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Human impacts on the functioning of African savannas

de Jonge, Inger K.

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Human impacts on the functioning of African savannas

The research presented in this thesis was carried out at the Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, The Netherlands according to the requirements of the Graduate School of Science (Faculty of Mathematics and Natural Sciences, University of Groningen).

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Human impacts on the functioning of African savannas

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Inger Kirsten de Jonge

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Promotor

Prof. dr. H. Olff

Copromotor

Dr. M.P. Veldhuis

Beoordelingscommissie

Prof. dr. M.P. Berg

Prof. dr. ir. F. van Langevelde

Prof. dr. C.L. Parr

Voor Cleo en Jan

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Chapter 1

General introduction

Inger K. de Jonge

Introduction

Savannas and grasslands are one of the most extensive vegetation types in tropical and subtropical regions (Solbrig *et al.* 1996, Scholes and Archer 1997). The savanna biome supports the livelihoods of millions of people through the provisioning of ecosystem services such as clean water, food, and forage for livestock while it also harbours unique and diverse flora and fauna (Sala and Paruelo 1997, Prins and Olff 1998, Murphy *et al.* 2016). However, anthropogenic impacts increasingly threaten savanna ecosystems (Osborne *et al.* 2018) and have caused widespread degradation through land-cover conversion and landscape fragmentation in recent decades (Lambin *et al.* 2003, Bond and Parr 2010). Especially on the African continent, where people regionally depend the most on environmental resources (Díaz *et al.* 2006) and human population is projected to at least double by the year 2050 in some countries (DESA 2019), savannas are under severe pressure. Concurrently, changes in rainfall regimes in combination with rising temperature are projected to lead to longer and more frequent droughts in savanna ecosystems (IPCC 2013) which together with elevated atmospheric [CO₂] form additional and possibly multiplicative threats to the ecological integrity of savannas (Parr *et al.* 2014, Stevens *et al.* 2016). Therefore, it is critical to better understand savanna ecosystem responses to anthropogenic change and to identify practices that secure the resilience of ecosystems functions and services.

Human impacts in African savanna ecosystems

The relationship between people and the environment has changed drastically over the course of the Anthropocene in African savannas (Olff and Hopcraft 2008, Malhi 2017). The dispersion of (agro) pastoralism ca. 4000 years ago from Ethiopia and the Nile valley marks the start of profound alterations to savanna landscapes. While the distribution of early hunter-gatherer humans was more or less restricted to small areas with high rainfall and soil fertility, the domestication of livestock allowed people to move into drier areas (Olff and Hopcraft 2008), which itself was enforced by growing population densities. In order to maximize livestock yields, traditional pastoralists are thought to have favoured grasslands over more wooded areas. Regular use of fire became an important tool for people to control bush encroachment, especially at higher annual rainfall conditions, while at the same time improving forage conditions for their livestock, especially on poorer soils (Lamprey and Reid 2004). Sedentary agriculture emerged around the same time as

pastoralism, but was more restricted and profitable in wetter, fertile areas such as along rivers. The ecological implications of these new forms of land-use may have been limited through disease transmission between wildlife and livestock and large scale droughts that regulated human densities through time (Olf and Hopcraft 2008). Yet, altered grazing regimes by large herds of livestock and the expansion of agricultural areas have marked the onset of compositional and structural changes in savannas.

Current day, pastoralism is widespread across Africa, including its driest regions, and still forms the basis of life for millions of people. However, where once the pastoral way of life coexisted with wildlife (Du Toit and Cumming 1999), ongoing human population growth is causing continental-scale replacement of wildlife with livestock with large consequences for ecosystem functions (Hempson *et al.* 2017). Semi-arid regions are expected to be affected first and most strong, where the release of ecological constraints on herbivore populations (through supplemental feed and water) drives fire suppression and woody plant encroachment (WPE) (Hempson *et al.* 2017). Moreover, intensified human land use associated with the transition from transhumance pastoralism to a predominantly sedentary lifestyle has resulted in ‘chronic’ grazing and browsing regimes by livestock with negative impacts on overall vegetation productivity. High intensity grazing and trampling compacts soils, reducing water infiltration and increasing soil temperature and evaporation rates (Veldhuis *et al.* 2014). The resulting abiotic stress may lead to higher mortality rates of vegetation (Buitenwerf *et al.* 2011), furthering negative effects on soil stability, which may ultimately put human-occupied arid and semi-arid savannas at the greatest risk of drought-driven vegetation shifts (Sankaran 2019).

Protected areas are of increasing importance to protect wildlife and to prevent further loss of biodiversity (Sinclair *et al.* 2002). However, even the largest protected areas are now under intense pressure around the globe (Jones *et al.* 2018, Veldhuis *et al.* 2019b). Conversion of natural habitats to agricultural fields proceeds increasingly closer to park boundaries of the Greater Serengeti Mara ecosystem (GSME), which coincides with the highest human population growth rates (Estes *et al.* 2012), as these were areas that for a long time were the least attractive for people due to human-wildlife conflicts. However, at higher population densities, migration to these areas is unavoidable as other areas become full (Veldhuis *et al.* 2019b). Immigration of people to areas just outside the park aggravate human-wildlife conflicts, which in turn creates antagonism between people and conservation objectives (Walpole *et al.* 2004). Shifts in land tenure policy from communal to individual landholdings and conversion of grazing land to cropland increasingly causes

agro-pastoralists living at the western side of the GSME to face a shortage of grazing land for their livestock (Kristjanson 2002). The resulting unsustainable use of resources just outside the border of protected areas increasingly limits the use of these areas by wild herbivore populations which in turn are compressed inside core protected areas (Veldhuis *et al.* 2019b). The resulting spatial compression in the centre of core protected areas, which has been further exacerbated by substantial illegal livestock grazing inside the GSME over the past decade, has strongly altered ecosystem functioning inside the park with consequences for the ecological stability and integrity of the entire ecosystem (Veldhuis *et al.* 2019b).

Human-driven alternative dynamic regimes

The vegetation composition and structure of savannas is highly dynamic, a characteristic that may explain their high resilience (Oliveras and Malhi 2016, Willis *et al.* 2018). Following ecological perturbations, such as strong changes in fire, grazing, or climate, open grasslands can shift to dense woodlands and back again to grasslands at decadal time scales. Such shifts between ‘alternative dynamic regimes’ (as each state is rarely stable) due to major ecological perturbations have been well documented for the GSME (Sinclair *et al.* 2008). For example, when the rinderpest outbreak at the end of the 19th century decimated large herds of livestock, people became strongly reduced in numbers, which in turn reduced the incidence of fire. As a consequence, cohorts of woody seedlings across the ecosystem were able to escape the fire trap which gave rise to increased woody cover in the decade following this perturbation (Sinclair *et al.* 2008). Alternatively, the Mara is experiencing an open savanna phase since the ban on ivory trade in 1989 resulted in the recovery of the elephant population (Dublin *et al.* 1990). High elephant densities reduced woody cover and prevented regeneration by removing seedlings, with consequences for woody plant cover until present day (Dublin *et al.* 1990).

The transitions between open savannas and closed woodlands are suggested to be driven by two alternative positive feedback loops which are characterized by contrasting disturbance regimes (Van Langevelde *et al.* 2003, Beckage *et al.* 2009, Oliveras and Malhi 2016). Fire and browsing herbivores maintain open savannas by preventing recruitment of trees and reducing trees to smaller size classes (Van Langevelde *et al.* 2003, Staver and Bond 2014). This indirectly favours grasses, which in turn promotes fire, giving rise to a fire-grass feedback maintaining grasslands even at high rainfall (Beckage *et al.* 2009, Oliveras

and Malhi 2016). Perturbation in the form of a drought year or fire suppression may disturb this feedback and potentially promote the alternative loop where the recruitment of trees may lead to increased shade and moist microclimates with negative effects on grass and fire incidence (Oliveras and Malhi 2016, Veldhuis *et al.* 2018).

Other than due to large ecological perturbations, large scale regime shifts are uncommon in protected savannas. This can be explained by the spatial and temporal interdependence of fire and herbivory as consumers of aboveground standing biomass (Wilcox *et al.* 2018). Herbivores, which are free to roam, are attracted to recently burned areas (Hempson *et al.* 2015) which allows other areas to accumulate enough fuel needed for fire. On longer time scales, this results in a shifting and heterogeneous mosaic consisting of both grass and tree dominated patches (Wilcox *et al.* 2018). The ongoing spatial compression of the GSME dissolves the interdependence of fire and herbivory, where increased grazing intensity prevents the accumulation of herbaceous biomass in increasingly large areas. In this light, human impacts in this savanna ecosystem can be seen as ecological perturbations that potentially cause regime shifts by changing the nature of disturbance.

Resistance and recovery

Given the dynamic nature of savannas, understanding the factors that control regime shifts in response to human impacts will benefit attempts to mitigate savanna degradation. Such factors may include a range of environmental conditions, which determine the response of the landscape to changes that promote switches to alternative regimes. For example, the potential of the woody component to *recover* from fire perturbation (promoted by the fire –grazer feedback) depends on resource availability (nutrients, water) which may make switches slow or less likely in more arid or oligotrophic savannas (Higgins *et al.* 2007). Woody plants that have not attained enough height during the fire free interval, will lose the majority of their aboveground structures in the next fire after which ‘the cycle’ restarts (Higgins *et al.* 2000). Over evolutionary time, woody plants are thought to have evolved different strategies to overcome this ‘fire trap’. Early bark growth and well protected epicormic buds may allow woody plants to ‘*resist*’ fire and resprout directly from surviving stems, while quick and vigorous basal resprouting allows fast ‘*recovery*’ through early height growth (Gignoux *et al.* 1997, Clarke *et al.* 2013, Charles-Dominique *et al.* 2015).

Resistance and recovery trade-offs might be common in ecology, causing the ‘resistance – recovery’ framework to increasingly become a popular concept to quantify the ability of an ecosystem to maintain its state and to recover from perturbation (Côté and Darling 2010, Hodgson *et al.* 2015, Nimmo *et al.* 2015). Theory predicts that there should be a compromise between the ability to grow fast under benign environmental conditions and to tolerate stress (Pianka 1970, Grime *et al.* 1997, Lambers *et al.* 2008). Vegetation that naturally occurs in stressful (e.g. arctic, saline, dry) environments tend to have lower growth potential but may possess relatively more adaptations against adverse conditions, such as thicker leaves (Lambers and Poorter 2004). Because arid savannas experience larger rainfall variability between years and have historically been exposed to fewer extreme drought events, they may be more ‘resistant’ to drought perturbations than mesic savannas as periods of water shortage may have promoted adaptations (traits) in the plant community to deal with drought (Greenwood *et al.* 2017, Sankaran 2019). Similarly, mesic savannas may experience faster post-drought recovery rates because of higher growth rates in the community. Ecological stability or ‘resilience’ can thus be achieved through high resistance in one system, while fast recovery ensures resilience in another (Hodgson *et al.* 2015).

In this thesis, I use the concepts of resistance to and recovery from perturbation to explain the impact of people on savanna ecosystems. The advantage of this general framework is that it is not linked to a biological level of organization and can be applied to measurements at the level of ecosystems (mesic versus arid savannas), landscapes, individual plants, or even plant parts (aboveground biomass) (Nimmo *et al.* 2015). A graphical representation of the different aspects of ‘resilience’ is given in Figure 1. Resistance can be defined as the capacity to withstand perturbations and is quantified by measuring the degree to which an ecosystem function or process is changed in response to perturbation (Pimm 1984). After the perturbation, recovery can be defined as the capacity to return its equilibrium and can be quantified by measuring the time needed to return to the pre-disturbance state (Pimm 1984).

Objective and thesis outline

With this thesis, I aim to contribute to a better understanding of anthropogenic impacts on the functioning of savanna ecosystems. Specifically, I attempt to show how components of ‘resilience’ can be used to study these highly dynamic, heterogeneous ecosystems and how we may use them to predict the outcome of human pressure on savanna function and

structure (**Chapter 2 and 3**). Second, I seek to quantify how and when human-occupied (and modified) landscapes facilitate or exclude wildlife in order to further ideas on how edge areas may be best managed to preserve both biodiversity and human livelihoods (**Chapter 4**). Lastly, I intend to contribute to the development of economic and reliable methods (**Chapter 5**) and experiments (**Chapter 2**) at ecological relevant time scales that support the estimation of key ecosystem functions such as aboveground net primary productivity (ANPP).

Fig. 1. Graphical representation of the response of an ecosystem function, process, or state to an ecological perturbation through time shown as a two part process consisting of resistance and recovery, which together constitute resilience. An ecological process or function may have high resistance to, but poor recovery from perturbation (orange line) and the other way around (blue line). Examples of such trade-offs are given in the main text.

First, in **Chapter 2**, I investigate to what extent the predominant displacement of wildlife by livestock in a pastoral village land adjacent to the GSME has altered the resistance to and recovery from perturbation. Using a novel method for imposing local drought conditions, this field study demonstrates that herbaceous vegetation in protected savanna landscapes possesses high recoverability but is not necessarily resistant to perturbation while the opposite is found for the village lands. The 'switch' can be partly explained by a reorganization of plant traits and attributes associated to the alternative regimes of fire versus grazing controlled landscapes. In **Chapter 3**, I assess whether a human-induced

regime shift in the form of fire suppression inside protected areas has different outcomes on the extent of woody plant encroachment (WPE) across environmental gradients in rainfall, lithology, soil texture, and geomorphology. The ecosystem-wide field study reveals that, besides direct effects of abiotic conditions on the speed of transition from an open, grassy savanna to a closed (sometimes impenetrable) woodland, there are important indirect pathways via tree functional types, which themselves can be linked to alternative strategies in being resistant or highly recoverable from fire.

Next, I evaluate the consequences of savanna landscape alterations (as a result of longer term fire suppression and livestock rearing) on wildlife occurrence in **Chapter 4**, where we used camera traps to compare the spatiotemporal distribution of various native ungulates, their main predator, and livestock across a soft-edge protected area boundary. The results show that not all wildlife species make (equally) use of human-occupied landscapes, with body size and feeding-guild as important traits that determine the suitability of edge areas. Furthermore, I show that the two most abundant wild herbivores avoid people and livestock during the day in the edge area, but are on average more present in village lands during prime foraging hours and high hyena activity implying benefits of short-grazed grazing lawns to these species, both in terms of resources and safety from predation. In **Chapter 5** I introduce a new methodology to estimate ANPP which is based on the combination of vegetation indices extracted from digital repeat imagery and remote sensing. Herbaceous vegetation in savannas is highly responsive to rainfall pulses, which underscores the need for novel tools that can capture short-term vegetation responses. Phenocams can do just that and I show in this chapter that a measure that captures moisture-driven day to day fluctuations in greenness improves productivity estimations.

Finally, in **Chapter 6** I integrate and synthesize the findings of the different chapters. I describe how resistance and recovery at different biological levels, from plants parts - to microhabitats in landscape resulting from biotic interactions - to entire landscapes, provide clues on how these units respond to human impacts. I furthermore reflect on the consequences of increasing human pressure for higher trophic levels and the future of human – wildlife coexistence, and discuss avenues for future research.

Study area

All data for this thesis were collected in the Greater Serengeti Mara ecosystem, a flagship savanna ecosystem at the Kenya-Tanzania border in East-Africa. The Serengeti-Mara ecosystem is characterized by the annual migration of around 1.3 million wildebeest, zebra and Thomson's gazelle that follows a seasonal rainfall gradient. The GSME consists of both strictly protected national parks and game reserves, including the Serengeti National Park (SNP) and the Masai Mara National Reserve (MMNR), and different wildlife management areas with varying resource use strategies (Fig. 2). There is a prominent rainfall gradient from ~350 mm MAP in the southeast to ~1200 mm MAP in the northwest part of the ecosystem (Sinclair 1995). Rainfall is highly variable but generally peaks during a short rain season in December and during the long rain season from March to May. Soils transition from volcanic ash-derived plains in the South-East to granite gneisses in the North (de Wit 1978, Jager 1982).

Vegetation is influenced by both rainfall and soil type and can be broadly classified into the South-eastern grass plains, West-central Acacia woodlands, and northern broadleaf woodlands (Herlocker 1974, Sinclair 1995). Savannas and woodlands are generally formed by a continuous layer of graminoids with a discontinuous layer of trees and/or shrubs. Principal tree species forming the woody component include *Vachellia tortilis*, *Vachellia robusta*, *Vachellia drepanolobium*, *Vachellia gerrardii*, *Commiphora trothea*, and *Balanites aegyptiaca* while common grass species include *Themeda triandra*, *Hyparrhenia filipendula*, *Sporobolus africanus*, *Digitaria macroblephara*, and *Panicum coloratum*.

