared LMMs for the following three predictors: 1) total herbivory using a linear or second-order polynomial function; 2) herbivore identity, using the presence/absence of the three herbivore types (cattle, wild mesoherbivores and megaherbivores); 3) herbivore identity, as in model 2, but including cattle-mesoherbivore and cattle-megaherbivore interactions. In all LMMs we coded block nested within year (2018/2019/2020) as the random effect. Because we were comparing herbivore-identity and total-herbivory approaches to modelling herbaceous community composition, we did not explore the effects of the covariates included in each model.

Table 3.1 Model selection comparing total herbivory and herbivore identity (presence/absence [P/A] of herbivore types) as predictors of herbaceous community composition (represented by the ordination axes, latent variables 1 and 2), species diversity metrics (effective number of species, evenness, and dominance), bare ground, total aerial cover, covers of annual/perennial grasses/forbs, and leafiness (measured by leaf-to-stem ratio). The 'TH/ID' column indicates whether total herbivory (TH) or herbivore identity (ID) was the more important predictor (ΔAIC > 2); *n* = 81.

Variable	**Model**	**df**	**AIC**	**TH/ID**
Latent variable 1 (primary ordination axis)	*~ cattle(P/A) × mega(P/A) + cattle(P/A) × meso(P/A) + (1|year/block)*	9	55.2	ID
	~ cattle(P/A) + mega(P/A) + meso(P/A) + (1|year/block)	7	66.9	
	~ poly(total herbivory,2) + (1|year/block)	6	116.3	
Latent variable 2 (secondary ordination axis)	*~ total herbivory + (1|year/block)*	5	99.5	TH
	~ cattle(P/A) + mega(P/A) + meso(P/A) + (1|year/block)	7	123.9	
	~ cattle(P/A) × mega(P/A) + cattle(P/A) × meso(P/A) + (1|year/block)	9	125.0	
Bare ground	*~ total herbivory + (1|year/block)*	5	472.6	TH
	~ cattle(P/A) + mega(P/A) + meso(P/A) + (1|year/block)	9	493.1	
	~ cattle(P/A) × mega(P/A) + cattle(P/A) × meso(P/A) + (1|year/block)	7	493.3	
Total cover	*~ cattle(P/A) + mega(P/A) + meso(P/A) + (1|year/block)*	7	690.5	ID
	~ cattle(P/A) × mega(P/A) + cattle(P/A) × meso(P/A) + (1|year/block)	9	691.4	
	~ poly(total herbivory, 2) + (1|year/block)	6	693.5	
Annual forbs absolute cover	*~ total herbivory + (1|year/block)*	5	131.6	TH
	~ cattle(P/A) + mega(P/A) + meso(P/A) + (1|year/block)	7	141.2	
	~ cattle(P/A) × mega(P/A) + cattle(P/A) × meso(P/A) + (1|year/block)	9	144.5	
Annual grasses absolute cover	*~ cattle(P/A) + mega(P/A) + meso(P/A) + (1|year/block)*	7	238.5	ID
	~ cattle(P/A) × mega(P/A) + cattle(P/A) × meso(P/A) + (1|year/block)	9	238.1	
	~ total herbivory + (1|year/block)	5	241.2	

Perennial forbs absolute cover	~ *poly(total herbivory,2) + (1|year/block)*	6	242.4	TH
	~ *cattle(P/A) × mega(P/A) + cattle(P/A) × meso(P/A) + (1|year/block)*	9	256.4	
	~ *cattle(P/A) + mega(P/A) + meso(P/A) + (1|year/block)*	7	268.9	
Perennial grasses absolute cover	~ *total herbivory + (1|year/block)*	5	162.3	TH
	~ *cattle(P/A) × mega(P/A) + cattle(P/A) × meso(P/A) + (1|year/block)*	9	164.5	
	~ *cattle(P/A) + mega(P/A) + meso(P/A) + (1|year/block)*	7	165.0	
Leafiness (leaf-to-stem ratio)	~ *poly(total herbivory,2) + (1|year/block)*	6	349.2	TH
	~ *cattle(P/A) × mega(P/A) + cattle(P/A) × meso(P/A) + (1|year/block)*	9	358.2	
	~ *cattle(P/A) + mega(P/A) + meso(P/A) + (1|year/block)*	7	366.7	
Effective number of species	~ *cattle(P/A) × mega(P/A) + cattle(P/A) × meso(P/A) + (1|year/block)*	9	278.8	ID
	~ *cattle(P/A) + mega(P/A) + meso(P/A) + (1|year/block)*	7	284.9	
	~ *poly(total herbivory,2) + (1|year/block)*	6	289.6	
Evenness	~ *poly(total herbivory,2) + (1|year/block)*	6	-204.4	TH
	~ *cattle(P/A) × mega(P/A) + cattle(P/A) × meso(P/A) + (1|year/block)*	9	-158.2	
	~ *cattle(P/A) + mega(P/A) + meso(P/A) + (1|year/block)*	7	-155.3	
Dominance	~ *cattle(P/A) × mega(P/A) + cattle(P/A) × meso(P/A) + (1|year/block)*	9	584.1	ID
	~ *total herbivory + (1|year/block)*	5	594.1	
	~ *cattle(P/A) + mega(P/A) + meso(P/A) + (1|year/block)*	7	601.0	

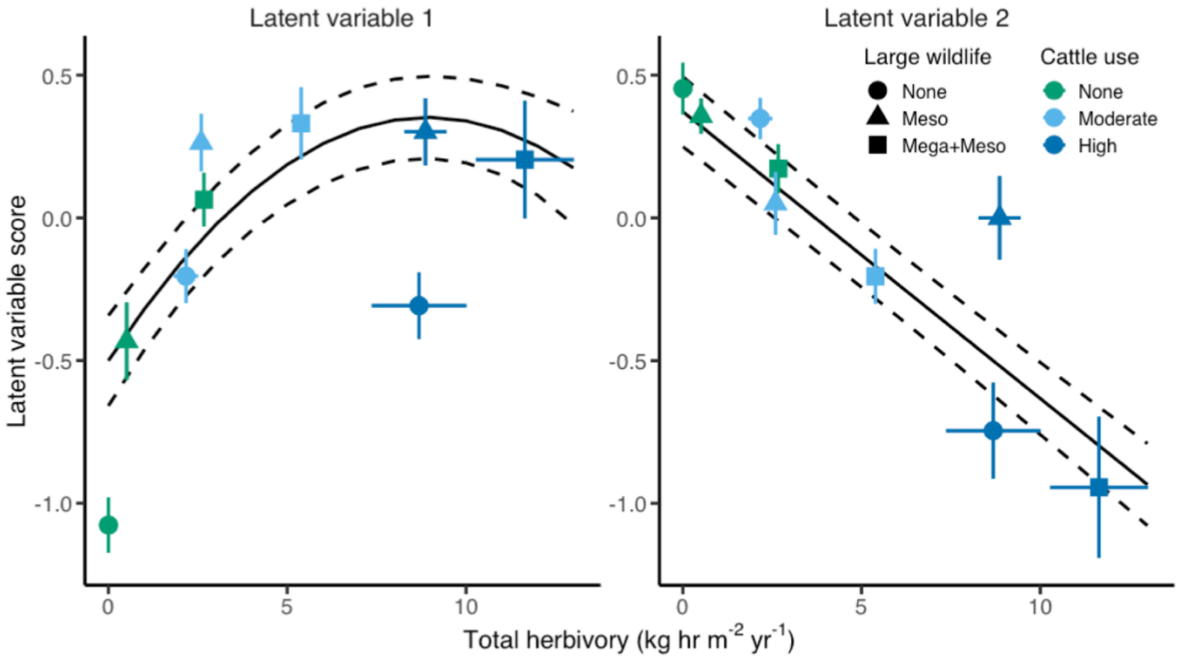

Figure 3.1 Responses of understory herbaceous community composition represented by latent variable model ordination axes 1 and 2. Regressions of ordination axes on total herbivory (means ± 1 SE). Fitted means (solid lines) and standard errors (dashed lines) of linear mixed models (*n* = 81). ‘Meso’ = accessible to wild mesoherbivores (50–1000 kg); ‘Mega’ = accessible to megaherbivores (elephant, giraffe); ‘None’ = no wild mesoherbivores/megaherbivores.

3.4 Results

3.4.1 Understory community composition is primarily shaped by herbivore identity, not total herbivory, at high cattle stocking rates

Understory community composition, represented by primary ordination axis, latent variable 1, was affected by both herbivore treatments and total herbivory (Figure 3.1). The treatments without high cattle stocking rates showed a similar relationship with total herbivory to that reported by Veblen et al. (2016). However, two lines of evidence suggest that high cattle stocking rate, as included in the present study, was the principal driver of understory community composition. Firstly, model selection showed that herbivore identity (presence/absence of herbivore types) was a more important predictor of herbaceous community composition (represented by latent variable 1) than total herbivory (Table 3.1). Secondly, treatments with high cattle stocking rates separated from other treatments in the ordination biplots, particularly along the secondary ordination axis – largely driven by annual grasses (Figure 3.2). The primary and secondary ordination axes (latent variables 1 and 2, respectively) explained 58% of the variation in herbaceous community composition and explained more of the variation of rarer species (Appendix 6: Figure S6.5).

The relative importance of herbivore identity and total herbivory varied across vegetation metrics. Total herbivory was a better predictor (Δ AIC > 2) of bare ground, leafiness (leaf:stem), evenness, and absolute covers of annual and perennial forbs, and perennial grasses. Meanwhile, herbivore identity was a better predictor of total herbaceous cover, annual grass cover, effective number of species and dominance (Table 3.1). Detailed statistical results are presented in Appendix 6: Tables S6.1–6.2.

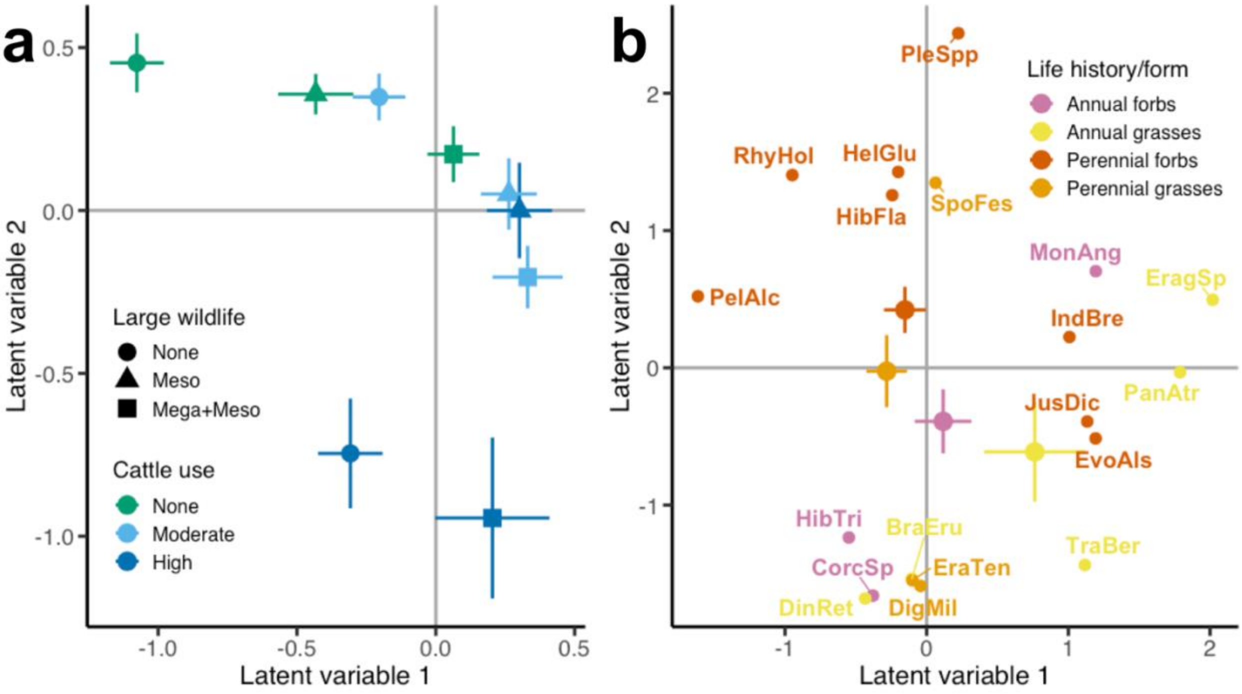

Figure 3.2 Biplots of understory herbaceous community composition represented by latent variable model ordination axes 1 and 2. Treatments responses (**a**) and latent variable coefficients for species (smaller points) and life history and life form groups (**b**; larger points; means ± 1 SE). ‘Meso’ = accessible to wild mesoherbivores (50–1000 kg); ‘Mega’ = accessible to megaherbivores (elephant, giraffe); ‘None’ = no wild mesoherbivores/megaherbivores. Only species with coefficients > |1| for either latent variable are shown. BraEru = *Brachiaria eruciformis*, CorcSp = *Corchorus* sp., DigMil = *Digitaria milanjiana*, DinRet = *Dinebra retroflexa*, EraTen = *Eragrostis tenuifolia*, EragSp = *Eragrostis* sp., EvoAls = *Evolvulus alsinoides*, HelGlu = *Helichrysum* (*Pseudognaphalium*) *glumaceum*, HibFla = *Hibiscus flavifolius*, HibTri = *H. trionum*, IndBre = *Indigofera brevicalyx*, JusDic = *Justicia diclipteroides*, MonAng = *Monsonia angustifolia*, PanAtr = *Panicum atrosanguineum*, PelAlc = *Pelargonium alchemilloides*, PleSpp = *Plectranthus* spp., RhyHol = *Rhynchosia holstii*, SpoFes = *Sporobolus festivus*, TraBer = *Tragus bertonianus*.

3.4.2 The effects of cattle and wild herbivores on the understory community are non-additive

Megaherbivores moderated the effects of cattle on understory community composition at both moderate and high stocking rates (Figs. 3.1–3.2). This was evidenced by the combined effect of cattle and megaherbivores on the primary ordination axis, latent variable 1, being weaker than the sum of their individual effects (megaherbivores × cattle, moderate: $Z = -2.4$, $p = 0.02$, high: $Z = -3.3$, $p < 0.001$).

Bare ground was positively related to total herbivory and was minimal in the absence of cattle (Figure 3.3; Appendix 6: Table S6.2). The combined effects of cattle at high stocking rates and wild mesoherbivores increased bare ground 96% more than the sum of their individual effects (mesoherbivores × cattle, high: $Z = 2.8$, $p = 0.004$). This led to over three times as much bare ground in the two treatments accessible to both mesoherbivores and cattle at high stocking rates compared to all other treatments. Total herbaceous cover was negatively related to total herbivory, exhibiting a quadratic response (Figure 3.3; Appendix 6: Table S6.2), but no interactive effects between domestic and wild herbivores on total cover were detected (Appendix 6: Table S6.1).

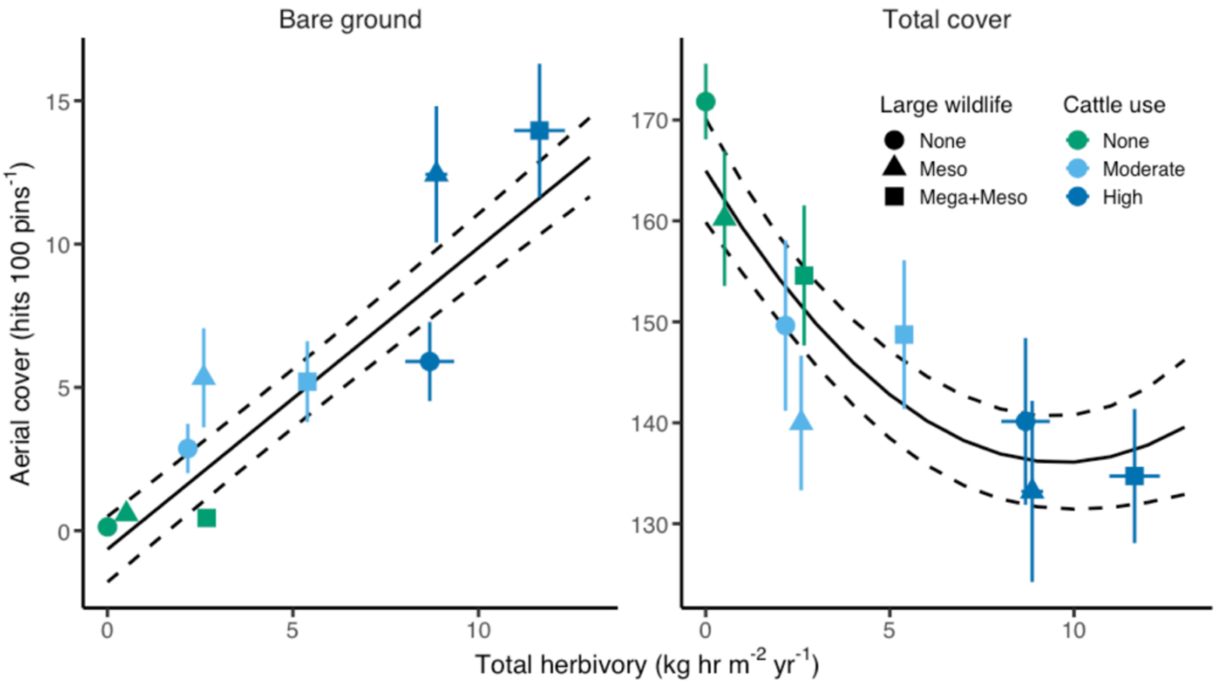

Figure 3.3 Responses of total herbaceous cover and bare ground to treatments and total herbivory (means ± 1 SE). Fitted means (solid lines) and standard errors (dashed lines) of linear mixed models ($n = 81$). 'Meso' = accessible to wild mesoherbivores (50–1000 kg); 'Mega' = accessible to megaherbivores (elephant, giraffe); 'None' = no wild mesoherbivores/megaherbivores.

Increasing total herbivory was associated with declines in absolute covers of perennial grasses, perennial forbs, and annual forbs (Figure 3.4a; Appendix 6: Table S6.2). Compared to the sum of their individual effects, the combined effect of cattle and wild mesoherbivores reduced perennial grass cover more (mesoherbivores × cattle, high: $Z = –3.0$, $p = 0.003$) and perennial forb cover less (mesoherbivores × cattle, high: $Z = 6.3$, $p < 0.001$; Figs. 3.4a and Appendix 6: Figure S6.6). This led to 11% and 28% lower covers for perennial grasses and forbs, respectively, in the two treatments accessible to both wild mesoherbivores and cattle at high stocking rates compared to the seven other treatments. Species-specific treatment effects on relative cover and its relationship with total herbivory for plant functional groups and the eight most common species are shown in Figure 3.4a and Appendix 6: Tables S6.1–6.2 & Figure S6.7.

Understory leafiness (leaf:stem) exhibited a quadratic response to total herbivory, where leafiness increased under increasing herbivory when total herbivory was below 5 kg hr m^{-2} yr^{-1}, but decreased as herbivory increased beyond that level. Interactive effects between cattle and wild mesoherbivores were evident in that understory leafiness was increased by the combined effect of cattle and wild mesoherbivores less than the sum of their individual effects, at both moderate and high stocking rates (mesoherbivores × cattle, moderate: $Z = –2.2$, $p = 0.04$, high: $Z = –3.6$, $p < 0.001$; Figure 3.4b). Species-specific treatment effects on understory leafiness for the five most common species are shown in Appendix 6: Table S6.3 & Figure S6.8.

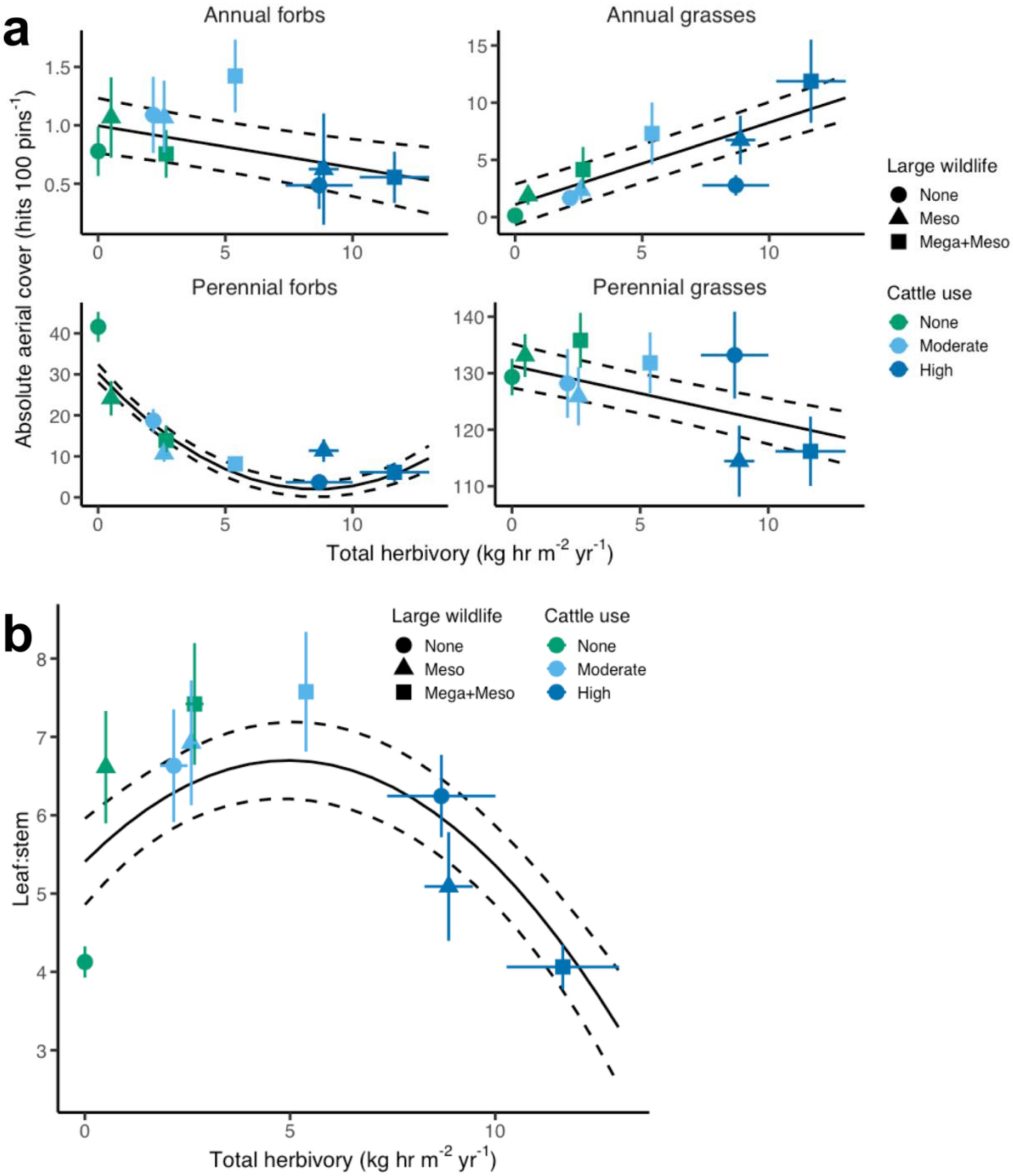

Figure 3.4 Relationships between total herbivory and both herbaceous cover and 'leafiness' (measured by leaf:stem) of understory plants. Regressions of the absolute covers of annual forbs, annual grasses, perennial forbs, perennial grasses (**a**), and leaf:stem (**b**) on total herbivory (means ± 1 SE). Fitted means (solid lines) and standard errors (dashed lines) of linear mixed models (*n* = 81). 'Meso' = accessible to wild mesoherbivores (50–1000 kg); 'Mega' = accessible to megaherbivores (elephant, giraffe); 'None' = no wild mesoherbivores/megaherbivores.

Wild mesoherbivores and cattle had positively synergistic effects on understory diversity (measured as effective number of species, evenness, and dominance), particularly at high stocking rates (Figure 3.5). The combined effect of wild mesoherbivores and cattle at high stocking rates on the effective number of species (mesoherbivores × cattle, high: $Z = 3.2$, $p = 0.002$) and evenness (mesoherbivores × cattle, high: $Z = 4.3$, $p < 0.001$) of the herbaceous community was greater than the sum of their individual effects. This led to 32% (equivalent to almost 2 species) and 33% higher diversity and evenness, respectively, in the two treatments accessible to both wild mesoherbivores and cattle at high stocking rates compared to the seven other treatments. The reduction of understory dominance by cattle and wild mesoherbivores combined was also stronger than the sum of their individual effects (mesoherbivores × cattle, moderate: $Z = –2.4$, $p = 0.02$, high: $Z = –4.5$, $p < 0.001$), leading to a 29% lower dominance in treatments accessible to both wild mesoherbivores and cattle than all other treatments.

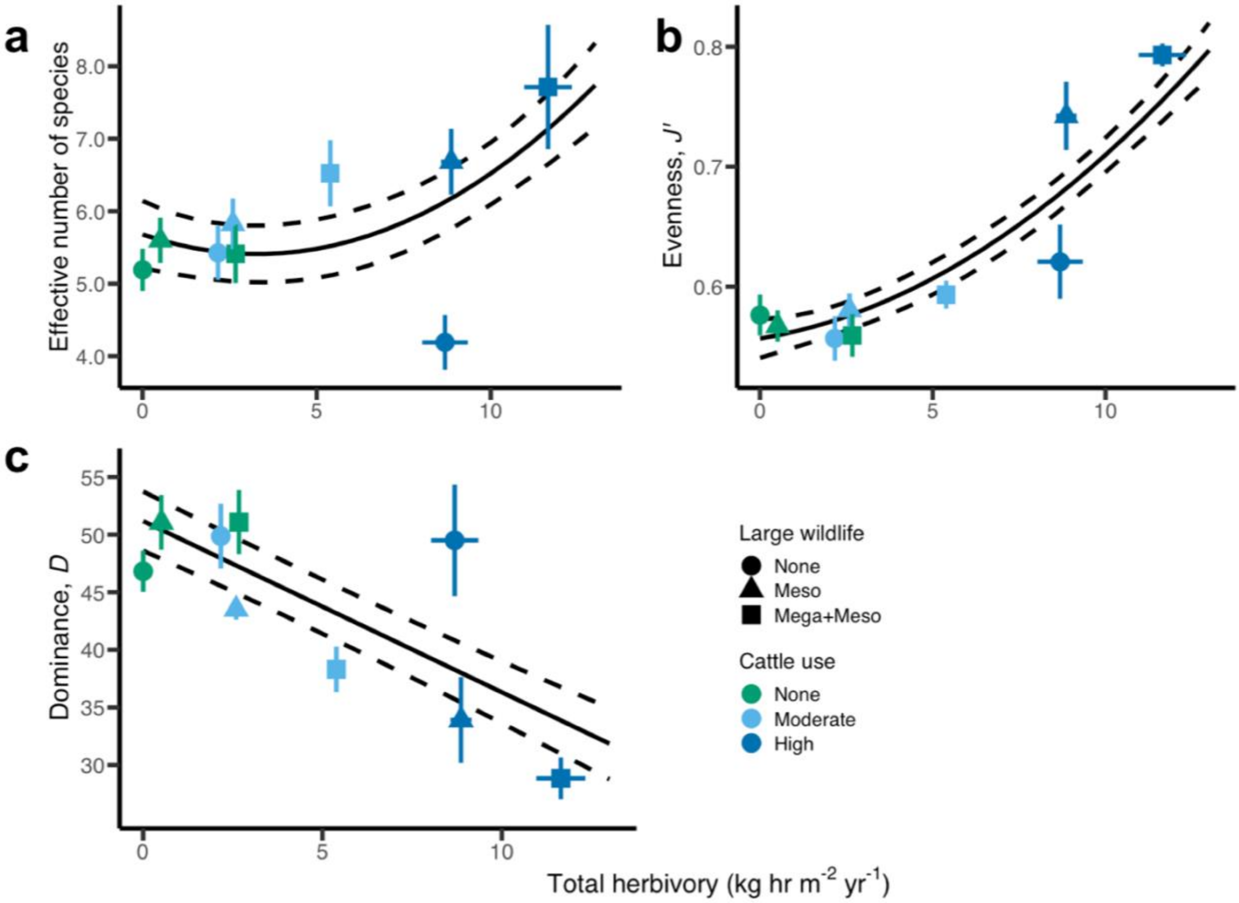

Figure 3.5 Treatment responses and regressions on total herbivory for diversity (**a**–**b**), and Berger-Parker dominance (**c**; means ± 1 SE). Fitted means (solid lines) and standard errors (dashed lines) of linear mixed models ($n = 81$). ‘Meso’ = accessible to wild mesoherbivores (50–1000 kg); ‘Mega’ = accessible to megaherbivores (elephant, giraffe); ‘None’ = no wild mesoherbivores/megaherbivores.