Due to the increase in agricultural areas and livestock densities, the area burned each year in the GSME has strongly decreased over the past 15 years, with fires increasingly restricted to core protected areas (Fig. 3). This has promoted woody cover especially along the margins of these protected areas (Veldhuis *et al.* 2019b).

The area between the western boundary of GSME and Lake Victoria is inhabited by Sukuma and Kuria. As agro-pastoralists, their village lands are generally divided into small-holdings where individual households use land for both agriculture and grazing. Some villages have a common grazing area which is grazed all year round. The area bordering the East of the GSME is mainly inhabited by Masai whose economic mainstay is pastoralism combined with small-scale subsistence farming. The predominantly communal grazing lands are grazed and browsed year-round by cattle and shoats.

Fig. 2. Protected areas in The Greater Serengeti-Mara Ecosystem (GSME). Protected areas are classified into three categories based on the presence of livestock and the intensity of border controls. Strict Nature Reserves with strong border control include Grumeti GR (1; 513 km²), Ikona WMA (2; 280 km²) and Ikorongo GR (3; 545 km²). Strict Nature Reserves with medium border control are Kijereshi GR (4; 94 km²), Maswa GR (5; 2756 km²) Serengeti NP (6; 13062 km²), Maasai Mara NR (7; 1578 km²) and Mau FR (8; 1649 km²). Protected Areas with Sustainable Resource Use are Maasai Mara Conservancies (9; 1413 km²), Loliondo GCA (10; 6185 km²), Ngorongoro CA (11; 8222 km²) and Makao WMA (12; 503 km²). The boundary of the GSME (dashed line) is defined as the areas used by the wildebeest migration (orange arrows) plus the upstream watershed areas connected to this (From: Veldhuis *et al.* 2019b).

Fig. 3. Map of the last year each area burned. Lines delineate the Core Protected Areas (CPA; black solid lines), Protected Areas with Sustainable Resource Use (PASRU; grey solid lines) and the boundary of the Greater Serengeti-Mara Ecosystem (GSME; black dotted lines) that represents the original area used by the migratory wildlife. Colours indicate the year each area last burned. Areas with no colour have not burned since 2001. The map was created using the MODIS MCD64 Burned Area Product (Giglio *et al.* 2009). Black stars represent the sites with long-term herbivore exclosures (from: Veldhuis *et al.* 2019b).

Chapter 2

High impact grazing pushes savanna ecosystems from a low resistance – high recovery system to a high resistance – low recovery system

Inger K. de Jonge, Christine Lijcklama à Nijeholt, Michiel P. Veldhuis, Han Olff

Abstract

Changes in rainfall regimes in combination with rising temperatures are projected to lead to longer and more frequent droughts in savanna ecosystems. Concurrently, human impacts in African savannas alter ecosystem functioning through changing disturbance regimes, which calls for a better understanding of how increasing human activities affect the resilience of savannas. The 'resistance – recovery' framework has become a general concept to quantify the response of ecosystems to perturbation. While conceptual and theoretical progress has improved the understanding of the links between ecological change and functional diversity, experiments in natural ecosystems are now needed to independently quantify resistance and recovery at the landscape level.

Here, we used a field-based experiment in an East-African savanna ecosystem to simultaneously measure both resistance to drought and recovery from above-ground biomass removal of herbaceous vegetation in a protected area (PA) and adjacent pastoral village lands (VL). Drought conditions were imposed on the vegetation using a novel method which involves the redirection of run-on rainfall water on a slope through gullies while pulse perturbations were performed by removing all aboveground standing biomass using a brush cutter. We considered the role of tree-grass interactions in altering resistance and recovery in each land use by measuring greenness underneath tree canopies and in paired inter-canopy plots before and during drought (resistance), and directly after and during a two month phase following pulse perturbation (recovery).

We found that herbaceous vegetation in VL was resistant to experimental drought, while vegetation greenness was significantly reduced in the PA. Conversely, vegetation greenness recovered fast in the PA compared to the VL from experimental pulse disturbance. Trees facilitated recovery of sub-canopy herbaceous vegetation, but only in the VL. Trees did not show any effect on resistance of sub-canopy vegetation to drought for both land-uses.

Our findings demonstrate that increasing human activities in the form of livestock grazing decrease the recovery potential, but may increase the resistance of savanna plant communities. This points towards a trade-off in resistance versus recovery at the landscape level, where a change in disturbance regime has likely shifted traits associated to coping with pulse disturbance (fire) to coping with press disturbance (herbivory and drought). We conclude that the use of the resistance-recovery framework is a promising way to experimentally assess the impacts of human activities on ecosystem functions and to identify elements (such as nurse trees) in the landscape that maintain response diversity.

Introduction

Discerning the mechanisms behind ecosystem responses to global environmental change is a central theme in ecology. While savannas are one of the most extensive biomes in the (sub) tropics (Solbrig *et al.* 1996, Scholes and Archer 1997), our understanding of the effects of climatic perturbations and land-use change on the functioning of the savannas is still relatively poor. Human population growth increasingly threatens the few remaining intact savanna ecosystems through a range of anthropogenic activities (Veldhuis *et al.* 2019b), including persistent alterations in fire and herbivory regimes through growing livestock numbers (Reynolds *et al.* 2007, Hempson *et al.* 2017). Concurrently, changes in rainfall regimes in combination with rising temperatures are projected to lead to longer and more frequent droughts in savanna ecosystems (IPCC 2013), which puts additional pressure on these ecosystems and the services they provide. It is therefore critical to understand the factors that determine the ecological stability towards these perturbations within savanna ecosystems in both natural and human-modified landscapes.

Ecological stability is a complex concept, which includes multiple components such as resilience, resistance, robustness, persistence, and variability (Donohue *et al.* 2013). Generally, signals of a high ecological stability of an ecosystem are that it does not experience unexpected major changes in ecosystem functions and/or characteristics in response to perturbation (a capacity known as ‘resistance’) and second, when it is capable of returning to its equilibrium or pre-disturbance state after a perturbation (a capacity known as ‘engineering resilience’, ‘recovery’ or ‘elasticity’) (Pimm 1984, Holling 1996). While initially a wide variety of terms describing similar aspects of stability complicated comparability between studies, there is now emerging consensus to define ‘resilience’ as a two part process of ‘resistance’ and ‘recovery’ (Côté and Darling 2010, McClanahan *et al.* 2012, Hodgson *et al.* 2015, Isbell *et al.* 2015). One of the reasons why this may be especially useful is because of potential trade-offs between resistance and recovery (Hodgson *et al.* 2015), where ‘resilience’ may be achieved through ‘resistance’ in one system and through fast ‘recovery’ in another. Empirical support for such trade-offs is limited in natural systems, but Donohue *et al.* (2013) showed that dimensionality of stability is much lower than one may expect if different components were not related.

Another advantage is that this ‘resistance – recovery’ framework can be seen as a general concept which is not linked to a biological level or organization and as such one can measure resistance and recovery of properties at the ecosystem level but also on the

level of communities, functional types, populations and individual plants (Nimmo *et al.* 2015). Different authors increasingly agree that response diversity and functional diversity are of great importance for the stability of ecosystem functions because they provide management options and allow scenario analysis for adequate responses to future change and disturbance (Tilman and Downing 1994, Hooper *et al.* 2005, Balvanera *et al.* 2006, Naeem *et al.* 2009). For example, having a range of species in a plant community that differ in their response to drought can stabilize the response of ecosystem process rates, thereby increasing recovery to perturbation (Van Ruijven and Berendse 2010). This confirms the 'insurance hypothesis' (Yachi and Loreau 1999) where the chance that a species with attributes or traits that confer resilience increases with higher species diversity (Yachi and Loreau 1999, Van Ruijven and Berendse 2010). This should however not be entirely due to chance; savannas are characterized by water-deficiency during prolonged periods of the year (Asner and Heidebrecht 2005) and as such, savanna trees and grasses have evolved a variety of traits that govern the ability of vegetation to tolerate or avoid droughts (Holloway-Phillips and Brodribb 2011, Craine *et al.* 2013, Sankaran 2019). Examples of typical drought avoidance traits are deep rootedness, leaf rolling, and leaf shedding while tolerance traits may include anatomical features of the xylem or widened leaves (Sankaran 2019). Some of these traits may be more associated to recovery while other govern resistance to drought. For example, high levels of resistance are generally associated with tolerance ('K', 'competitor' strategies), while recovery may be more associated to rapid regrowth and resprouting ('r', ruderal or colonizer strategies) (Pianka 1970, Tilman 1988, Grime *et al.* 1997, Nimmo *et al.* 2015). As the distribution of traits can be predicted from environmental conditions through principles of community assembly (Wright *et al.* 2004, Ackerly and Cornwell 2007, Sonnier *et al.* 2010), resistance and recovery capacities are likely not random across the landscape and may depend on combinations of disturbance regimes, environmental conditions, or resource availability. Heavy sustained grazing by livestock increases soil temperature and evaporation rates, thereby increasing abiotic stress to grasses (Veldhuis *et al.* 2014). The soil drying effect of intense grazing through soil compaction may cause a shift in functional composition towards a drought tolerant grass community in savanna ecosystems (Veldhuis *et al.* 2014) with potential consequences for the resistance and recovery potential of the herbaceous layer compared to a natural system with lower grazing pressure.

Within land use types, trees may be an important driver of grass layer resistance and recovery capacity as they change resource availabilities. Under some conditions, trees facilitate understory vegetation through the amelioration of abiotic conditions such as light

and temperature (Belsky *et al.* 1993, Moreno 2008, Dohn *et al.* 2013). Especially in regions which experience prolonged period of droughts, trees may protect palatable grasses and other herbaceous vegetation from desiccation by increasing air humidity and reducing soil evaporation under the canopy shade. Moreover, trees may increase water availability to sub-canopy vegetation through hydraulic lift (Ludwig *et al.* 2003). Trees with taproots can penetrate into deep soil layer which enables them to extract water during dry spells. A part of this water is lost via the tree's shallow lateral roots, which is then redistributed in upper soil layers where it may become available to sub canopy vegetation (Ludwig *et al.* 2003). Lastly, savanna trees can be seen as 'island of fertility' (Belsky 1994) where elevated soil nutrients underneath crown canopies are associated to grasses with higher nutrient status (Treydte *et al.* 2007). Both the modification of environmental conditions and the altered functional composition (traits) may change the ability of the herbaceous vegetation to resist perturbation and / or to recover from perturbation.

While the resistance – recovery framework is theoretically appealing, there are limited empirical studies in natural field settings that quantify both components simultaneously, which may be especially complicated in highly dynamic and heterogeneous systems such as savannas. Assessment of resistance and recovery requires both cross-sectional measurements that capture relevant environmental gradients (e.g. legacies from past disturbance regimes in pastoral lands) as well as longitudinal monitoring where an ecological unit is measured before, during, and after a perturbation (Nimmo *et al.* 2015). Here, we set up a field-based experiment to quantify both resistance and recovery of herbaceous vegetation to perturbation across two contrasting land uses. For resistance, we overcame issues with longitudinal monitoring by adopting a factorial design in which an experimental drought treatment was used to measure resistance in space rather than through time. For the recovery component, we used a separate 'pulse' perturbation experiment in which all aboveground biomass was removed, so that the recovery measurements are not affected by the system's resistance. Specifically, we asked 1) in what ways resistance and recovery of the herbaceous layer to perturbation are different between protected areas (historically exposed to pulse-disturbance) and pastoral village lands (history of press-disturbance), 2) in what ways trees modify resistance and recovery of herbaceous vegetation underneath crown canopies (microhabitat), and 3) whether differences in resistance and recovery between land use and microhabitat can be explained by characteristics and traits of the herbaceous vegetation.

Material and Methods

Study area and design

We conducted our work within the greater Serengeti-Mara ecosystem which encompasses ~25000 km² of Northern Tanzania and Southern Kenya and includes the Serengeti National Park (SNP) and adjacent land management units and game reserves in Tanzania and the Masai-Mara reserve in Kenya. The study site is situated in the North-eastern corner of the Serengeti National Park and adjacent village lands within the Loliondo Game Controlled Area (LGCA) which lies east of the park. LGCA is home to numerous wildlife populations and is part of a key dispersal area for migrating wildlife from Serengeti National Park. For this reason, Loliondo has long played a central role in both conservation discussions and the growing village-based tourism industry. Traditional land use of the village lands is pastoralism by local Masai. Rainfall is highly variable but generally peaks during the short rain season in December and during the long rain season from March-May. Based on the Climate Hazards Group Infrared Precipitation (CHIRPS) dataset over the period 2009-2019, mean annual precipitation in this area is around 1000 mm. Vegetation is characterized by a tree-grass mixture, with *Vachellia gerrardii* dominating the mid-slope catenae position and *Vachellia robusta* dominating the lower catenae position.

The experiment was set up across the border of the Serengeti National Park and the adjacent village lands of Ololosokwan (Loliondo). In both areas, we selected three sites (paired block design) with similar tree density and always halfway the catenae sequence. Within site, three plots were selected inside the park and in the village lands, of each 40 by 40 meters. These plots were randomly assigned to one of the following treatment groups: 'control', 'drought', and 'pulse perturbation' (Fig. 1). Nested within the treatment plots, we assessed the effect of tree-grass interactions through paired sub-canopy and inter-canopy subplots of 1 m² (Fig. 1). The distance between sub- and intercanopy subplots was set at the crown diameter of the tree canopy, measured from the edge of the crown. Only medium sized (crown diameter 2.5 – 5 meters), live trees were selected.

Resistance

The resistant component of resilience was quantified through a drought experiment that was initiated in May 2016. The rolling landscape of our study system allowed us to experiment with a novel method to create drought conditions through the use of V-shaped gullies (Fig. 2). The gully redirects rainfall away from the plot, that would normally run over the landscape as overland flow, and gradually infiltrate in the soil (Fig. 2). We developed

this method after we found that herbaceous savanna vegetation was consistently lower in aboveground standing biomass, lower in cover, and had altered species composition in areas situated behind gullies which are repeatedly re-opened by the park management each year to divert water from heavy rainfall events alongside roads frequented by tourists in the Serengeti NP (Fig. S1). We chose NDVI as the response variable as it has been shown to be related to a variety of plant physiological and biophysical parameters such as leaf area index (LAI), green vegetation density, aboveground biomass, chlorophyll content, photosynthetic activity and overall vegetation health (Sellers *et al.* 1992, Nagler *et al.* 2004, Byrne *et al.* 2011).

Fig. 1. Location of the study area in the GSME across two contrasting land-uses: the SNP (protected area, PA) and the LGCA (pastoral village lands, VL) and a graphical representation of the experimental design

We assessed resistance to drought by analysing the ratios of post-experiment (2017) to pre-experiment (2016) vegetation greenness of paired subplots across treatment plots (control – drought) for each block. Pre-experiment vegetation greenness was measured at the same time when gullies were constructed (May 2016) and post-experiment vegetation greenness was measured every month throughout the long rain season (February to June 2017). We took several measurements over the following rain season to consider the role of phenological state on resistance. NDVI was measured using a ground-based system (4-channel SKR-1850 radiometer, Skye instruments). The radiometer was attached on a hand-held pole at a height of 1.25 m, which the manufacturer calculated as the distance above the ground necessary to achieve a 0.25 m² circular sampling area. To cover the whole plot, we took four measurements which were averaged.

Fig. 2. One of the constructed gullies that surround a plot in the national park (upper picture) and a visualization of the process of gradual drying of herbaceous vegetation through the re-direction of rainfall inputs.

Recovery

In order to quantify the recovery component of resilience, we have carried out a ‘pulse experiment’ in which we perturbed the herbaceous vegetation by removing all above-ground herbaceous vegetation up until the root crown with a brush cutter (Honda, UMK 425 LE). This was done at the end of the dry season in October 2016, in order to catch the recovery after the first rains of the short rain season. We then used the aforementioned ground-based NDVI measurement system to assess recovery trajectories for each subplot by measuring NDVI every four days. We monitored recovery for a limited period of time (two weeks after the first rain event following the perturbation) as herbivores will eventually eat away ‘recovered’ green plant material and this will occur faster in village lands. Here, we assume that the initial recovery potential is representative of recovery speed to baseline level (e.g. to levels of an undisturbed vegetation state). Because soil NDVI is highly variable (Montandon and Small 2008) and can greatly influence the outcome especially at low NDVI of the vegetation component (Baret and Guyot 1991), recovery was quantified as the absolute difference between the disturbed state (right after perturbation) and the recovered state. This ensures that the large contribution of the soil component of NDVI (after biomass removal) does not influence the recovery measurements.

Species composition and traits

At the onset of the experiment in May 2016, we visually estimated the percentage cover of each grass species in each 1 m² subplot. The (much lower) cover of the remaining herbaceous vegetation was aggregated to functional types as ‘forbs’, ‘sedges’, and ‘nitrogen fixers’. Distribution of traits was limited to the grass functional group as the herbaceous layer was dominated by this group in both the protected area ($M = 0.88$, $SD = 0.06$) and the village lands ($M = 0.90$, $SD = 0.08$), and also not to mix in a strong phylogenetic signal in the trait responses. Across all plots, we recorded 31 grass species and for each species we collated a mix of life-history, morphological, and physiological traits that may be important in determining competitive ability and response to environmental constraints (drought) and disturbances (grazing): 1) Life cycle (annual, perennial); 2) growth-form (caespitose, mat-forming); 3) photosynthetic subtype (NADP-ME, NAD-ME, and PCK); 4) culm height; 5) leaf width, and 6) leaf length. All traits, except for photosynthetic subtype, were derived from the GrassBase trait database, which offers standardized descriptions on grass species compiled from literature (Clayton *et al.* 2016). Information on photosynthetic subtype for each species was derived from Ingram (2010), Ghannoum *et al.* (2002), and Fish *et al.* (2015).

Root biomass and aboveground standing biomass

At the end of the rain season of 2017, we collected twelve soil cores from the village land and ten from the protected area. Soil cores were taken from control plots, adjacent to a random selection of subplots up until a depth of 15 centimetres. From these soil cores, we separated roots of herbaceous vegetation through wet sieving into 'rhizomes' and 'non-rhizomatous' roots. While root traits (such as elongated rhizomes) can be predicted from species composition, some species exhibit high plasticity in root geometry and root allocation and as such we field measured the distinction. Root biomass was measured after all material was oven-dried. At the same locations, we approximated aboveground standing biomass using a calibrated disc-pasture meter. Two measurements were averaged for each location before using a calibration equation ($R^2 = 0.83$) specific to the Serengeti to convert height (cm) of the disc into herbaceous biomass (kg ha^{-1}) (Unpublished data Smith *et al.*). From these measurements, we calculated root to shoot ratios and rhizome to shoot ratios.

Data analysis

Linear Mixed Models (LMMs) were fitted using the *nlme* package (Pinheiro *et al.* 2017) to assess the effect of the fixed factors 'treatment' (control – drought), 'land-use' (protected area – village lands), and 'canopy' (sub-canopy – inter-canopy) on the post-experiment (2017) to pre-experiment (2016) ratio of NDVI. Subplot within block were included as random effects to account for the paired design. We considered all possible interactions, including a three-way interaction between treatment (disturbance regime), management (park versus village land), and canopy (under versus outside tree canopy). Full models with significant interactions were used for model interpretation. LMMs were also used to examine the effect of land-use and canopy on the recovery of NDVI after the pulse perturbation and on root biomass of the herbaceous vegetation. Tukey contrasts from post hoc tests for mixed-effects models were used to examine pairwise comparisons with the *lsmeans* package (Lenth and Lenth 2018).

Multivariate RLQ analysis and fourth corner analysis were used in a complementary way to get insights into the relationships between species composition, species traits and environmental conditions (Dray *et al.* 2014). RLQ analysis relates a matrix of environmental variables by samples (R), the species abundance by samples matrix (matrix L) and the species by traits matrix (Q). Prior to the RLQ analysis, correspondence analysis (CA) was computed on the species-site matrix while Hill and Smith ordination was used for both the environmental variables-site matrix and the species-traits matrix (Hill and Smith 1976).

The result of the RLQ analysis is a three-way ordination that visualizes trait-environment relationships. In order to quantify these relationships, we used the fourth-corner statistic to test the correlation of traits and environmental variables to RLQ axes (Dray and Legendre 2008). The significance of each correlation was tested with 49999 permutations with two different permutation models, as recommended by Dray and Legendre (2008). The first one (Model 2 in Dray *et al.* 2014) permutes the site vectors and tests whether the distribution of species is dependent upon the environmental variables. The second model (Model 4 in Dray *et al.* 2014) permutes the species vectors and tests whether the distribution of species depends on their traits. The two models are then combined, where a trait is only considered to be significantly correlated if the *P*-values of both models are lower than $\alpha = 0.05$. Lastly, we used the false discovery rate method to adjust the maximum *P*-value for multiple comparisons between traits and axis. All quantitative trait values were log-transformed prior the analyses. The ordination analyses, RLQ statistics and significance tests were all performed using the *ade4* package (Dray and Dufour 2007). All analyses were performed in the statistical environment R, version (3.6.1) (R development Core Team 2019).

Results

Resistance and recovery

Time series of the ground-based NDVI measurements throughout the rainy season of 2017 show an increase in NDVI between February and March, indicating the start of the season (SOS) and a decrease in NDVI between May and June, reflecting the end of the season (EOS) (Fig. 3). Because NDVI values in June approach the soil-component NDVI values (0.200 – 0.300) in the village lands, we limited the resistance analysis to the months March – May. Prior to the onset of the drought treatment in 2016, NDVI values were generally lower in protected area than in village lands due to temporary high grazing intensity by migratory ungulates (Fig. 3). The low pre-experiment NDVI values in 2016 caused a significantly higher post (average March - May 2017) to pre-experiment NDVI in protected areas compared to village lands (LMM, land use effect, $F_{1,14} = 287.98$, $P < 0.001$) (Fig. 4). The drought treatment significantly impacted NDVI of herbaceous vegetation in protected areas (Tukey contrast between control and drought, $P = 0.003$), while no measurable differences in post to pre NDVI were found in village lands (Fig. 4). Tree canopy did not affect the impact of the drought treatment (LMM, canopy effect, $F_{1,49} = 2.64$, $P = 0.111$). The effect of the drought treatment was consistent throughout the season (March to May) and as such we only report the results of the model where we used the average of post to pre NDVI ratios.

The experimental pulse perturbation revealed differences in recovery potential of herbaceous vegetation between land uses that was dependent upon canopy (LMM, interaction effect land-use and canopy, $F_{1,16} = 8.28$, $P = 0.011$). Tukey contrasts showed that inter-canopy vegetation had significantly lower recovery potential than sub-canopy vegetation in village lands ($P < 0.001$) (Fig. 5), while there was no effect of tree canopy in protected area ($P = 0.733$). Furthermore, recovery potential of sub-canopy herbaceous vegetation in village lands was not significantly different from sub-canopy microhabitat ($P = 0.987$) and inter-canopy microhabitat ($P = 0.978$) in protected area.

Fig. 3. Time-series of mean ground-based NDVI in protected areas (dark-green) and village lands (light-green) starting in 2016 (prior to gully creations, pre-experiment) and throughout the wet season of 2017 (post experiment). Error bars show the standard deviation of the mean.

Root to shoot and rhizome to shoot ratios

Root to shoot ratio of the herbaceous vegetation was higher in village lands than in protected areas (LMM, land use effect, $F_{1,9} = 10.70$, $P = 0.010$) and in sub-canopy microhabitat (LMM, canopy effect, $F_{1,10} = 10.73$, $P = 0.010$). Tukey contrasts revealed that sub-canopy root to shoots ratio in village lands was significantly higher than all other groups while inter-canopy root to shoot ratio in protected area was significantly lower than other groups (Fig. 6). The effect of canopy on rhizome to shoot ratio was dependent upon management, where sub-canopy rhizome to shoot ratio was significantly higher than inter-canopy microhabitat, but only in the village lands (LMM, interaction effect land-use and canopy, $F_{1,9} = 5.95$, $P = 0.037$) (Fig. 6). Tukey contrasts furthermore showed that there was no difference in rhizome to shoot ratio between inter-canopy microhabitat in village lands and the protected area (Fig. 6).

Fig. 4. The effect of drought on herbaceous vegetation for each land use, expressed as the ratio of post experiment (average of growing season 2017) to pre experiment (2016) NDVI. Solid and dashed lines represent inter-canopy and sub-canopy plots respectively (N = 72).

Fig. 5. Recovery of herbaceous vegetation in terms of NDVI after pulse perturbation in protected area (left panel) and village land (right panel) for the paired combination of sub-canopy and inter-canopy subplots (N = 36).

Grass communities and traits

The RLQ analysis showed that separation in species composition and traits was generally low in our dataset, as indicated by the rather low eigenvalues of both axes (axis 1: 0.19, axis 2: 0.12). This implies that grass communities across land-use and microhabitat were relatively similar with multiple shared species. Across the combinations of land use (P versus V) and canopy (i versus s), inter-canopy habitat in village land (Vi) and sub-canopy

habitat in protected areas (Ps) were the most important categories in the RLQ in terms of contribution to total inertia, of which Ps was significantly ($P = 0.025$) correlated, while Vi was marginally significantly correlated ($P = 0.054$) with the first RLQ axis (Fig. 7, Table 1). The first axis explained 58% of co-inertia and showed a marginally significant correlation with NAD-ME ($P = 0.088$), meaning that inter-canopy microhabitat in village lands may be associated to this photosynthetic subtype, while sub-canopy habitat in protected areas may have low cover of species with this subtype (Fig. 7). The second axis, explaining 38% of co-inertia, correlated with sub-canopy habitat in village lands and significantly separated 'mat-forming' grass species from 'caespitose' grass species meaning that sub-canopy microhabitat was associated to mat-forming grasses (Fig. 7, Table 1).

Fig. 6. Root to shoot ratio (top panel) and rhizome to shoot ratio (bottom panel) in the Protected Area (PA) and Village Land (VL) and for inter-canopy and sub-canopy subplots ($N = 22$). Groups marked with similar letters were not different (Tukey contrast, $P > 0.05$).

Fig. 7: Ordination diagrams of the first two RLQ axes displaying the positions of grass species in the RLQ space (A) and the co-variation of plant functional traits and environmental groups (combinations of land use and canopy) (B). Environmental groups (Pi, Ps, Vi, Vs) and traits with significant associations to RLQ axis 1 or 2 are shown in bold-italic, while marginal significant associations are given in italics. Full species names for the codes in A can be found in Table S1.

Table 1: Pearson correlations (r) of traits and the environmental groups (combinations of land use and canopy) with RLQ axes 1 and 2 according to the fourth-corner statistics.

	Axis 1	Axis 2
Traits		
Life cycle (annual)	-0.17	0.04
Growth-form (mat-forming)	-0.01	0.31*
Photosynthetic subtype		
NADP-ME	-0.03	0.04
NAD-ME	-0.26*	-0.04
PCK	0.23	-0.01
Culm height	0.12	-0.08
Leaf width	0.17	0.11
Leaf length	0.12	-0.06
Environment		
Pi	0.05	-0.17
Ps	0.28*	-0.02
Vi	-0.21*	-0.12
Vs	-0.08	0.26*

Significance codes: * $P < .1$; ** $P < 0.05$; *** $P < 0.01$; **** $P = 0.001$.

Discussion

Our findings suggest that increasing human activities in the form of livestock grazing decrease the recovery potential, but may increase the resistance of savanna plant communities. The results point into the direction of a trade off in resistance versus recovery at the landscape level, where a change in disturbance regime has likely shifted traits associated to tolerance to pulse disturbance (fire) on one side, versus press disturbance (herbivory and drought) on the other side. Similar trade-offs have been suggested in plant physiology research, which are explained as a compromise between the ability to grow fast under benign environmental conditions and to tolerate stress (Lambers *et al.* 2008). In terms of resilience, this may be extended into trade-offs between individuals, species, communities and entire landscapes, which are inherently fast recoverable in response to perturbation versus those that are not affected by the stress and do not experience major changes in ecosystem functions or other ecological process rates (Nimmo *et al.* 2015). Further, we showed that heterogeneity in the form of trees and associated microhabitat can locally improve the recovery potential of sub-canopy vegetation and thereby of the whole landscape. As the village lands had more livestock but also more trees, these effect compensate each other in their effect on resilience. The identification of drivers that improve resistance or recovery, such as the inclusion of trees in pastoral village lands, is therefore particularly valuable for conservation management in the face of recurring and intensifying disturbance (Standish *et al.* 2014).

Resistance of herbaceous vegetation to drought

Herbaceous vegetation in the protected area was impacted by the drought treatment while vegetation in village lands did not show any response to the experimental gullies (Fig. 4). This implies that the vegetation in protected areas was less resistant (meaning that it was less able to maintain the same level of productivity as the control treatment) to the reduction in water supply compared to the vegetation in village lands. Higher resistance of herbaceous vegetation to drought in village lands can be explained by the history of persistent grazing in pastoral village lands. Due to soil drying effects of high intensity grazing, the herbaceous community in village lands may have evolved to deal with continuous water stress and may thereby be more resistant to experimental drought than the community in the protected area. Physiological tolerance to drought between and within savanna grass species is highly variable (Craine *et al.* 2013) and depends on multiple life-history attributes, including allocation patterns to roots and drought avoidance strategies (Sankaran 2019). Generally, savanna plants with deep roots and that

allocate relatively more to roots than to shoots perform better under droughts (Holdo and Nippert 2015, Sankaran 2019). In this study, drier conditions associated to livestock grazing may have promoted higher root to shoot ratios of the herbaceous layer in the village lands (Fig. 6), which in turn contributed to the higher resistance to experimental drought.

Higher rhizome to shoot ratios may have additionally promoted resistance underneath tree canopies in village lands (Fig. 6). Even though we did not find differences in resistance to drought between sub and inter-canopy microhabitat in village lands, their resistance may have been promoted through different processes. In savannas, a clear functional distinction can be made between 'lawn grasses' and 'bunch grasses', where lawn grasses are characterized by traits that enable plants to withstand both grazing and drought (Coughenour 1985, Veldhuis *et al.* 2014). Examples of traits associated to lawn grasses include basal tillering, elongated rhizomes, and extravaginal branching (Archibald *et al.* 2019). Overall lateral growth-form is adaptive against grazing because leaf material is kept close to the soil, reducing accessibility to herbivores and because stronger root networks associated to mat-forming grasses prevent uprooting (Archibald *et al.* 2019). At the same time, rhizomatous clonal grasses store carbohydrates, nutrients and water in rhizomes (Bai *et al.* 2010) which may improve resistance to drought. This was confirmed by a study performed on different ecotypes of *Cynodon dactylon*, which showed that ecotypes with large rhizomatous networks had superior drought resistance (Zhou *et al.* 2014). These rhizomatous networks may have improved resistance in this study as the RLQ ordination showed that mat-forming grasses were associated to sub-canopy habitat in village lands (Fig. 7), where some subplots were dominated (cover > 50%) by extensive mats of either *Andropogon greenwayi* or *Digitaria abyssinica*.

High grazing pressure in village lands may have additionally shifted the grass community towards a higher cover of NAD-ME species (Fig. 7). While the correlation between inter-canopy microhabitat in village lands and this photosynthetic subtype is only marginally significant, the RLQ ordination showed an association between the two. NAD-ME species are shown to be more drought-adapted than NADP-ME species and possess traits that enable higher water use efficiency at the leaf level (Ghannoum *et al.* 2002). Lastly, high resistance of herbaceous vegetation may have been promoted by phenotypic plasticity of grasses. The RLQ analysis showed only little separation in species composition and traits, meaning that the grass community across land-use and tree-canopy microhabitat was relatively similar. Furthermore, all but one subplot included the abundant and highly variable grass species *Themeda triandra*. In dynamic environments such as savannas, plasticity would not be

dispensable, as a fixed phenotype would be poorly adjusted to variable conditions in water availability and disturbance (Valladares *et al.* 2007). The trait data for each grass species were extracted from literature in this study and therefore does not take into account possible plasticity within species, so the trait differences presented here are likely to be conservative.