3.5 Discussion

Although individual effects of large wild herbivores and livestock on herbaceous vegetation are well documented (Frank et al. 2016; Koerner et al. 2018; Pakeman et al. 2019; Porensky et al. 2016; Seymour et al. 2010; Staver et al. 2019; van der Plas et al. 2016), to our knowledge, this study provides the first experimental evidence of the separate and combined effects of wild herbivores and cattle at more than two stocking rates (i.e. more than simply presence versus absence) on vegetation. After 11 years of high cattle stocking rate treatments (24 years after the exclosures were established), the data showed that understory community composition was primarily shaped by herbivore identity rather than total herbivory and the effects of cattle stocking rate interacted with the presence of large wild herbivores (mesoherbivores and megaherbivores). Wild mesoherbivores amplified the effects of high cattle stocking rates in terms of increasing bare ground and reducing perennial grass cover, while they tempered the positive effects of high cattle stocking rates on increasing understory leafiness. The quadratic response of leafiness to total herbivory suggests that forage quality peaks at intermediate herbivory. These changes in forage quantity and quality have important implications for both large wild herbivore conservation and cattle production. Understanding these non-additive interactions between cattle and large wild herbivores will aid in managing mixed-use rangelands and implementing ecological restoration and/or rewilding globally. Notably, the measured effects and interactions may differ in areas with different large wild herbivore assemblages or different spatio-temporal patterns of herbivory.

3.5.1 Cattle at high stocking rates do not functionally replace large wild herbivores in shaping understory community composition

Herbivore identity was more important than total herbivory in explaining understory plant community composition when including high cattle stocking rates (Table 3.1). Cattle at high stocking rates shifted the understory plant community in quantitatively different ways from large wild herbivores or moderate cattle stocking rates, and in ways that were not predicted by total herbivory alone (Figure 3.1). In a previous study of the same exclosure experiment that did not consider high cattle stocking rates, Veblen et al. (2016) concluded that cattle at moderate stocking rates functionally replace large wild herbivores, and that total herbivory was the primary driver of plant community composition. Our results are consistent with those of Veblen et al. (2016) when disregarding high cattle stocking rate treatments. However, our findings provide a strong caveat to those of Veblen et al. (2016), suggesting a threshold of cattle grazing intensity exists beyond which their impacts change, akin to thresholds documented in other rangelands (Bestelmeyer et al. 2015; Briske et al. 2003; Vetter 2005). In other words, cattle stocked at moderate rates were able to mimic herbivory by the assemblage of large wild herbivores, but unique effects of cattle on understory community composition became apparent at high cattle stocking rates. Because each herbivore species has a unique morphology and dietary profile (Table 1 in Veblen et al. 2016), albeit with some overlap (Kartzinel et al. 2015), increased prevalence of any one herbivore species, wild or domestic, may cause understory community composition to shift in ways that are not governed by total herbivory (Tóth et al. 2016). This suggests that an increase in the density of any single herbivore, domestic or wild, may shift understory plant communities in specific ways that are otherwise muted when the species is at moderate densities. Further research would be required to confirm this. However, the ability of cattle at moderate stocking rates to mimic the effects of an assemblage of large wild herbivores on understory vegetation may also be because their relative consumption of grasses and forbs reflects the overall relative consumption of grasses and forbs by the grazers, mixed feeders, and browsers represented in the large wild herbivore assemblage.

3.5.2 Cattle stocking rate interacts with large wild herbivore accessibility to shape understory vegetation

Under high cattle stocking rates, the negative effects of herbivory on forage quantity and quality were enhanced more than additively in the presence of wild mesoherbivores, as evidenced by more bare ground, lower perennial grass cover, and lower understory leafiness. Some understory community metrics also exhibited non-linear relationships with total herbivory – relationships that are likely to share similar mechanisms to those underlying interactive effects between cattle and large wild herbivores. For example, perennial forb cover was both nonlinearly related with total herbivory and reduced by high cattle stocking rates less in the presence of wild mesoherbivores (predominantly plains zebra *Equus quagga*; Figure 3.4a). These patterns are partly explained by perennial forbs (dominated by unpalatable *Helichrysum* (*Pseudognaphalium*) *glumaceum*) resisting further reductions in cover despite increased herbivore pressure (Appendix 6: Figure S6.7), possibly via compensatory growth or increased production of defensive chemicals that reduce palatability (Quintero & Bowers 2013). Similarly, relative cover of the palatable dominant perennial grass, *Brachiaria lachnantha,* decreased with total herbivory at a greater rate as herbivory increased (Appendix 6: Figure S6.7) and was impacted non-additively by interactions between cattle at high stocking rates and both wild mesoherbivores and megaherbivores. These patterns can be explained by i) *B. lachnantha* being pushed beyond physiological thresholds as total herbivory was increased by wild and domestic herbivores (Appendix 6: Figure S6.7); or ii) foraging behaviour and dietary selectivity being altered by the presence of other herbivore species resulting in greater preference for *B. lachnantha* (Odadi et al. 2013).

The interactive effects between cattle at both moderate and high stocking rates and wild mesoherbivores on understory 'leafiness' (leaf:stem) may be due to a combination of compensatory growth and differences in palatability between leaves and stems (Figure 3.4b). The positive effect of cattle on understory leafiness was dampened where wild mesoherbivores were present. This suggests that herbivory of leaves (selected over stems due to greater palatability) by both wild and domestic animals begins to non-additively outweigh defoliation-enhanced leaf growth (McNaughton et al. 1983).

The interactions between cattle at high stocking rates and wild mesoherbivores in their effects on diversity (effective number of species and evenness; Figure 3.5) may, in part, be driven by herbivory-induced suppression of dominance (Koerner et al. 2018) and increased light availability (Borer et al. 2014), both of which are important determinants of understory species diversity in grasslands globally. Similarly, for annual grasses (Figure 3.4a), previous research suggests that such suppression of dominance can open up spaces that are subsequently colonised by non-dominant short-lived species such as annual grasses (Porensky et al. 2013; Fynn & O’Connor 2001). Consequently, both diversity and annual grass cover may be influenced by the amount of bare ground. Cattle at high stocking rates increased bare ground non-additively where mesoherbivores were present (Figure 3.3). This may have occurred because, beyond a certain threshold of bare ground, animals (domestic and/or wild) increase their preference for bare patches for locomotion, exacerbating trampling, and/or bare patches become more difficult for plants to colonise. Dominance itself may be expected to rise with total herbivory as unpalatable species replace palatable species (Vetter 2005; Seymour et al. 2010). However, more research is needed to test these hypothetical underlying processes and the relative influence of each component.

3.5.3 Implications for management

Our findings echo those of other studies (Eldridge et al. 2016, 2018; Liu et al. 2015), highlighting the importance of considering the combined impacts of domestic and wild herbivores, their identities, and their interactions in shaping understory plant communities in mixed-use rangelands. Because understory community composition responded primarily to herbivore identity when high cattle stocking rates were included (Table 3.1), total herbivory by wild and domestic species may not be a useful predictor of herbaceous community composition when cattle densities are increased in mixed-use rangelands. Evidence of non-additive effects of cattle and large wild herbivores indicates that land managers must be mindful of interactive effects when adjusting cattle stocking rates. For example, in areas where wild mesoherbivores are present, increasing cattle stocking rates from moderate to high can lead to disproportionately lower understory leafiness (Figure 3.4b) and more bare ground (Figure 3.3). Similarly, non-linear responses of understory community composition to total herbivory (Figure 3.1) indicate that the magnitude of the effect of increasing herbivore stocking rates depends on the existing level of herbivory.

When managing for understory diversity, increasing cattle stocking rates may increase or reduce diversity depending on the presence of large wild herbivores (Figure 3.5). While diversity declined when cattle were stocked at high rates in the absence of large wild herbivores, the combination of large wild herbivores and cattle at high stocking rates led to reduced dominance and increased species diversity and evenness. However, the plant species that benefitted most from this herbivore combination were annual grasses, mirroring other studies (e.g. Porensky et al. 2013; Fynn & O'Connor 2001). Compared to perennial grasses, annual grasses in this system are less palatable, are a more ephemeral forage resource, and are less capable of resisting water erosion (Riginos & Herrick 2010). Ultimately, our results suggest that cattle should preferably be stocked at moderate rates in mixed-use rangelands not only to minimise direct negative impacts on large wild herbivores of conservation importance (Kimuyu et al. 2017), but also to avoid shifts in understory cover, community composition, forage quality, and soil erosion that are undesirable for both cattle production and conservation objectives. Importantly, our results support previous studies from this and other systems that suggest that moderate grazing by cattle does not cause effects that are unique or undesired by most land managers. However, there appears to be a threshold, between 2 and 10 kg hr m^{-2} yr^{-1} in our system (Appendix S6: Figure S6.3), at which the unique effects of a single species (in this case cattle), manifest in the understory plant community.

3.6 Supporting information

Appendix 6. Supporting data

3.7 References

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Chapter 4: Equity in ecosystem restoration (published in Restoration Ecology)

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4.1 Abstract

The importance of equity has been emphasised in climate change, biodiversity loss, land degradation, and ecosystem restoration. However, equity implications are rarely considered explicitly in restoration projects. Although the role of equity has been studied in the context of biodiversity conservation and environmental governance, environmental variables are often ignored in equity studies, and spatial analyses of equity are lacking. To address these gaps, we use a mixed methods approach, integrating spatially explicit ecological and social data to evaluate, through an equity lens, a restoration project in a semi-arid rangeland social-ecological system in Kenya. We use questionnaires and semi-structured key informant interviews to explore four dimensions of equity: distributional, procedural, recognitional and contextual. Our results show that restoration employment and distance to the restoration site strongly influence perceived distributional and procedural equity. Employment and distance to restoration site can interact in counterintuitive ways in their influence on aspects of perceived equity, in this case, the fairness of site selection. Our findings exemplify that equity dimensions are intimately linked, and trade-offs can occur between equity dimensions, across socio-temporal scales, and in choosing the ethical framework to apply. Our work demonstrates how restoration is influenced by different dimensions of equity and we opine that incorporating equity in project planning and implementation processes can improve restoration outcomes. We emphasise the importance of respecting plurality in the values systems and ethical frameworks that underlie what is considered equitable, while negotiating trade-offs between diverse ethical positions in the design and implementation of ecosystem restoration projects.

4.2 Implications for practice

- Ecological outcomes of restoration projects may benefit from improving equity.
- Different dimensions of equity are intimately linked, and trade-offs can exist between equity dimensions, in the choice of ethical framework to apply, and across socio-temporal scales (e.g. focal/other communities or current/future generations), as well as between equity and ecological objectives of restoration. Consequently, maximizing equity in one particular dimension may come at the expense of another equity dimension or the ecological outcomes of restoration.

- Restoration practitioners should be mindful that factors influencing perceived equity can interact in counterintuitive way and must respect a plurality of value systems and ethical frameworks when negotiating trade-offs between diverse ethical positions.

4.3 Introduction

The importance of equity has been highlighted across multiple global-scale issues such as climate change (IPCC 2014), biodiversity loss (CBD 2013), land degradation (IPBES 2018), and ecosystem restoration (SER 2020). The United Nations Decade on Ecosystem Restoration (2021–2030) stresses the importance of recognition and procedural aspects of equity: the participation of relevant stakeholders, including women, young people, persons with disabilities, indigenous peoples and local communities (UN 2019). Ecosystem restoration is inherently value laden and prone to disagreement and compromise (Egan et al. 2011; Jordan 2003). Restoration often involves (in)equity, from the structural societal disparities that can underly ecological degradation that necessitates restoration (IPBES 2018; Schell et al. 2020) to restoration prioritisation (Crossland et al. 2018; Dallimer & Stringer 2018) and the distribution of the costs and benefits associated with restoration work (Jewitt et al. 2014). Equity can be defined as the ‘fair or just treatment of individuals or groups’ (Law et al. 2017), and is comparative, principally concerned with relationships between people (McDermott et al. 2013). Equity has many facets, including social (human-centred equity), environmental (equity related to environmental issues), intergenerational (responsibilities to future generations), and the consideration of non-human life (Schlosberg 2013) or entities (e.g. spirits; Martin et al. 2016). The importance of equity has been discussed in the context of biodiversity conservation and ecosystem governance, often in the form of environmental justice (Sikor et al. 2014; Martin et al. 2013). However, in conservation research, qualitative methods are poorly implemented and reported (Young et al. 2018), while environmental variables are seldom included in equity studies (Friedman et al. 2018) resulting in many knowledge gaps. Equity is rarely addressed in restoration projects (but see Jewitt et al. 2014), as are social science methods more generally (Wortley et al. 2013; Aronson et al. 2010). We aim to contribute towards filling these gaps by employing a mixed methods approach to considering a restoration project through an equity lens.

Equity can be decomposed into four dimensions: distributional, procedural, recognitional, and contextual (Pascual et al. 2014). Distributional equity refers to the equitable sharing of costs, benefits, rights, responsibilities and risks. Most equity studies focus on distributional equity, because it is the most recognisable and easiest to quantify (Friedman et al. 2018). Procedural equity refers to equitable involvement of stakeholders in making rules and decisions. Recognitional equity refers to the respect for knowledge systems, values, social norms, and rights of stakeholders. Contextual equity refers to the broad social, economic, political, and cultural contexts, both past and present, that influence the ability of an actor to participate in decision making, ensure fair distribution, and gain recognition; for example, power dynamics, ethnicity, gender, age and education (Pascual et al. 2014).

Motivations for considering equity in restoration projects can be instrumental (outcomes based, e.g., utilitarian), intrinsic (fundamental, e.g., virtues), or both – as is also the case for restoration itself. Implementing restoration equitably in order to improve project success is an example of instrumental motivation. Pursuing equity because it is inherently right or valuable, regardless of benefits to restoration outcomes, characterises intrinsic motivation. The motivation for equity is predicated on ethical frameworks. Different ethical frameworks can lead to different perspectives on what is considered equitable, which can conflict (Law et al. 2017).

We assess both ecological and social aspects of a restoration project by addressing three main questions: i) 'what effect did the restoration work have on invasive species prevalence and animal (domestic and wild) habitat use?', ii) 'what role does equity play in ecosystem restoration?', and iii) 'how do spatial attributes influence equity?'. By investigating how restoration work is influenced by different dimensions of equity, we explore how incorporating equity in planning and implementation processes could influence restoration success.

4.4 Methodology

4.4.1 Conceptual framework and research design

Building on work by others, we develop a conceptual framework for how equity relates to restoration (Figure 4.1), in order to frame the concepts that underpin our research design. We adapt the conceptual framework relating equity to payments for ecosystem services schemes developed by Pascual et al. (2014). We incorporate the role of equity in ecosystem degradation and the need for restoration reviewed by IPBES (2018), as well as the trade-offs identified by Law et al. (2017). In short, our conceptual framework illustrates that the four dimensions of equity influence drivers of ecosystem degradation, and thus the need for restoration, while impacting the efficiency and effectiveness of restoration outcomes via feedbacks, both positive and negative. Trade-offs can exist between equity dimensions, in the choice of ethical frameworks to be applied, and across socio-temporal scales (e.g. focal/other communities or current/future generations), as well as between equity and ecological objectives of restoration. We developed this hypothetical framework *a priori* to organise our thinking and the research design. We did not intend to systematically validate it during the research.

The stages of our research process, listed chronologically, were as follows: 1) identify the community's most highly prioritised ecological issue (*Opuntia stricta* invasion) and co-develop possible solutions (ecological restoration); 2) develop a research question ('what is the role of equity in restoration?'); 3) co-develop methodology for restoration work; 4) implement the restoration work; 5) organise a scoping workshop to frame the equity issues; 6) conduct questionnaires designed using important equity-related questions identified in the scoping workshop; 7) identify key informants using stakeholder mapping (using a power/interest matrix) and conduct key informant interviews using semi-structured approach based on the results of the questionnaires. We followed the iterative nature of grounded theory, in which the results of data analysis informed further data collection.

4.4.2 Study site

Livestock grazing lands cover 80% of Kenya's area and account for over 12% of gross domestic product (Allan et al. 2017). We conducted this study in a 6,816 ha predominantly Maasai communally managed rangeland, called Makurian group ranch (hereafter, Makurian), in Laikipia, Kenya. The ethnicity of the community is almost entirely Mukogodo Maasai. Kenya is a biodiversity hotspot in which livestock-keeping plays an important role for livelihoods and culture. Rainfall is weakly trimodal with a pronounced dry season December-March. From 2001 to 2019, annual rainfall averaged 460 mm yr^{-1} (range: 231–929 mm yr^{-1}, annual coefficient of variation: 35%). Soils are haplic and chromic luvisols and vegetation is predominantly *Acacia etbaica* (syn. *Vachellia etbaica*) and *A. drepanolobium* (syn. *V. drepanolobium*) savanna. *Opuntia stricta* is a problematic cactus species that has become invasive and/or naturalised in many countries (CABI 2020). *Opuntia stricta* was introduced to Laikipia by a colonial administrator in the 1950s and has spread exponentially, assisted by rangeland degradation (reduced vegetation cover and increased soil erosion) associated with livestock grazing and settlements (Strum et al. 2015). The dispersal of *O. stricta* is aided by wildlife that consume its fruit, particularly baboons *Papio anubis* and elephants *Loxodonta africana*. The attraction of elephants to pastoral settlements, where the cactus is often more prevalent, may increase human wildlife conflict (Strum et al. 2015). In the study area, *O. stricta* was perceived by local residents as a more severe issue than insufficient grazing, largely because it restricts access to pasture and its glochids (small barbs) lead to secondary infections and sometimes death in livestock (Shackleton et al. 2017).

4.4.3 Restoration work

This project focuses on reinstating ecological functionality (rather than aiming for recovery relative to a local native ecosystem) and could be thought of as 'rehabilitation' (between 'repairing ecosystem function' and 'initiating native recovery' on the restorative continuum; Gann et al. 2019). However, the project aimed to assist the recovery of an ecosystem that has been degraded/damaged/destroyed, so we use the term 'restoration'.

Community leaders – members of the group ranch committee and representatives of the eleven 'clusters' (or sub-communities) within Makurian, called *nyumba kumi* –, identified a restoration site to fit three co-established criteria: 1) *O. stricta* cover >50%; 2) conserved for dry season grazing, because higher herbaceous cover in conserved areas may slow *O. stricta* reestablishment (Strum et al. 2015); and 3) proximity to a building to securely store tools. The group of community leaders, together with the lead researchers (HW and EK), co-developed a list of alternative approaches to *O. stricta* management including: i) mechanical removal with heavy machinery; ii) manually assisted dispersal of flightless biocontrol agent, cochineal *Dactylopius opuntiae*; iii) burning spines and glochids to allow safe ingestion by livestock, and iv) manual removal. From this list, manual removal was chosen based on expected cost-effectiveness. Cut and/or uprooted cacti were collected into tall piles, which is cheaper than alternatives such as burning or burying. Another rationale behind the piles was to encourage passive cochineal establishment (each pile had at least one infected cactus), without costly propagation and spreading of the biocontrol agent. We purchased tools (wheelbarrows, hoes, spades, gloves, machetes, garden forks, rakes) and employed community members to manually clear the cactus. Community leaders chose employment over volunteering, despite acknowledging the risks of ‘crowding out’ values, in which moral obligations to restore ecosystems are replaced by finance or regulation (Moon & Cocklin 2011). A total of 91 individuals were employed (59 males, 32 females; median age: 34 years, age range: 21–58 years), each for between 5 and 17 days, in January/February 2020 (the dry season), clearing a 21-ha area located in one cluster. Prior to this clearing event, between April and July 2019, the tools were used for 1-day voluntary *O. stricta* clearing events in all eleven clusters at sites chosen at the cluster level. The purpose of this was to 1) share the benefits of *O. stricta* clearing across all clusters, and 2) develop an effective piling technique (e.g. pile size) for the 21-ha restoration work. The importance of voluntary work in restoration has been recognised, with respect to project implementation and sustainability as well as the wellbeing of volunteers (Egan et al. 2011). Before and after the 21-ha area was cleared, the tools were equally distributed among the clusters, where they rotated among households to clear *O. stricta* around homesteads.

4.4.4 Data collection and analysis

We assessed local perceptions of various aspects of equity. Although perceptions are often criticised for being subjective, inaccurate and unreliable, they provide an important form of evidence in conservation and environmental management (e.g. Bennett 2016). The distributional and procedural pillars of equity were evaluated primarily using the questionnaires and key informant interviews. We assessed recognitional equity using participant observation practiced throughout the project, while assessing contextual equity using a literature search and key informant interviews.

The scoping workshop attendees were selected through stratified random sampling to include men and women of varying ages, both employed and not employed by the restoration project, from all eleven clusters. All selected individuals attended the workshop. The scoping workshop was structured as a large focus group discussion to both frame and identify equity issues. The large number of participants ($n = 44$) had the advantage of more balanced representation (four randomly selected men/women who were employed/not employed by the project from each cluster), but increased the potential for biases due to group think, dominance effects, production blocking, information cascades, and/or social loafing (Mukherjee et al. 2018).

Both questionnaires and unstructured key informant interviews are suitable methods for monitoring and evaluating projects involving communities (Mukherjee et al. 2018). The questionnaires collated low-resolution perspectives of a large representative sample of the community (n = 232), while the key informant interviews allowed a more in-depth, higher-resolution exploration of equity-related issues with a small number of respondents (n = 4, one male/female community leader and local government official). The key informant interviews were also used to provide context and clarity in interpreting the questionnaire responses. EK, who is a member of the Makurian group ranch, translated between English and Maa and conducted the questionnaires alone to reduce bias in the responses (e.g. respondents would feel more comfortable expressing criticisms). The sample size for the questionnaires was such that at least one individual from each household willing to be interviewed took part. The questionnaires included binary (yes/no) and Likert scale (1–5) questions, as well as a priority ranking exercise to order the issues covered in the questionnaire by relative importance (1–12, 12 being the most important). We conducted the questionnaires orally, in person, and one-to-one (Appendix 8). We conducted key informant interviews as a mixed-sex group (one man, HW, one woman, CC, and one male interpreter, EK) in an attempt to elicit more balanced and complete responses. This was a recommendation by several community members, particularly regarding gender equity issues.

In the process of analysing key informant interviews, we borrow from constructivist grounded theory. This variant of classic, positivist, grounded theory (Glasser & Strauss 1967; Chametzky 2016) aims for interpretive understandings and situated knowledges, reflecting on positionality and particularities, and views data as value laden and co-constructed by researchers and research participants (Charmaz & Bryant 2010). We used participant observation throughout the project to add data that were not captured in the interviews (Reed & Dougill 2010).

We recorded variables of interest that may influence perceptions of equity: distance from homestead to restoration site (using the *distance to nearest hub* function in QGIS version 3.4.8), individual/household wealth (sum of the number of cattle, sheep, goats, donkeys, and camels multiplied by their respective exchange values – for details see Appendix 7: Table S7.1), employment status (employed or not employed by the restoration project), gender, age, marital status.

We assessed *O. stricta* densities and domestic and wild animal habitat use as ecological outcomes of restoration. To do this, we counted *O. stricta* plants and dung piles along 20 100-m belt transects (Kimuyu et al. 2017), 10 of which were within the restoration site and the other 10 in an adjacent control site with comparable slope, soil type, vegetation type, and land management (conserved for dry season grazing). These transects were sampled eight months after *O. stricta* was cleared to ensure that dung deposited prior to the restoration work had disintegrated and were not counted.

Maps of the probability of *O. stricta* presence (occurrence probability) were produced using the Land Degradation Surveillance Framework methodology (Winowiecki et al. 2018). At 654 random sampling locations we recorded *O. stricta* presence/absence in a 1,000 m^2 area using the Invasive Species Mapper application (https://www.rcmrd.org/). We employed a machine learning algorithm, extreme gradient boosting, to predict *O. stricta* occurrence probability using all eight bands of Landsat 8 tier 1 surface reflectance imagery (dropping plots for which the quality assessment band indicated cloud cover) taken as close in time as possible to the field surveys. We randomly assigned 70% of the field data for training and 30% for validation. The predictions performed well, evidenced by *O. stricta* presence/absence being correctly predicted in 83% of validation data.

For the literature search to investigate the role of contextual equity, we used ‘Maasai’, ‘colonial’ and ‘Laikipia’ as search terms in Google Scholar. Although alternative methodologies such as gathering expert knowledge can provide more detailed and nuanced understandings of contextual equity, we chose a literature search to provide a broader range of perspectives and because both past and present contexts of the region have been extensively studied (e.g. Hughes 2006; Letai & Lind 2013). To search for literature to help develop a conceptual framework and a theoretical equity-restoration relationship, we used the search terms ‘equity’ or ‘justice’ with either ‘ecosystem/ecological restoration’ or ‘conservation’ in Google Scholar.

We used analysis of variance (ANOVA) to test correlations between i) perceptions of equity (de Winter & Dodou 2010) and variables of interest (distance, employment status, wealth, gender, age), ii) densities of animal dung piles and *O. stricta* plants. *Opuntia stricta* densities and wealth were log-transformed to normalise. All statistical analyses were performed in R version 3.6.2 (R Core Team 2019).

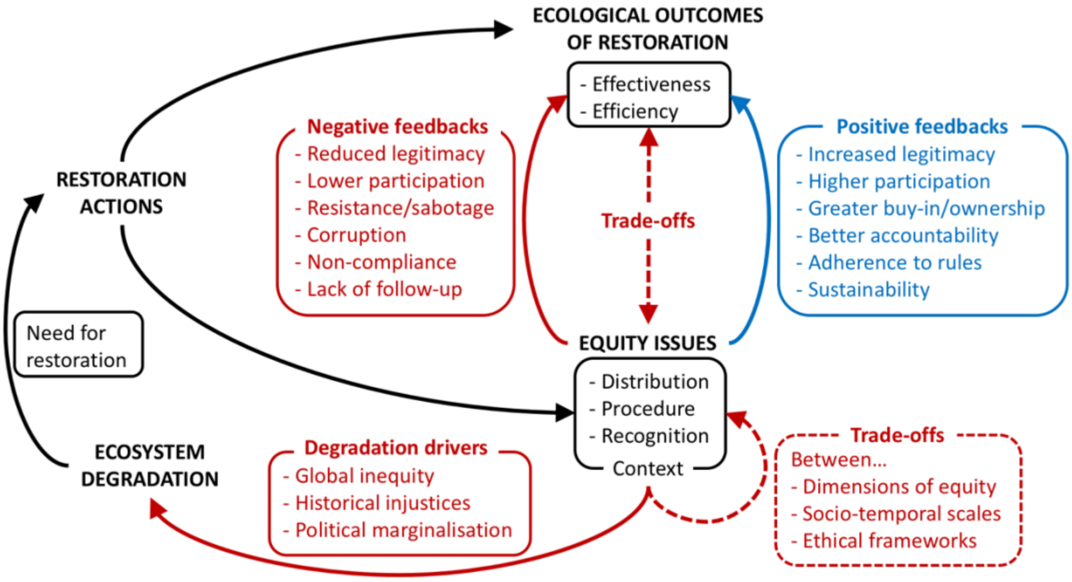

Figure 4.1 Conceptual framework for the role of equity in restoration, highlighting processes that positively (blue) or negatively (red) impact restoration or equity objectives. Adapted from Pascual et al. (2014).

4.5 Results

4.5.1 Restoration outcomes

Remote sensing derived predictive maps show that Makurian has the highest mean *O. stricta* occurrence probability of all communally managed properties in Laikipia (Makurian = 0.57, restoration site = 0.63; Appendix 7: Figure S7.1). The belt transects revealed that *O. stricta* densities were 41% lower in the restoration site compared to the control site ($F = 3.4$, $p = 0.08$) eight months after restoration work, during which nearly all cacti were uprooted. The cacti in the cleared area were re-establishing from fragments and were therefore smaller than mature plants in the control site (personal observation). Dung surveys revealed that livestock were preferentially herded in rehabilitated areas. The density of dung piles of sheep, goats, and cattle decreased 60% ($F = 8.0$, $p = 0.01$), 69% ($F = 10.9$, $p = 0.004$), and 36% ($F = 4.3$, $p = 0.05$) for every 1,000 plants ha^{-1} increase in *O. stricta* density (Figure 4.2). Dung surveys also revealed a preference by elephants – the primary human-wildlife conflict species – for areas with higher *O. stricta* density (180% greater dung pile density for every 1,000 plants ha^{-1} increase in *O. stricta* density, $F = 1.7$, $p = 0.21$), but this result was not statistically significant. Although responsibility towards the needs of wild species was not explicitly considered by the community, zebras (*Equus quagga*) and hares (*Lepus* spp.) appeared to prefer rehabilitated areas, respectively showing 90% ($F = 4.8$, $p = 0.04$) and 82% ($F = 6.0$, $p = 0.03$) lower dung pile density for every 1,000 plants ha^{-1} increase in *O. stricta* density.

The perceived benefits of the restoration work were 25% higher among individuals employed by the project compared to those not employed ($F = 99.6$, $p < 0.001$). Perceived benefits declined by *c*. 9% for every 10 km from the restoration site overall ($F = 6.6$, $p = 0.01$) and for those not employed by the project ($F = 5.2$, $p = 0.02$), but declined non-linearly with distance to restoration site amongst those employed (second degree polynomial: $F = 4.4$, $p = 0.02$). Most (89%) benefited from *O. stricta* clearing around their homestead, while many reported livestock health improvements (96%, in every case due to reduced consumption of *O. stricta*), increased shade (100%, due to removal of cacti beneath trees), ease of passage through the area (100%), and reduced conflicts with wildlife (97%).