We propose that the experimental gullies are a novel, field-based method to offer an economic alternative to rainfall manipulation experiments. Rain-out shelters are mostly used until now, but these are more sensitive to destruction by people or wildlife and can have considerable microclimate effects. While we could not collect quantitative data on actual water budgets and surface flows, the reduction in NDVI in the drought treatment in protected areas suggests that the manipulation was successful. A possible caveat is that the effect of the drought treatment was not measurable in village lands as aboveground herbaceous biomass was not able to accumulate here due to continuous grazing as the growing season progressed. The direct supply of water through rainfall (which we are not able to manipulate here), may have been enough to support the initial stage of regrowth after persistent defoliation by livestock. However, the positive effect of trees on the recovery of herbaceous vegetation in the village lands (Fig. 5) shows that livestock did not remove the effect of canopy and means that there are measurable differences in NDVI, regardless of grazing pressure and the limited potential for biomass accumulation. Moreover, gullies showed observable marks of water flows and we observed water run-on collection inside the gullies (Fig. 2, small picture). Concurrently, patchy senescence of herbaceous vegetation was observed in one of the plots in the village lands (Fig. 8), suggesting that resistance may depend on (unmeasured) local variation in the landscape. The local senescence in this experimental plot additionally supports the claim that the effect of reduction in water run-on can be measured. Future testing of this promising method across different landscapes would benefit from the use of exclosures to allow for biomass accumulation and simultaneous monitoring of infiltration across treatments during rainfall events.

Recovery from perturbation

Recovery of herbaceous vegetation was faster in protected areas than in village lands, but only for inter-canopy subplots (Fig. 5). These results can be partly explained by absolute root biomass differences. Recovery can be slowed without stored reserves, and larger root systems generally allow for quick emergence and resprouting after rainfall (Snyman 2005). Besides resistance, higher root to shoot and rhizome to shoot biomass in sub-canopy microhabitat may have also promoted recovery in village lands. Higher relative root and rhizome biomass in sub-canopy microhabitat are the consequence of tree-grass

interactions but whether it is the outcome of a positive or a negative interaction is unclear. Trees may simultaneously compete for and increase resources to understory grasses in both time and space (Bruno *et al.* 2003, Callaway 2007, Brooker *et al.* 2008), where the net outcome of tree-grass interactions is determined by the balance between the strength of competitive and facilitative processes. In general, and in accordance with the stress gradient hypothesis, competition is expected to have stronger effects on fitness and productivity under low stress conditions (Brooker and Callaghan 1998). Higher stress in village lands, due to persistent livestock grazing, may therefore explain why we only found a positive effect of trees on the recovery of vegetation in village lands. High rhizome to shoot ratios (Fig. 6) and high cover of mat-forming grasses (Fig. 7) in sub-canopy microhabitat in village lands may indicate drier conditions underneath canopies due to evapotranspiration by trees. While the overall effect of nurse trees on herbaceous vegetation is positive, dense networks of rhizomatous ‘mats’ associated to sub-canopy subplots may thus have arisen in response to competition for water as they increase competitive ability by improving rainfall interception at the expense of tree lateral roots. Alternatively, high recovery is linked to stored reserves which may be improved by facilitative effects by trees as they elevate soil nutrients underneath their crown canopies (Belsky 1994, Treydte *et al.* 2007).

Fig. 8. Image of one of the plots subjected to experimental drought in village lands which experienced (local) senescence of the herbaceous vegetation. See Fig. S2 for actual ground-based NDVI values in this plot (Photo credit: Inger de Jonge).

Fast recovery of the herbaceous layer in the protected area after pulse perturbation (Fig. 5) can be explained by alternative strategies associated to fire versus grazer dominated states (Hempson *et al.* 2019). While the protected area in our study area is characterized by frequent fires, fire has been suppressed for more than fifteen years in the Ololosokwan pastoral village lands (Veldhuis *et al.* 2019b). Frequent burning promotes grasses with traits

that make them flammable while grazing is thought to promote palatable, grazing-lawn grasses (Hempson *et al.* 2019). These positive feedbacks suggest that grassy ecosystems have alternative stable states or ‘regimes’ (Hempson *et al.* 2019) with potential implications for resistance to and recovery from perturbation. Besides being highly flammable, fire grasses are characterized by rapid post-fire regrowth enabled by high photosynthetic rates (Ripley *et al.* 2015). While fire may provide specific cues to vegetation for regrowth, herbaceous vegetation response to the complete removal of above-ground standing biomass in our pulse experiment likely reflects the typical ‘fast recovery’ of fire grasses. Fast recovery in these natural landscapes with recurrent fires is considered adaptive as it limits the establishment opportunity of other grasses and plants (Ripley *et al.* 2015), which is of less concern in intensely grazed landscapes.

Conclusion

This study shows that human activities can push savanna ecosystems from a low resistance – high recovery system to a high resistance – low recovery system. Loss of resilience may be a continuous process where initial or intermediate stages are characterized by gradual switches in resistance and recovery that can be closely monitored. As such, these indices can give clues whether a landscape approaches a regime that is grazing-controlled and which elements (e.g. ‘nurse’ trees) in the landscape can provide a ‘helpful resilience-favouring’ regime that would promote transitions back to a fire-controlled savanna (Standish *et al.* 2014). In addition, trees increase the recovery potential in these village lands offering an important tool to mitigate the predicted consequences of climate change in these human-dominated landscapes.

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Supporting Information

Fig. S1. The effect of road-side gullies in the Serengeti National Park on vegetation height (height of longest grass individual), compressed vegetation height as measured with a disk-pasture meter, and percentage bare ground (visual estimation) (N = 40) at 10 and 50 meters distance from the road at both sides from the gully (where negative values represent the plots downslope of the gully). Letter codes give significance ($P < 0.05$) across distance classes (Kruskal-wallis test). Measurements were performed during the short rain season of 2015 as part of a pilot study.

Table S1: Functional traits of grass species found in this study.

species	Species code	lifecycle	Growth-form
Andropogon greenwayi	Angr	perennial	matforming
Aristida pilgeri	Arpi	perennial	caespitose
Bothriochloa insculpta	Boin	perennial	caespitose
Brachiaria semiundulata	Brse	annual	caespitose
Cenchrus ciliaris	Ceci	perennial	caespitose
Chloris gayana	Chga	perennial	matforming
Chloris pycnothrix	Chpy	annual	caespitose
Cymbopogon caesius	Cyca	perennial	caespitose
Cynodon dactylon	Cyda	perennial	matforming
Dactyloctenium aegyptium	Daae	annual	matforming
Digitaria macroblephara	Dima	perennial	caespitose
Digitaria abyssinica	Diab	perennial	matforming
Eragrostis racemose	Erra	perennial	caespitose
Eragrostis tenuifolia	Erte	perennial	caespitose
Eustachys paspaloides	Eupa	perennial	caespitose
Harpachne schimperi	Hash	perennial	caespitose
Heteropogon contortus	Heco	perennial	caespitose
Hyparrhenia filipendula	Hyfi	perennial	caespitose
Hyperthelia dissoluta	Hydi	perennial	caespitose
Microchloa kunthii	Miku	perennial	caespitose
Panicum coloratum	Paco	perennial	caespitose
Panicum maximum	Pama	perennial	caespitose
Setaria sphacelata	Sesp	perennial	caespitose
Sporobolus africanus	Spaf	perennial	caespitose
Sporobolus festivus	Spfe	perennial	caespitose
Sporobolus fimbriatus	Spfi	perennial	caespitose
Sporobolus iocladius	Spio	perennial	caespitose
Sporobolus pellucidus	Sppe	perennial	caespitose
Sporobolus pyramidalis	Sppy	perennial	caespitose
Eleusine multiflora	Elmu	annual	caespitose
Themeda triandra	Thtr	perennial	caespitose

Information on lifecycle, growth-form, culm height (cm), leaf width (mm), and leaf length (cm) were collected from GrassBase (Clayton *et al.* 2016). Information on photosynthetic subtype of each species was deduced from Ingram (2010), Ghannoum *et al.* (2002), and Fish *et al.* (2015).

Photosynthetic subtype	Culm height	Leaf width	Leaf length
NADP-ME	60	4	10
NADP-ME	150	2	35
NADP-ME	200	8	30
PCK	40	15	4
NADP-ME	50	10	25
PCK	220	9	50
PCK	50	5	10
NADP-ME	120	8	30
NAD-ME	40	4	12
PCK	70	7.5	25
NADP-ME	100	5	15
NADP-ME	60	10	12
NAD-ME	80	5	10
NAD-ME	70	3	30
NAD-ME	80	5	18
NAD-ME	52	5	19
NADP-ME	100	8	30
NADP-ME	200	4	30
NADP-ME	300	6	30
NAD-ME	60	2	8
NAD-ME	100	10	30
PCK	200	35	40
NADP-ME	300	17	50
PCK	110	4	40
PCK	60	2	7
PCK	100	5	30
NAD-ME	80	5	30
PCK	75	2	15
PCK	160	10	50
NAD-ME	45	6	26
NADP-ME	200	8	30

Fig. S2. Effect of the gully on herbaceous greenness (NDVI) in one of the drought treatment plots in village lands. Dashed lines represent the gully, where distance is given in the direction of the slope (negative value are inside the drought plot)

Chapter 3

Woody plant encroachment in response to human-induced alterations in fire regime is mediated by functional strategy in an East African savanna

Inger K. de Jonge, Stijn J. Berger, Michiel P. Veldhuis, Han Olff

Abstract

Increasing woody plant encroachment in savanna ecosystems has raised widespread concerns about its potential impact on ecosystem functioning and services. But it is unclear if such encroachment can be explained mostly from regional gradients in land use, fire regime and herbivory, or whether local variation in hydrology and soil conditions is also important, and why. Especially the indirect effect of the environment, through determining the distribution of functional diversity and thus differential capacity of woody species to respond to changing fire and herbivory, is rarely considered.

Here, we used an ecosystem-wide field study in an East-African savanna to assess the role of environmental gradients in rainfall, lithology, soil texture and geomorphology in explaining structural variation in woody plant encroachment across an anthropogenically induced fire suppression gradient. Second, we explored whether the spatial distribution of alternative strategies of woody plants to escape fire and herbivory (bark and height investment, mechanical herbivory defences and growth form) can be predicted from environmental factors, and how this mediates vegetation response to altered fire regimes.

The results show that woody plant encroachment in response to fire suppression is strongest in areas with finer soil textures, lower soil fertility, at intermediate catenae positions and is weaker at the highest rainfall end, together accounting for 41% of total deviance in stem density. Using structural equation modelling, we find support for alternative causal involvements of plant functional strategy, where rainfall, soil sand content and grazing reduce the chance that woody communities are comprised of shrub-like trees, a growth form that increases human-driven woody plant encroachment when dominant in the local community.

These findings demonstrate that the extent of woody plant encroachment in response to alterations in fire regime is highly context-dependent, in both direct and indirect ways. We show how the interplay between environmental factors and functional strategy explain structural variation in encroachment, yielding a new direction for advancing our mechanistic understanding of woody plant encroachment.

Introduction

Savannas cover a large part of the earth's surface and play an important role in the functioning of the biosphere and in supporting people's needs through the provisioning of ecosystem services (Sala and Paruelo 1997, Asner *et al.* 2003, Bond 2008). Over the last decades, a large part of the world's grassland and savanna's is undergoing a transition from herbaceous to woody plant dominance. This has stimulated research on understanding the biotic and abiotic drivers of these vegetation shifts, because such shifts have large ecological consequences for ecosystem functions and services (Eldridge *et al.* 2011, Ratajczak *et al.* 2012, Sala and Maestre 2014). An increasing number of studies link the phenomenon, a process known as 'woody plant encroachment', to regional changes in land use, fire regime and herbivory and global changes in climate (Stevens *et al.* 2016, 2017, Venter *et al.* 2018). Yet, a large amount of variation in the extent and structure of woody plant encroachment at local scales remains poorly understood. Particularly in East-African savannas, where wildlife is being replaced by livestock at an alarming pace, there is no clear framework that explains the strong local heterogeneity in the response of vegetation to fire exclusion.

Over the last two decades, fire and herbivory have been identified as two key processes with strong control over woody cover in savanna ecosystems above a set threshold in mean annual precipitation (MAP) of ~650 mm (Sankaran *et al.* 2005, Lehmann *et al.* 2014). Fire and browsing herbivores maintain open savannas by preventing recruitment of trees and / or reducing trees to smaller size classes (Van Langevelde *et al.* 2003, Staver and Bond 2014). This process indirectly favours grasses, which themselves promote fire, giving rise to a fire-grass feedback maintaining grasslands even at high rainfall (Beckage *et al.* 2009, Oliveras and Malhi 2016). Grazing herbivores can disturb this positive feedback by reducing fuel loads, thereby decreasing fire intensity or suppress fire all together (Scholes and Archer 1997). Sustained grazing over time may even promote an alternative feedback, where woody plants that have escaped the fire and browse traps increase shade, thereby limiting grass growth and thus fuel loads, promoting further woody cover (Oliveras and Malhi 2016). These 'alternative dynamic regimes' explain the dynamic character of savannas and the strong declines or increases of woody cover at decadal time scales in response to ecological perturbations (e.g. large reduction in herbivore populations due to disease outbreaks) (Dublin *et al.* 1990, Sinclair *et al.* 2008). Currently, increased livestock grazing in and around remaining natural savanna landscapes prevents the accumulation of biomass in increasingly large areas. The resulting 'human-driven' fire suppression has promoted woody cover especially along the margins of protected areas (Veldhuis *et al.* 2019b), but with very variable outcomes on local scales.

Not only rainfall, but also soil properties and geomorphology are known to provide context to the effects of fire and herbivory on woody vegetation (Devine *et al.* 2017) with both direct and indirect causal pathways (Fig. 1). Direct effects of environmental factors may for example include facilitation of tree growth at high rainfall and soil nutrient availability which encourages canopy closure in the absence of fire (Higgins *et al.* 2007, Murphy and Bowman 2012). However, the same conditions may increase productivity of grasses and whether trees are favoured may thus depend on factors that affect tree-grass competition, such as rainfall variability (including intensity and intermittency) or soil texture (February *et al.* 2013, d’Onofrio *et al.* 2015). Environmental factors can additionally influence encroachment through complex interactions with legacy effects of historic land use (Fig. 1). For example, high rainfall in combination with strong seasonality can lead to high fire frequencies, which in turn suppresses trees at the sapling stage (Bond and Van Wilgen 1996, Higgins *et al.* 2000). These so-called ‘gullivers’ maintain themselves by photosynthesis in between fires, but under intense disturbance regimes, changed growing conditions, or other habitat alterations, their densities may fall with consequences for the future woody plant encroachment once fire is excluded from the landscape.

Fig. 1. Conceptual models showing current views (left) on how human-driven woody plant encroachment through fire suppression (*hd-WPE*) is determined by abiotic environmental factors (*ENV*), sapling densities (*SAP*) and legacy effects of historic disturbance regimes (*h-DIS*). In this study we hypothesize (right) an additional mechanism via tree functional traits (*F*, orange lines). As outlined in the conceptual models, the indirect effects of the environment on woody encroachment can follow three pathways; through (1) tree recruitment bottlenecks, which may affect encroachment potential, (2) functional strategies that control tree growth and recruitment densities and (3) legacy effects of historic disturbance regimes such as fire return interval and the amount of grazing and browsing, before fire suppression by humans started, which in turn may affect recruitment bottlenecks and functional strategies.

In this study, we hypothesize an additional indirect effect of environmental conditions on the variability of woody plant encroachment via functional traits (Fig. 1, Hypothesis). Recently, Osborne *et al.* (2018) provided an overview of ways with which ecological adaptations of woody plants and grasses mediate the impacts of changing land use, alterations in herbivory and fire regimes, and climate change on woody cover. For example, savanna trees are resilient to tree cutting due to their ability to resprout, a trait that many savanna trees have evolved to cope with top-kill or stem damage due to fire or mega herbivores (Tredennick and Hanan 2015, Twine and Holdo 2016). Over the past years several useful frameworks have been developed to understand alternative life-history strategies of plants, where species are generally subdivided into resisters, tolerators and avoiders of fire, herbivory and drought (Gignoux *et al.* 1997, Archibald and Bond 2003, Staver *et al.* 2012, Dantas and Pausas 2013, Zizka *et al.* 2014, Archibald *et al.* 2019).

Here, we assess the importance of four alternative strategies of woody plants that are potentially relevant to understanding woody plant encroachment, namely *early bark investment*, *strong height investment*, *growth-form*, and *mechanical herbivore defence*. The first two are suggested to be indicative of two contrasting strategies to escape from fire (Gignoux *et al.* 1997, Dantas and Pausas 2013). Trees investing in height growth attempt to locate their canopy as quick as possible above the flame zone before the next fire. They generally rely on high starch reserves in underground crown buds which enable quick and vigorous post-fire *recovery* (Clarke *et al.* 2013). Early bark growth and well protected epicormic buds may allow woody plants to *resist* fire and resprout directly from surviving stems (Gignoux *et al.* 1997, Charles-Dominique *et al.* 2015). As the capacity for fast recovery is generally linked to rapid growth rates, the dichotomy between suites of traits that promote recovery from fire versus those that promote resistance may be helpful in predicting the speed of woody plant encroachment.

The third strategy, *growth-form* is related to a functional distinction that can be made between woody plants that grow as ‘trees’, as ‘trees that are sometimes shrubs’ or ‘shrubs’ (Zizka *et al.* 2014). Zizka *et al.* (2014) found delayed reproduction and promoted investment in height growth for species with a tree-shaped growth form. At the landscape level, poor recruitment may limit the potential of woody plant encroachment and considering functional types that are indicative of lower recruitment are therefore relevant. The role of recruitment is difficult to assess in this context; recruitment by seed is thought to be traded off against sprouting and therefore limited in ecosystems

that are prone to fire (Bond and Midgley 2001). At the same time, we know only little about differences between species and functional types in their sprouting behaviour when it comes to sprouting intensity (density-wise), environmental cues, and root suckering.

The last strategy, *mechanical herbivory defence*, is thought to have evolved to resist browsing by mammalian herbivores. In south African savannas, *Vachellia* and *Senegalia* saplings have adaptations that are structured by a single trade-off in fire and herbivory (Staver *et al.* 2012). Herbivory adapted species resist browsing by forming wide, cagey crowns with large thorns which prevents herbivores from reaching leaves in the inner area of the crown while fire adapted species tend to be less branched and have more of a pole-like structure (Archibald and Bond 2003). The tendency for branching and horizontal growth has potential consequences for vegetation structure when species with these traits are released from fire in areas prone to human disturbance.

There is a need to investigate whether and how these strategies are related to each other and assess their importance and specific roles in mediating vegetation response to alterations in fire and grazing regimes (Osborne *et al.* 2018). Although trait-based approaches have emerged as a very promising way to understand mechanisms that structure plant communities through ecological filtering (Ackerly and Cornwell 2007, Sonnier *et al.* 2010), attempts to use these traits to understand local vegetation changes in response to changed disturbance regimes have so far been limited. Here, we explore the indirect effects of environmental gradients on woody plant encroachment via their effect on functional diversity. Specifically, we ask: 1). To what extent community means of *early bark investment*, *strong height investment*, *growth-form*, and *mechanical herbivore defence* can be predicted from environmental gradients in MAP, soil properties and geomorphology and 2) to what extent the effect of environmental gradients on woody plant encroachment can be explained via indirect effects on functional traits.

Material and Methods

Study area and design

We conducted our work within the greater Serengeti-Mara ecosystem which encompasses approximately 25000 km² of Northern Tanzania and Southern Kenya and includes the Serengeti National Park (SNP), adjacent land management units and game reserves in

Tanzania and the Masai-Mara reserve in Kenya. There is a prominent rainfall gradient from ~350 mm MAP in the southeast to ~1200 mm MAP in the northwest part of the ecosystem (Sinclair 1995). Rainfall is highly variable but generally peaks during a short rain season in December and during the long rain season from March-May. Soils transition from volcanic ash-derived plains in the South-East to granite gneisses in the North (Jager 1982). Vegetation is influenced by both rainfall and soil type and can be broadly classified into the South-eastern grass plains, West-central Acacia woodlands, and northern broadleaf woodlands (Sinclair 1995)

Satellite-imagery have revealed substantial illegal grazing by livestock inside protected areas, leading to large-scale fire suppression along the margins of protected areas (Veldhuis *et al.* 2019b). In this study, we quantified woody plant encroachment in zones inside protected areas subject to at least ten years of this form of human-driven fire suppression across the ecosystem. Vegetation plots (N = 192) followed a paired design, where each plot in a zone of human-induced fire suppression is paired with a plot in a control zone with no human disturbance, experiencing the same abiotic environmental conditions (Fig. 2). The study was designed to capture important resource gradients, which may affect functional strategy and overall productivity of savanna vegetation. At the largest spatial scale, vegetation plots are therefore distributed over a rainfall gradient from 650 MAP to 1100 MAP. On local scales we included the effect of catenae (Fig. 2b), which is a major source of landscape heterogeneity in this ecosystem, associated with strong soil differentiation and redistribution of rainfall (Khomu *et al.* 2011). Lastly, plots were located to maximize local variation in soil sand content and exchangeable bases. Sand content (as a component of soil texture) is an appropriate indicator of hydraulic properties of the soil, with important consequences for water availability in savanna's (Rodríguez-Iturbe and Porporato 2007). The sum of exchangeable bases, which include potassium (K), calcium (Ca), magnesium (Mg) and sodium (Na), was used as an indicator of soil nutrient status.

Human-driven woody plant encroachment

Around each central location of a plot we determined woody density within four size classes based on stem diameter at 30 cm height (size class 1; < 1 cm stem diameter, size class 2; > 1 and < 4 cm, size class 3; > 4 and < 15 cm; and size class 4; > 15 cm). Rather than using a fixed size plot, we sampled the closest individuals to a fixed GPS point, resulting in circular plots which are density dependent in size. This secures a similar sampling effort for different size classes instead of the strong oversampling of saplings and under sampling of large individuals characteristic of fixed plot sizes. For size class 1 and 2 we sampled the nearest 20 individuals,

for size class 3 the nearest 15 individuals and for size class 4 the nearest ten individuals. Densities were then calculated for each size class by dividing the number of individuals by the (variable) sampled area assuming a circular plot with the distance to the furthest sampled individual as radius. As catenae gradients cause relatively fine-scale landscape heterogeneity, we never sampled beyond a radius of 50 meters resulting in ‘treeless’ vegetation plots in at least some areas. For each individual, the species identity was determined. We recorded stem diameter using an electronic calliper for trees with stems thinner than 15 cm, otherwise a tape measure was used to measure stem circumference (diameter was calculated assuming round stems). Quantification of human-driven encroachment was restricted to the size class of size class 3, as the goal of the study was to determine what changed in terms of vegetation structure during the last 10 to 15 years as a result of human-induced fire suppression, while younger individuals reflect changes in shorter time spans.

Fig. 2. Study design showing vegetation plots (N = 192) along the margins of the ecosystem in zones of human driven fire suppression and control zones with no fire suppression (a). Plots follow a paired design where each plot in a zone of human-induced fire suppression (FS) is paired with a plot at the same catenae position in a control zone with no human disturbance (C) (b). Zones of high human activity in protected areas are readily visible through ‘livestock’ tracks (red lines in b). Vegetation plots were always kept at least 100 meters away from these tracks and 250 meter away from the park boundary. The red colours in the figure on the right reflect a high catenae position, while the blue colours reflect a low catenae position, calculated as the deviation from mean elevation (DEV), which measures the topographic position of the central point using TPI (neighbourhood of 1500 m) divided by the standard deviation of the elevation.

Recruitment limitation of tree establishment

Trees can be low in abundance because they hardly recruit (e.g. due to low seed set, seed or seedling predation, or unsuitable environmental conditions for seedlings), or because of low survival from the sapling to tree stage. The first explanation for low tree density, and thus an open vegetation, is called recruitment limitation (Nathan and Muller-Landau 2000). In a similar way as how we calculated tree density, we calculated densities for both sapling size classes (size class 1 and 2). We consider both groups for quantifying recruitment limitation as control zones are distributed across the ecosystem, causing variation in disturbance regimes year to year. This has consequences for interpreting saplings densities in the youngest classes, as one zone could have burned during one year, while another zone burned the preceding year. Therefore, we classified areas as being recruitment limited when the density of total saplings was lower than four individuals per 100 m², as this density would be needed to reach a closed canopy assuming each individual reaches a crown diameter of at least six meters at maturity. While some (smaller) woody species, such as *Dichrostachys cinerea* and *Ormocarpum trichocarpum*, may not reach crown diameters of six meters, they can reproduce vegetatively, reducing the importance of actual sapling density. Each control plot was thus binary classified as being recruitment limited or not.

Disturbance legacies

In order to explain the variability in woody plant encroachment, we consider both the legacy effect of historic disturbance regimes (before human-induced fire suppression started) and 'current' disturbance regimes. Increasing human activities in boundary zones have not only led to fire exclusion, but have most likely also led to changes in the intensity and frequency of grazing and browsing by native ungulates. We used dung counts in transects of 50 m long and 2 m wide across vegetation plots to estimate abundance of livestock, grazing wildlife (including mixed-feeders) and browsing wildlife in both control plots (historic disturbance) and fire suppression plots (current) (see Table S1 for species list and functional guilds). The historic fire regime in control plots was considered by calculating the proportion of years with fire between 2000 and 2016 using the MODIS MCD64A1 Burned Area Product Collection 6 (Giglio *et al.* 2009), assuming that this frequency reflects the historic fire regime of the fire-suppressed paired sites.

Functional strategies

For 17 of the most abundant woody species, together accounting for 93% of all the individuals observed in the vegetation plots in the study, we sampled ≥ 20 individuals (stem diameter ≥ 1 cm, ≤ 8 cm) and measured the stem diameter, stem height and bark

thickness. Only for *Vachellia nilotica* (N = 5) and *Albizia harveyi* (N = 6) we used fewer individuals as we did not encounter more saplings of these two species. We measured bark thickness using a standard bark gauge to the nearest millimetre (Haglof, Barktax, Sweden). Thickness and stem diameter were measured between 10 and 50 cm height, as this is the zone of fire impact on tree stems. The gauge was inserted until resistance by the sapwood was felt. *Early bark investment* was quantified for each species by taking the slope of the regression between stem diameter and bark thickness (Hempson *et al.* 2014).

Diameter-height allometry is informative of how fast a woody plant gains height relative to stem diameter and was therefore used to quantify *height investment* for each of the 17 species. We used the same individuals that were measured to quantify *early bark investment*, but discarded individuals which were heavily browsed or damaged. We used additional measurements on undamaged woody plants up till a height of 12 meters. Both height and stem diameter were log transformed in order to fit linear regressions. For each species, we extracted the slope of the regression between height and stem diameter as a measure of *height investment*.

For *growth form*, we adopted the classification of woody plants into ‘trees’ (T), ‘trees that are sometimes shrubs’ (SST), and ‘shrubs’ (S), first used by Zizka *et al.* (2014). None of the woody species that we encountered identify as shrubs without occasionally growing as trees, so we discarded the S category. Information on *growth form* of woody plants were extracted from Herlocker (1974), which until now offers the most complete description of vegetation in the Serengeti-Mara ecosystem, and from a collection of East-African reference sources (Brenan 1960, Wickens 1973, Gillett 1991, Sands 2003).

Mechanical herbivore defence was classified as being ‘high’ or ‘low’ based on traits that mediate bite size of herbivores such as the presence of hooks and leaf to spine ratio (Cooper and Owen-Smith 1986, Charles-Dominique *et al.* 2015, Charles-Dominique *et al.* 2019). While structural defences, such as cagey architecture, are indicative of mechanical defence as well, they are less suitable in this study as ‘caginess’ is highly variable within species and inducible upon increased levels of browsing. Species with either hooks (generally, the *Senegelia* species) or larger spines than leaves were classified as having ‘high’ mechanical herbivore defence while species having neither were classified as having ‘low’ mechanical defences.

Community means

Community means for each trait were calculated based on the presence of species in the fire suppression plots. The calculation of community means was restricted to the fire suppression plots because multiple control plots were without woody individuals. Because fire suppression may have released the constraints for particular functional types, only species with individuals belonging to size classes 3 and 4 were used to calculate the community mean for each trait. Trait values for each species were summed and divided by the total amount of species present. Generally, trait based models of plant community assembly assume that community weighted mean (CWM) trait values reflect the optimal strategy in a particular site, given the regional species pool (Shipley *et al.* 2011). As such, species with traits that are nearest to CWM values in that site, are expected to have the highest fitness and thus the highest abundances (Shipley *et al.* 2011). In this study, 'abundance' is influenced by human-driven fire suppression. Because our goal is to assess the causality between multiple environmental factors and human-driven woody plant encroachment, we consider community means (CM's) instead of CWM's.

Environmental gradients

We used a modified topographic position index (TPI) algorithm to construct a landform map based on a digital elevation model (DEM), derived from global C-band shuttle radar topographic mission (SRTM), with 30 m pixel resolution. TPI measures the relative topographic position of a central point as the difference between the elevation at this point and the averaged elevation within the direct neighbourhood (Weiss 2001). The TPI values typically range between -1 and 1, where positive values indicate that the central point is located higher than the surroundings while negative indicate a position lower than the surroundings. By using TPI at different scales (e.g. different neighbourhood sizes), both major landscape units, such as mountains and alluvial areas, and smaller features such as catenae positions along pediplains and minor drainages can be distinguished (Grohmann *et al.* 2009). Recently, de Reu *et al.* (2013) showed that multi-scale TPI can produce erroneous classifications in heterogeneous landscapes. The Deviation from mean Elevation (DEV), which measures the topographic position of the central point using TPI divided by the standard deviation of the elevation (SD), was found to produce more accurate landform classifications in heterogeneous landscapes (De Reu *et al.* 2013). As the Serengeti-Mara ecosystem is an example of geomorphological heterogeneity due to volcanism, we performed the landscape classification using DEV with a neighbourhood of 1500 m. The produced map was then used to distribute the five plots over a local catenae gradient (Fig. 2b).

We used digital maps from Africa Soils Information Service for both soil sand content (w%) and exchangeable bases (cmol/kg) at a resolution of 250 m as measures of respectively soil texture and soil fertility (Hengl *et al.* 2017). As most water and nutrient uptake takes place in the soil's top layers, we used the depth horizon of 5 – 15 cm for both soil properties (sd2) (February and Higgins 2010). MAP was calculated based on the 0.05° gridded rainfall dataset from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) (Funk *et al.* 2015)

Data analysis

Bivariate relationships between trait values of woody species were analysed with Pearson's correlations to assess whether traits of woody species in the study area are independent from each other and can be considered as 'alternative' strategies. To assess how community means of traits, disturbance regimes, woody plant density and recruitment limitation are related to environmental gradients (MAP, soil sand content, exchangeable bases, catenae position, and a quadratic term for catenae position), we used a series of Generalized Linear Models (GLM's) with different error distributions and link functions. Quasi-binomial distribution and logit link function were used to assess the effect of environmental gradients on the community means of *growth-form* (proportion of species identifying as 'T's in the community) and *mechanical herbivore defence* (proportion of species with 'high' mechanical herbivore defences in the community). We analysed variation in tree densities in fire suppression zones (human-driven WPE), grazer abundance, browser abundance, and livestock abundance across environmental gradients with GLM's assuming a negative binomial distribution with a logarithmic link function. We opted for a negative binomial distribution because of overdispersion and a quadratic relationship between the mean and variance (Ver Hoef and Boveng 2007). For the binary variable recruitment limitation, we used GLM's with a binomial distribution and logit link function. Lastly, we used multiple linear regression to relate environmental factors to community means of the principal component axis which summarizes *early bark investment* and *height investment* (see results, first section).

For all models, we first constructed a maximal model including all predictors and stepwise eliminated non-significant terms (based on *P*-values) to yield a minimal adequate model (Crawley 2012). Full models were used to construct partial residual plots using the *Visreg* package (Breheny *et al.* 2019) and compute standardized beta-coefficients using the *Quantpsych* package (Fletcher and Fletcher 2010) to assign relative importance to predictor variables. Model fit was assessed using D^2 which is the proportion of deviance explained by each model relative to the null model. All models were tested for multicollinearity (variance inflation < 2.0) using the *car* package (Fox *et al.* 2012).

We used structural equation modelling (SEM) to analyse via which pathways environmental conditions affect human-driven woody plant encroachment. The goal of SEM is to understand causal relationships in systems by evaluating the statistical fit between abstract ecological theories and empirical data (Shipley 2000, Grace 2008). We chose the SEM approach because we aim to evaluate both the direct effects of the environment as well as its indirect effects, via functional traits, disturbance regimes, and recruitment limitation on human-driven WPE. We used the conceptual models described in Fig. 1 to develop a series of structural equation models (SEM's) and tested their fit based on AIC using the *PiecewiseSEM* package (Lefcheck 2018). In order to make objective comparisons between models with varying numbers of predictors and responses, we made the models nested prior to model evaluation (Lefcheck 2016). All analyses were performed in the statistical environment R, version (3.6.1) (R development Core Team 2019).