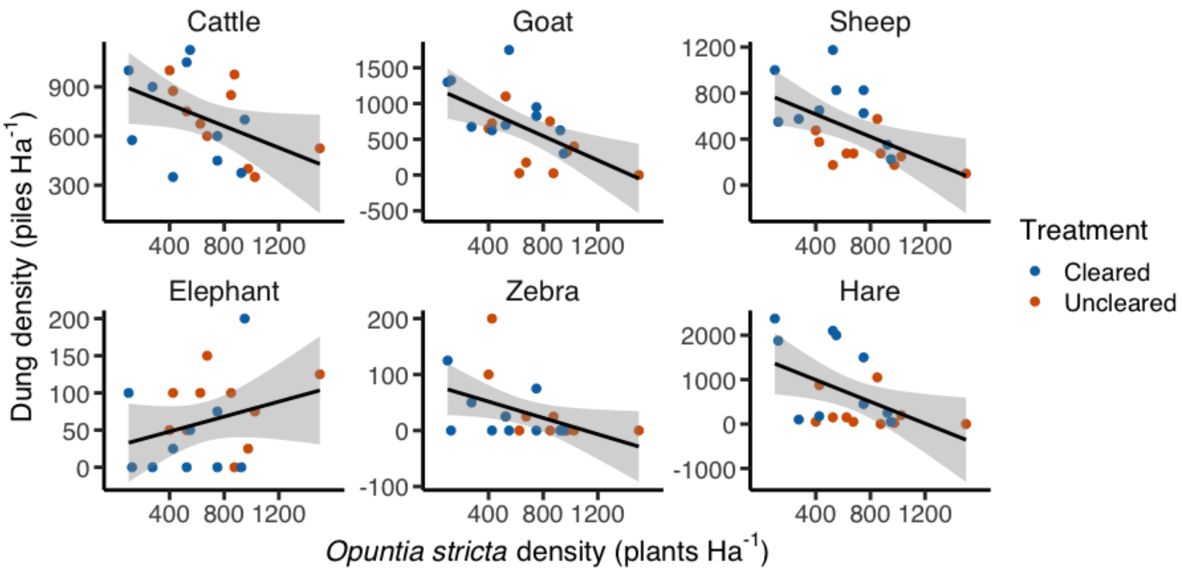

Figure 4.2 Correlations between *Opuntia stricta* density and dung pile densities of domestic (top row) and wild (bottom row) species. Dung densities are a proxy for habitat use. Trend lines show linear models with standard errors.

4.5.2 Equity in restoration

Our results show a variety of ways in which equity plays a role in restoration work. We consider the results of each of the four pillars of equity in turn starting with contextual equity to situate the results of the distributional, procedural and recognitional pillars. We then present a theoretical relationship between equity and the degree to which ecological outcomes of restoration are met, developed from a combination of our empirical data (questionnaires and key informant interviews) and a literature search.

4.5.3 Contextual equity

Contextual equity encompasses both present and past contexts. Historical injustices play a key role in contemporary ecosystem degradation – and therefore the need for restoration – in Maasai community managed rangelands in Laikipia. This began in the early 1900s when Maasai territory was greatly reduced by the British colonial government forcibly moving certain Maasai sections into two reserves, the northern of which included part of what is now Laikipia (Hughes 2006). Although these reserves were committed to the Maasai in perpetuity under the 1904 Maasai Agreement, the British reneged on the agreement in 1911, moving the Maasai from the northern reserve into an expanded southern reserve to make way for European settlement. This latter move was sanctioned by a second agreement, but Maasai contend that their leaders signed under duress (Hughes 2006). The Maasai who remained in Laikipia were predominantly from the Mukogodo sections, who affiliated with forest-dwelling Cushitic-speaking foragers (hunters, gatherers and beekeepers), who were treated more sympathetically by colonial administrators (Cronk 2004). The Mukogodo Maasai also lost access to grazing land and key resource areas through the demarcation of a forest reserve in the 1930s and land privatisation and subdivision for both agriculturalist Kikuyu and elite Maasai, during and after independence in 1963 (Letai & Lind 2013). This history of land expropriations and associated suppression of mobility, together with population growth, increased pressure on the remaining rangelands accessible to the Mukogodo Maasai, contributing greatly to land degradation.

By contrast, the key informant interviews revealed a perception, held particularly by the two local government officials, that weak governance was one of the primary drivers of land degradation, not poverty or marginalisation. They pointed to the considerable income from selling sand harvested from seasonal rivers at the group ranch level, a small proportion of which could be used to finance restoration efforts. One key informant stated that “if sand harvesting was well managed, Makurian would be one of the richest group ranches in the area…and…should not have any problems [with land degradation]”. Another key informant commented “these group ranches are not so poor to the extent that they can’t sustain some of these [restoration] projects on their own”.

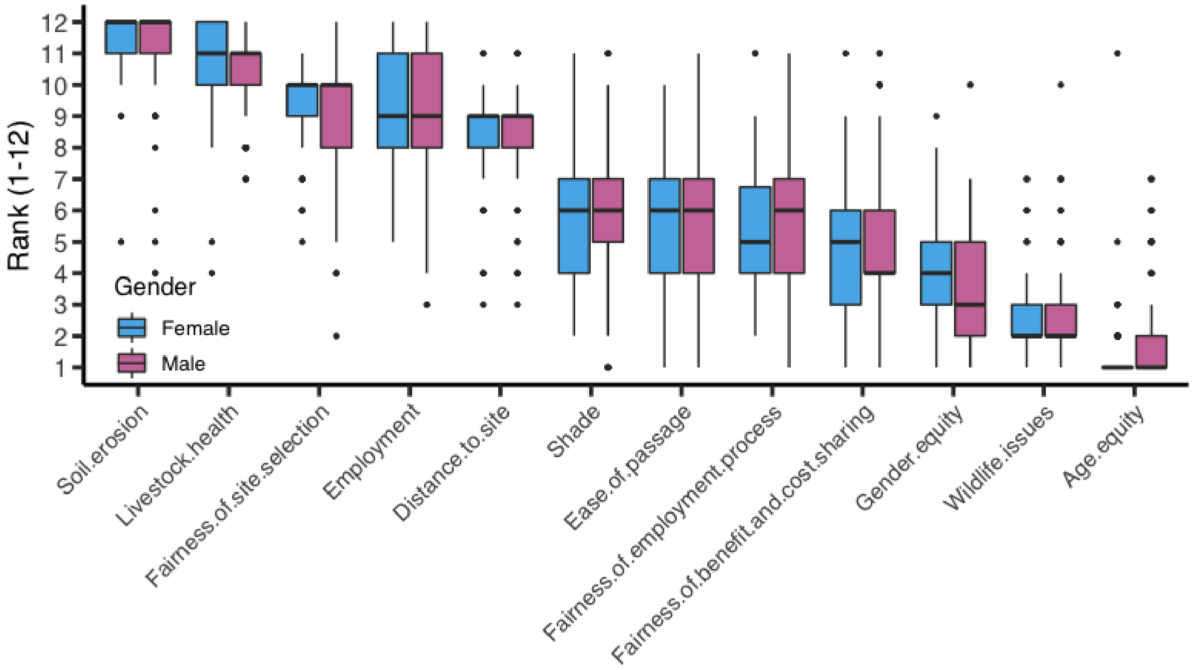

Figure 4.3 Priority ranking of issues covered in the questionnaires (lowest = 1, highest = 12) by gender (female, *n* = 82; male, *n* = 150).

4.5.4 Distributional equity

The mean perceived distributional equity (fairness of the distribution of costs and benefits of restoration) was 4.1 of 5. Perceived distributional equity was 5% greater for people employed than those not employed by the restoration project ($F = 33.2$, $p < 0.001$). Among those employed, perceived distributional equity increased 20% with every 10 km from the restoration site ($F = 4.0$, $p = 0.05$). One of the suggestions from key informant interviews as to how to improve equity was to organise clearing events within each cluster. This would mitigate the inequity stemming from people living further away benefiting less, particularly for those employed. Another suggestion was to involve disabled people, either directly or by prioritising their relatives for employment.

The community ensured that poorer families received a greater share of the benefits of employment. Over 96% of respondents reported that poorer families (poverty was subjectively defined by respondents) were prioritised for employment, which was corroborated by the result that employed individuals were 18% poorer than those not employed by the project ($F = 21.6$, $p < 0.001$). Distributional equity appeared to be influenced by age but not gender. Less than 23% of respondents (women: 28%, men: 20%) felt that gender affected how costs and benefits were shared. By contrast, 87% of respondents felt that age affected how costs and benefits were shared, largely because old people were deterred by the distance to the restoration site due to physical mobility constraints. Gender equity (mean rank = 3.7 of 12) and age equity (mean rank = 1.6 of 12) issues were considered comparatively less important than procedural equity issues (Figure 4.3). The key informant interviews suggested that the gender imbalance in employment (ratio of women to men, 1:1.8) was not viewed as a significant inequity, even by women, because of traditional gender roles.

However, the key informants unanimously maintained that employment of women led to greater benefits to families, children in particular, as women tend to spend their income on commodities that benefit the family (e.g. food), while men often spend their income on alcohol and drugs. This led to greater intergenerational equity (benefit-sharing within families) and, to the extent that employed women were from poorer families, to greater equity among families. The two female key informants suggested that women would also perform restoration work more effectively and should be prioritised for employment. The community leader commented: “I have seen women are the best casual workers and also the money they get from working reaches the children”. The local government official stated: “a lot of times I am working with women, I have a better workforce in women than men – I don’t know, I could be biased.”

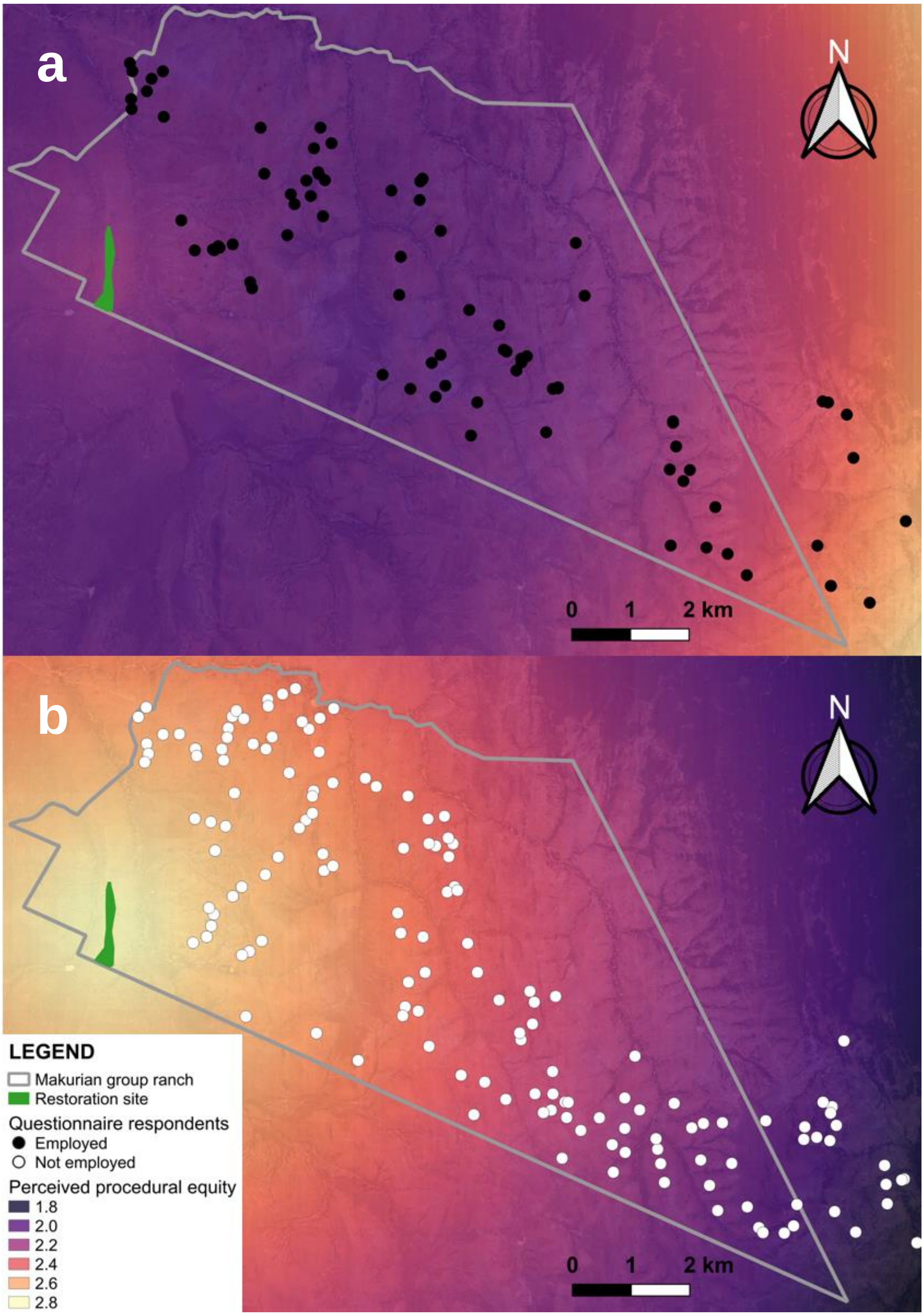

Figure 4.4 Predictive maps of perceived procedural equity of restoration site selection (1–5, Likert scale) by questionnaire respondents who were employed (**a**) or not employed (**b**) by the project. Predictions are based on the relationship between perceived procedural equity and distance to restoration site (km). This relationship is non-linear (second-degree polynomial) for those employed

and linear for those not employed. The background shows a Bing maps satellite image. Employment appears to have a negative effect on perceived fairness of restoration site selection among those living closer to the site, illustrating that the effects of distance can be non-linear and counterintuitive.

4.5.5 Procedural equity

One of the main elements of positive feedback on the project from the key informant interviews was for providing employment to all clusters, because many development projects only work with and benefit individual clusters. One community leader mentioned “There are NGOs who are only creating conflict within the community by engaging only one cluster”. The mean perceived procedural equity was 4.1 of 5 for fairness of employment process and 2.3 of 5 for fairness of site selection. The priority ranking exercise showed that aspects of procedural equity (fairness of site selection, mean rank = 9.1 of 12) were perceived to be more important than aspects of distributive equity (fairness of cost and benefit sharing, mean rank = 4.8 of 12; Figure 4.3). Perceived fairness of the employment process was 5% greater for those employed than respondents not employed ($F = 27.0$, $p < 0.001$) and, among those employed, increased 10% with every 10 km from the restoration site (employed: $F = 3.4$, $p = 0.07$, not employed: $F = 0.7$, $p = 0.41$). Perceived fairness of the restoration site selection process was 12% lower for those employed than respondents not employed ($F = 8.1$, $p = 0.004$) and decreased 25% with every 10 km from restoration site ($F = 5.8$, $p = 0.02$) and among respondents not employed by the project ($F = 17.0$, $p < 0.001$), but increased non-linearly with distance from restoration site among those employed (second degree polynomial, $F = 3.6$, $p = 0.03$; Figure 4.4 and Appendix 7: Figure S7.2). The cluster most frequently proposed for future restoration work (40% of respondents) was also one of the most central (reducing distance to restoration site) and had the third highest *O. stricta* prevalence of all clusters (Figure 4.5).

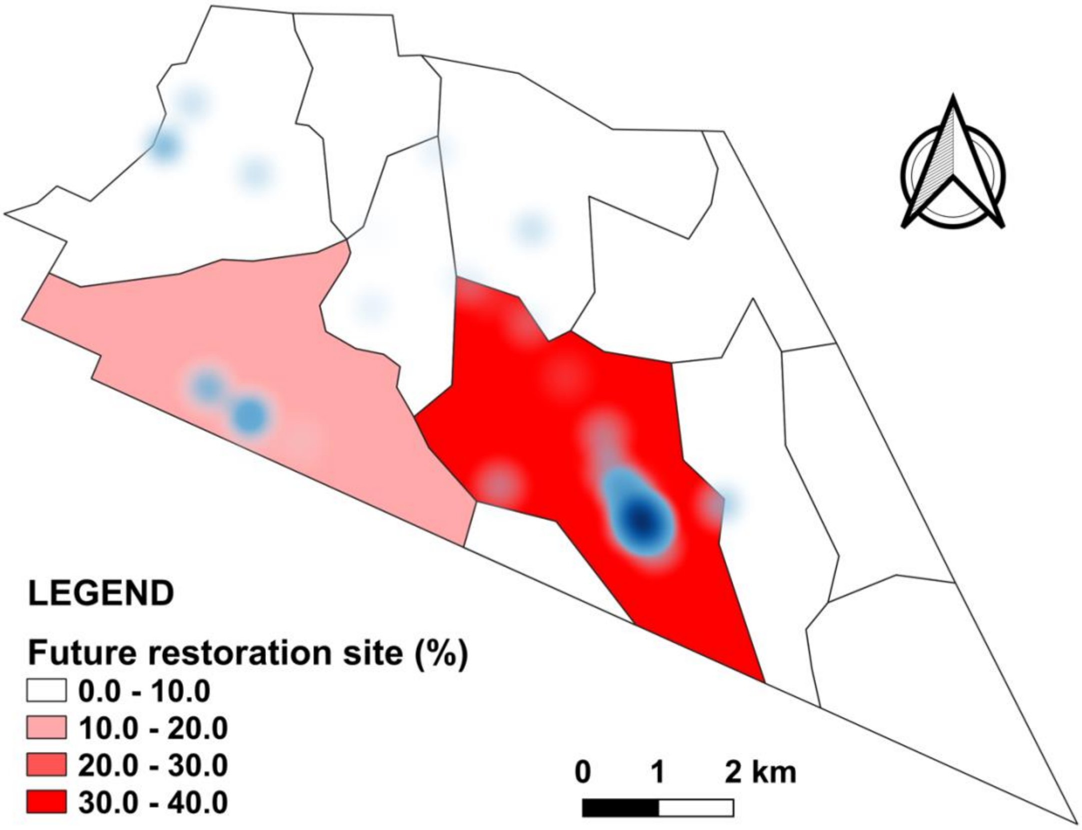

Figure 4.5 Proposed future restoration sites. Heatmap (blue) shows point density of proposed sites and the shading (red) illustrates the proportion of respondents proposing the future site should be in a particular cluster. The central location of the future site proposed by the majority of respondents highlights the importance of distance to the restoration site.

4.5.6 Recognitional equity

The process of employment and restoration site selection also involves recognitional equity, in particular between project implementors and community members. The community's socio-cultural norms and traditional decision-making processes were respected by not imposing rules, such as setting employment quotas for clusters, gender and/or age group. The values of community members were also respected in deciding on the restoration approach and setting of restoration goals. For example, community members were employed (as opposed to volunteering) as per the community's request, showing that they valued employment to an extent that outweighed the risk of crowding out and hindering the sustainability of restoration activities (valued by the project coordinators). Regarding restoration goals, the community decided to fill gullies with uprooted *O. stricta* plants in some areas, because cacti establishing there would reduce soil erosion – a high priority issue (mean rank = 11.4 of 12). Participant observation during the restoration work revealed that community members felt that filling gullies with uprooted *O. stricta* plants was ethically sound, despite admitting the heightened risk of cladodes (flat stems) establishing in communities downstream. Recognising and endorsing this ethical position would create inequity for downstream communities, which exemplifies equity trade-offs across social scales. As a compromise, the community decided, under no pressure from the project leaders, to fill only small gullies in areas with little runoff and thus reduced risk of cacti washing into seasonal rivers.

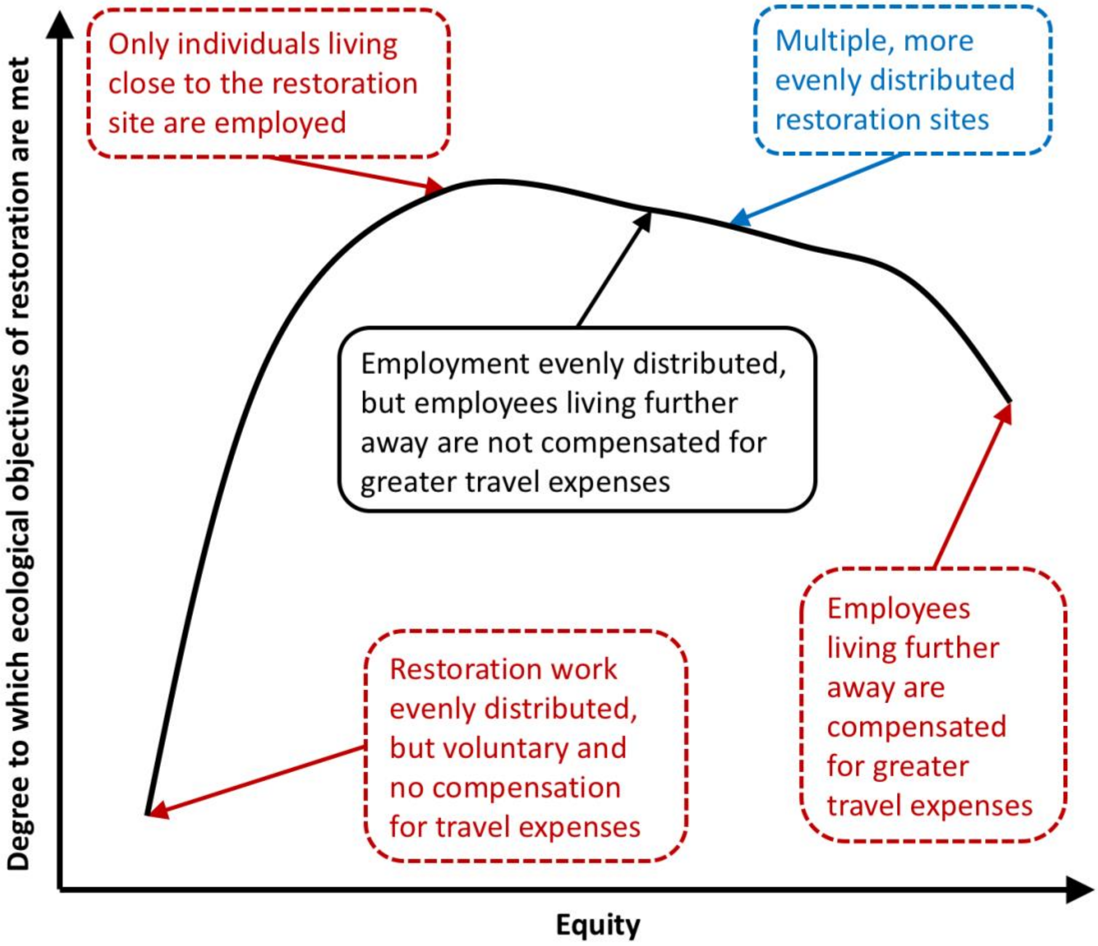

Figure 4.6 Hypothetical relationship between equity and the degree to which ecological objectives of restoration are met. Potential alternatives to the approach taken in this project (black) that would be more (blue) or less (red) optimal regarding restoration and/or equity objectives are highlighted. Adapted from Halpern et al. (2013).

4.5.7 Theoretical equity-restoration relationship

We use our empirical data to build on research from the literature search to construct a hypothetical relationship between equity and the degree to which restoration outcomes are met (Figure 4.6). It includes potential outcomes of alternative approaches to the restoration project suggested in key informant interviews. For example, the suggestion from two key informants of organising multiple clearing events across Makurian would also increase employment of women, who were deterred by the distance to the restoration site and associated transport costs, time, and risk of encounters with elephants. One key informant commented: “Most of the women had a problem because of the distance to the site – also fear of elephants when it is dark […] Maybe you can organise so that people do [restoration] work in their respective areas.” This approach of smaller but more evenly distributed restoration sites may have increased perceived equity with little change to meeting certain restoration objectives (specifically, total area cleared). However, smaller cleared areas may be more rapidly recolonised by *O. stricta* due to greater edge effects, thus diminishing restoration effectiveness and sustainability. A limitation of this hypothetical relationship between equity and the degree to which restoration outcomes are met (Figure 4.6) is its simplistic representation of two multidimensional variables. However, we believe that it provides a useful heuristic model.

4.6 Discussion

All four dimensions of equity played a role in this ecosystem restoration project. Employment and distance were key correlates of perceived equity (particularly distributional and procedural equity) and sometimes interacted. Our spatially explicit analysis of perceived distributional and procedural equity shows that the effects of distance can be non-linear and counterintuitive. Employment appeared to have a negative effect on perceived fairness of restoration site selection among those living closer to the site (Figure 4.4a). This surprising result may be because the influx of herders and their livestock from further afield attracted by and utilising the restoration site (evidenced by dung surveys and key informant interviews) triggered resentment in people living closer to the site. This resentment for ‘free-riders’ was more prominent for employees, who invested time and energy in restoring the area, which outweighed their perceived benefits of employment. Alternatively, among those living close to the restoration site, non-employed individuals may have felt that they particularly benefited because they avoided the physical labour associated with the restoration work. Both of these effects may have occurred simultaneously to produce the observed patterns, but both highlight that investment of time and energy may outweigh monetary benefits in determining aspects of perceived equity, even in poor communities. The concept of ‘spatial justice’ has been applied in urban areas (Soja 2008; Schell et al. 2020) and there is a growing interest in ‘pixelizing the social’ and mapping social values (Nahuelhual et al. 2016; Liverman 1998), but the use of geographic information systems (GIS) in equity studies is rare (Friedman et al. 2018). Our results also echo other work (Martin et al. 2016; McDermott et al. 2013), emphasising the importance of moving beyond distributional and procedural equity to consider the contextual and recognitional dimensions of equity that influence restoration work.

Regarding contextual equity, the role of historical injustices in the need for restoration was not raised during the key informant interviews, which may be due to the positionality of HW and CC, both of whom are white Kenyan descendants of British colonial settlers. By studying colonial history, particularly of Laikipia, we strived to mitigate what McIntosh (2016) calls ‘structural oblivion’ – a state of ignorance, denial, and ideological myopia that emerges from an elite social structural position. However, respondents may have, consciously or not, avoided the topic of colonialism for fear of triggering the shame and anxiety associated with a form of moral ‘double consciousness’ – the ‘sense of always looking at one’s self through the eyes of others, of measuring one’s soul by the tape of a world that looks on in amused contempt and pity’ (DuBois 1996) –, as experienced by white Kenyans (McIntosh 2016). The influence of positionality should be reflected upon when analysing social data (positionality statements for HW, EK and CC are included in Appendix 7).

Regarding recognitional equity, respecting different values and social norms necessitates the appreciation and celebration of the plurality of ethical frameworks (Schlosberg 2013; Sikor et al. 2014; Law et al. 2017). Our results exemplify that this diversity of values systems can lead to trade-offs between conflicting ethical positions. Trade-offs between equity objectives of different actors at different scales (e.g. between focal and downstream communities – and project coordinators – regarding filling gullies with *O. stricta*), mirrors similar issues for ecological objectives of restoration (Brancalion & Holl 2020). The dominant form of equity in international discourses is structured by a utilitarian ethical framework, focussing on the distributional dimension of equity, contemporary individuals as the ‘justice subjects’ (the stakeholders considered), and merit – as opposed to equality, need or deservedness – as the ‘criterion’ or decision-making guideline that organises relationships between justice subjects. It may not necessarily be appropriate to impose this dominant form of equity in the Global South (Sikor et al. 2014). Using the example of this study, one cluster was given fewer employment opportunities because it had an active development project providing jobs clearing *O. stricta* (i.e. emphasising needs over merit as the equity criterion). Prioritisation of poorer families provides a similar example.

Although we did not explicitly evaluate the role of power dynamics, the balance of power between project leaders and community members and among community members is likely to have influenced perceptions of equity. For example, despite clear communication from the project leaders to community members that they were merely facilitating the project, aspects of their positionality (e.g. education) may have led to unconsciously perceived authority of the project leaders over community members. The power structures within the community also determine collective decision-making. The considerable distance between the chosen restoration site and the location of the future restoration site most frequently proposed by respondents suggests that these power dynamics influenced the restoration site selection.

Our results also highlight that different dimensions of equity are intimately linked. For example, the respect for socio-cultural norms (recognitional equity) during the employment process influenced the perceived fairness of the employment process (procedural equity), which, in turn, affected the perceived fairness of cost and benefit sharing (distributional equity), because employment played a key role in perceived benefits. In this study, trade-offs occurred between equity dimensions. For example, asking community members to propose the next restoration site may appear to some to be a more democratic process than allowing community leaders to make this decision, increasing procedural and distributional equity. However, over a quarter of respondents answered ‘anywhere’ and only 40% suggested a specific location, which suggests indifference. More importantly, this would undermine traditional decision-making processes, reducing recognitional equity.

Different aspects of equity, such as gender and age equity, can interact in a way that the level of marginalisation experienced is more than the sum of marginalisation along each axis, termed ‘intersectionality’ (Lau 2020). Although we did not explore intersectionality in this study, awareness of its effects may aid in meeting equity objectives in restoration. Although incorporating equity into ecosystem restoration will add an extra level of complexity and cost, we opine that it will lead to more effective, efficient and successful restoration work. The validity of this proposition should be investigated in future research by comparing similar restoration projects with differing degrees of equity, ensuring that diverse dimensions of equity and restoration success are considered.