Results

Tree functional traits

Woody species found in the Serengeti-Mara ecosystem show differences in functional trait values for both *early bark investment* and *height investment* (Table S2). The results of the Pearson correlation tests between these two traits show that they were highly correlated ($r = 0.80$, $N = 17$, $P < 0.001$) (Table 1, Fig. S1) implying that differences between species are driven by one adaptive strategy. Therefore, we summarized the values for these traits in one principal component (from here onwards *bark to height investment*), of which the community means are considered in the rest of the study. No correlations were found between *bark to height investment* and the other functional traits (data not shown), implying that these traits were independent from each other and that their distribution across environmental gradients and their roles in mediating impacts of fire suppression can be assessed separately.

Community trait means across environmental gradients

Community means of growth form were best predicted by MAP ($P < 0.001$) and soil texture ($P < 0.001$) where woody plant communities in areas with higher MAP and higher fraction of sand had relatively more T's than SST's (Fig. 3, Table 2). Catenae was the only significant predictor of the community mean for *bark versus height investment*, where communities consisted relatively more of species investing in bark and/or less

in height higher up the catenae ($P < 0.001$) (Fig. 3, Table 2). Lastly, community means of the proportion of mechanically defended tree species were higher at low MAP ($P < 0.001$) and at lower catenae position ($P = 0.004$).

Table 1. Correlation between the measured functional traits for the most abundant woody species found in the study areas ($N = 26$). Pearson correlation coefficients are shown, with associated significance levels.

Functional trait	T1	T2	T3	T4
T1. Early bark investment†	-	0.80***	-0.42	-0.15
T2. Diameter - height allometry†		-	-0.08	0.22
T3. Mechanical herbivore defence (high)			-	0.32
T4. Growth-form (tree)				-

† Early bark investment and diameter-height allometry were measured for a total of 17 species. The class that is given a value of 1 for the binary variables Mechanical herbivore defence and Growth-form (0/1-coding) is given between brackets. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Historic and current disturbance regimes

The environmental gradients showed different associations with historic disturbance regimes across the ecosystem (all model summaries can be found in Table S3). In control areas, dung counts of grazing herbivores were highest in areas with high exchangeable bases (ANODEV, Deviance = 49.9, $d.f. = 1,94$; $P < 0.001$) and high fractions of sand (ANODEV, Deviance = 30.65, $d.f. = 1,93$; $P < 0.001$). Dung counts of browsers were highest in drier areas (ANODEV, Deviance = 16.11, $d.f. = 1,94$; $P < 0.001$) and in areas with lower fractions of sand (ANODEV, Deviance = 8.72, $d.f. = 1,93$; $P = 0.003$). The chance of a fire in control areas in the last 16 years increased with MAP (ANODEV, Deviance = 8.69, $d.f. = 1,94$; $P < 0.001$) and exchangeable bases (ANODEV, Deviance = 1.04, $d.f. = 1,93$; $P < 0.001$). The main form of disturbance in areas subject to human-mediated fire suppression (current disturbance) is grazing livestock (cattle) (Fig. S2). Similarly to grazing wildlife, dung counts of livestock were found to be highest in areas with high exchangeable bases (ANODEV, Deviance = 5.75, $d.f. = 1,94$; $P = 0.017$) and with higher fraction of sand (ANODEV, Deviance = 4.07, $d.f. = 1,93$; $P < 0.044$).

Recruitment limitation and human driven woody plant encroachment

Recruitment limitation in control areas was poorly predicted by environmental factors, with a total explained deviance of only 13% (Table 3). The minimal adequate model showed that the chance to find at least four saplings per 100 m² decreases with fraction of sand ($P <$

0.001) and with exchangeable bases ($P < 0.001$). Human-driven WPE in terms of woody plant densities in fire suppression zones was reasonably predicted based on environmental factors, with a total explained deviance of 41% (Table 3). All environmental predictors were part of the minimal adequate model, with the strongest effect of fraction sand ($P < 0.001$), which had a negative effect on the density of woody plants in fire suppression plots (Fig. 4). Soil fertility ($P < 0.001$) and MAP ($P = 0.044$) both had negative effects on woody plant encroachment, while catenae had a significant non-linear effect on encroachment with highest tree densities at intermediate catenae positions ($P = 0.009$) (Table 3, Fig. 4).

Table 2. Analysis of deviance results for environmental factors ‘fraction of sand’ (Sand), ‘Exchangeable bases (EXBA), ‘catenae position’ (Catenae), and MAP used in generalized linear models explaining variability in the community means of different functional traits. The minimal adequate model was obtained by elimination of non-significant terms, beginning from the maximal model.

Variable	Predictor	df	Res. Deviance	Prop. Deviance	Res. d.f.	F	P
Growth-form	null		61.39		95		
	MAP	1	55.19	0.10	94	14.49	<.001
	Sand	1	49.89	0.09	93	12.36	<.001
	EXBA	1	49.71	<0.01	92	0.42	0.515
	Catenae	1	49.70	<0.01	91	0.02	0.885
Bark to height investment	null		56.35		95		
	Catenae	1	41.82	0.26	94	32.69	<.001
	Sand	1	40.64	0.02	93	2.65	0.088
	MAP	1	40.53	<.01	92	0.23	0.533
	EXBA	1	40.44	<.01	91	0.20	0.654
Mechanical herbivore defence	null		53.97		95		
	MAP	1	42.42	0.21	94	33.87	<.001
	Catenae	1	39.42	0.06	93	8.81	0.005
	EXBA	1	39.25	<.01	92	0.48	0.447
	Sand	1	39.21	<.01	91	0.14	0.710

The proportion deviance (prop. Deviance in table) is the proportional decrease in residual deviance relative to the null model. The ordering of predictors in the model is based on significance (p-value) in order to demonstrate the added importance (in terms of explained deviance) for each predictor.

Fig. 3. Partial residual plots of the variability in community means of growth form, bark versus height investment and mechanical defence against herbivores explained by MAP, fraction of sand, exchangeable bases and catenae position. The partial residuals plots are based on a full model and allow for the evaluation of the effect of each variable on the response variable, given the effect of the other predictors in the model. The vertical axis has been transformed to show the response of the dependent variable, and as such the residuals are displayed as a rug at the bottom of each panel. See Supplementary Table 2 for a summary of the models.

Alternative pathways for the effect of environmental factors on Woody plant encroachment

Structural equation models indicated that gradients in environmental conditions can impact human-driven woody plant encroachment in multiple ways, through direct and indirect effects (Fig. 5). The SEM which yielded lowest AIC values included indirect effects via community mean of *growth form*, historic disturbance in grazing, and recruitment limitation of saplings (Fisher's $C = 31.23$, d.f. = 34, $P = 0.604$) (Fig. 5, A). Including historic disturbances into the structural equation model improved statistical fit ($\Delta AIC > 2$), implying

that at least part of the effects of the environment were likely to run via 'contexts' shaped by fire regime and grazer abundances. The results of this SEM show that *growth-form* had a negative effect on the density of encroachment, indicating that areas with relatively more woody species that identify as *T*'s rather than *SST*'s were less encroached ($P < 0.001$). Control plots which were classified as being not recruitment limited had a positive association to woody plant encroachment found in fire-suppression plots ($P = 0.016$). Both *growth form* and recruitment limitation were influenced by historic disturbance by grazers. The proportion of species that identify as *T*'s in the community was positively associated with grazer abundance ($P = 0.028$) and recruitment limitation increased with grazer abundance ($P < 0.001$). Recruitment limitation was additionally affected by historic fire regime, where low fire frequencies were associated to recruitment limitation ($P = 0.037$).

Table 3. Analysis of deviance results for environmental factors 'fraction of sand' (Sand), 'exchangeable bases' (EXBA), 'catenae position' (Catenae), and MAP used in generalized linear models explaining variability in human-driven woody plant encroachment (woody plant density in fire suppression plots, negative binomial regression) and recruitment limitation (binomial regression). The minimal adequate model was obtained by elimination of non-significant terms, beginning from the maximal model.

Variable	Predictor	df	Res. Deviance	Prop. Deviance	Res. d.f.	P
hd-WPE	null		178.96		95	
	Sand	1	144.64	0.19	94	<.001
	EXBA	1	118.44	0.15	93	<.001
	Catenae	1	117.01	0.01	92	0.231
	Catenae ²	1	110.20	0.04	91	0.006
	MAP	1	106.14	0.02	90	0.045
Recruitment limitation	null		129.69		95	
	Sand	1	120.94	0.07	94	0.003
	EXBA	1	113.15	0.06	93	0.005
	Catenae	1	110.38	0.02	92	0.096
	MAP	1	109.67	0.01	91	0.340

The proportion deviance (prop. Deviance in table) is the proportional decrease in residual deviance relative to the null model. The ordering of predictors in the model is based on significance (p-value) in order to demonstrate the added importance (in terms of explained deviance) for each predictor.

Regarding the environmental factors, the results of this SEM show that the fraction of sand had direct ($P < 0.001$) as well as indirect effects via *growth form* ($P = 0.021$) and grazer abundance ($P < 0.001$) on woody plant encroachment. The effects of MAP on woody plant

encroachment is found to be complex, with multiple indirect pathways and no direct effects. MAP had negative indirect effects via growth-form ($P < 0.001$) and a negative indirect effect via historic fire disturbance ($P = 0.006$) and historic grazer disturbance ($P < 0.001$). On the other hand, positive indirect effects of MAP on woody plant encroachment include the negative effect of MAP on historic grazer abundance ($P = 0.004$) and the positive effect that historic fire disturbance has on the chance that areas are not recruitment limited. The non-linear effect of catenae position appeared to be direct, with highest levels of encroachment at intermediate catenae position ($P = 0.045$). Additionally, the model with best statistical fit included an indirect positive effect through recruitment limitation, where the chance of areas being recruitment limited decreased higher up the catenae ($P = 0.043$). The negative effect of soil fertility (exchangeable bases) on human induced woody plant encroachment was both direct and indirect via a positive effect on historic grazer disturbance (both $P < 0.001$).

Fig. 4. Partial residual plots of the variability in human-drive encroachment of woody plants in plots subject to fire suppression explained by MAP (mm), sand (g/100g), exchangeable bases (cmolc kg⁻¹) and catenae position. The partial residual plots are based on a full model and allow for the evaluation of the effect of each predictor on the response variable, given the effect of the other predictors in the model. The vertical axis has been transformed to show the response of the dependent variable, and as such the residuals are displayed as a rug at the bottom of each panel. Note that the effect of catenae is non-linear, hence a beta-coefficient is lacking. See Table 3 for a summary of the model.

Fig. 5. Results of alternative SEM models (A – C) explaining variability in human-driven woody plant encroachment (hd-WPE). The coloured boxes display environmental abiotic factors included in the SEM's; MAP, fraction of sand (SAND), exchangeable bases (EXBA), and catenae position (CAT). Black boxes represent response variables included in the SEM's; community mean of *growth-form* (GF), historic disturbance by grazers (grazers), historic disturbance due to fire frequency (Fire), tree recruitment limitation (RL), and current livestock disturbance (livestock). Black arrows represent positive effects while grey arrows represent negative effects, with the exception of the effect of catenae (CAT), which has a quadratic effect on encroachment, with highest levels at intermediate catenae position (model A). Dashed arrows represent non-significant paths and dashed boxes represent response variables that were not included in the respective model. R² values associated with the response variables are Nagelkerke's pseudo R² and are indicative of the proportion of explained variation by relationships with other variables. No standardized path coefficients are available as the SEM is based on Generalized linear models (Lefcheck *et al.* 2017). Instead, we used p-values to visualize relative importance of relationships through arrow widths.

Historic disturbance by browsers did not have significant relationships to community means of *growth form* or recruitment limitation and were therefore not included in SEM models. Additionally, it appeared that current disturbances by native grazers or browsers did not have significant effects on human-driven encroachment. Also, community mean values of *bark versus height investment* and *mechanical herbivore defence* had no significant effect on woody plant encroachment. In alternative SEM's, current livestock disturbance had significant negative effects on woody plant encroachment (Fig. 5, B and C), where livestock disturbance itself was found to be higher at higher soil fertility and higher in areas with more *T*'s in the community. While AIC values of these alternative models are higher than model A ($\Delta AIC > 2$), they did produce acceptable fits in terms of Fisher's C and significance.

Discussion

The goal of this study was to understand local variation in human-driven woody plant encroachment and whether functional diversity has a role in mediating vegetation response to human-induced fire suppression through livestock grazing. Here, we showed how this variation can be explained through various causal pathways in which environmental gradients in rainfall, soil texture, soil fertility, and catenae predict the intensity of woody plant encroachments through effects on (pre-human interference) disturbance regimes, recruitment limitation, and community means of *growth form*. The SEM results provide a new framework in which we can understand the role of environmental factors in predicting woody plant encroachment in situations where anthropogenic pressures change ecosystem functioning.

Traits across environmental gradients

Woody species in the Serengeti-Mara ecosystem show variation in functional traits that are thought to be related to the way in which they cope with disturbances in fire and herbivory (Table S2). At least three independent traits can be distinguished for woody species (*growth form*, *bark versus height investment*, and *mechanical herbivore defence*) (Table 1), which were chosen based on existing frameworks on alternative life-history strategies. This suggests that woody plants can, to a certain extent, have different combinations of these traits; species with relatively high resistance against browsers through mechanical defence can for example exhibit an resistance (e.g. *Vachellia nilotica*) or tolerance (e.g. *Vachellia seyal*) strategy towards fire as indicated by their trait value for *bark versus*

height investment (Table S1). The results show that community means of *growth-form*, *bark versus height investment* and *mechanical herbivore defence* are also explained by different combinations of environmental gradients (Fig. 3, Table 2). Both *growth-form* and *bark versus height investment* are considered to be important indicators of fire escape strategy (Gignoux *et al.* 1997, Dantas and Pausas 2013, Zizka *et al.* 2014), implying that environmental gradients predict which combination of traits are most adaptive to cope with fire.

Zizka *et al.* (2014) showed that woody species that identify as T's have different resprout strategies after fire than SST's, where T's invested in less but bigger shoots than SST's. This difference could make SST's less competitive in areas with very frequent fires. While we did find an increase in the proportion of T's in the community with MAP (Table 2, Fig. 3), which is positively associated to fire frequency (Table S3), the SEM with the best statistical fit did not include a direct relationship between historic fire frequency and community means of *growth form* (Fig. 5A). While SEM's should be seen as 'hypothesis generating' rather than actual scientific support for 'one mechanism', there could be other effects (and pathways) associated to soil sand content and MAP that favour T's over SST's. East-African savannas are highly seasonal, which means that woody plants simultaneously face periodic droughts, fire and herbivory. Risks associated to drought, such as cavitation, increase with tree height which explains why many trees are dropping their leaves in the dry season. However, there are also difference in root systems between T's and SST'; excavation of four savanna woody species revealed that root systems of species identifying as SST's were relatively shallow and laterally extensive, while roots of the two T's were more prevalent in deeper soils (O'Donnell *et al.* 2015). At the most extreme, we find T's such as *Vachellia tortilis*, typically found on sandy soils, using deep taproots to extract water from deeper soil layers (Belsky 1994). A higher community mean of *growth-form* on sandy soils can perhaps be explained by reduced drought associated risks for T's compared to SST's as more rain will percolate to deeper soil layers. Another potential pathway (as revealed by the SEM) goes via historic grazing disturbance which was directly positively associated to *growth-form* (Fig. 5, A). A possible explanation is that trees, by channelling more resources to one big shoot (Zizka *et al.* 2014), are less sensitive to the negative impacts of high grazing disturbance (repeated trampling or bulk grazing).

The most adaptive strategy for woody plant in savannas should be the outcome of multiple drivers, acting at the same time. Dantas and Pausas (2013) showed that there are relatively more 'corky' species (*early bark investment*) in Neotropical savannas than in African savannas and that this can be explained by the presence of browsers in the latter. The lanky

strategy (thinner bark, *height investment*) is suggested to be more adaptive in areas that experience high levels of browsing pressure as early height growth will locate the canopy above the influence zone of both fire and browsers (Bond *et al.* 2012, Dantas and Pausas 2013). Such interactive effects of different disturbances in shaping plant traits has received only little attention and we are just beginning to understand to what extent traits associated with resistance and tolerance against fire and herbivory are aligned (Archibald *et al.* 2019). The interaction between the two may be a possible explanation for the contrasting effects of catenae position on the community means of *mechanical herbivore defence* and *bark versus height investment*. At lower catenae positions, we found relatively more 'lanky' (*height investment*) species and more species with high mechanical herbivore defence (Fig. 3, Table 2). While we didn't find a significant effect of catenae position on dung counts of native browsers or grazers in this study, impacts of native herbivores over longer time periods may have been higher. Catenae position affects particle and colloid transport processes (which generally lead to richer soils) and redistributes water which makes areas positioned low at the catenae more attractive to herbivores, as long as visibility is high (Anderson *et al.* 2010, Khomo *et al.* 2011). At the same time, 'corky' strategy may be more adaptive higher up the catenae; low productivity may restrict the ability of a resprouter to re-occupy a site after a disturbance event and may promote traits associated with typical fire resisters, such as bark investment (Hoffmann *et al.* 2012). Lastly, fire intensity is expected to be higher at lower catenae positions due to higher fuel loads. Trees investing in bark attempt to protect meristems from heat and generally have epicormic buds which allow them to resprout directly from surviving stems (Trollope and Tainton 1986). The success of protecting stems and buds may drop with increasing fire intensity (Williams *et al.* 1999), leading to increases in top-kill in young trees (Higgins *et al.* 2012).

Variability in human-driven woody plant encroachment

Human-driven woody plant encroachment was strongest in areas with finer soil textures, lower soil fertility, at intermediate catenae positions and is weaker under higher rainfall conditions. The SEM results suggest that these effects are mediated by functional strategy via community means of *growth-form* (Fig. 5A). An explanation for increased woody plant encroachment in areas which favour SST's over T's may be higher or faster rates of recruitment after the removal of fire from the landscape. T's delay reproduction and allocate more resources to height growth (Zizka *et al.* 2014). Woody communities that are dominated by T's thus require large, mature trees in the vicinity in order to encroach an area over short time spans. In contrast, areas which favour SST's have high potential rates of woody recruitment even in the absence of large individuals.

Another explanation for higher woody plant encroachment in areas which favour SST's is differences in root suckering between species and functional types. Two abundant SST's in East-African savannas, *Ormocarpum trichocarpum* and *Dichrostachys cinerea*, are known for their clonal life-history and their vigorous root suckering (Wakeling and Bond 2007, Anderson *et al.* 2015). Root suckering species keep their regenerative organs (including bud banks) and resource reserves underground, making them less sensitive to impacts of fire (Clarke *et al.* 2013). This explains why root suckering as a trait is quite common in savannas, especially in woody plants with unprotected aboveground buds and / or with low bark growth rates (Charles-Dominique *et al.* 2015, Charles-Dominique *et al.* 2017). Root-suckering plants have plenty belowground sites for resprouting and therefore need to allocate less resources to bark protection. This may make root suckering species more likely to be top-killed by fire than non-root suckering species, but production of numerous root suckers after fire is suggested to be more efficient in terms of regeneration of foliage than canopy resprouting (Charles-Dominique *et al.* 2015). In this study, SST's such as *O. trichocarpum*, *D. cinerea*, *Vachellia gerrardii*, and *Vachellia drepanolobium* had locally high sapling densities and the highest reported in this study. Whether these saplings were actual root suckers is unclear as this would have required excavation of the root system. However, high sapling densities in combination with reports that these species are reputable for their root suckering abilities (Bellefontaine 1997), points towards a trade-off in allocation of resources where T's may invest more in height gain to escape the fire-trap while SST's may rely more on underground structures because of their vulnerability to disturbance in terms of top-kill. Root suckering is, however, not exclusive to SST's and the reputability of *Combretum molle* to produce root suckers (Bellefontaine 1997) may explain why this species is locally encroaching (Fig. 6).

We hypothesized that contrasting strategies to escape fire can mediate vegetation response to fire suppression through increased post-fire resprouting. This was based on frameworks first proposed by Gignoux *et al.* (1997) which described these strategies as *hide-and-resprout* versus *stay-and-resist*. Investment in below-ground buds and reserves and root suckering is typical of *hide-and-resprout* strategy. In this study, we captured these two alternative strategies by sorting woody species based on *early bark versus height investment* but community means were not predictive of woody plant encroachment. An explanation is that encroaching ability of woody plants after fire suppression is best reflected by a full vector of community mean values, not just the value of single traits or in this case a combination of two traits. In that light, the functional distinction between different *growth forms* may have captured best the multivariate phenotype that can quickly encroach areas, even though there

are exceptions where species that identify as T's have traits that allow them to encroach locally. Community means of *mechanical herbivore defence* also did not affect woody plant encroachment in terms of density. Because of the tendency of herbivory adapted species to form wide 'cagey' crowns upon disturbance (Archibald and Bond 2003, Staver *et al.* 2012), higher community means of mechanical herbivore defence may be more indicative of the structure of encroachment (horizontal vs vertical growth). Especially when fire suppression goes hand in hand with moderate stem cutting (another common human activity in margins areas of protected areas), herbivore adapted woody plants may resprout horizontally, with consequences for vegetation structure and penetrability.

Fig. 6. Pictures showing areas dominated by *Combretum molle* at different stages of human-induced fire suppression. Image A shows an 'control' area far from the park boundary with recurrent fire disturbance and higher herbaceous biomass. Livestock grazing suppresses fire closer to park boundaries where a stand of *C. molle* saplings arises (B). Given the root-suckering ability of this species, the observation that these saplings are relatively even-sized, could be explained by a post-fire 'root-suckering event'. With continued human induced fire suppression, these saplings transition to bigger size classes and give rise to woody plant encroachment (C and D).

Pathways via recruitment limitation and *growth-form* were independent (as indicated by the absence of correlation in errors) and follow different causal structures (Fig. 5A). Recruitment limitation increased with historical disturbance from grazers, while grazers were positively associated to areas with higher soil fertility and higher soil sand content (Fig. 5A). Grazing is often suggested to have indirect, facilitating effects on woody plants by reducing grass competition (Riginos 2009, February *et al.* 2013), but we found the opposite effect for the smallest size classes in the Serengeti-Mara ecosystem. Small saplings may not be able to overcome repeated trampling and consumption by bulk grazers in areas frequented by grazers (Sinclair 1995), ultimately giving rise to recruitment limited areas. This is partly in agreement with Morrison *et al.* (2019), who show that the net effect of herbivory on seedling survival was negative. While grazers reduce the growth potential of grasses and thereby the competition between grasses and trees (Goheen *et al.* 2010), woody plants are confronted with multiple demographic bottlenecks (Holdo *et al.* 2014), where the effects of herbivores may switch from being negative in the earliest phase of establishment to positive when juvenile seedlings grow in the absence of grasses (Morrison *et al.* 2019). High grazing pressure may therefore have especially negative effects on woody plant recruitment in areas that were already recruitment limited.

Besides the indirect effects of the environment via disturbance, *growth-form* and recruitment limitation, the best SEM revealed direct effects of soil fertility, soil texture, and catena position (Fig. 5A). Human-driven woody plant encroachment is overall slower in areas with higher soil sand content, which seems to be in contrast with earlier work on both woody plant encroachment and woody cover in general (Sankaran *et al.* 2008, Case and Staver 2017). Sandy soils allow for deeper water infiltration which may favour trees over grasses (Walker and Noy-Meir 1982). In our study, fire suppression goes hand in hand with increased levels of grazing by livestock which may have limited the role of tree-grass competition. This means that the sign of the effect of soil texture can switch depending on types of human interference. We were not able to assess whether livestock incursions have been constant through time and how this may have impacted the rate of encroachment through altering tree-grass competition or trampling effects. This makes interpretation of the direct, negative effect of soil fertility on human-driven encroachment difficult. In alternative SEM's (Fig. 5 B,C), current disturbance of livestock negatively impacts encroachment, while livestock disturbance itself is highest in areas with higher soil fertility. This, together with the result that direct associations between soil properties and recruitment limitation become insignificant when historic grazing disturbance is added to SEM's, points towards an indirect effect of soil via past disturbances that we have not measured.

Conclusion

Continued pressure on savanna ecosystems as a result of human population growth in East Africa (and beyond) requires new approaches with which we can understand the specific effects of human activities in savannas. In this study, we confirm the potential of using trait-based approaches to understand human-induced vegetation change (Osborne *et al.* 2018). We showed that environmental conditions can predict the spatial distribution of plant strategies across the landscape, which in turn mediate human-driven plant encroachment. As an explorative study, we have focused on easy measurable traits and broad functional distinctions. A better understanding of which properties associated to *growth-form* explain the density of trees in encroached areas is needed. Field-based observations point towards specific traits, such as root suckering, but data is only available for a limited number of species in our study system for such difficult assessable belowground traits. Based on our results, we expect that improved understanding of finer-scaled variation in community means of functional strategy will be key to explain remaining variation in human-driven plant encroachment and will greatly inform management practices.

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Supporting Information

Table S1. List of herbivore species with information on their functional guild (grazer, mixed-feeder, browser)

Species	Scientific name	Functional guild
Buffalo	<i>Syncerus caffer</i>	Grazer
Cattle	<i>Bos taurus</i>	Grazer
Dik dik	<i>Madoqua kirkii</i>	Browser
Duiker	<i>Sylvicapra grimmia</i>	Browser
Eland	<i>Tragelaphus oryx</i>	Mixed feeder
Elephant	<i>Loxodonta africana</i>	Mixed feeder
Giraffe	<i>Giraffa camelopardalis</i>	Browser
Goat	<i>Capra aegagrus hircus</i>	Browser
Grant's gazelle	<i>Nanger granti</i>	Mixed feeder
Hartebeest	<i>Alcelaphus buselaphus</i>	Grazer
Impala	<i>Aepyceros melampus</i>	Mixed feeder
Oribi	<i>Ourebia ourebi</i>	Mixed feeder
Reedbuck	<i>Redunca redunca</i>	Grazer
Roan	<i>Hippotragus equinus</i>	Mixed feeder
Sheep	<i>Ovis aries</i>	Grazer
Suni	<i>Neotragus moschatus</i>	Browser
Thomson's gazelle	<i>Eudorcas thomsonii</i>	Mixed feeder
Topi	<i>Damaliscus lunatus</i>	Grazer
Wilbebeest	<i>Connochaetes taurinus</i>	Grazer
Zebra	<i>Equus quagga</i>	Grazer

Table S2. Trait values (*Height investment*: Height – stem, *Mechanical herbivore defence*: Defence, *Early bark investment*: Stem – bark) and functional type (*Growth form*) for 26 woody species found in vegetation plots.

Species	Height - stem	Growth form	Defence	Stem - bark
<i>Albizia harveyi</i>	1.018	Tree	low	0.089
<i>Balanites aegyptiaca</i>	1.125	Tree	high	0.134
<i>Combretum molle</i>	1.056	Tree	low	0.122
<i>Commiphora africana</i>	1.108	Tree or Shrub	low	0.198
<i>Commiphora trothea</i>	1.067	Tree or Shrub	low	0.173
<i>Cordia ovalis</i>	-	Tree or Shrub	low	-
<i>Dichrostachys cinerea</i>	0.984	Tree or Shrub	low	0.094
<i>Grewia bicolor</i>	-	Tree or Shrub	low	-
<i>Grewia fallax</i>	-	Tree or Shrub	low	-
<i>Kigelia africana</i>	1.157	Tree	low	0.207
<i>Ormocarpum trichocarpum</i>	1.036	Tree or Shrub	low	0.126
<i>Rhus natalensis</i>	-	Tree or Shrub	low	-
<i>Sclerocarya birrea</i>	-	Tree	low	-
<i>Senegalia polyacantha</i>	1.031	Tree	high	0.096
<i>Senegalia senegal</i>	1.073	Tree or Shrub	high	0.124
<i>Terminalia mollis</i>	-	Tree	low	-
<i>Vachellia drepanolobium</i>	1.002	Tree or Shrub	high	0.084
<i>Vachellia gerrardii</i>	1.061	Tree or Shrub	high	0.119
<i>Vachellia hockii</i>	1.056	Tree or Shrub	low	0.158
<i>Vachellia nilotica</i>	1.059	Tree	high	0.146
<i>Vachellia robusta</i>	1.071	Tree	low	0.117
<i>Vachellia seyal</i>	1.043	Tree	high	0.102
<i>Vachellia sieberiana</i>	-	Tree	high	-
<i>Vachellia tortilis</i>	1.042	Tree	high	0.096
<i>Vachellia xanthophloea</i>	-	Tree	high	-
<i>Ziziphus mucronata</i>	-	Tree or Shrub	low	-

Fig. S1. Relationship between the trait values *early bark investment* and *height investment* for 17 woody species found in the study area

Fig. S2. Dung counts grouped by functional groups (browsers, grazers, and livestock) in control plots (C) and fire suppression plots (FS)

Table S3. Analysis of deviance results for environmental factors ‘fraction of sand’ (Sand), ‘Exchangeable bases (EXBA), ‘catenae position’ (Catenae), and MAP used in generalized linear models explaining variability in the historic and current disturbance regimes. The minimal adequate model was obtained by elimination of non-significant terms, beginning from the maximal model.

Variable	Predictor	df	Res. Deviance	Prop. Deviance	Res. d.f.	F	P
Historic Grazers	null		186.02		95		
	EXBA	1	136.12	0.27	94	-	<.001
	SAND	1	105.47	0.16	93	-	<.001
	Catenae	1	104.63	<.01	92	-	0.360
	MAP	1	104.63	<.01	91	-	0.964
Historic Browsers	null	1	130.74		95		
	MAP	1	114.63	0.12	94	-	<.001
	SAND	1	105.91	0.07	93	-	0.003
	EXBA	1	105.77	<.01	92	-	0.709
	Catenae	1	105.75	<.01	91	-	0.872
Historic Fire	null	1	17.81		95		
	MAP	1	9.12	0.49	94	112.61	<.001
	EXBA	1	8.08	0.06	93	13.49	<.001
	Catenae	1	7.87	0.01	92	2.81	0.097
	SAND	1	7.87	<.01	91	<.01	0.962
Current Livestock	null	1	126.64		95		
	EXBA	1	120.89	0.05	94	-	0.017
	SAND	1	116.83	0.03	93	-	0.044
	Catenae	1	115.86	<.01	92	-	0.325
	MAP	1	115.44	<.01	91	-	0.517

The proportion deviance (prop. Deviance in table) is the proportional decrease in residual deviance relative to the null model. The ordering of predictors in the model is based on significance (p-value) in order to demonstrate the added importance (in terms of explained deviance) for each predictor.

Chapter 4

**Body size and feeding guild predict
spatiotemporal habitat choice of large
African herbivores in response to human
use of a savanna landscape**

Inger K. de Jonge, Remo Wormmeester, Michiel P. Veldhuis, Han Olff

Abstract

The compatibility of people and wildlife in East-African savannas is increasingly being questioned, especially at the current human population densities and associated pressures (such as livestock grazing) that cause wildlife now to disappear from rangelands and retract inside protected areas (PAs). Intensifying human activities at the edge of PAs are hereby compromising the ecological integrity of the few remaining habitats for wild herbivore populations. This calls for the development of strategies that can preserve both biodiversity and human livelihoods, which requires an understanding of how human modified landscapes are facilitating or excluding different wildlife species in savanna ecosystems.

In this study, we used camera traps to compare the spatiotemporal distribution of 12 native ungulate species in Serengeti National Park with adjacent communal village lands. We compared the relative use of village lands for each species in both the wet and the dry season and additionally assessed detailed changes in habitat preference between the two land uses over the diel cycle for the two most abundant herbivores, wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*), and their most common predator in the study area, spotted hyena (*Crocuta crocuta*).

The results show seasonal differences in the utilization of village lands and protected areas, as well as strong shifts in herbivore habitat use over the diel cycle. The variation in the spatial patterns between herbivores was mainly associated to body size, where smaller, gregarious species made relatively more use of village lands than larger species. Furthermore, the results show that wildebeest and zebra mainly used village lands from pre-dusk to midnight, which was the opposite of daytime activity of Masai pastoralists and their livestock. Activity in village lands peaked around dusk for both wildebeest and zebra, which largely overlaps with peaks in hyena activity.