4.7 Supporting information

Appendix 7. Positionality statements and supporting data
Appendix 8. Questionnaire

4.8 References

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Chapter 5: Discussion and Synthesis

5.1 Introduction

Slowing and reversing the ongoing global biodiversity declines through ecosystem restoration requires a deeper, integrated understanding of both underlying biophysical processes, such as livestock-wildlife interactions (Schieltz & Rubenstein 2016), as well as important human aspects, such as equity (Elias et al. 2021). This is particularly the case for drylands that tend to be rich in biodiversity but can be home to people lagging behind in terms of human development (James et al. 2013; IPBES 2018; Stringer et al. 2017). Through a literature review, I identified three key questions in light of important and urgent knowledge gaps: 1) To what extent can livestock at different stocking rates functionally replace large wild herbivores in their effects on plant and animal communities? 2) Do the effects of livestock at different stocking rates interact non-additively with the effects of large wild herbivores? 3) What socio-economic factors influence the equity of ecosystem restoration efforts? To address these knowledge gaps, I focussed on rangeland social-ecological systems in central Kenya, employing both biophysical and social science methods. The results suggest that cattle can functionally replace large wild herbivores in their impacts on smaller wildlife assemblages, which appear to respond primarily to total herbivory and vegetation structure (Objective 1). However, understory vegetation is more sensitive to herbivore identity, particularly at high cattle stocking rates (Objective 2). Both smaller wildlife and understory vegetation communities are shaped in complex ways by the interactive effect of large wild herbivores and domestic herbivores at varying stocking rates (Objectives 1 and 2). Aspects of perceived equity in a rangeland restoration project were also influenced in complex ways by the interactions between employment status and distance to the restoration site (Objective 3). These interactions between biophysical and socio-economic variables should be taken into account when planning future ecosystem restoration efforts.

In this chapter, I synthesise the key findings across and between the three integrated papers presented in Chapters 2, 3, and 4 in order to inform future ecological restoration projects within Laikipia county, as well as in other similar rangeland social-ecological systems across the globe. The findings from this thesis will be particularly applicable to tropical semi-arid rangeland social-ecosystems similar to those investigated in this thesis, but certain insights may also be applicable in other rangeland systems more broadly. For example, it has been noted that the dry-season/wet-season cycles of tropical grasslands are analogous to the seasonal cycles of temperate grasslands, as both are fundamentally cycles of growth and senescence (Tree 2019). Therefore, the processes that govern temperate and tropical grasslands may not be as dissimilar as they superficially appear and insights from one may, in certain cases, be transferable to the other. I then propose future directions for research that would build on the findings of this thesis and make further important contributions to our understanding of both human and biophysical dimensions of ecosystem restoration in rangeland social-ecological systems.

5.2 Key findings that address the research objectives

Four key findings emerged from this research, which address all three research objectives:

1) The diversity of smaller-bodied wild vertebrates responds to total herbivory regardless of herbivore identity and cattle stocking rate – in other words, it does not matter whether the herbivory is by wild or domestic herbivores. This effect appears to be mediated by vegetation structure.
2) At high cattle stocking rates, understory plant community composition responds primarily to herbivore identity as opposed to total herbivory.
3) Cattle stocking rate and large wild herbivore presence interact in complex ways, in some cases moderating and in other cases enhancing each other’s effects on smaller-bodied wild vertebrates and understory plant communities.
4) Distance to restoration site and employment by the restoration project can strongly affect perceived equity among community members and can interact in their influence on certain dimensions of perceived equity, in this case procedural equity. As perceived equity can influence ecological outcomes of restoration, planning restoration projects to improve equity, including spatial considerations of site selection, will directly benefit community-based restoration projects.

5.3 Implications for ecosystem restoration in the rangeland social-ecological systems of Laikipia

In addition to the broader implications for the management of rangeland social-ecological systems highlighted above, the findings from this research also have more specific implications for the management of rangeland social-ecological systems in Laikipia county. Lessons can be drawn from this thesis that are relevant to addressing the multiple objectives of land managers, including biodiversity conservation, livestock production, economic viability, and the preservation of cultural traditions. Below, I detail three key implications of this thesis for ecosystem restoration in rangeland social-ecological systems in Laikipia county. These mirror the three broader implications detailed above, but with greater emphasis on the local context within Laikipia county. Here, I aim to provide specific recommendations that can be applied in a practical manner by land managers and other residents of Laikipia county.

5.3.1 Altering vegetation using livestock stocking rates and wild herbivore presence to meet conservation and ecosystem restoration goals

The results of this thesis (Chapter 2) suggest that properties in Laikipia that support both cattle and large wild herbivores (> 50 kg) may be enhancing biodiversity by facilitating smaller-bodied wildlife (10–70 cm shoulder height). However, even properties that actively exclude large wild herbivores (e.g. Mogwooni) are likely to have similar effects, because the smaller wildlife appeared to be responding to total herbivory rather than herbivore identity. This effect is likely to be localised to the habitat patches being grazed and may not occur if a large area is grazed homogeneously even at the same cattle stocking rate – although, further research would be required to test this hypothesis. The positive effect of cattle grazing on smaller wildlife diversity may also occur in properties with much lower cattle stocking rates, such as Lewa (0.01 to 0.08 cattle ha^{-1}) or Ol Jogi Pyramid (0.0 to 0.09 cattle ha^{-1}; unpublished data). In these properties, the grazing effect may be limited to the sites being grazed by cattle and/or the sites being grazed by large wild herbivores, the latter of which may have a greater effect if the large wild herbivores are at higher densities than in properties with high cattle stocking rates. Whether properties with higher cattle stocking rates have lower densities of large wild herbivores has not yet been systematically tested, and this should be an important avenue for future research.

Properties that are stocked at much higher stocking rates (> 3 cattle ha^{-1} and > 4 sheep/goats ha^{-1}), which tend to be communally managed rangelands (e.g. Makurian, Kurikuri, and the Naibunga conservancies), far exceed the stocking rates investigated in this thesis. This means that they are unlikely to experience the positive benefits of grazing on smaller wildlife diversity. Firstly, the high livestock stocking rates, particularly of sheep and goats, reduces forage availability to the extent that grazing begins to have a negative effect on biodiversity. Secondly, the extensive grazing impacts at these high livestock stocking rates may preclude benefits to smaller wildlife, which may be facilitated by grazed patches surrounded by a matrix of less grazed habitat but suppressed by homogeneous grazing at the same stocking rate.

It may be that the positive effect of grazing on smaller wildlife diversity will be limited to or stronger on vertisols (colloquially known as ‘black cotton soils’). Whether this phenomenon is also true of other dominant soil types across Laikipia such as luvisols (colloquially known as ‘red soils’) would also require further research. However, the strong correlations between the local diversity of smaller wildlife (and all wildlife 0.05–1,000 kg) suggest that a similar effect might occur on other soil types, although the strength of the relationship may differ. If this is the case, lower cattle stocking rates on luvisols will achieve comparable benefits to smaller wildlife diversity, because vertisols tend to have taller grass. Properties that have both vertisols and luvisols (e.g. Mpala, Ol Pejeta) could consider adapting stocking rates accordingly depending on soil type if they seek to enhance the local diversity of wildlife (0.05–1,000 kg).

There are several efforts to restore rangeland health and, in some cases, rewild rangelands in Laikipia. In areas that are currently heavily grazed by domestic animals (> 3 cattle ha^{-1} and > 4 sheep/goats ha^{-1}), reducing livestock stocking rates to within a range that is comparable to those tested in this thesis is likely to increase the diversity of both large and smaller wild herbivores. Alternatively, it may be possible to alter grazing regimes in such a way as to allow relatively high stocking rates, such as well managed seasonal grazing arrangements with neighbouring rangelands. The social, economic, and cultural implications of these shifts in livestock management would of course need to be considered. Ecosystem restoration and rewilding efforts that involve reducing livestock stocking rates in areas that currently support diverse large wild herbivore communities should consider the effects of this destocking on overall herbivory. If large wild herbivore densities do not increase to match the reduction in livestock stocking rates, this could have a negative impact on smaller wildlife. However, this may represent a return to conditions prior to significant impact by pastoral communities (i.e. before *c*. 1,000 BC; Lane, 2011), and would not be of concern if the smaller wildlife populations are not threatened. This assumes that large wild herbivores were not at significantly higher densities in the past. Alternatively, large wild herbivore populations may not increase in response to destocking of domestic animals in the short term due to a temporal lag, or over the longer term due to ecological constraints imposed by the anthropogenic habitat fragmentation over the past century. In the former case, the ecosystem may equilibrate over time or land managers could mitigate any potential negative impacts on smaller wildlife by destocking domestic animals gradually. If habitat fragmentation is the primary constraint, then efforts to connect suitable habitat (e.g. using fence gaps and corridors) and/or efforts to restore degraded habitat will be necessary.

Rangeland managers of private properties in Laikipia generally make livestock grazing decisions based on the availability of forage and water, but rarely consider understory species composition. Those who do commonly monitor the abundance of one of the palatable dominant perennial grasses, *Themeda triandra*, and possibly the less preferred dominant perennial grasses *Pennisetum stramineum* and *P. mezianum*. Therefore, I will focus on the rangeland management implications for these dominant perennial grass species, in addition to the implications for total herbaceous cover and understory leafiness (and indication of forage quality). Total cover responded more strongly to herbivore identity (the presence or absence of cattle or large wild herbivores) than total herbivory, so the species composition of wild and domestic herbivores will determine total cover to a greater extent than the total herbivory by domestic and wild herbivores. As only a few properties monitor the densities of large wild herbivores, it would be more practical to continue to monitor total cover directly. The saturation of the relative cover of *T. triandra* as total herbivory increased suggests that this species is resilient to rising herbivore stocking rates, at least until around 12 kg hr m^{-2} yr^{-1}. This corroborates previous reports that this species responds positively to herbivory (Veblen et al. 2016). However, there is likely to be a threshold beyond which the effect of herbivory becomes negative. On the other hand, the relative cover of *P. mezianum* increased more rapidly as total herbivory increased, while the relative cover of *P. stamineum* was uncorrelated with total herbivory. This suggests that rangeland managers should be cautious when increasing herbivore stocking rates due to the greater-than-additive increases in the relative dominance of less preferred grass species such as *P. mezianum*. Land managers in communally managed areas that tend to be home to communities with a long cultural history of pastoralism, can be more familiar with a larger range of understory plant species and hold traditional ecological knowledge of their influences on livestock health (Homewood 2009). However, it is difficult to extrapolate the relationships between herbivore stocking rates and understory plant community composition, because the typical grazing pressure far exceeds that of KLEE.

Understory leafiness was highest in treatments with both wild mesoherbivores (50–1,000 kg) and megaherbivores (> 1,000 kg; elephant and giraffe), whether they had cattle at moderate stocking rates or no cattle at all. However, leafiness was lowest in plots with wild mesoherbivores, megaherbivores, and cattle and high stocking rates as well as plots that excluded all large herbivores. This implies that forage quality could be improved in areas that support both cattle and large wild herbivores (i.e. most private properties) by ensuring cattle stocking rates are around 0.10 to 0.15 cattle ha^{-1}. More heavily grazed areas (> 3 cattle ha^{-1} and > 4 sheep/goats ha^{-1}), which tend to be communally managed rangelands (e.g. Makurian, Kurikuri, and the Naibunga conservancies), would need to reduce herbivore stocking rates in order to improve forage quality.

5.3.2 Accounting for the presence of large wild herbivores when determining livestock stocking rates

For properties that actively exclude large wild herbivores (e.g. Mogwooni), the implications of increasing cattle stocking rates on understory vegetation and wildlife can be based on the effects of the KLEE treatments that exclude large wild herbivores. However, distilling practical recommendations that can be implemented by rangeland managers of mixed-use rangelands poses a challenge, due to the complex nature of the interactions between cattle and large wild herbivores in influencing smaller wildlife diversity and shaping understory plant communities. For this reason, it may be necessary for land managers in mixed-use rangelands (i.e. most properties) to simply be aware that non-additive effects can occur where domestic and wild herbivores share rangeland landscapes. Moreover, it may be more practical for rangeland managers in mixed-use systems to monitor the responses of wildlife and vegetation directly, rather than to attempt to predict the outcomes of interactive effects between wild and domestic herbivores on the ecosystem when altering herbivore stocking rates. Rangeland managers do monitor forage availability visually and often have a wealth of personal experience. This may be augmented by more systematic, but low cost, vegetation and wildlife monitoring, which can be recorded in a format that is readily communicated and understood.

5.3.3 Equity and the socio-economic factors that influence it in ecosystem restoration projects

Here I elaborate on specific implications of this thesis for Makurian group ranch and other communally managed rangelands in Laikipia. The importance of employment by the restoration project and the distance from restoration site in influencing perceived equity relating to the restoration project has several implications for future ecosystem restoration projects within Makurian group ranch and in other communally managed rangelands in Laikipia. Firstly, due to the poverty and lack of economic opportunities in communally managed rangelands in Laikipia, the demand for employment in these areas is very high. The findings in Chapter 4 illustrate that restoration projects that focus on activities that create employment in local communities, will both benefit community members as well as increase perceived equity. For example, choosing manual removal of invasive plants such as *Opuntia stricta* with simple hand-held tools would create more employment opportunities that mechanical removal using heavy machinery. Due to the low cost of labour in poorer countries and the high cost of purchasing and operating specialised machinery that is often imported, approaches that increase employment opportunities also reduce the costs of restoration activities. Secondly, the importance of employment in determining perceived procedural equity also means that the process by which employees are selected is critical. As with any benefit to a community, inherent inequities and power imbalances can lead to unfair distributions of employment opportunities, as documented in Chapter 4. Thirdly, the importance of the distance to the restoration site suggests that future restoration projects should attempt to ameliorate its negative impacts on perceived equity as well as on the ecological outcomes of restoration. For example, assuming an identical budget, smaller-scale restoration projects distributed among villages or clusters of a larger community would reduce the distance to the local restoration site, compared to a single large restoration site. This may lead to tradeoffs with ecological restoration objectives that call for larger treated sites or require additional coordination such that the aggregate benefits are captured at the landscape scale. For instance, stronger edge effects associated with smaller restoration sites may allow invasive species to re-establish more rapidly. However, there may also be additional socio-economic and equity advantages to smaller-scale distributed restoration sites. Shorter commuting distances could allow more women to gain employment in restoration projects, which would increase gender equity and potentially lead to more direct economic benefits to the families of the employed individuals. This is because income received by men is less likely to reach the family than income received by women, as documented in Chapter 4.

5.4 Implications for ecosystem restoration in rangeland social-ecological systems globally

The findings from this research have clear implications for the management of rangeland social-ecological systems. In particular, lessons can be drawn from this thesis to guide the ecosystem restoration efforts that are becoming ever more critical for addressing the current biodiversity crisis. Below I detail three key implications of this thesis for ecosystem restoration in rangeland social-ecological systems.

5.4.1 Altering vegetation using livestock stocking rates and wild herbivore presence to meet conservation and ecosystem restoration goals

The results of this thesis (Chapter 2) suggest that reintroduction of locally extirpated large wild herbivores, as in trophic rewilding efforts (Donlan 2005; Seddon et al. 2014; Svenning et al. 2016), can enhance the diversity of smaller wildlife and the habitat use of specific species (e.g. steenbok, helmeted guineafowl, crested and yellow-necked francolins, cattle egrets, starlings, and shrikes). Failing this, domestic animals such as cattle are likely to have similar effects and increasing their stocking rates can enhance local diversity of smaller wildlife in savannas. The strong response of smaller wildlife diversity to grass height suggests that even mechanical mowing would also have a similar effect (Cromsigt & Olff 2006). Similarly, species that responded strongly to megaherbivore-induced tree density changes (i.e. duikers, servals, and bushbabies) may also respond to manual thinning of trees (Riginos & Grace 2008). This implies that reintroducing megaherbivores may have a negative effect on the habitat use and possibly populations of these species that prefer areas with higher tree densities. Promoting biodiversity is a common goal of ecosystem restoration (Hughes et al. 2018; IPBES 2018) and the results of this thesis suggest that this may be achieved in savannas by using herbivory as a tool to alter understory and overstory vegetation structure. Overall biodiversity would be more greatly enhanced by reintroducing an assemblage of extirpated large wild herbivores than the introduction of cattle, even if their effects on grass height and smaller wildlife diversity are comparable.

Grazing, whether by wild or domestic herbivores, not only reduces grass height, but also shifts the understory plant community composition (Veblen et al. 2016). For example, wild mesoherbivores and cattle at moderate and high stocking rates all increased the cover of annual grasses and reduced perennial forb cover (Chapter 3). Megaherbivores also reduced the cover of perennial forbs. The results of this thesis confirm those of Veblen et al. (2016) that the removal of native large wild herbivores can alter understory community composition. This suggests that trophic rewilding efforts that involve the reintroduction of locally extirpated large wild herbivores can restore understory plant community composition. In this this thesis (Chapter 3), I show that the overall composition of the understory community (measured by the primary ordination axis) is altered by grazing in a way that appeared to be driven largely by total herbivory when excluding the high cattle stocking rate treatments. This result was in agreement with Veblen et al. (2016), suggesting that total herbivory is more important than herbivore identity in shaping understory community composition at moderate cattle stocking rates. However, the results of this thesis show that, at high cattle stocking rates, the understory community composition shifts in ways that are better predicted by herbivore identity than total herbivory. This implies that cattle can mimic the effects of, and thus functionally replace, large wild herbivores in shaping the understory community composition at moderate but not high cattle stocking rates. Therefore, restoring and/or maintaining native savanna understory plant community composition may necessitate a reduction of cattle stocking rates in areas where they are too high. The quadratic response of understory leafiness to total herbivory suggests that leafiness (and thus forage quality) is maximised at intermediate combined stocking rates of domestic and wild herbivores (*c*. 3–7 kg hr m^{-2} yr^{-1}).

In practice, the ‘moderate’ and ‘high’ stocking rates at KLEE can be considered ‘low’ and ‘moderate’, respectively, in comparison to stocking rates observed in many communally managed rangelands within and beyond Laikipia. For example, the ‘moderate’ cattle stocking rate at KLEE is designed to mimic the stocking rate of the private ranch in which it is located (Mpala), as well as other similar ranches, at 0.10 to 0.15 cattle ha^{-1}. (Veblen et al. 2016; Young et al. 2018). These cattle stocking rates are similar to other private ranches in the county, such as Borana (0.11 to 0.21 cattle ha^{-1}), Suyian (0.07 to 0.29 cattle ha^{-1}), Ol Pejeta (0.23 to 0.27 cattle ha^{-1}), Ol Jogi Ranch (0.14 to 0.24 cattle ha^{-1}; unpublished data). For rangelands that stock multiple domestic herbivore species it is important to account for the overall impact of all livestock when comparing stocking rates. For example, another private ranch, Lolldaiga Hills, that keeps both cattle and sheep stocks cattle at 0.15 to 0.29 cattle ha^{-1} and stocks sheep at 0.08 to 0.23 sheep ha^{-1} (unpublished data). The questionnaires revealed that the cattle stocking rate at Makurian was 2 to 3 times that of Mpala, at 0.35 cattle ha^{-1} (Chapter 4). Once the stocking rates of sheep (0.80 sheep ha^{-1}) and goats (0.63 goats ha^{-1}) are included, the total grazing pressure of domestic animals far exceeds that of the ‘high’ stocking rates at KLEE. Consequently, rangelands with livestock stocking rates comparable to those of Makurian will likely require stocking rates to be lowered in order to restore understory community composition.

As well as contrasts in stocking rate and herd composition, livestock grazing management also differs between privately and communally managed rangalands in Laikipia and elsewhere – broadly, rotational versus continuous grazing. However, several communally managed rangelands are beginning to implement rotational grazing systems and therefore more similar to the high cattle stocking rate treatment at KLEE. If this trend continues, it may be possible to draw greater inference from the results of KLEE to the broader landscape.

5.4.2 Accounting for the presence of large wild herbivores when determining livestock stocking rates

The evidence of interactive effects between cattle at different stocking rates and the presence of wild mesoherbivores and megaherbivores implies that the presence of large wild herbivores should be taken into account when adjusting domestic animal stocking rates. These non-additive livestock-wildlife effects impacted both smaller wildlife and understory vegetation. The interactive effects were in some cases moderating, such that the effects of domestic and wild herbivores dampened each other (Chapter 2). Their combined effect was therefore less than the sum of their individual effects. For example, the local diversity of smaller wildlife was enhanced by cattle at high stocking rates and wild mesoherbivores, but less so in the presence of the other. Similarly, cattle at high stocking rates and wild mesoherbivores increased understory leafiness (leaf-to-stem ratio), but reduced understory leafiness in the presence of the other. The livestock-wildlife interactive effects were in other cases augmentative, such that the effects of domestic and wild herbivores were enhanced by each other. In other words, their combined effect was greater than the sum of their individual effects. For example, the amount of bare ground was increased by cattle at high stocking rates more in the presence of wild mesoherbivores. Similarly, ostrich habitat use was increased by wild megaherbivores more so in the presence of cattle at moderate stocking rates.

Land management practices that aim to increase the local diversity of smaller wild herbivores in savannas may be able to achieve this through grazing, whether by wild or domestic herbivores. However, the dampening interactive effects between cattle and wild mesoherbivores means that raising cattle stocking rates will enhance local smaller wildlife diversity to a similar degree when alone compared to when wild mesoherbivores are present. Land management practices that aim to improve forage quality by increasing understory leafiness should consider the interactive effects between cattle and wild mesoherbvores. Past a certain threshold, increasing cattle stocking rates would be expected to reduce understory leafiness where wild mesoherbivores are present.

Despite the largely negative effects of livestock grazing on wildlife from the published literature, I show that grazing, even by livestock, can have beneficial effects on smaller-bodied wildlife and can therefore be used as a tool in ecosystem restoration (Chapter 2). However, rangeland managers should be cautious when increasing cattle stocking rates in the presence of wild megaherbivores, because bare ground may increase to a greater extent than would be predicted based on the additive effects of cattle and megaherbivores. Similarly, because perennial grass cover is reduced more by cattle at high stocking rates and wild mesoherbivores when together than each individually, rangeland managers should be cautious when increasing stocking rates.

5.4.3 Considering equity and the socio-economic factors that influence equity in ecosystem restoration projects

The results of this thesis showed that different dimensions of the perceived equity of restoration projects can be influenced by socio-economic factors, such as employment by the restoration project and the distance to the restoration site (Chapter 4). Because equity can influence the ecological outcomes of conservation projects (Halpern et al. 2013; Pascual et al. 2014), future ecosystem restoration projects should take into consideration the influence of socio-economic factors that influence equity. In this thesis, the perceived fairness of restoration site selection (an aspect of procedural equity) was influenced in an interactive manner by employment by the project and distance to the restoration site. This implies that future ecosystem restoration projects need to be cognisant of potential interactive effects such as these, which can affect both social and ecological outcomes. Equity issues are rarely considered in ecosystem restoration projects, so the approach taken in this thesis provides an example of how other restoration projects may assess equity alongside ecological indicators.

These complex interactions between determinants of perceived equity, which in turn can influence the ecological outcomes of restoration, demonstrate that a profound understanding of the ecological dimensions of restoration alone is insufficient for improving the outcomes of future ecological restoration efforts. This also highlights the importance of continuing to explore the influences of equity and the socio-economic factors that influence it in shaping ecosystem restoration outcomes, in an integrated manner alongside the traditional ecological indicators. Recent research has also highlighted the role of a variety of issues relating to equity in ecosystem restoration, including social equity (Kandel et al. 2021), gender equity (Crossland et al. 2021; Kariuki & Birner 2021), power dynamics (Mansourian 2021), social inclusion (Sigman & Elias 2021), indigenous ethics (Lee et al. 2021), and inequities stemming from colonial history (Sen et al. 2021).

5.5 Sharing research findings

Sharing the knowledge generated is an important part of knowledge coproduction more specifically. To this end, together with Elijah Kirobi (co-author of Chapter 4), I prepared a summary of the findings in Chapter 4 in the Maa language that was formally submitted to the Makurian group ranch (Appendix 9). We prepared the report in a way that is accessible to the leaders of the Makurian community and that can be communicated verbally to illiterate members of the Makurian community. Similarly, I wrote a summary of key findings relevant to the wider Laikipia ranching and conservation community, to be circulated via email (Appendix 10). Future research may benefit from evaluating feedback from stakeholders, such as community members, ranch managers, and conservationists, to iteratively generate priority research questions and guide avenues for further applied research.

5.6 Directions for future research

There are several additional questions that precipitated from this thesis that I believe would be important to investigate in future research. I elaborate on these knowledge gaps below, discussing how addressing them may further deepen our understanding of the biophysical and human dimensions of ecosystem restoration in dryland social-ecological systems.

5.6.1 Covering a broader range of stocking rates, grazing regimes, and domestic animal species compositions (and their interactive effects)

Through this thesis, I attempted to begin to address the issue of the lack of research comparing different livestock stocking rates, particularly with respect to effects on wildlife. However, consideration of more than three stocking rates would have provided a more complete picture, particularly in identifying thresholds. In addition, there are many other aspects of livestock grazing regimes that are important in determining the effects of domestic animals, including the timing, duration, intensity, and frequency (Briske et al. 2011; Vetter et al. 2005; Zietsman 2014). Future studies should account for variations in these parameters, because they could significantly influence the effect of livestock grazing even if animal densities or stocking rates remain constant (Briske et al. 2003, 2008; Gosnell et al. 2020; Hawkins 2017; Hawkins et al. 2017; Odadi et al. 2017). Because different domestic animals vary in their feeding behaviour and dietary composition (Kartzinel et al. 2019), it would be beneficial for future research to investigate their unique effects of, for example, cattle, sheep, goats, and camels. In practice, these different domestic animal species are often kept together in the same rangeland system, so evaluating interactive effects between them may also be important.

5.6.2 Contrasting wild herbivores assemblages (and interactions among them)

In this thesis I focused on a savanna rangeland system in central Kenya. The direct effect of large wild herbivore assemblages on smaller wildlife and plant communities may depend on the composition of the large wild herbivore assemblage. Therefore, future research could replicate similar experiments in other ecosystems with different mesoherbivores and/or megaherbivore assemblages. For example, the predominantly grazing white rhinoceros *Ceratotherium simum* is likely to have contrasting impacts on vegetation and smaller wildlife to those of the predominantly browsing megaherbivores (elephants and giraffe) in the focal ecosystem of this thesis (Kartzinel & Pringle 2020). Similarly, an ecosystem comprising a different mesoherbivore assemblage may also produce contrasting results, particularly if the mesoherbivore species represented different feeding guilds (e.g. grazer-dominated versus browser-dominated; Kartzinel et al. 2015).

5.6.3 Climatic mediation

Climatic factors play a crucial role in mediating relationships among plant and animal communities in rangeland social-ecological systems (e.g. Long et al. 2017). For example, there is evidence that rainfall mediates the effects of cattle on plains zebra habitat use (Kimuyu et al. 2017), as well as the effects of large wild herbivores on cattle weight gain (Odadi et al. 2011). Savanna understory vegetation is also strongly shaped by drought cycles (Porensky et al. 2013; Riginos et al. 2018). It is therefore likely that rainfall will also mediate the relationships investigated in this thesis. If I had conducted these studies over a decade or more (through drought cycles) I may have been able to assess the nature and extent of the climatic mediation of, for example, the effects of cattle and large wild herbivores on smaller wildlife and understory plant communities. Such studies will become increasingly important given current and projected climate change (IPCC 2021).

5.6.4 The influence of power dynamics within communities in shaping equity outcomes

One important aspect of the social dimensions of ecosystem restoration efforts that I did not explicitly address relates to power dynamics (Mansourian 2021). Power dynamics exist between the project leaders and the community members as well as among community members, which can influence equity outcomes. For example, the focus on using the community's existing institutions to select employees for the restoration project promoted an aspect of recognitional equity – recognition of cultural and customs. However, the power structures inherent in these institutions may lead individuals to feel that process of employee selection was unfair – an aspect of procedural equity. Likewise, consciously or unconsciously perceived authority of project leaders and/or researchers over community members could lead to power imbalances in decision making. The nature and influence of power dynamics in shaping decision making could be examined more explicitly in future restoration projects. Reflecting on them may aid in ameliorating any detrimental effects that power imbalances may have on social or ecological outcomes of restoration. This includes, for example, ensuring that the most marginalised community members do not lose out further as a result of restoration activities.

5.6.5 Assessing contextual and recognitional dimensions of equity through local perceptions

In this thesis, I used a literature review to evaluate contextual equity and participant observation to assess recognitional equity. However, these two dimensions of equity could have been investigated using other methods such as interviews. Interviews may be more appropriate for evaluating contextual equity in areas in which the contemporary and historical context has not been well documented. Interviews could also have benefited the evaluation of recognitional equity, although this would have taken more time than questionnaires and, to accommodate it, the sample size would have to be compromised. Although they are associated with their own limitations, such as local bias, perceptions of contextual and recognitional equity may provide a more detailed and nuanced picture of these dimensions of equity than literature reviews and participant observation.

5.6.6 Explicit treatment of the role of spatio-temporal scale in both biophysical and social aspects of ecological restoration

Issues relating to spatial and temporal scale are ubiquitous in scientific research (Chase et al. 2019; McGill et al. 2015; Shea & Chesson 2002). For example, the observed effect of grazing on the diversity of small-bodied wildlife may have been due to the small scale of the treatments (Chapter 2). The 0.25-ha high cattle stocking rate treatment plots were nested within a 1-ha moderate cattle stocking rate treatment plots, located within a matrix of savanna habitat surrounding KLEE. This means that smaller wildlife may have been responding to the spatial and/or temporal heterogeneity created by the treatments rather than or as well as the treatments themselves. Consequently, replicating the experiment at larger spatial scales may have had contrasting effects. Ideally, similar experiments would need to be set up at different scales in order to test the effects of scale explicitly, but this is likely to be prohibitively expensive. One alternative would be to use observational studies, which are less costly to scale up, but they have disadvantages over manipulative experiments that relate to challenges in determining causality.

Increasing the spatial scale of the equity study (Chapter 4) would have introduced a broader perspective of equity that included neighbouring communities. Crucially, this would have included analysis of risks for communities living downstream who would be impacted by restoration decisions that may, for example, increase the spread of the exotic cactus via rivers, such as filling gullies with cleared cacti. Analogously, expanding the temporal scope of the equity study would have explicitly incorporated future generations into equity considerations. Implications of restoration actions for broader social scales could also be examined, such as tradeoffs between local, national, and international perceptions of equity that relate to the contrasting values systems at the different levels of social organisation, which in turn impact restoration projects (Brancalion & Holl 2020).

5.7 Conclusions

To conclude, in this thesis, I explored the biophysical and human dimensions of rangeland social-ecological systems in an African savanna. I focused on livestock-wildlife-vegetation interactions and the socio-economic factors that influence equity in restoration projects. Regarding the biophysical dimension, the results of the thesis suggest that the effects of grazing on small-bodied wildlife diversity is largely driven by total herbivory, while grazing shapes understory plant communities in ways that are more sensitive to herbivore identity when cattle stocking rates are increased. Therefore, cattle appear to functionally replace large wild herbivores in their effects on smaller wildlife, but not on understory plant communities at higher cattle stocking rates. In addition, non-additive or interactive effects can occur between domestic and wild herbivores. Regarding the social dimension, perceived equity is affected by employment by the restoration project and the distance to the restoration site, which can interact in their influence on certain aspects of equity. These biophysical and social patterns should be considered in an integrated manner during ecosystem restoration projects, which are likely to grow in number as the UN Decade on Ecosystem Restoration (2021–2030) progresses and we strive to meet SDG targets such as LDN. Future research would particularly benefit from more detailed investigations into the diverse parameters of livestock grazing regimes, the role of climatic mediation, the evaluation of contextual and recognitional equity through perceptions, and the explicit treatment of power dynamics and spatio-temporal scale effects.

5.8 References

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Appendices

Appendix 1. Other first authored and co-authored papers supporting the thesis

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Ebel CR, Case MF, Kimuyu DM, Langendorf RE, Porensky LM, Veblen KE, Wells HBM, Young TP, Hallett LM (in review with Frontiers in Ecology and Evolution) Top-down control of biotic stability mechanisms by large mammalian herbivores.

Appendix 2. The importance of long-term social-ecological research for the future of restoration ecology (published in Restoration Ecology)

Authors: Harry B. M. Wells, Andrew J. Dougill, Lindsay C. Stringer

A2.1 Abstract

In the face of rapid environmental and cultural change, long-term ecological research (LTER) and social-ecological research (LTSER) are more important than ever. LTER contributes disproportionately to ecology and policy, evidenced by the greater proportion of LTER in higher impact journals and the disproportionate representation of LTER in reports informing policymaking. Historical evidence has played a significant role in restoration projects and it will continue to guide restoration into the future, but its use is often hampered by lack of information, leading to considerable uncertainties. By facilitating the storage and retrieval of historical information, LTSER will prove valuable for future restoration.

A2.2 Implications for practice

- Rapid changes such as climate change and human population growth render long-term social-ecological research (LTSER) more important than ever to guide future restoration efforts.
- Historical knowledge in various forms (history as information and reference, history as revealing the future, and history as enriching cultural connections) has played a significant role in restoration and will continue to be important for future restoration. This implies that LTSER will be important for restoration into the future through encoding and storing social-ecological memory.
- LTSER will inform effective integration of restoration as a management tool, which will need to be employed routinely in all aspects of human engagements to counterbalance inevitable extractive/destructive activities in a more intensely human-dominated future.

A2.3 Introduction

The benefits of long-term ecological research (LTER) are widely acknowledged (Müller et al. 2010; Lindenmayer et al. 2012) and LTER contributes disproportionately to ecology and policy (Hughes et al. 2017). Monitoring the impacts of key environmental variables requires long-term studies partly because many variables change slowly, but also because spatial and temporal variability pose challenges distinguishing “signal” from “noise” (Singh et al. 2013) — particularly in dynamic environments such as drylands (Stringer et al. 2017). Moreover, long-term studies allow processes at multiple timescales to be captured, while complementing and providing more robust results than shorter-duration monitoring (Hughes et al. 2017). In 2003, recognition of the importance of integrating ecological and social dimensions led to the development of long-term social-ecological research (LTSER; Singh et al. 2013; Dick et al. 2018). Here, we explore how LTSER will benefit future restoration following the historical knowledge typology out- lined by Higgs et al. (2014): (1) history as information and reference, (2) history as revealing the future, and (3) history as enriching cultural connections.

A2.4 History as information and reference

History has played in important role in restoration ecology and its significance is unlikely to diminish (Higgs et al. 2014). The role of history as information and reference includes history as range of variability (of system variables), legacy (signatures of influences of the past), and reference (information concerning past ecosystem states and trajectories). Regarding history as reference, long-term perspectives help to determine what is "natural" and to disentangle natural variability from other, potentially significant trends; examples include animal population dynamics, biological invasions, climate variability, fire regimes, and ecosystem health evaluations (Willis & Birks 2006). In each case, short-duration studies are incapable of capturing longer-term trends and cycles that provide valuable information to guide restoration actions. LTSER also reduces susceptibility to "shifting baselines" (Corlett 2016) and provides key information where contemporary reference ecosystems are lacking or where all ecosystems have changed. Long-term monitoring enables the characterization of ecosystem dynamics and the definition of process-based and multifaceted reference models (e.g. Balaguer et al. 2014). LTSER will also help to elucidate legacy effects – the influence of the past on the structure and function of a social-ecological systems (SES) – thus informing the prescription of restoration treatments that account for the constraints or challenges on future states or trajectories imposed by these legacies.

Unlike history as reference and legacy, historical range of variability (HRV) is expected to become less important to restoration due to rapid cultural and environmental changes (Higgs et al. 2014). However, HRV may continue to be valuable for future restoration (1) in other locations that shift into a similar range of environmental conditions as a study site, or (2) where environmental variables return within a similar range in the same location. For history as information more generally, long-term monitoring will be critical for detecting small but significant changes and recording responses to infrequent, unexpected, and potentially critical events (Hughes et al. 2017; Mirtl et al. 2018). For example, long-term studies revealed that short-term monitoring of plant community composition incorrectly predicted the success of restoration treatments that ultimately failed and vice versa (Herrick et al. 2006). Moreover, LTSER can play a significant role in assessing susceptibility to degradation and thus inform restoration planning, particularly in highly variable environments (Miehe et al. 2010). Similarly, LTSER also enables assessments of population declines and extirpation risk, which are crucial for targeting restoration efforts. Long-term monitoring is also required for tracking progress toward national commitments such as Sustainable Development Goal target 15.3 on land degradation neutrality (Cowie et al. 2018) and for restoration funding schemes based on payments for ecosystem services, such as Regen Network (www.regen.network). Furthermore, continuous monitoring will facilitate the prioritization process for targeting restoration investments (Dallimer & Stringer 2018), adjustment of restoration objectives, adaptation of management strategies, and evaluation of restoration success (Herrick et al. 2006).

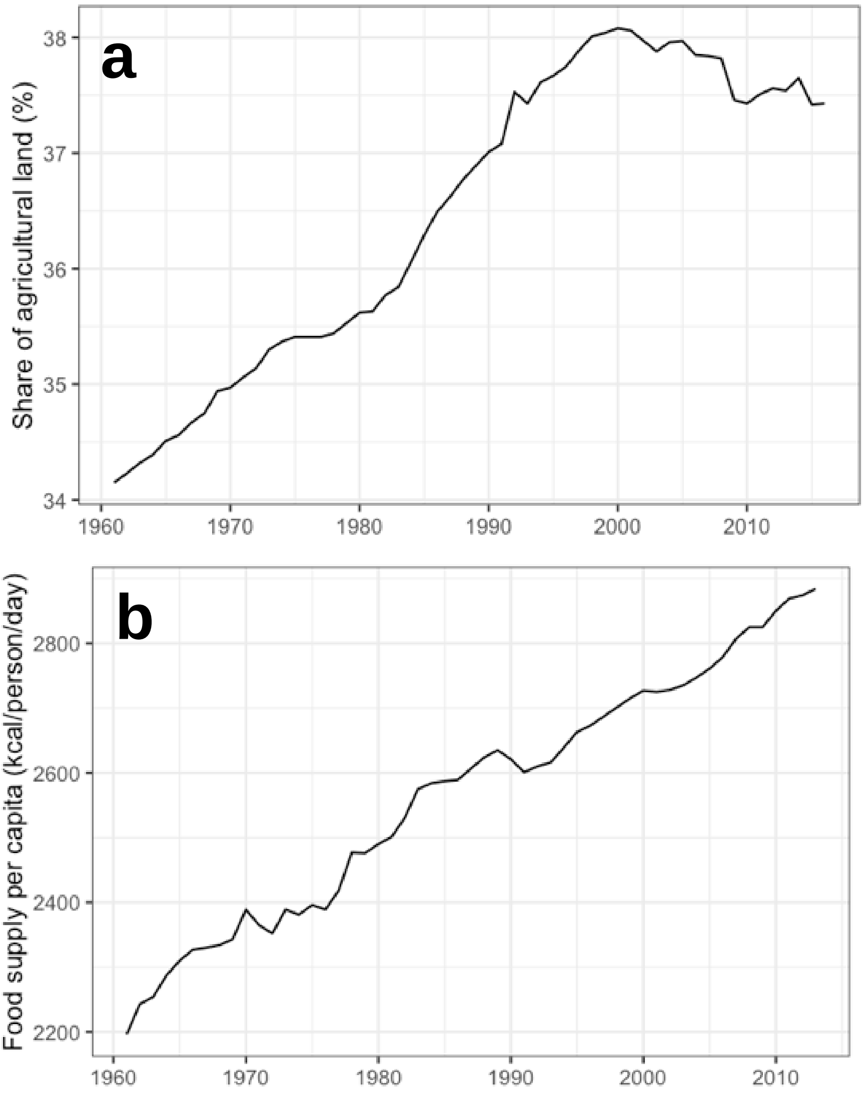

Figure S2.1 Global trends in the share of agricultural land (**a**) and per capita food supply (**b**) between 1961 and 2013. Data from FAO (www.fao.org/faostat/en/#data) accessed June 2019.

A2.5 History as revealing the future

Long-term monitoring also augments the benefits of history as revealing the future, which includes history as scenario (past scenarios and actual events) and experiment (natural experiments). LTSER would improve scenario planning and prediction of SES dynamics under future conditions. Here, we expand on two examples: (1) human population growth and land use change and (2) climate change.

Human population growth, increasing purchasing power and rising per capita consumption and land use change have negatively impacted biodiversity and ecosystem services (IPBES 2019). Although human population continues to rise, it is generally agreed that intensifying production on existing arable land is sufficient to meet humanity's future food demands (Cherlet et al. 2018). In fact, the global agricultural land share has been declining since 2000, while per capita food supply has maintained a positive trend (FAO 2017; Figure S2.1). This indicates that increased efficiencies in food supply have allowed more people to be fed on less land, suggesting an increase in abandoned agricultural land, which creates opportunities for restoration if unexploited for other land uses (e.g. urban development; Queiroz et al. 2014). More space-efficient intensive agricultural practices often have detrimental ecological impacts, which them- selves necessitate the integration of restorative processes (e.g. to enhance biodiversity and ecosystem services). Changes in the share of agricultural land vary by country; parts of Europe and Oceania experienced the largest declines from 1996 to 2016 (Figure S2.2a). The number of people living in rural areas is also projected to decline from 2020 to 2100 (UN-DESA 2018), which may create restoration opportunities in rural areas in which population densities are declining. These projections are also heterogeneous internationally (Figure S2.2b); the rising rural populations expected in many African countries will likely pose challenges for restoration. In regions experiencing agricultural land expansion and rising rural populations (e.g. Tanzania, Niger), restorative agriculture, agroforestry, and sustainable agricultural intensification is likely to take precedence over restoration in the coming decades. LTSER will help us identify restoration opportunities by increasing our understanding of how SESs are responding to these and other anthropogenic trends, such as technological development, female empowerment, and climate change, as they unfold.

Similarly, LTSER will allow us to monitor the nature and rate of biodiversity change in response to climate change, thus guiding restoration planning. A well-designed network of long-term monitoring sites could act as a warning system for future climate impacts (Prach & Walker 2011). Unfortunately, the spatiotemporal resolution of current global climate projections is low, rendering site-level planning informed by climate projections difficult for restoration practitioners. Long-term records of climatic variables will be valuable for restoration planning by enabling global climate projections to be downscaled (Ekström et al. 2015). This is particularly pertinent in developing countries with low densities of climate stations and regions for which climate models show high uncertainty, or where contrasting climate trends are experienced at finer scales (e.g. Schmocker et al. 2016).

Regarding history as experiment, we extend its definition beyond natural experiments to include planned experiments and monitoring. Of course, natural experiments will continue to be valuable, particularly when documented through long-term observation, but rigorous long-term experiments will have several advantages including planned comparisons, replication, and improved inference. A third aspect of history as revealing the future is history as virtue (the quality of being historical). If historicity indeed becomes “restoration’s virtue of the future” (Higgs et al. 2014), LTSER will be an effective means of facilitating the development of this virtue by storing social-ecological memory for future restoration ecologists and practitioners to access. This social-ecological memory will be valuable in guiding future restoration decisions.

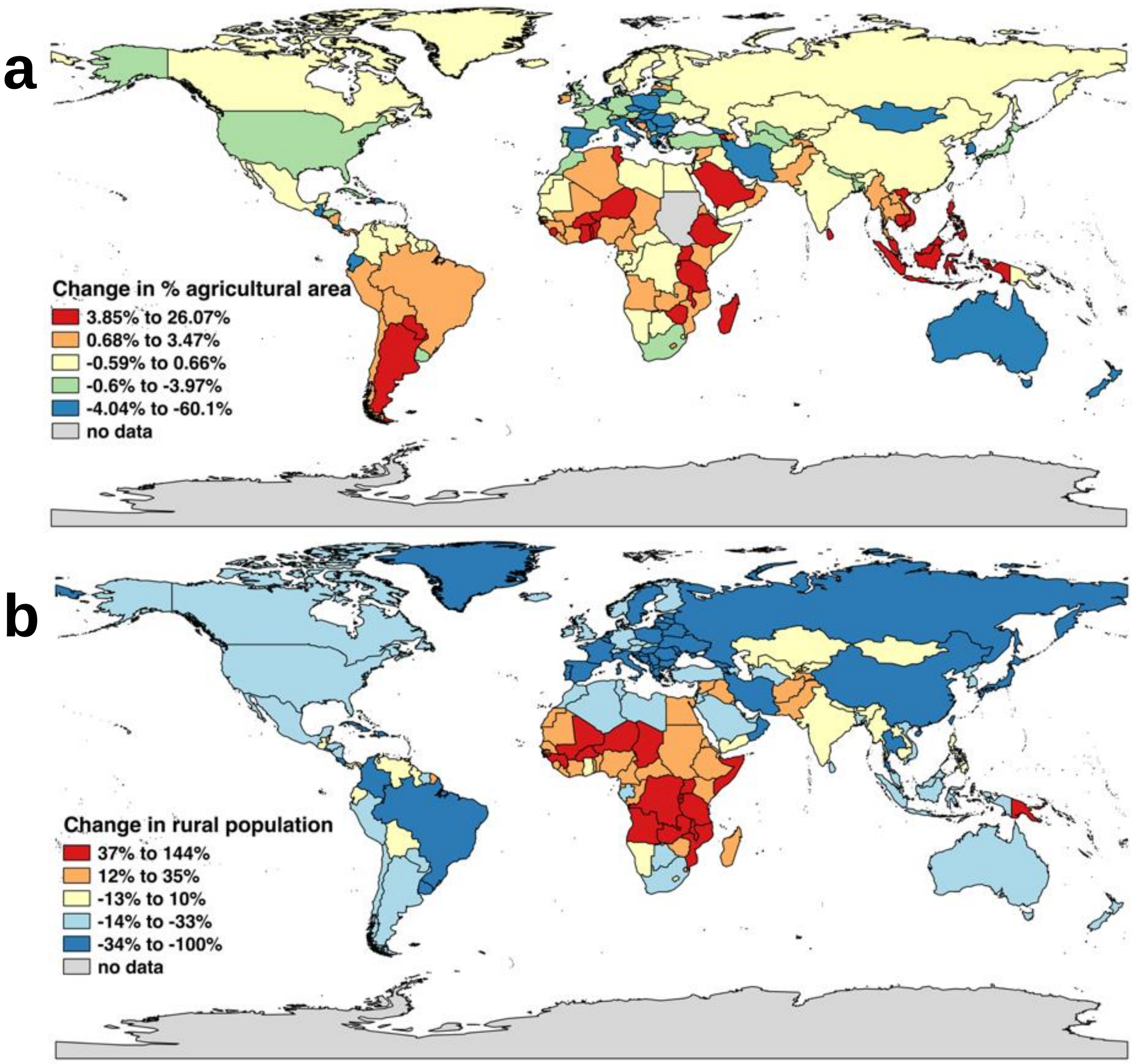

Figure S2.2 Maps of (**a**) change in share of agricultural land as a percentage of total land area between 1996 and 2016, and (**b**) projected change in rural population from 2020 to 2050. Data from UN-DESA 2018.

A2.6 History as cultural connections

Generating social-ecological memory will also benefit history as enriching cultural connections, which includes history as place (reinforcing sense of place), governor (exercising caution in interventions and limiting exuberant actions), and redress (reinstating disturbance regimes). Of these, the last may be the most well recognized as it relates to the reestablishment of historical cultural practices and associated disturbance regimes. In this and other aspects of history as enriching culture, LTSER will be particularly important as it emphasizes the integration of human dimensions into LTER by encouraging collaboration across multiple disciplines and knowledges (e.g. ‘scientific’ and ‘local’).

Unfortunately, history as enriching cultural connections has received little attention in restoration ecology thus far, but its prominence is likely to grow (Higgs et al. 2014). Another major gap is the diversity of LTER and LTSER sites, the majority of which are in the United States and Europe while very few are in developing nations (Singh et al. 2013).

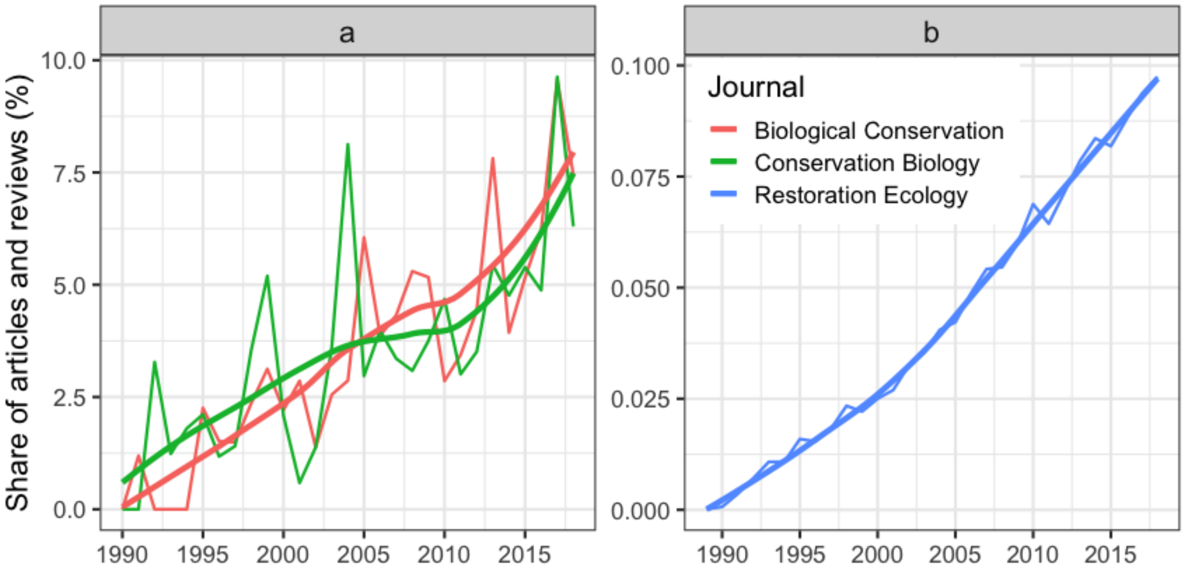

Figure S2.3 Increased interest in restoration. The share of articles and reviews in Biological Conservation, Conservation Biology (**a**) and Restoration Ecology (**b**) in Web of Science using both ‘restor*’ and ‘ecology*’ as search terms. Values are expressed as a percentage of total articles and reviews in each journal (**a**) or all journals (**b**). Trend lines show loess regressions.

A2.7 Looking ahead

To summarize, the importance of the various facets of historical knowledge to restoration implies that LTSER will be a significant asset for future restoration, complementing other long-term approaches (e.g. paleoecology). Large-scale, long-term studies are of particular importance (Fischer et al. 2010) – these are becoming more common in invasion ecology and community ecology and are sorely needed for restoration ecology to graduate from a site- and situation-specific discipline to a more globally applicable science (Montoya et al. 2012). Restoration commands a growing share of peer-reviewed publications and the proportion of articles and reviews concerning restoration within leading conservation journals is also rising (Figure S2.3). Restoration may yet come to dominate the field of conservation, as envisaged by Young (2000). Taking a long-term perspective, maintenance of diverse, productive, and functional ecosystems requires that restoration is integrated into SES management as a continuous process rather than as a means to an end (i.e. a self-sustaining system requiring little/no intervention). For example, employing restoration to mitigate climate change may mark the start of the routine use of restoration as a tool for geo-climatic engineering into the future. Similarly, implementing restoration in areas experiencing high human population densities today will equip us with the techniques required to incorporate restorative activities ubiquitously in the more intensely human-dominated landscapes of the future, counterbalancing inevitable extractive/destructive activities. Finally, we will benefit from incorporating restoration principles into all aspects of human activities including product design, industry, architecture, and urban planning.

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Appendix 3. Ethical Review Approval

The Secretariat
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Tel: 0113 343 4873
Email: ResearchEthics@leeds.ac.uk

UNIVERSITY OF LEEDS

Henry Wells
School of Earth and Environment
University of Leeds
Leeds, LS2 9JT

Social Sciences, Environment and LUBS (AREA) Faculty Research Ethics Committee
University of Leeds

22 March 2021

Dear Harry

Title of study:	**Identifying the benefits, limitations and tradeoffs (both socioeconomic and biophysical) associated with the application of a novel rangeland restoration technology: Insights from Laikipia, Kenya.**
Ethics reference:	**AREA 18-151**

I am pleased to inform you that the above research application has been reviewed by the Social Sciences, Environment and LUBS (AREA) Faculty Research Ethics Committee and I can confirm a favourable ethical opinion as of the date of this letter. The following documentation was considered:

Document	Version	Date
AREA 18-151 New_ethical_review_form_HW_2019 (2).doc	2	10/05/2019
AREA 18-151 Fieldwork_Assessment_Form_HighRisk_HW_25Jan19.docx	1	10/05/2019
AREA 18-151 DataManagPlan_2019_HW.docx	1	09/05/2019
AREA 18-151 Semi Structured Interview for Mobile Boma Local Knowledge Study.docx	1	09/05/2019
AREA 18-151 Verbal_Informed_Consent_Protocol_HW_2019.docx	1	09/05/2019

Committee members made the following comments about your application:

- Well informed application with the ethical issues clearly addressed.

Please notify the committee if you intend to make any amendments to the information in your ethics application as submitted at date of this approval as all changes must receive ethical approval prior to implementation. The amendment form is available at http://ris.leeds.ac.uk/EthicsAmendment.

Please note: You are expected to keep a record of all your approved documentation and other documents relating to the study, including any risk assessments. This should be kept in your study file, which should be readily available for audit purposes. You will be given a two week notice period if your project is to be audited. There is a checklist listing examples of documents to be kept which is available at http://ris.leeds.ac.uk/EthicsAudits.

We welcome feedback on your experience of the ethical review process and suggestions for improvement. Please email any comments to ResearchEthics@leeds.ac.uk.

Yours sincerely

Jennifer Blaikie
Senior Research Ethics Administrator, the Secretariat
On behalf of Dr Kahryn Hughes, Chair, AREA Faculty Research Ethics Committee

CC: Student’s supervisor(s)

Appendix 4. Verbal informed consent protocol

Verbal Informed Consent Protocol

Title: Combining local and scientific knowledges to map the costs, benefits and fairness of rangeland rehabilitation through *Opuntia stricta* removal and improve restoration planning.

Invitation paragraph: 'You are being invited to take part in a research project. Before you decide to participate, it is important that you understand the purpose of the research and what it will involve. Please listen carefully to the following information. Feel free to discuss it with others if you wish and ask me any questions if anything is unclear or you would like more information. Take your time to decide whether or not you would like to take part.'

Purpose of project: 'The purpose of this project is to compile perspectives of Makurian group ranch community members on the costs, benefits and fairness of rangeland rehabilitation through *Opuntia stricta* clearing and opinions on where future restoration work should take place. The information gathered will be combined with predictive maps of *Opuntia stricta* density to improve planning and outcomes of future *Opuntia stricta* management work.'

Why have I been chosen?: 'You have been chosen as you have knowledge relating to rangeland rehabilitation through *Opuntia stricta* clearing, including the costs, benefits and fairness with which the restoration work was conducted.'

Do I have to take part?: 'It is up to you to decide whether or not to take part in this project. You may withdraw at any time without giving reason, until the analysis stage when all data are anonymised.'

What do I have to do?: 'This University of Leeds PhD project runs from October 2018 till September 2021 and you will be involved on one occasion, for the duration of this interview (less than 1 hour). I will ask you about rangeland rehabilitation through *Opuntia stricta* clearing and you are free to discuss any aspect of this topic in depth.'

What are the possible disadvantages and risks of taking part?: 'There are no risks or disadvantages to taking part in this interview.'

What are the possible benefits of taking part?: 'Although there are no immediate benefits of taking part, the results of the research will be shared with you and all participants at the end of the project. You will therefore have access to the perspectives and experiences of other participants.'

What will happen to the results of this project?: 'Information that you provide will be anonymised (so that it is not traceable to you) before being shared with other participants and others wishing to use the information (e.g. other researchers or land managers).'

What type of information will be sought from me and why is the collection of this information relevant for achieving the research project's objectives?: 'Perspectives from Makurian community members on costs, benefits and fairness of restoration activities will be collected. This information will contribute to achieving the project's objectives by guiding future restoration work.'

Who is organising/funding the research?: 'This research is funded by the University of Leeds Doctoral Scholarship and the World Agroforestry Centre (ICRAF).'

Will I be recorded?: 'You will not be recorded.'

Contact for further information: Tel.: +254 202 120 0888; Email: eehw@leeds.ac.uk

Appendix 5. Supporting information for Chapter 2: Supporting data

A5.1 Supplementary tables

Table S5.1 Statistical results for responses of habitat use to treatments [*habitat use ~ M*C + W*C + (1|Block)*] and diversity to vegetation [*diversity ~ grass height + (1|Block)*; *diversity ~* Acacia drepanolobium *density + (1|Block)*] for smaller mammals when carnivores (servals and jackals) are excluded; $p < 0.05$ are in bold; Mega = wild megaherbivores, Meso = wild mesoherbivores; $n = 27$.

	Standardised habitat use		**Effective number of species**	
Fixed effects	***Z***	***p***	***Z***	***p***
Cattle(moderate)	1.51	0.132	1.67	0.096
Cattle(high)	-0.41	0.682	4.42	**<0.001**
Mega	-1.77	0.078	1.56	0.119
Meso	0.41	0.682	1.96	0.050
Mega*Cattle(moderate)	0.36	0.720	-1.39	0.165
Mega*Cattle(high)	-0.52	0.601	-1.15	0.250
Meso*Cattle(moderate)	-0.36	0.721	0.38	0.701
Meso*Cattle(high)	2.59	**0.010**	-0.94	0.346
Grass height	-1.66	0.098	-3.12	**0.002**
A. drepanolobium density	3.57	**<0.001**	3.57	**<0.001**

Table S5.2 Statistical results for responses of habitat use to treatments [*habitat use ~ M*C + W*C + (1|Block)*] for smaller mammals and birds and responses of smaller wildlife diversity to treatments [*diversity ~ M*C + W*C + (1|Block)*] during December 2019 and January 2020, when grass height did not significantly differ between treatments; *p* < 0.05 are in bold; Mega = wild megaherbivores, Meso = wild mesoherbivores; models were fitted separately for each species group.

		Standardised habitat use		**Effective number of species**	
Group	**Fixed effects**	***Z***	***p***	***Z***	***p***
Smaller mammals	Cattle(moderate)	1.01	0.615	NA	NA
	Cattle(high)	-3.66	**<0.001**	NA	NA
	Mega	-4.34	**<0.001**	NA	NA
	Meso	0.64	0.524	NA	NA
	Mega*Cattle(moderate)	1.68	0.092	NA	NA
	Mega*Cattle(high)	1.17	0.242	NA	NA
	Meso*Cattle(moderate)	-0.56	0.578	NA	NA
	Meso*Cattle(high)	3.35	**0.001**	NA	NA
Birds	Cattle(moderate)	0.52	0.601	NA	NA
	Cattle(high)	0.67	0.505	NA	NA
	Mega	0.50	0.620	NA	NA
	Meso	0.29	0.773	NA	NA
	Mega*Cattle(moderate)	0.60	0.550	NA	NA
	Mega*Cattle(high)	-0.94	0.357	NA	NA
	Meso*Cattle(moderate)	-0.35	0.724	NA	NA
	Meso*Cattle(high)	0.70	0.484	NA	NA
Smaller wildlife	Cattle(moderate)	0.59	0.557	0.06	0.951
	Cattle(high)	-0.29	0.773	2.26	**0.009**
	Mega	-0.32	0.751	1.60	0.110
	Meso	0.21	0.836	0.26	0.794
	Mega*Cattle(moderate)	0.02	0.981	-1.62	0.104
	Mega*Cattle(high)	-0.35	0.325	-2.51	**0.012**
	Meso*Cattle(moderate)	0.58	0.566	0.65	0.513
	Meso*Cattle(high)	1.42	0.155	-0.97	0.335

Smaller mammals = mammal species 10–70 cm shoulder height

Birds = bird species < 50 kg living/foraging primarily on the ground

Smaller wildlife = combined mammal and bird species 10–70 cm shoulder height able to access all plots unimpeded

Table S5.3 Statistical results for species-level habitat use responses to treatments [$\textit{habitat use} \sim M*C + W*C + (1|Block)$]; $p < 0.05$ are in bold; Mega = wild megaherbivores, Meso = wild mesoherbivores; $n = 27$; species modelled separately.

	Cattle(mod)		**Cattle(high)**		**Mega(yes)**		**Meso(yes)**		**Mega(yes) × Cattle(mod)**		**Mega(yes) × Cattle(high)**		**Meso(yes) × Cattle(mod)**		**Meso(yes) × Cattle(high)**	
Variable	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***
duiker	1.87	0.061	-0.59	0.554	-0.94	0.347	-1.24	0.216	-0.68	0.499	-0.24	0.810	-0.58	0.566	1.36	0.172
steenbok	-0.02	0.988	-0.02	0.988	0.74	0.461	0.76	0.445	-0.10	0.924	-0.95	0.340	1.65	0.098	2.02	**0.044**
warthog	0.50	0.615	0.20	0.838	0.19	0.847	1.33	0.184	-2.12	**0.034**	-0.78	0.437	1.48	0.138	1.07	0.284
hare	0.00	1.000	0.24	0.814	0.00	1.000	0.00	1.000	0.11	0.912	0.58	0.563	0.00	1.000	0.23	0.821
baboon	0.44	0.659	1.12	0.264	0.44	0.659	0.39	0.700	0.12	0.902	-0.80	0.423	0.01	0.989	0.05	0.960
bushbaby	0.65	0.517	-0.68	0.500	-3.15	**0.002**	2.86	**0.004**	1.46	0.143	1.31	0.191	-2.02	**0.045**	-0.71	0.481
serval	1.15	0.252	0.17	0.866	-0.36	0.717	0.52	0.602	-0.79	0.431	0.27	0.789	0.79	0.431	0.65	0.561
jackal	0.26	0.769	-0.01	0.994	-0.77	0.439	0.75	0.451	0.62	0.536	-0.49	0.621	-0.13	0.896	-1.51	0.131
striped hyaena	-0.07	0.944	-0.51	0.612	-2.71	**0.007**	2.56	**0.011**	1.26	0.228	2.37	**0.018**	-0.66	0.508	-0.72	0.470
spotted hyaena	-0.43	0.669	0.16	0.876	0.64	0.524	0.99	0.323	0.13	0.899	1.06	0.289	0.83	0.405	0.02	0.981
ostrich	0.00	1.000	0.00	1.000	3.06	**0.002**	1.21	0.227	2.22	**0.026**	0.23	0.820	-0.53	0.596	-0.54	0.592
helmeted guineafowl	1.29	0.199	2.12	**0.034**	-0.05	0.959	0.57	0.572	0.23	0.820	-0.17	0.864	-0.06	0.953	1.00	0.315
crested francolin	0.44	0.658	1.02	0.308	0.12	0.905	-0.09	0.932	-1.04	0.299	-0.67	0.502	1.05	0.293	1.30	0.193

yellow-necked francolin	0.32	0.748	1.08	0.280	0.02	0.986	0.12	0.908	0.57	0.570	1.45	0.147	0.59	0.558	0.63	0.529
cattle egret	2.09	**0.037**	2.53	**0.011**	-0.13	0.899	-1.07	0.285	-0.84	0.399	1.20	0.232	-1.51	0.132	-1.24	0.215
black-bellied bustard	0.97	0.331	0.39	0.695	0.44	0.659	1.05	0.296	1.64	0.101	-0.53	0.599	-1.87	0.062	-0.17	0.867
buff-crested bustard	0.37	0.709	0.51	0.611	0.00	1.000	0.00	1.000	-0.40	0.690	-1.87	0.062	0.31	0.760	2.13	**0.033**
starling	0.14	0.893	0.13	0.896	0.00	0.997	0.11	0.911	-0.43	0.666	-1.22	0.224	0.67	0.500	2.40	**0.016**
shrike	0.31	0.753	1.20	0. 230	0.00	1.000	0.00	1.000	-0.71	0.475	1.97	**0.049**	0.49	0.624	-0.07	0.946

Table S5.4 Statistical results for species-level responses to vegetation [*habitat use* ~ *grass height* + *(1|Block); diversity* ~ Acacia drepanolobium *density* + *(1|Block)*]; $p < 0.05$ are in bold; models were fitted separately for each species.

	Grass height			***A. drepanolobium* density**		
Species	***F***	***n***	***p***	***F***	***n***	***p***
duiker	0.28	27	0.781	3.95	27	**<0.001**
steenbok	-2.11	27	**0.035**	-0.09	27	0.930
warthog	-1.64	27	0.101	-0.57	27	0.568
hare	-1.05	27	0.292	-0.44	27	0.659
baboon	-1.14	27	0.254	-0.27	27	0.787
bushbaby	0.88	27	0.381	2.14	27	**0.033**
serval	-1.53	27	0.127	2.88	27	**0.004**
jackal	-1.81	27	0.071	1.75	27	0.080
striped hyaena	-0.84	27	0.402	1.21	27	0.226
spotted hyaena	-1.44	27	0.150	-1.65	27	0.098
ostrich	-1.87	27	0.061	-1.76	27	0.079
helmeted guineafowl	-6.33	27	**<0.001**	0.16	27	0.874
crested francolin	-2.50	27	**0.012**	1.00	27	0.317
yellow-necked francolin	-3.74	27	**<0.001**	0.30	27	0.761
cattle egret	-2.37	27	**0.018**	-1.65	27	0.099
black-bellied bustard	-1.58	27	0.115	0.14	27	0.888
buff-crested bustard	-1.21	27	0.227	1.74	27	0.083
starling	-2.37	27	**0.018**	0.35	27	0.726
shrike	-2.03	27	**0.042**	0.52	27	0.603

A5.2 Supplementary figures

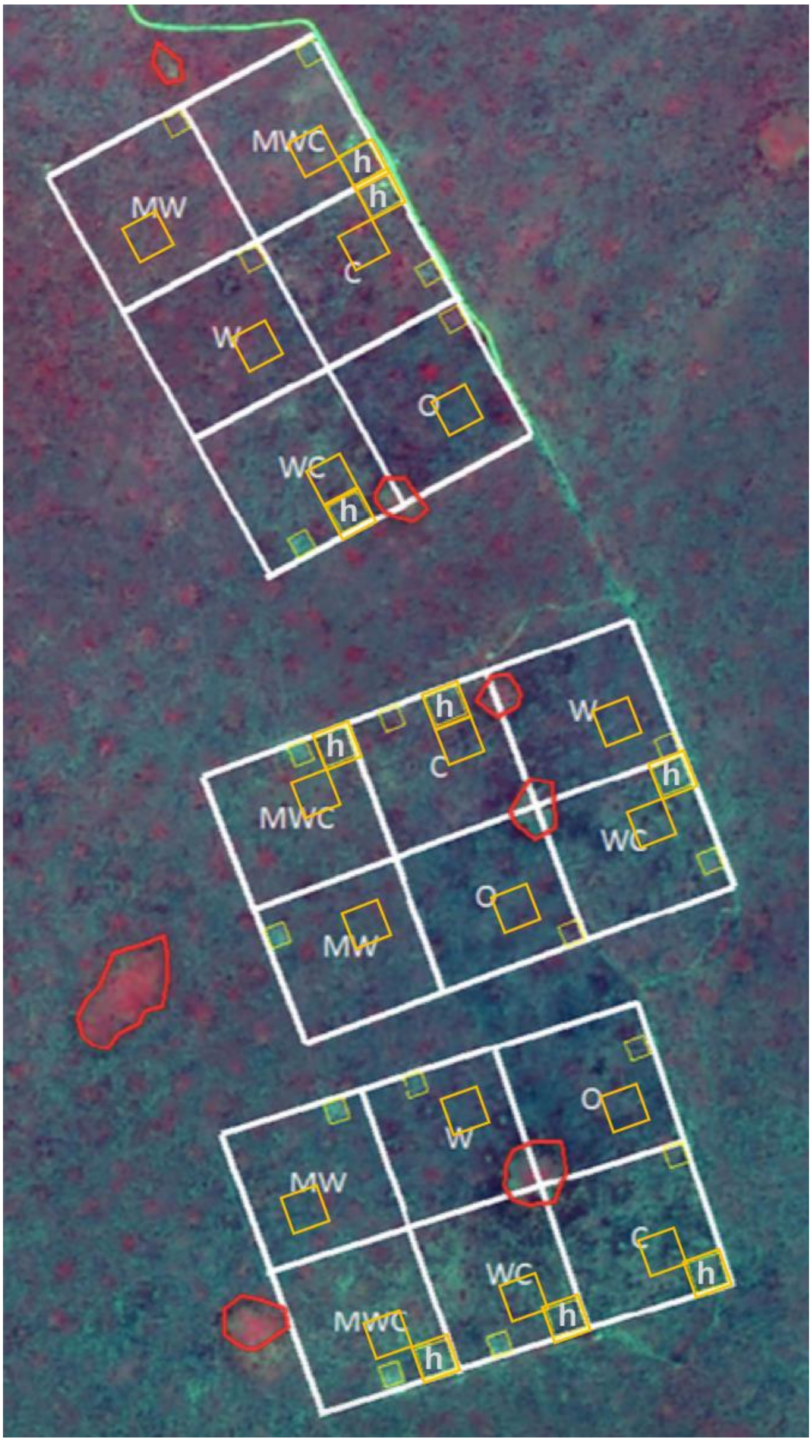


Figure S5.1 Kenya Long-term Exclosure Experiment layout showing the 27 50 × 50 m subplots (large orange squares; the letter ‘h’ identifies high cattle stocking rate treatments) within 4-Ha treatment plots (white squares). ‘C’ = only cattle allowed (moderate); ‘W’ = wild mesoherbivores allowed; ‘M’ = megaherbivores (elephant, giraffe) allowed; ‘O’ = meso- and mega-herbivores excluded. Anthropogenic glades (red polygons) and 30 × 30 m burn treatments (small yellow squares) are also shown. Underlying satellite image (23 May 2013) is in false colour.

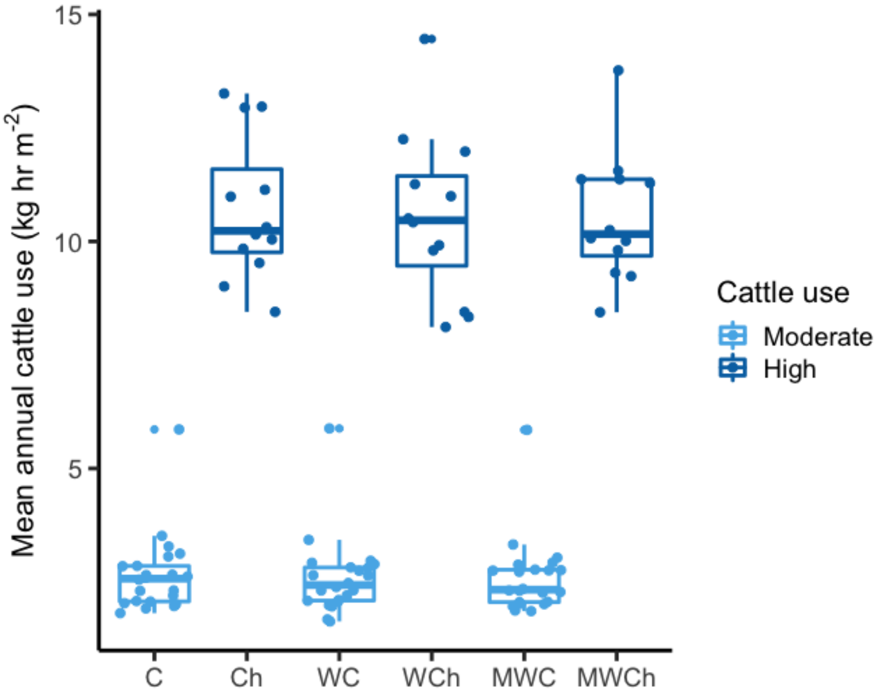


Figure S5.2 Annual cattle habitat use intensity by treatment (1998–2020). Cattle use is calculated by summing the product of the number of cows, calves and bulls multiplied by their respective average body mass, multiplied by the number of hours spent in each plot per year, divided by the plot size. ‘C’ = cattle allowed (moderate); ‘Ch’ = cattle allowed (high); ‘W’ = wild mesoherbivores allowed; ‘M’ = megaherbivores (elephant, giraffe) allowed; ‘O’ = meso- and mega-herbivores excluded.

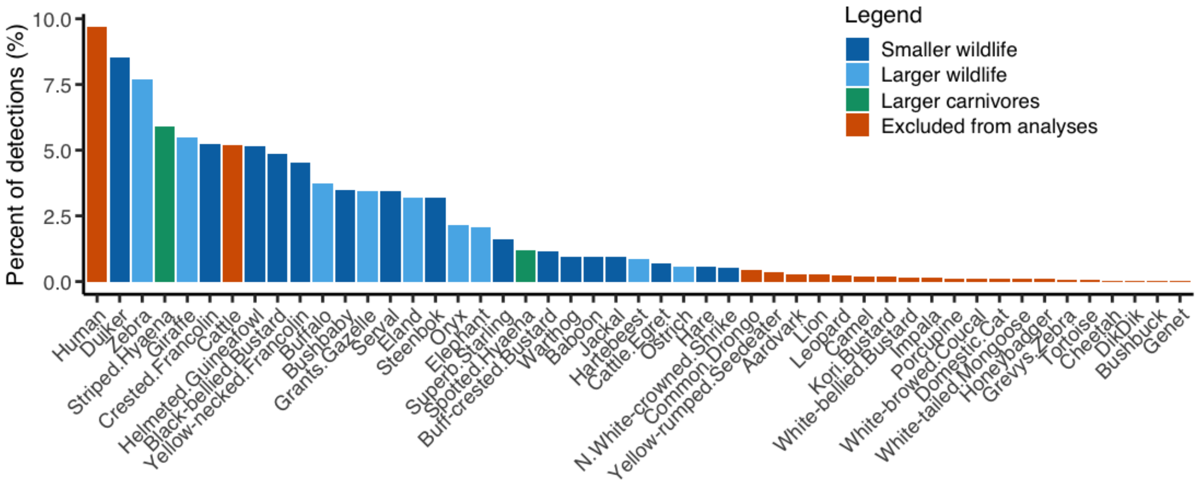


Figure S5.3 Species-level independent camera trap detections (images taken 1 hr apart) as a percentage of total independent detections (*n* = 6672) for all 49 species. Smaller wildlife = mammal and bird species 10–70 cm shoulder height (s.h.), (*n* = 16); Larger wildlife = herbivores > 50 kg (*n* = 9); Larger carnivores (spotted and striped hyaenas, *n* = 2). Wild species accounting for < 5 independent detections per 100 trap nights and humans and other domesticated species were excluded from analyses (*n* = 22). Density estimates of the larger herbivores are given in Veblen et al. (2016).

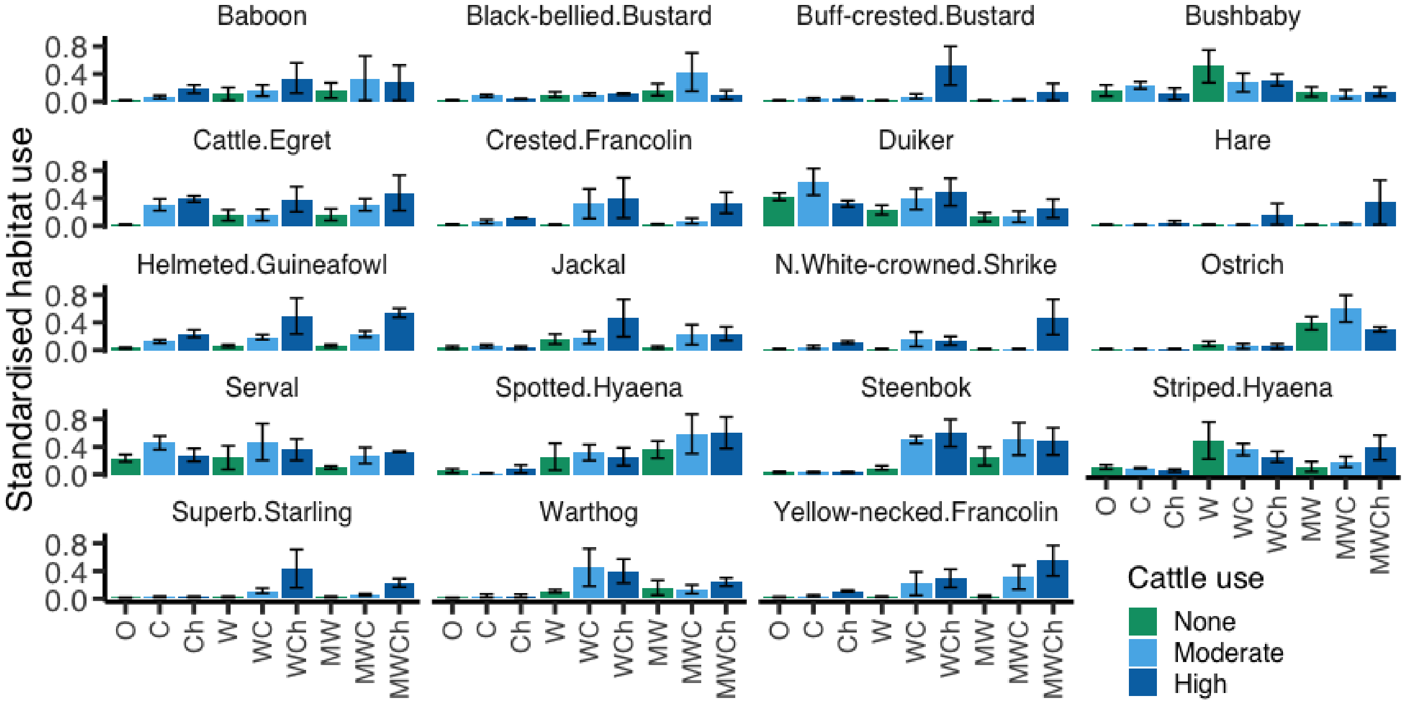


Figure S5.4 Treatment effects on species' habitat use (means ± 1 SE). Habitat use is standardised and rescaled by converting images per trap nights to an open unit interval (0,1) then compressing to remove 0s and 1s. 'C' = cattle allowed (moderate); 'Ch' = cattle allowed (high); 'W' = wild mesoherbivores allowed; 'M' = megaherbivores (elephant, giraffe) allowed; 'O' = meso- and mega-herbivores excluded.

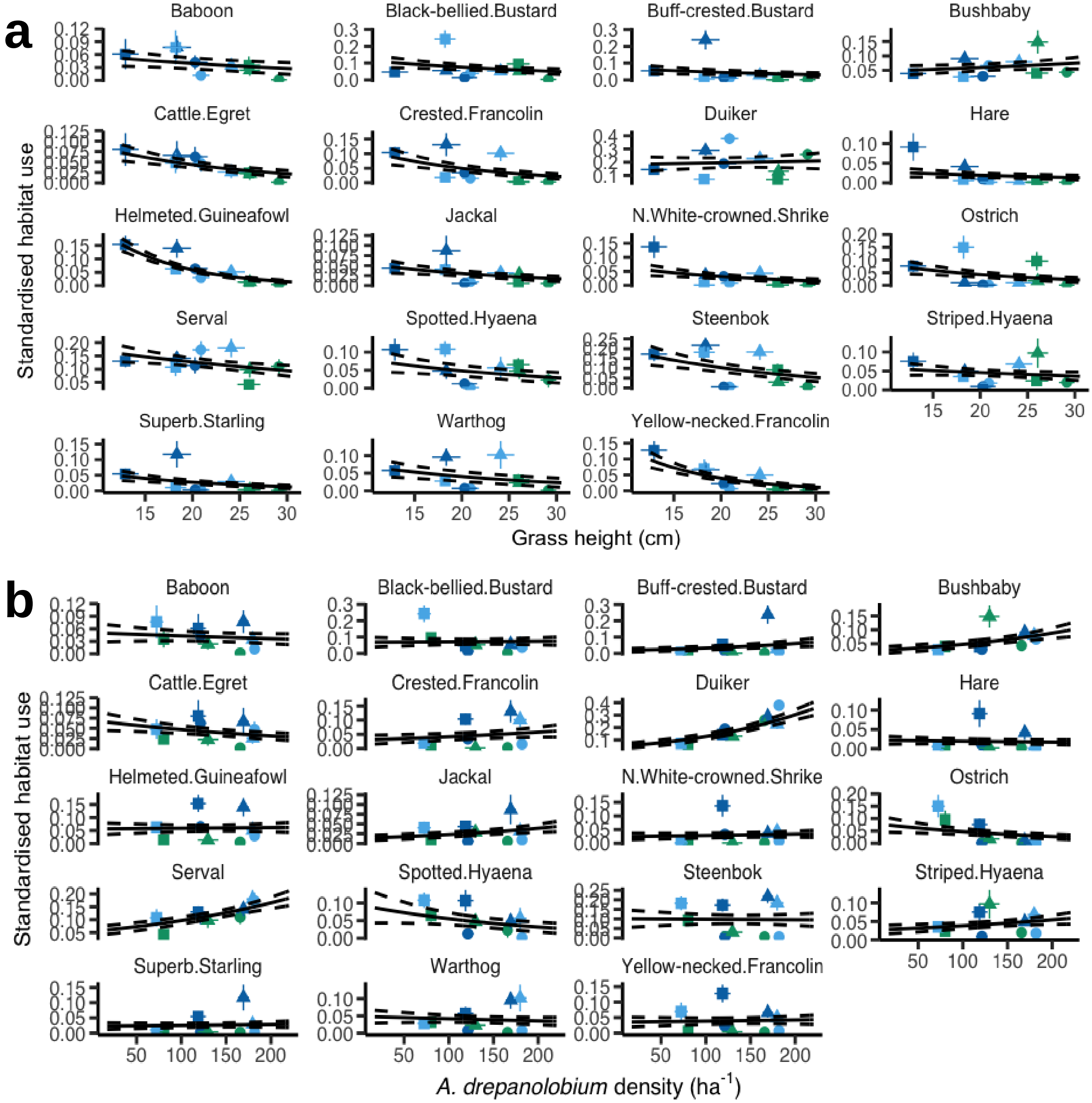


Figure S5.5 Species level responses to grass height (**a**) and *Acacia drepanolobium* density (**b**) (means ± 1 SE). Habitat use is standardised and rescaled by converting images per trap night to an open unit interval (0,1) then compressing to remove 0s and 1s. Fitted means (solid lines) and standard errors (dashed lines) of beta-distributed linear mixed models (species modelled separately): *habitat use ~ grass height + (1|Block)*. Scales differ between species. Larger wildlife presence indicated by filled circles (none), triangles (wild mesoherbivores), and squares (wild megaherbivores). Cattle use indicated by green (none), light-blue (moderate), and dark-blue (high).

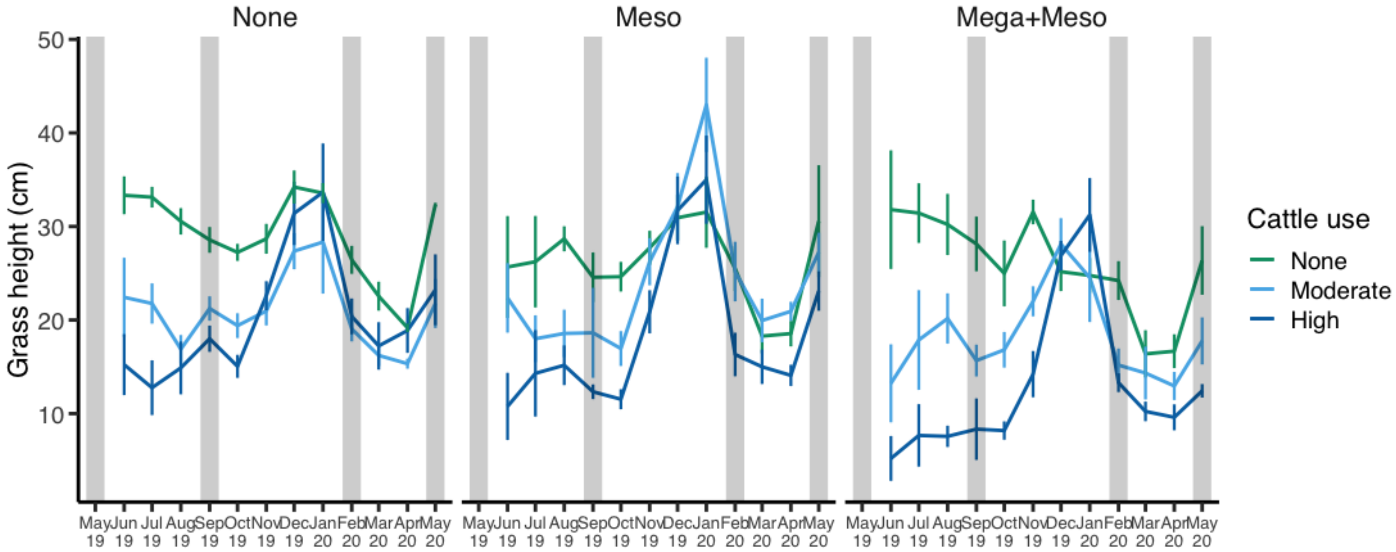


Figure S5.6 Monthly grass height by treatment (means ± 1 SE). Plots are faceted by large wildlife accessibility: ‘Meso’ = accessible to wild mesoherbivores (50-1000 kg), ‘Meso+Mega’ = accessible to both wild mesoherbivores and megaherbivores (elephant and giraffe), ‘None’ = no wild mesoherbivores or megaherbivores. Grey bars indicate cattle grazing events.

A5.3 Supplementary references

Veblen KE, Porensky LM, Riginos C, Young TP (2016) Are cattle surrogate wildlife? Savanna plant community composition explained by total herbivory more than herbivore type. Ecological Applications 26(6):1610–1623 https://doi.org/10.1890/15-1367.1

Appendix 6. Supporting information for Chapter 3: Supporting data

A6.1 Supplementary tables

Table S6.1 Statistical results for herbivore treatment effects for community ordination axes (latent variables 1 and 2), diversity metrics (effective number of species, evenness, and dominance), total herbaceous cover, bare ground, absolute covers of annual/perennial forbs/grasses, and understory ‘leafiness’ (leaf:stem), and the eight species each comprising > 1% of total cover ($p < 0.05$ are in bold; $n = 81$).

	Cattle(mod)		**Cattle(high)**		**Mega(yes)**		**Meso(yes)**		**Mega(yes) × Cattle(mod)**		**Mega(yes) × Cattle(high)**		**Meso(yes) × Cattle(mod)**		**Meso(yes) × Cattle(high)**	
Variable	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***
Latent variable 1 (primary ordination axis)	6.9	**<0.001**	6.1	**<0.001**	3.9	**<0.001**	5.1	**<0.001**	-2.7	**0.02**	-3.3	**<0.001**	-1.0	0.32	-0.0	0.84
Latent variable 2 (secondary ordination axis)	-0.8	0.45	-8.7	**<0.001**	-1.3	0.18	-0.7	0.49	-0.4	0.72	-3.9	**<0.001**	-1.0	0.30	4.3	**<0.001**
Effective number of species	0.5	0.62	-2.1	**0.03**	-0.4	0.69	0.9	0.38	1.3	0.18	1.8	0.07	0.0	0.99	3.2	**0.002**
Evenness	-0.9	0.37	2.1	**0.04**	-0.4	0.72	-0.4	0.67	0.7	0.50	1.9	0.06	1.1	0.28	4.3	**<0.001**
Dominance	1.0	0.33	0.9	0.39	0.0	0.99	1.4	0.18	-1.2	0.24	-1.2	0.25	-2.4	**0.02**	-4.5	**<0.001**
Total cover	-3.5	**0.001**	-5.0	**<0.001**	-0.9	0.38	-1.8	0.07	1.6	0.11	0.8	0.43	0.2	0.83	0.5	0.61
Bare ground	1.8	0.07	3.8	**<0.001**	-0.1	0.93	0.3	0.77	0.0	1.00	0.8	0.44	0.9	0.34	2.8	**0.004**
Annual forbs absolute cover	0.5	0.60	-1.7	0.09	-0.3	0.75	0.0	1.00	0.9	0.35	0.5	0.60	-0.2	0.86	-0.2	0.86
Annual grasses absolute cover	2.3	**0.02**	2.9	**0.004**	1.1	0.28	2.4	**0.02**	0.9	0.36	0.3	0.75	-1.4	0.16	-0.2	0.83

Perennial forbs absolute cover	-6.4	<**0.001**	-13.9	<**0.001**	-3.9	<**0.001**	-4.8	<**0.001**	2.0	**0.05**	0.4	0.72	1.1	0.27	6.3	<**0.001**
Perennial grasses absolute cover	-0.3	0.77	-0.6	0.56	0.5	0.64	-0.7	0.49	0.4	0.66	-0.1	0.93	-0.8	0.44	-3.0	**0.003**
Leafiness (leaf:stem)	3.3	**0.001**	2.8	**0.006**	1.1	0.29	3.2	**0.001**	-0.1	0.89	-1.7	0.09	-2.0	**0.04**	-3.3	<**0.001**
Brachiaria lachnantha relative cover	0.8	0.45	-0.4	0.68	0.0	0.99	1.1	0.27	-1.3	0.20	-3.1	**0.002**	-1.9	0.05	-3.6	<**0.001**
Themeda triandra relative cover	5.9	<**0.001**	10.4	<**0.001**	2.2	**0.03**	3.8	<**0.001**	0.1	0.90	0.4	0.69	-1.1	0.26	-4.6	<**0.001**
Pennisetum straminium relative cover	-0.8	0.45	-1.2	0.22	-1.1	0.27	-1.0	0.30	-0.3	0.77	-1.5	0.14	0.6	0.55	2.2	**0.03**
Pennisetum mezianum relative cover	-0.4	0.70	2.4	**0.02**	-0.2	0.85	1.7	0.08	1.5	0.13	4.1	<**0.001**	-0.4	0.73	-1.6	0.11
Bothriochloa insculpta relative cover	3.9	<**0.001**	0.7	0.50	1.8	0.08	2.3	**0.02**	-2.0	**0.04**	-3.8	<**0.001**	-0.5	0.63	1.9	0.05
Lintonia nutans relative cover	-1.6	0.12	-1.2	0.22	1.0	0.34	-0.9	0.39	0.1	0.93	1.5	0.12	2.0	**0.04**	2.9	**0.004**
Helichrysum glumaceum relative cover	-4.9	<**0.001**	-13.6	<**0.001**	-3.1	**0.002**	-4.8	<**0.001**	0.7	0.48	-0.3	0.80	0.0	1.00	5.7	<**0.001**
Brachiaria eruciformis relative cover	1.8	0.07	2.4	**0.02**	0.9	0.36	2.1	**0.04**	0.5	0.62	-1.1	0.26	-0.4	0.71	-0.1	0.89

Table S6.2 Regressions against total herbivory for community ordination axes (latent variables 1 and 2), diversity metrics (effective number of species, evenness, and dominance), total herbaceous cover, bare ground, absolute covers of annual/perennial forbs/grasses, and understory ‘leafiness’ (leaf:stem), and relative covers of the eight species each comprising > 1% of total cover (*p* < 0.05 are in bold; *n* = 81).

		Linear		**Second order polynomial**		
Variable	**Function**	***Z***	***p***	***Z***	***p***	**R^2_{marg}**
Latent variable 1 (primary ordination axis)	~ *poly(total herbivory, 2) + (1|year/block)*	-5.3	**<0.001**	2.7	**0.006**	0.15
Latent variable 2 (secondary ordination axis)	~ *total herbivory + (1|year/block)*	9.6	**<0.001**	NA	NA	0.42
Effective number of species	~ *poly(total herbivory, 2) + (1|year/block)*	3.9	**<0.001**	2.7	**0.008**	0.16
Evenness	~ *poly(total herbivory, 2) + (1|year/block)*	10.2	**<0.001**	2.3	**0.02**	0.57
Dominance	~ *total herbivory + (1|year/block)*	-6.3	**<0.001**	NA	NA	0.28
Total cover	~ *poly(total herbivory, 2) + (1|year/block)*	-5.3	**<0.001**	2.7	**0.006**	0.15
Bare ground	~ *total herbivory + (1|year/block)*	9.6	**<0.001**	NA	NA	0.42
Annual forbs absolute cover	~ *total herbivory + (1|year/block)*	-2.6	**0.01**	NA	NA	0.05
Annual grasses absolute cover	~ *total herbivory + (1|year/block)*	5.6	**<0.001**	NA	NA	0.14
Perennial forbs absolute cover	~ *poly(total herbivory, 2) + (1|year/block)*	-10.4	**<0.001**	6.4	**<0.001**	0.48
Perennial grasses absolute cover	~ *total herbivory + (1|year/block)*	-3.0	**0.003**	NA	NA	0.05
Leafiness (leaf:stem)	~ *poly(total herbivory, 2) + (1|year/block)*	-2.2	**0.03**	-3.8	**<0.001**	0.16
Brachiaria lachnantha relative cover	~ *poly(total herbivory, 2) + (1|year/block)*	-9.6	**<0.001**	-3.0	**0.002**	0.49
Themeda triandra relative cover	~ *poly(total herbivory, 2) + (1|year/block)*	9.5	**<0.001**	-0.5	**<0.001**	0.58
Pennisetum straminium relative cover	~ *total herbivory + (1|year/block)*	-1.1	0.26	NA	NA	0.02
Pennisetum mezianum relative cover	~ *poly(total herbivory, 2) + (1|year/block)*	7.0	**<0.001**	2.8	**0.005**	0.40
Bothriochloa insculpta relative cover	~ *total herbivory + (1|year/block)*	0.5	0.65	NA	NA	0.00

Lintonia nutans relative cover	*~ total herbivory + (1|year/block)*	4.3	**<0.001**	NA	NA	0.19
Helichrysum glumaceum relative cover	*~ poly(total herbivory, 2) + (1|year/block)*	-11.7	**<0.001**	6.5	**<0.001**	0.61
Brachiaria eruciformis relative cover	*~ total herbivory + (1|year/block)*	5.1	**<0.001**	NA	NA	0.24

Table S6.3 Statistical results for herbivore treatment effects on understory 'leafiness' (leaf:stem) for the five most common species; $p < 0.05$ are in bold; $n = 81$.

	Cattle(mod)		**Cattle(high)**		**Mega(yes)**		**Meso(yes)**		**Mega(yes) × Cattle(mod)**		**Mega(yes) × Cattle(high)**		**Meso(yes) × Cattle(mod)**		**Meso(yes) × Cattle(high)**	
Species	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***	***Z***	***p***
Brachiaria lachnantha	3.8	**<0.001**	1.9	0.05	1.1	0.28	3.4	**<0.001**	-1.3	0.19	-1.7	0.10	-0.7	0.51	-0.6	0.57
Themeda triandra	2.5	**0.01**	2.3	**0.02**	0.4	0.70	3.0	**0.002**	1.0	0.30	-0.9	0.39	-2.5	**0.01**	-2.9	**0.004**
Pennisetum straminium	-0.2	0.84	-1.3	0.18	2.0	**0.04**	-0.7	0.50	-1.5	0.14	-2.0	**0.05**	1.1	0.25	1.4	0.17
Pennisetum mezianum	-1.9	0.06	-2.0	**0.05**	-1.4	0.15	-1.0	0.32	1.2	0.22	1.1	0.28	1.5	0.13	1.2	0.22
Lintonia nutans	0.4	0.71	-1.0	0.30	-0.6	0.55	-0.4	0.70	0.7	0.50	0.7	0.51	-0.5	0.64	0.7	0.50

A6.2 Supplementary figures

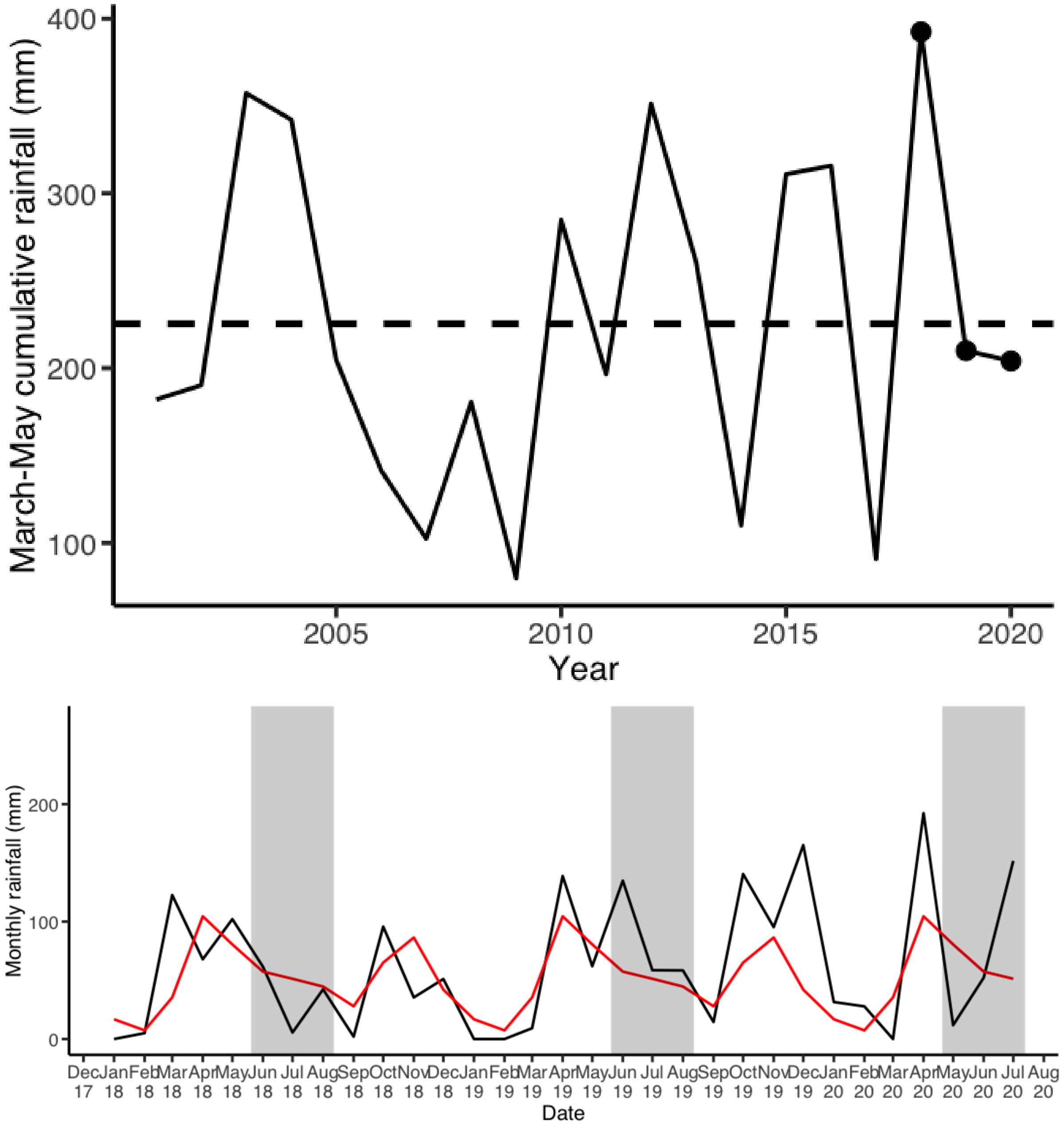


Figure S6.1 March–May ‘wet season’ rainfall for 2001–2020 (**a**) and monthly rainfall for 2018–2020 (**b**). All values are averaged across the three sampling blocks. Black points indicate years sampled in this study. Red line shows mean monthly rainfall for 2001–2020. Grey bars represent herbaceous vegetation sampling periods.

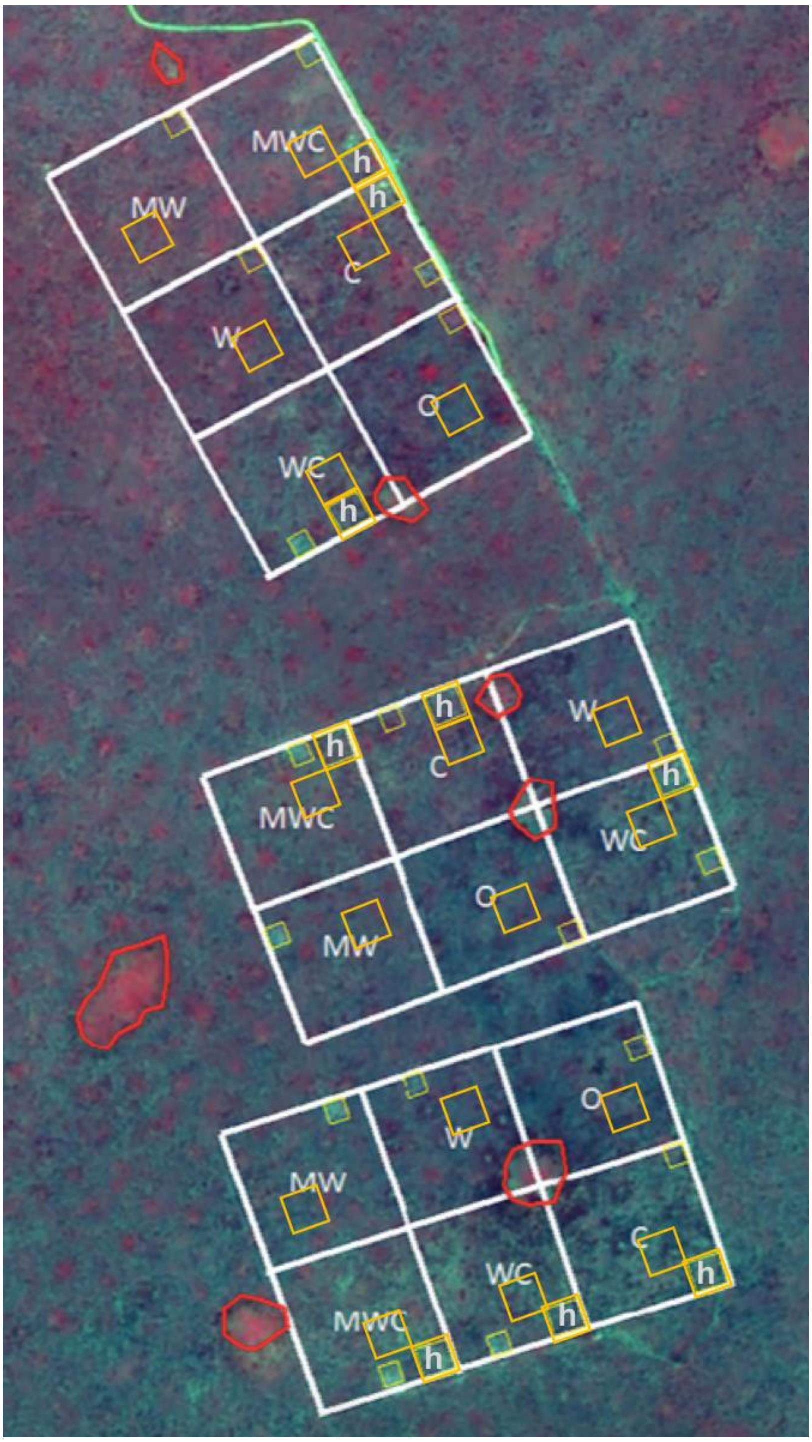


Figure S6.2 Kenya Long-term Exclosure Experiment layout showing the 27 50 × 50 m subplots (large orange squares; the letter ‘h’ identifies high cattle stocking rate treatments) within 4-ha treatment plots (white squares). ‘C’ = only cattle allowed (moderate); ‘W’ = wild mesoherbivores allowed; ‘M’ = megaherbivores (elephant, giraffe) allowed; ‘O’ = wild mesoherbivores and megaherbivores excluded. Anthropogenic glades (red polygons) and 30 × 30 m burn treatments (small yellow squares) are also shown. Underlying satellite image (23 May 2013) is in false colour.

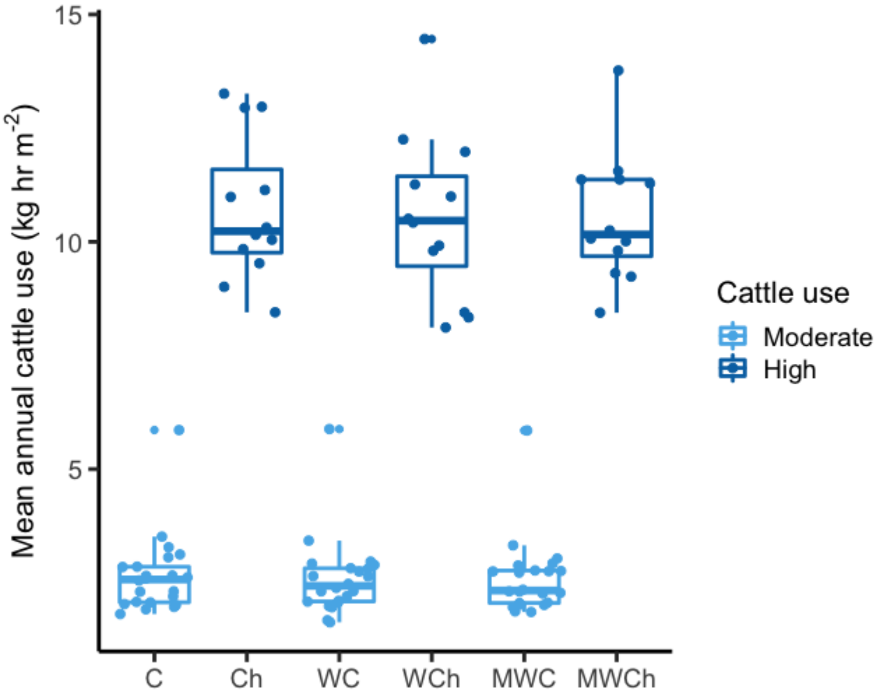


Figure S6.3 Annual cattle use intensity by treatment (1998–2020). Cattle use is calculated by summing the product of the number of cows, calves and bulls multiplied by their respective average body mass, multiplied by the number of hours spent in each plot per year, divided by the plot size.

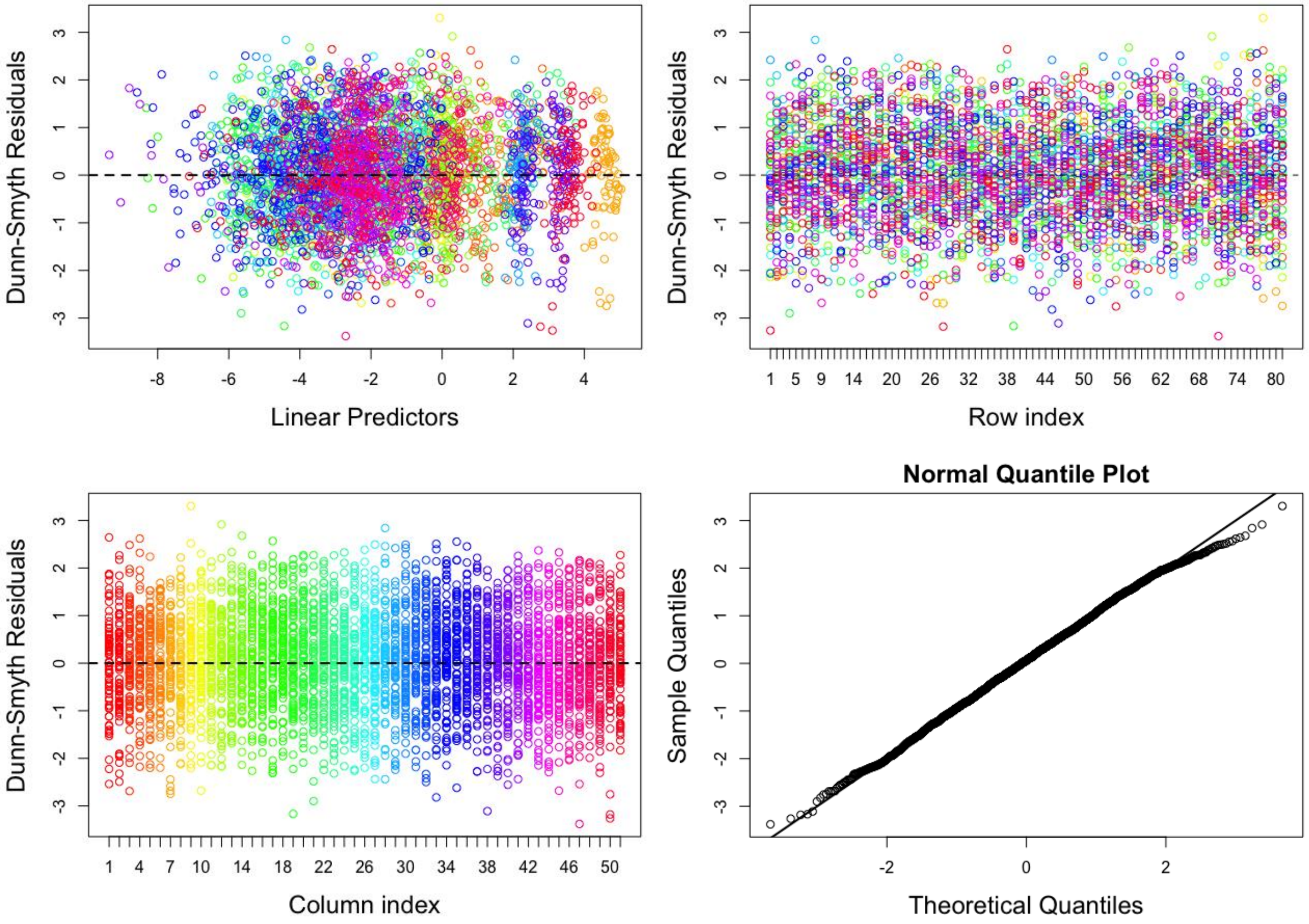


Figure S6.4 Plots for residual analysis. Row index = sites (*n* = 81). Column index = species (*n* = 51), each represented by a different colour.

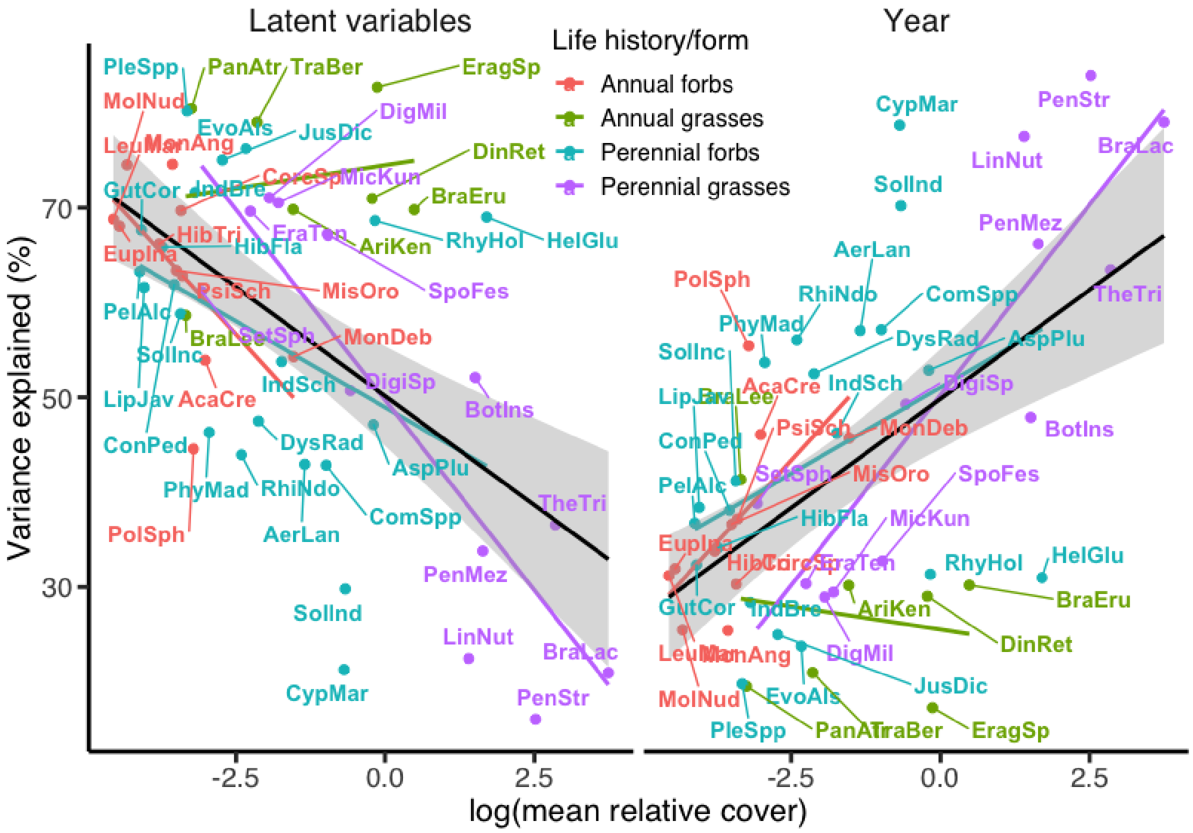


Figure S6.5 Variance partitioning shows that more of the variation in rarer species is explained by the ordination axes (latent variables 1 and 2) while inter-annual variation (random effect of year) explains more of the variation in more common species. Trend lines represent linear regressions coloured by life history and life form; the black line shows the overall trend with standard errors in grey. AcaCre = *Acalypha crenata*, AerLan = *Aerva lanata*, AriKen = *Aristida kenyensis*, AspPlu = *Aspilia pluriseta*, BotIns = *Bothriochloa insculpta*, BraEru = *Brachiaria eruciformis*, BraLac = *B. lachnantha*, BraLee = *B. leersioides*, ComSpp = *Commelina* spp., ConPed = *Conyza pedunculata*, CorcSp = *Corchorus* sp., CypMar = *Cyperus* & *Mariscus* spp., DigiSp = *Digitaria* sp., DigMil = *D. milanjiana*, DinRet = *Dinebra retroflexa*, DysRad = *Dyschoriste radicans*, EragSp = *Eragrostis* sp., EraTen = *E. tenuifolia*, EupIna = *Euphorbia inaequilatera*, EvoAls = *Evolvulus alsinoides*, GutCor = *Gutenbergia cordifolia*, HelGlu = *Helichrysum* (*Pseudognaphalium*) *glumaceum*, HibFla = *Hibiscus flavifolius*, HibTri = *H. trionum*, IndBre = *Indigofera brevicalyx*, IndSch = *I. schimperi*, JusDic = *Justicia diclipteroides*, LeuMar = *Leucas martinicensis*, LinNut = *Lintonia nutans*, LipJav = *Lippia javanica*, MicKun = *Microchloa kunthii*, MisOro = *Misopates orontium*, MolNud = *Mollugo nudicaulis*, MonAng = *Monsonia angustifolia*, MonDeb = *Monechma debile*, PanAtr = *Panicum atrosanguineum*, PelAlc = *Pelargonium alchemilloides*, PenMez = *Pennisetum mezianum*, PenStr = *P. stramineum*, PhyMad = *Phyllanthus maderaspatensis*, PleSpp = *Plectranthus* spp., PolSph = *Pollichia campestris*, PsiSch = *Psilotrichum schimperi*, RhiNdo = *Rhinacanthus ndorensis*, RhyHol = *Rhynchosia holstii*, SetSph =

Setaria sphacelata, SolInc = *Solanum incanum*, SolInd = *S. indicum*, SpoFes = *Sporobolus festivus*, TheTri = *Themeda triandra*, TraBer = *Tragus bertonianus*.

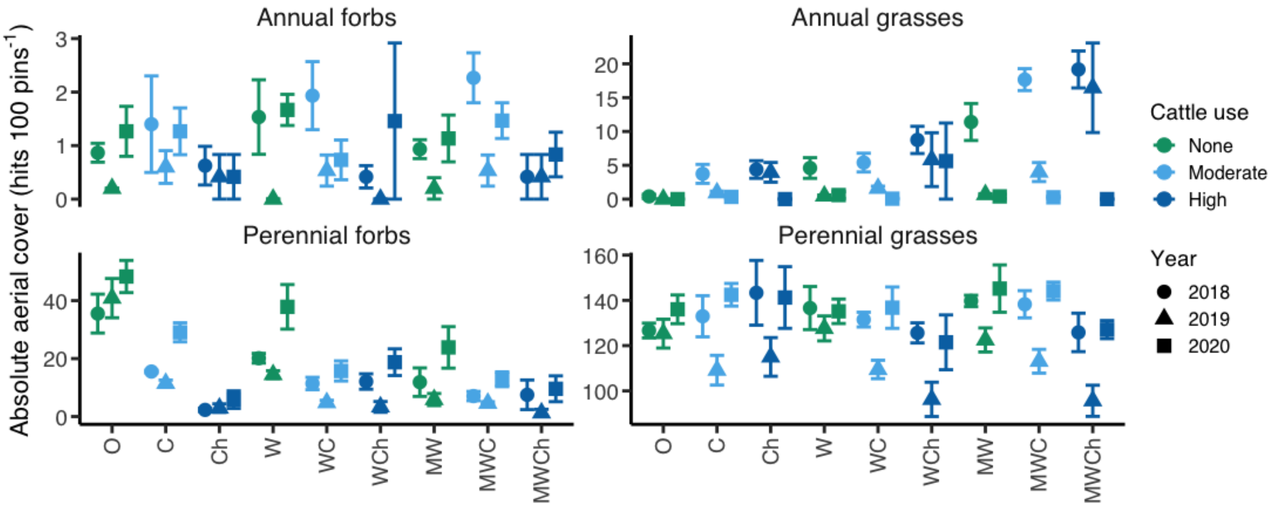


Figure S6.6 Annual treatment effects of absolute aerial cover by life history and life form. ‘C’ = cattle allowed (moderate intensity); ‘Ch’ = high cattle stocking rates; ‘W’ = wild mesoherbivores allowed; ‘M’ = megaherbivores (elephant, giraffe) allowed; ‘O’ = cattle mesoherbivores and megaherbivores excluded.

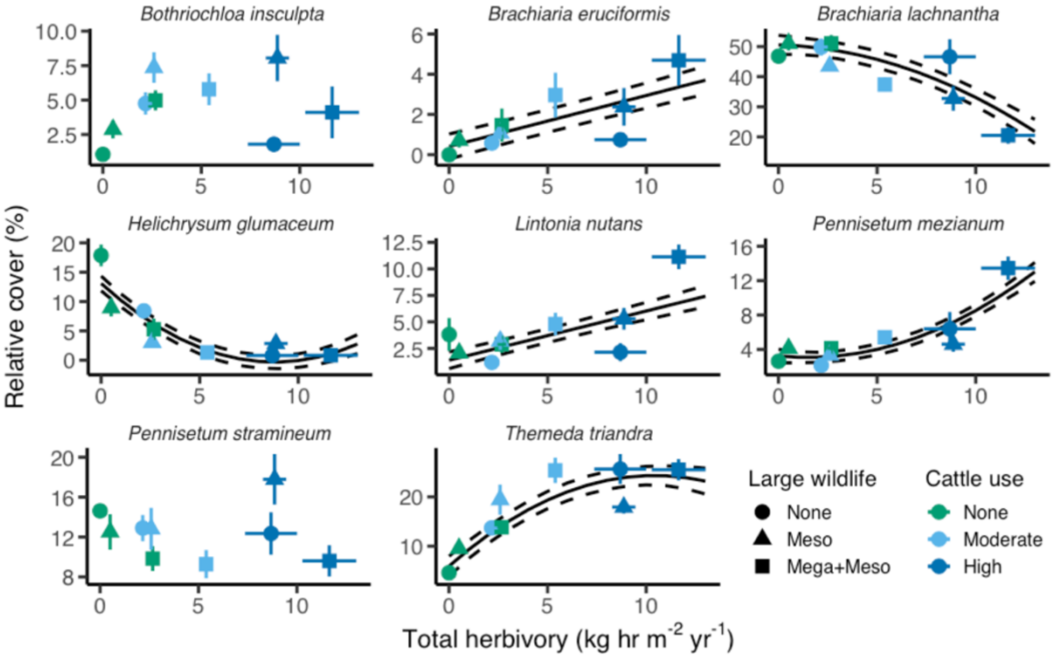


Figure S6.7 Relationships between relative cover and total herbivory for the eight species each comprising > 1% of total cover (means ± 1 *SE*). ‘Meso’ = wild mesoherbivores (50–1,000 kg) allowed; ‘Mega’ = megaherbivores (elephant and giraffe) allowed; ‘None’ = no wild mesoherbivores/megaherbivores. Fitted means (solid lines) and standard errors (dashed lines) of linear (*Brachiaria eruciformis* and *Lintonia nutans*) and second-order polynomial (*Brachiaria lachnantha*, *Helichrysum* (*Pseudognaphalium*) *glumaceum*, *Pennisetum mezianum*, and *Themeda triandra*) regressions.

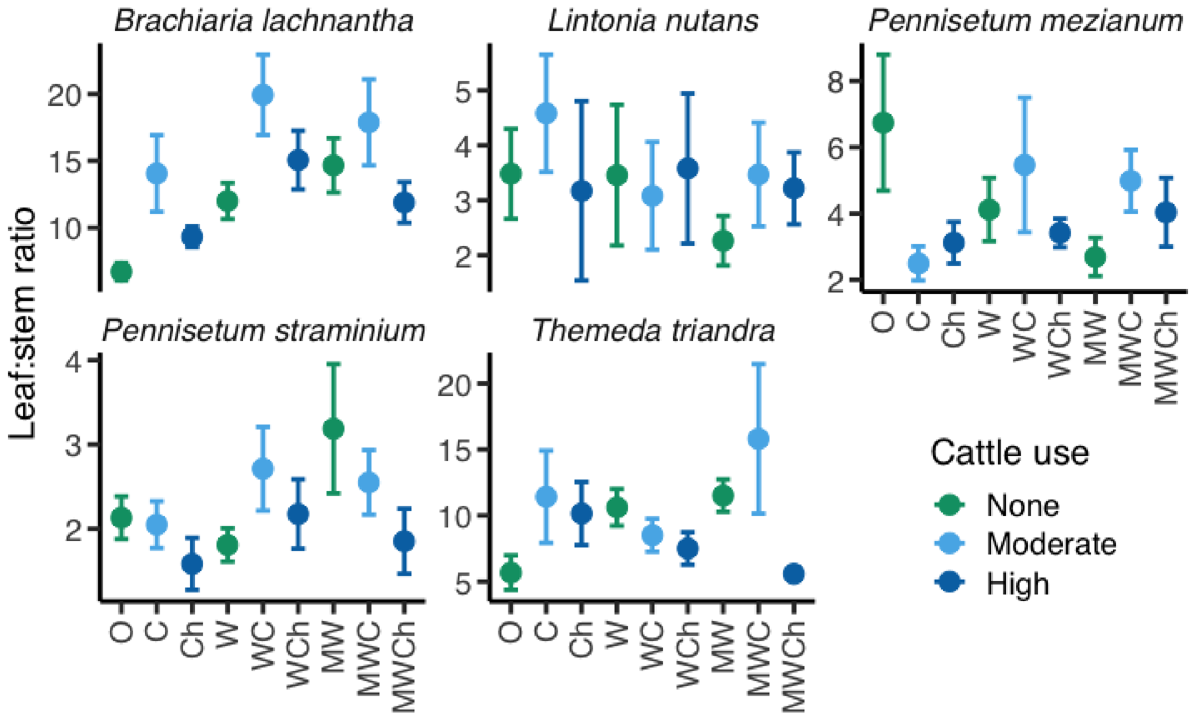


Figure S6.8 Leaf-to-stem ratio responses to treatments for the five most common species (means ± 1 SE). 'C' = cattle allowed (moderate intensity); 'Ch' = high cattle stocking rates; 'W' = wild mesoherbivores allowed; 'M' = megaherbivores (elephant, giraffe) allowed; 'O' = cattle mesoherbivores and megaherbivores excluded.

Appendix 7. Supporting information for Chapter 4: Positionality statements and supporting data

A7.1 Positionality statements:

Each of the individuals involved in social data collection have written a positionality statement (including age, sex, ethnicity, education, personality and interests) to aid in the interpretation of the social science results.

Elijah H. Kirobi:
I am a 27-year-old man, my ethnicity is Maasai, and am a member of Makurian Group Ranch. I hold a diploma in Tourism Management from Maasai Mara University and am currently pursuing a degree in Tourism Management at Kenyatta University. I was a youth representative – an elected individual who represents the interests of community members under 35 in group ranch meetings. Current members of the group ranch committee have encouraged me to run for secretary of the 15-member committee. I perceive myself as a humble person who acts with integrity and I like to work with people with mutual respect. I love my community and strive to secure the rights of its members and further its development. I am willing to help where I can when people are in need or are experiencing difficulties. I like to see community members coming up with ideas to improve their lives of that of their families. I enjoy walking in nature while looking after livestock, fetching water or looking for honey with friends in the forest.

Cadia L. Chen:
I am a 26-year-old woman, with European and Israeli heritage. I grew up at Mount Nyiru in Samburu county and therefore have experience living with Samburu people, who are close relatives of the Maasai. I am a permaculture designer and also work at tourist camps and lodges as a relief manager, mostly in Laikipia. I was educated in British and international private schools in Kenya and France, respectively. I studied Liberal Arts and Sciences at Quest University, Canada. I speak English and Kiswahili fluently and some Samburu – a Maa language. I am a friendly and inquisitive person and am interested in learning about people. I sometimes feel ashamed of the way some white Kenyans, particularly the older generations, view and treat black Kenyans. This motivates me to gain a deeper understanding of myself and other Kenyans of all ethnicities. I am also interested in ecological issues and in developing land management practices that lead to more resilient landscapes.

Harry B. M. Wells:
I am a 26-year-old, ethnically white-Asian man, and am a final year PhD student at the University of Leeds. I grew up on Lolldaiga Hills – a livestock ranch and conservation area that neighbours

Makurian Group Ranch. Prior to studying Biology for undergraduate and masters levels at the University of Bristol, I was educated under the British system in Kenya and the UK and under the Japanese system in Kenya and Japan. I have a quiet and reserved personality. I have a strong feeling of what is morally right/wrong but am also open to seeing things from new perspectives. My primary interests are in restoring degraded ecosystems and gaining a deeper understanding of our local ecosystems to improve land management. I would like to work to maintain the landscape's integrity and rich biodiversity, while ensuring that local people are benefiting from these healthy ecosystems. As a descendant of a colonial settler family, I feel ashamed of Britain's colonial history – particularly in Kenya. However, I feel that what we do as individuals today is more important. I feel that land degradation is a symptom of social disfunction, and that restoration is a way to heal both ecosystems and human communities.

A7.2 Supplementary tables

Table S7.1 Livestock relative values used for individual and household wealth metric. This wealth proxy was calculated by summing the number of animals of each species multiplied by their respective exchange values. For example, a value of five indicates that one adult cow will commonly be exchanged for five sheep/goats. It is important to note that this cultural exchange value does not reflect market values.

Species	Cattle	Goats	Sheep	Donkey	Camels
Relative exchange value	5	1	1	12	12

A7.3 Supplementary figures

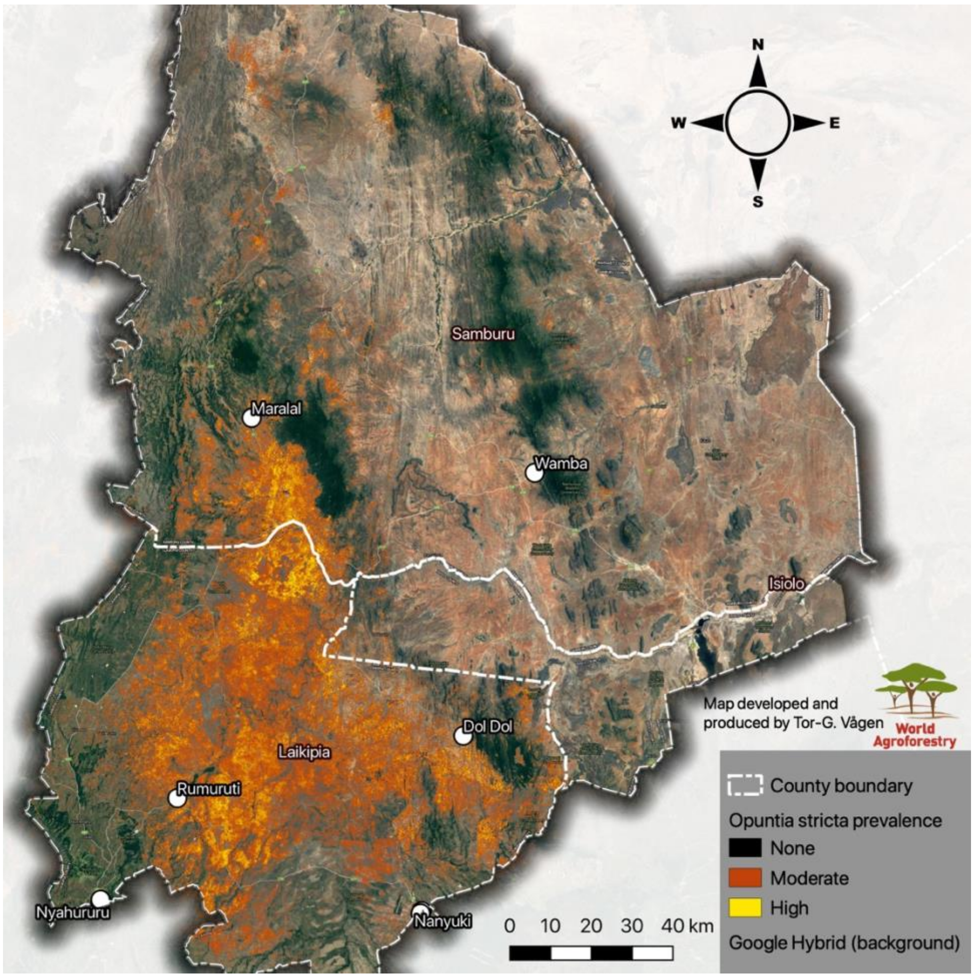


Figure S7.1 *Opuntia stricta* occurrence probability in Laikipia and Samburu counties. This map was produced by employing a machine learning algorithm, extreme gradient boosting. As input, we used *O. stricta* presence/absence field data sampled at 654 1,000-m^2 random locations together with all eight bands of Landsat 8 tier 1 surface reflectance imagery (dropping plots for which the quality assessment band indicated cloud cover) taken as close in time as possible to the field surveys.

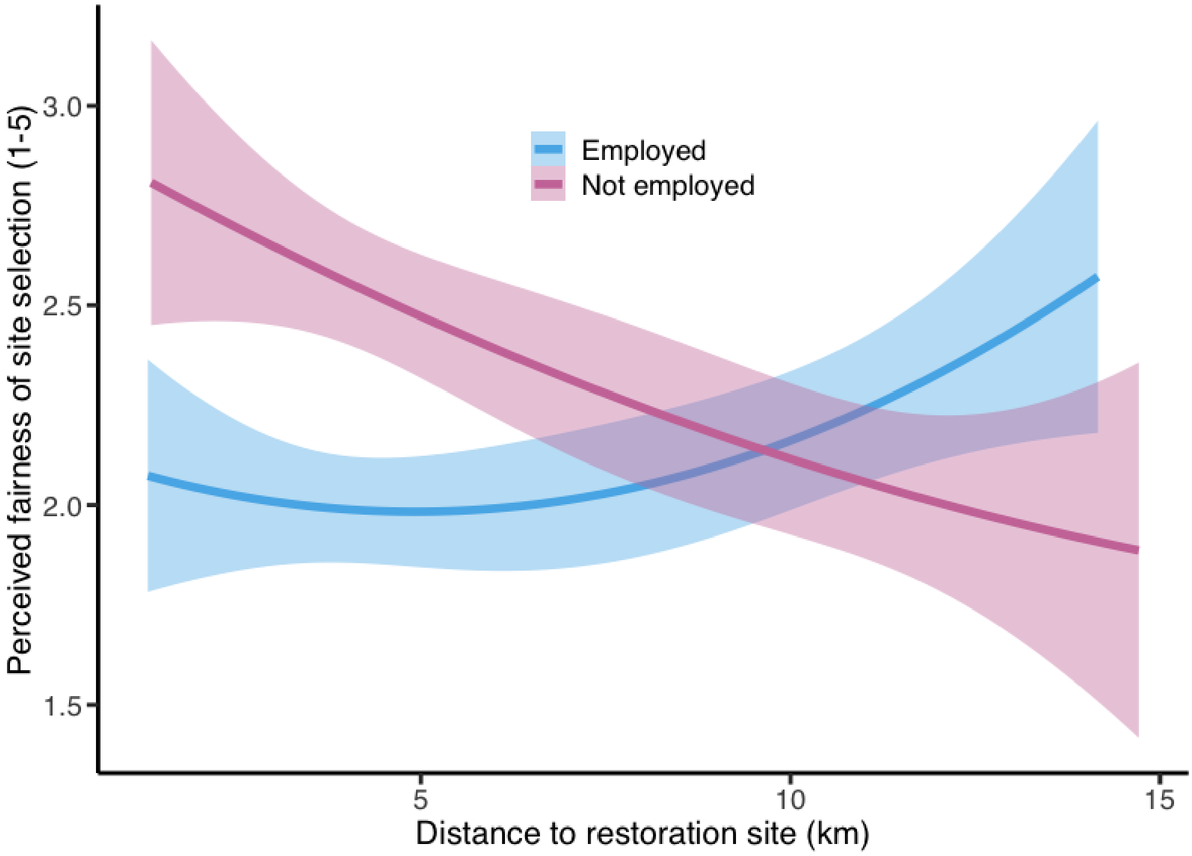
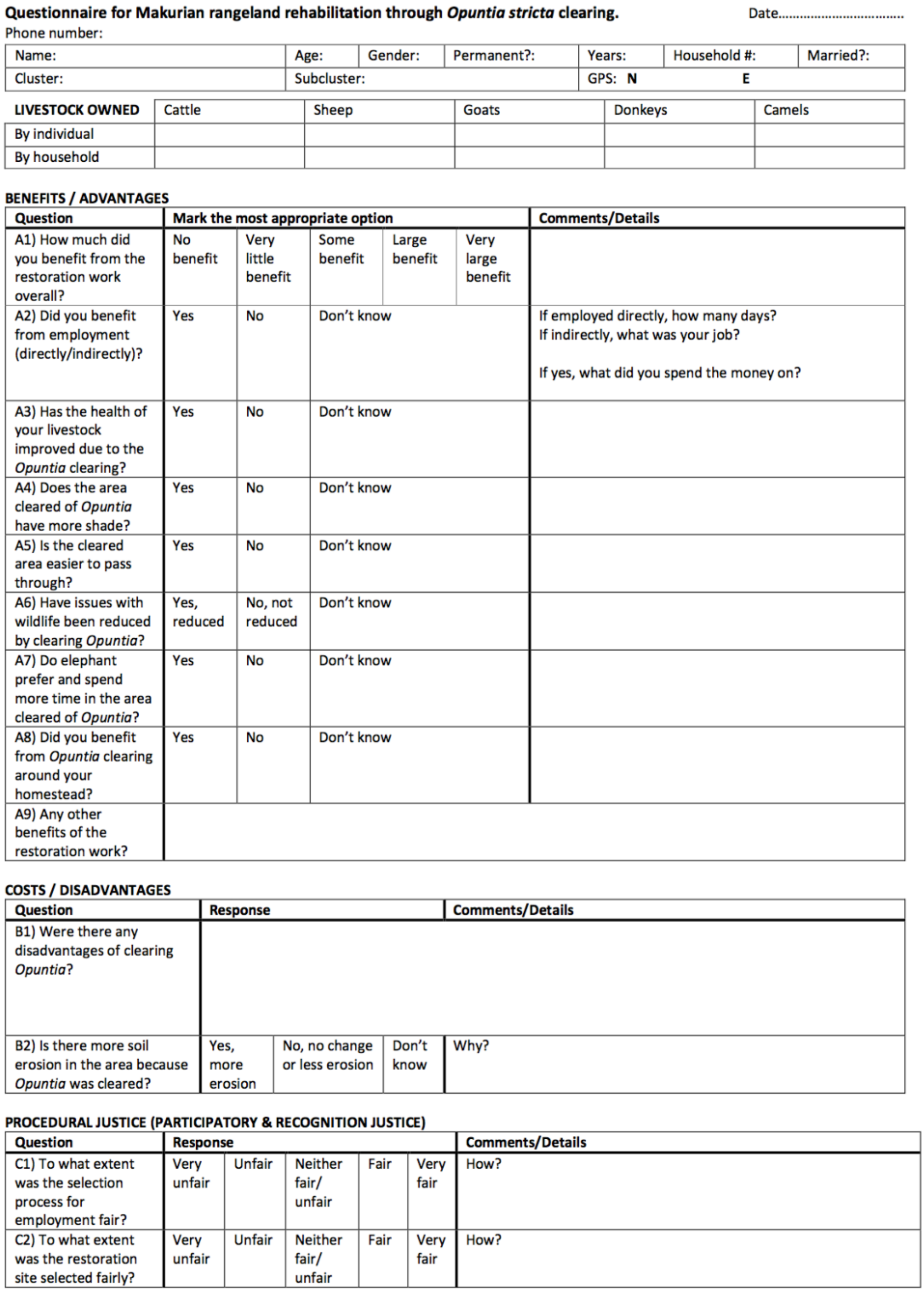


Figure S7.2 Interactions between distance to restoration site and employment in their relationship with perceived procedural equity of restoration site selection. Fitted lines show second-order polynomial functions ± standard errors (shaded ribbons).

Appendix 8. Supporting information for Chapter 4: Questionnaire



Questionnaire for Makurian rangeland rehabilitation through *Opuntia stricta* clearing. Date……………………………

Phone number:

Name:	Age:	Gender:	Permanent?:	Years:	Household #:	Married?:
Cluster:	Subcluster:			GPS: **N** **E**		

LIVESTOCK OWNED	Cattle	Sheep	Goats	Donkeys	Camels
By individual					
By household					

BENEFITS / ADVANTAGES

Question	**Mark the most appropriate option**					**Comments/Details**
A1) How much did you benefit from the restoration work overall?	No benefit	Very little benefit	Some benefit	Large benefit	Very large benefit	
A2) Did you benefit from employment (directly/indirectly)?	Yes	No	Don't know			If employed directly, how many days? If indirectly, what was your job? If yes, what did you spend the money on?
A3) Has the health of your livestock improved due to the *Opuntia* clearing?	Yes	No	Don't know			
A4) Does the area cleared of *Opuntia* have more shade?	Yes	No	Don't know			
A5) Is the cleared area easier to pass through?	Yes	No	Don't know			
A6) Have issues with wildlife been reduced by clearing *Opuntia*?	Yes, reduced	No, not reduced	Don't know			
A7) Do elephant prefer and spend more time in the area cleared of *Opuntia*?	Yes	No	Don't know			
A8) Did you benefit from *Opuntia* clearing around your homestead?	Yes	No	Don't know			
A9) Any other benefits of the restoration work?						

COSTS / DISADVANTAGES

Question	**Response**			**Comments/Details**
B1) Were there any disadvantages of clearing *Opuntia*?				
B2) Is there more soil erosion in the area because *Opuntia* was cleared?	Yes, more erosion	No, no change or less erosion	Don't know	Why?

PROCEDURAL JUSTICE (PARTICIPATORY & RECOGNITION JUSTICE)

Question	**Response**					**Comments/Details**
C1) To what extent was the selection process for employment fair?	Very unfair	Unfair	Neither fair/ unfair	Fair	Very fair	How?
C2) To what extent was the restoration site selected fairly?	Very unfair	Unfair	Neither fair/ unfair	Fair	Very fair	How?

C3) Were poorer families prioritised for employment?	Yes	No	Don't know			Why?
C4) Should women have been able to start work 30 minutes earlier and end 30 minutes later?	Yes	No	Don't know			
C5) How fairly was the restoration work conducted overall?	Very unfair	Unfair	Neither fair/ unfair	Fair	Very fair	
C6) How else could the process have been conducted more fairly?						

DISTRIBUTIVE JUSTICE

Question	**Response**					**Comments/Details**
D1) Were people living further away disadvantaged?	Yes	No	Don't know			How?
D2) Did age affect how costs & benefits were shared?	Yes	No	Don't know			How?
D3) Did gender affect how costs & benefits were shared?	Yes	No	Don't know			How?
D4) Would benefits & costs of *Opuntia* clearing have been shared more fairly if more people were each employed for fewer days?	Yes	No	Don't know			Why?
D5) How fairly were the costs & benefits shared overall?	Very unfair	Unfair	Neither fair/ unfair	Fair	Very fair	
D6) How else could the benefits & costs have been shared more fairly?						

RANKING BENEFITS/COSTS & SOCIAL JUSTUCE ISSUES (1=least important, 12=most important)

Employment	Livestock health	Wildlife issues	Shade	Ease of passage	Soil erosion	Fairness of employment process	Fairness of site selection	Fairness of benefit/cost sharing	Gender equity	Age equity	Distance to restoration site

FUTURE RESTORATION WORK

Question	**Response**	**Comments/Details**
E1) Where should future *Opuntia* clearing be done?	 GPS: **N** **E**	Why?

Question	**Response**
F1) What does 'land degradation' mean to you?	
F2) What does 'land restoration' mean to you?	

Any other comments relating to the rehabilitation work regarding cost, benefits, and fairness?..

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Appendix 9. Report of research findings to Makurian group ranch in Maa

A9.1 Erisio tiatua eramatare onkulupuo

Nkoroki natumeki te group ranch Makurian

Harry B. M. Wells, Elijah H. Kirobi, Cadia L. Chen, Leigh A. Winowiecki, Tor-Gunnar Vågen, Muhammad N. Ahmad, Lindsay C. Stringer, Andrew J. Dougill

Eniatua

kebaiki netiake swam too mpashi nemeidinga olmatundai na ore loitikoshi onkitejon nenyor sii ninche mpashi nawang. Ketii ilbulabul oitodolu ajo enyor itomia eneidinga olmatudai

Naituruk too nkikilikwanat

1) enkop, 2) biotisho o swam, 3) engelunoto o mpaashi to lningo, 4) esiai, 5) elakwani empaashi nageluno, 6) oloip, 7) enkiimata, 8) ramati tialo enkigeroe, 9) esidano edupoto ongarata, 10) erisio tenkalo ntomonok, 11) mbaa o mwesi, 12) erisio tenkalo o esirio pooki/ilporori.

Erisio neitu ebata

Enkironya enkitoria olashumpa leukoloni, olteleyiok, onshalari erikore naidikidikore naishoo enkop meinyalari keidim makurian ataramata nkulupua eneyena tankarake emirare osunya

Erisio eworoto

Keilep eworoto erisio too lelo oigero alang lemeigero, etoponari eworoto too lelo olakuniki amu kore lolakwa nedol ana enotito esiai. Kore nkulie kitopuat o nkulupo neiyieu neese to nkuto pooki petaaniki pooki. Teneigeri ntomonok neidim dupoto atabai ilmareita

Enekuniaiyioki eririo

Kore enkigerore naa sidiai to loigeroki o too lelo onyikita

Eyiolounot erisio

Teneyiolouni enumieki ena yeunot e makurian na keidim olosho ataasaki ate (matonyokanuk ilpoori to lmatundai.)

Erisio naiyiolounoi

Kedamuni neilepunyeki yeunto emakurian keidim atoriiko mbaa oloshoo tiatua pooki (e.g. aiiput ilpoori to Olmatundai)

Unkulie kitopuat enkenye

Kore iltunga’na kumo tiatua onwan o tomon naa ol-kinyei etijo eiyeuni Kenya neduyeki olmatundai

Enkiroroto nabayie

Keponari erisio eramatere enkop o mbaa natii nilepunyeki mbaa enkitopuata enkop, kake kore mbaa are neidim aitayutu olarambal.

Appendix 10. Report of research findings to local land managers and conservationists

Twelve months of camera trapping in a long-term exclosure experiment on black cotton savanna shows that grazing, whether by cattle or large wild herbivores (>50 kg), increases the local diversity of smaller wildlife (10–70 cm shoulder height).

For more information see:

Wells HBM, Kimuyu DM, Odadi WO, Dougill AJ, Stringer LC, Young TP (2021) Wild and domestic savanna herbivores increase smaller vertebrate diversity, but less than additively. Journal of Applied Ecology 58:953–963 https://doi.org/10.1111/1365-2664.13843

Cattle can mimic the effects of an assemblage of large wild herbivores (>50 kg) in shaping savanna understory plant community composition when the cattle are at moderate (~2.1 kg hr m^{-2}), but not high stocking rates (~10.5 kg hr m^{-2}).

For more information see:

Wells HBM, Porensky LM, Veblen KE, Riginos C, Stringer LC, Dougill AJ, Young TP (2021) At high stocking rates, cattle do not functionally replace wild herbivores in shaping understory community composition. Ecological Applications

The perceived equity of community-based rangeland rehabilitation through the removal of an invasive cactus, *Opuntia stricta*, was strongly influenced by whether individuals were employed for restoration work and the distance to the restoration site.

For more information see:

Wells HBM, Kirobi EH, Chen CL, Winowiecki LA, Vågen T-G, Ahmad MN, Stringer LC, Dougill AJ (2021) Equity in ecosystem restoration. Restoration Ecology 29(5):e133385 https://doi.org/10.1111/rec.13385