These results illustrate that some species adjust their habitat choice in response to human use of landscapes, but not all species. At the same time, clear preference in specific times of the day of some wildlife species for village lands implies that benefits outweigh costs during these periods. A further exploration of how these edge areas fit into the risk-resource landscape experienced by wildlife will benefit effective management of edge areas, facilitating the future coexistence of people and wildlife in African savannas around protected areas.

Introduction

People and wildlife have coexisted in East-Africa for at least 500,000 years but the continuation of this coexistence is increasingly being questioned (Du Toit and Cumming 1999, Lamprey and Reid 2004, Veldhuis *et al.* 2019b). In this region, most native ungulate populations once occurred outside formally protected areas (PAs) (Western 1989), as still is the case in Kenya, but rapid human population growth, growing livestock populations, and changing land use have degraded and fragmented pastoral rangelands over the past decades (Ogutu *et al.* 2009) increasingly restricting wildlife to protected areas (PAs), as in Tanzania. Concurrently, edge areas of PAs are experiencing high rates of immigration and land conversion which squeezes wildlife even further inside core-protected areas, threatening the ecological integrity of last remaining habitats (Estes *et al.* 2012, Ogutu *et al.* 2012, Geldmann *et al.* 2019, Veldhuis *et al.* 2019b). Fencing, the hard separation of people and wildlife, is hardly considered a viable strategy in the large PAs in East-Africa (Hayward and Kerley 2009, Ogutu *et al.* 2012, but see Packer *et al.* 2013), which urges rethinking of the management of these edge areas (DeFries *et al.* 2007). The transition from transhumance pastoralism to a predominantly sedentary lifestyle has resulted in high-intensity grazing by livestock in edge areas, which in turn is altering landscapes through changes in species composition and vegetation structure (Western *et al.* 2009). Theoretically, wildlife can still disperse into these human-dominated landscapes, yet we know only little about the degree through which humans around protected areas facilitate or exclude wildlife through time.

The interaction between livestock and wildlife is often viewed as being competitive due to shared habitat and overlapping resources (Voeten and Prins 1999), but in some contexts, livestock can facilitate wildlife and vice-versa (Odadi *et al.* 2011). Competitive effects may arise when resources become limited during the dry season but heightened grazing pressure in the wet season may alternatively improve forage quality (Odadi *et al.* 2011). Grazing during the rainy season removes dead standing biomass which promotes regrowth of high quality forage (McNaughton *et al.* 1997). But, the benefit of improved quality may not be outweighed by reduced quantity (Voeten *et al.* 2010). Other positive effects may occur via redistribution of soil nutrients in pastoral lands through the use of ‘bomas’, which increase spatial heterogeneity and local diversity (Augustine *et al.* 2011, Marshall *et al.* 2018). Pastoralists use these temporary corrals to manage their livestock resulting in the concentration of large quantities of dung and urine in small areas. Abandoned boma sites (often referred to as ‘glades’) may persist for decades and attract native (lactating) ungulates as they provide forage resources of high nutritional quality (Augustine *et al.* 2011, Reid 2012).

Boma settlements in pastoral lands can additionally change the predation risk perceived by herbivores through repelling or attracting predators (Kolowski and Holekamp 2006). Human activity and presence of domestic dogs around bomas can markedly decrease attacks from lions (*Panthera leo*), leopards (*Panthera pardus*) and hyenas on livestock from which wild herbivores may profit as well (Ogada *et al.* 2003). According to the principles of the landscape of fear concept (Laundré *et al.* 2001), animals weigh predation risk (fear) to gains (food and resources), which means that herbivore populations are both regulated by direct predation but also by an 'intimidation' or 'perceived risk' effect (Preisser *et al.* 2005, Creel and Christianson 2008). Besides the discouraging effect of human activity on predators, edge areas may additionally 'feel' safer as reduced grass heights improve the ability to detect or escape from predators (Laundré *et al.* 2010, Riginos 2015).

Wild ungulates species are not equally regulated by resource quantity, resource quality and predation (Prins and Olff 1998, Hopcraft *et al.* 2010). Small-bodied herbivores have smaller gastrointestinal systems and higher energy expenditure per unit mass, which means they have to select highly nutritious food (Demment and Van Soest 1985). Alternatively, larger herbivores can extract enough energy from less nutritious food, but only if it occurs in enough quantity (Wilmschurst *et al.* 2000). Small grazers may therefore profit of nearby pastoral lands in edge areas while larger grazers are likely to be excluded due to shortage of resources. These effects may be less straightforward for browsers. Due to a history of heavy grazing and resulting fire suppression, pastoral village lands in areas with sufficient rainfall have been subject to an increase of woody plant biomass (Reid *et al.* 2008). Resources for this feeding guild may thus be in surplus, especially for large species such giraffe (*Giraffa camelopardalis*) and elephant (*Loxodonta africana*) as they feed up high and thereby do not compete with browsing goats (*Capra hircus*). Body size also influences species vulnerability to predation (Sinclair *et al.* 2003). Populations of smaller sized species are relatively more regulated by predation because they are preyed upon by many predators while larger species are only preyed upon by larger predators (Olff *et al.* 2009, Hopcraft *et al.* 2010). The largest 'mega' herbivores (>1000 kg) are not preyed upon at all, since they are too big for any predator to handle (Owen-Smith 1988). If there are benefits of pastoral lands in terms of safety from predation, this smaller herbivores would benefit more than larger ones.

Still, the 'landscape of fear' is not a fixed spatial pattern of perceived risk. Free-ranging herbivores are expected to adaptively change their habitat selection across the diel cycle as local predation risk in specific habitats increases or decreases, e.g., due to changes in activity of predators (Palmer *et al.* 2017, Kohl *et al.* 2018). In this context, Masai pastoralist

activities in village lands add to this dynamic landscape of fear as well. While hunting wildlife for consumption is culturally unacceptable to Masai (Goldman 2007), their activities during daytime may be perceived as a risk by wildlife and therefore exclude wildlife during certain periods. This exclusion may be amplified by thermal stress which constrains large bodied herbivores from daytime foraging in open habitats and forces them to rest in the shade during the hottest hours of the day (Owen-Smith and Goodall 2014, Owen-Smith and Traill 2017).

Spatial and temporal heterogeneity in the quality and quantity of food resources and security from predation in savanna landscapes hence play a major role in the distribution of native ungulate assemblages. While our understanding of the spatial distribution by African wild herbivores is relatively advanced in protected areas (Anderson *et al.* 2010, 2016, Hopcraft *et al.* 2012), we generally lack information on how neighbouring human-occupied areas fit into the risk-resource landscape experienced by wildlife. Here, we assess the spatiotemporal distribution of African native ungulates across the boundary of the Serengeti National Park in Tanzania into the neighbouring Loliondo communal pastoral village lands. Specifically we asked 1) in what way do feeding guild, body size and seasonality control relative occurrence in pastoral lands versus adjacent protected areas and 2) how does the activity over the diel cycle of two abundant herbivores, zebra and wildebeest, relate to the diel cycle of Masai pastoralist and their main predator (spotted hyena) in this area.

Methods and materials

Study area and design

The study was conducted in the Greater Serengeti-Mara ecosystem (GSME) in East-Africa, one of the largest remaining PAs in the world and home to abundant and diverse wildlife. The GSME includes the Serengeti National Park (SNP) in Tanzania and the Masai Mara National Reserve in Kenya where human activities are restricted. They are bordered by multiple types of land management, such as game reserves, wildlife management areas, conservancies, game controlled areas and regular village lands, each with their own management objectives and regulations. We performed our camera trapping study in the North-eastern corner of the system, where the SNP borders the Lolondio Game Controlled Area (LGCA) (Fig. 1). The LGCA is mainly inhabited by Masai whose economic mainstay is livestock keeping through herded, free-ranging grazing (pastoralism). Communal grazing

lands in Ololosokwan are grazed and browsed year-round by cattle and shoats. Mean annual precipitation is approximately 1000 mm. Rainfall is highly variable in the entire region but generally peaks during the short rain season from December – January and during the long rain season from March – June, while the peak of the dry season falls in July and August when it generally does not rain at all. The landscape is characterized by gently rolling granitic pediplains (Jager 1982), and the vegetation can be classified as savanna woodlands. The area is frequented by a diverse suite of resident ungulates as well as migratory wildebeest, zebra and Thomson's gazelle (*Eudorcas thomsonii*).

We deployed 12 camera traps in the Ololosokwan communal grazing lands and adjacent protected area. Study sites (N = 6) were located between two to five kilometres away from the park boundary at both sides. Sites followed a block design (A – C), where each site within the PA is paired with a site in the village lands and each site consisted of two plots (Fig. 1). The plots were located in the same landform and geology (as indicated by geomorphology and dominant tree species) in the PA and the village land. Each plot was placed approximately halfway the catenae gradient (for definition and history of the concept, see Borden 2020) to control for potential elevated predation risk in drainages due to reduced overview of the surroundings.

Fig. 1. Map showing the location of the study area within the GSME (left panel) and the study design showing location of blocks (A – C) in the SNP and adjacent communal village lands of Ololosokwan (right panel). Sites in the village lands are solely used for livestock husbandry and situated between the park boundary and Masai bomas (purple dots).

Data collection and processing

At each plot, we fitted camera traps (Bushnell Trophy Cam, model 119736) to collect motion-triggered images of wildlife within timeframes of three weeks during the rainy season (28th of May – 17th of June) and the dry season (8th of August – 28th of August) of 2016. Cameras were attached on single standing trees at 2.5 meters from the ground and with an viewing angle set in such a way that approximately 20 percent sky was visible in each frame. In this way, we ensured a wide view of the entire plot that captures both small and larger wildlife species, even in taller grass. Cameras were set to take picture (field scan) every 15 min., and were in addition motion-triggered (with 10 seconds in between motion triggered captures). The camera trapping period encompassed 504 trap days resulting in total number of 88,463 images. To make sure that detection area during the daytime matches the detection area during the night, animals were only counted up to 15 meters away from the camera (marked with a stone in the field) as the infrared light of the camera only illuminates up to this distance. To minimize double counting of individuals that remained within the field of view of the camera for prolonged periods of time, we used ten minute time slots in which we used the image within each sequence with the most individuals for scoring. This ensures statistical independence of measurements as individual animals are unlikely to stay in the same place (in front of camera's) longer than 4 to 5 minutes in these systems (Palmer *et al.* 2017).

Body size and feeding guild

Information on the body weight of wild herbivores present in the study area were derived from Maloiy *et al.* (1982), Smith *et al.* (2003), and Hopcraft *et al.* (2015), where body weights estimated on East-African population were favoured in case of multiple reports, and sexes were averaged. Information on feeding guilds was extracted from Hofmann and Stewart (1972).

Data analysis

The dataset to assess the spatial distribution of different wild herbivore species across land uses consisted of the sum of all individuals scored at each plot per season. These sums were used to calculate the log response ratio for each paired combination of plots across land use as follows:

$$\text{Response ratio} = \text{Log} \frac{N_{VL} + C}{N_{PA} + C} \quad (1)$$

Where N_{VL} represents the number of individuals of a specific species in the village lands and N_{PA} represents the number of individuals of a specific species in the protected area. A constant (C) with a value of 0.01 is added to enable zero values to be used in the calculation of the response ratio. Positive response ratio values signify a preference for village lands for a given species, while negative values mean preference for protected areas. We fitted Gaussian Linear Mixed Models (LMMs) using the *nlme* package (Pinheiro *et al.* 2017) to examine whether log response ratios were significantly different from zero for each species separately, for both seasons. In these analyses, block was added as a random effect. Estimates of the log response ratios were derived through REML and 95% confidence intervals were obtained from the likelihood profile. For species that occurred in both land uses during both seasons, we additionally used LMMs to test for the effect of season as a fixed factor, using a likelihood ratio test.

To assess the role of body size and feeding guild on relative occurrence of village lands, we averaged log response ratios for each species over the blocks. This was done to be able to include less abundant species which only occurred in a subset of blocks or plots. Because of an interactive effect between season and feeding guild and the requirements of homogeneity of regression slopes in ANCOVA's, we used the average log response ratio over both seasons for each species. The dataset thus included a log response ratio value for each species and information on that species feeding guild (fixed factor) and body weight (covariate). Body weight was log-transformed to meet the assumptions of a linear relationship between dependent and response variables.

For wildebeest and zebra, we obtained sufficient data over the study period to also estimate their preference over the diel (day-night) cycle and assess whether they occurred more in village lands at specific times of the day. To this purpose, we used the counts of animals captured by cameras at each site, each day and each hour of the day. Rather than 'abundance' such counts of photographic rates should be interpreted as an index of activity as these rates can increase because more individuals use a particular site or because individuals use that site more often (Sollmann 2018). The focus of this part of the study was on the wet season, as these two species made only limited use of village lands during the dry season. A similar analysis during the dry season would require more data (more trap days). The counts of animals captured by cameras at each site, each day and each hour of the day contained many zeros and can therefore not be used in standard GLM's for count data, using a poisson error distribution. Instead, specialized statistical models should be used that can accommodate data with excess zeros, such as zero-inflated models

(Martin *et al.* 2005). Here, we assume that the zero counts in the data set are a mixture of structural zeros and random zeros. For example, browsers that prefer woodlands, such as giraffe, will likely avoid more open grassy areas leading to structural zeros as opposed to random zeros. But not all woodlands can be continuously used by giraffe, resulting in the inclusion of random zeros in the dataset. Because the non-zero counts were overdispersed (having a greater variance than expected based on the assumed distribution), we fitted zero-inflated GLMs assuming a negative binomial distribution (ZINB) with a logarithmic link function for the count portion of the data and a logit link function for the zero portion of the data using the *GlmmTMB* package (Magnusson *et al.* 2017). Site within block was used as a random effect and we accounted for within site temporal autocorrelation by including an AR1 covariance structure for the temporal covariance between observations from hour to hour within sites. Due to the cyclic nature of diel data, the candidate models included periodic components, represented by pairs of sine and cosine functions over the day with a fundamental period of 24 hours and one to three harmonics of 12, 8, and 6 hour periodicity to modulate the signal (Nelson 1979). The model was specified as:

$$\begin{aligned} \text{Log}(\text{count}(x)) = & \alpha_0 + (\alpha_1 \cos \frac{2 \pi x}{24} + \beta_1 \sin \frac{2 \pi x}{24}) \\ & + (\alpha_j \cos \frac{h_j 2 \pi x}{24} + \beta_j \sin \frac{h_j 2 \pi x}{24}) \end{aligned} \quad (2)$$

With x representing the hour of the day and h representing the j_{th} harmonic, where a full model would comprise all three harmonics. The periodic components were first included in the zero portion of the model, then in the count portion, and lastly in both the zero and count portions. A null model (intercept-only for both the count and the zero portion) was considered as well, which assumed that activity was constant across the diel cycle. Models were evaluated based on AIC scores, where the least-complex but still sufficient fitting model was selected when ΔAIC was lower than 2 (Burnham and Anderson 2004). Land use was included as a fixed factor and interaction terms between periodic components and land use were tested. To put the change in activity across the diel cycle in village lands and protected areas in the context of a ‘landscape of fear’, we additionally modelled hyena activity over the diel cycle. Activity models for livestock over the diel cycle was limited to village lands as no livestock incursions into protected areas were recorded during the study period. All analyses were performed in the statistical environment R, version (3.6.1) (R development Core Team 2019).

Results

Wildlife occurrence in protected area and pastoral village lands

Considering all species with more than one occurrence during the study period, a total number of 7333 animals were scored, representing 13 species (Table S1). Hyena was the only predator species that was observed, with a total number of 119 records. Out of the 13 wild herbivores, we found that wildebeest, zebra, impala (*Aepyceros melampus*), Thomson's gazelle, eland (*Tragelaphus oryx*), topi (*Damaliscus lunatus*), hartebeest (*Alcelaphus buselaphus*), Grant's gazelle (*Nanger granti*), and elephant occurred both in protected areas and in adjacent village lands. Giraffe only occurred in the village lands while dik dik (*Madoqua kirkii*), duiker (*Sylvicapra grimmia*) and buffalo (*Syncerus caffer*) were only observed in the protected area during both seasons.

Log response ratios of species occurring in both land use types revealed that wildebeest, zebra, impala, eland, and hyena all occurred more in the protected area than in village lands in the dry season and that their relative occurrence in village lands significantly increased in the rain season (Table 1, Fig. 2). The results furthermore show that there is no effect of land use on the occurrence of these four species during the rainy season, as signified by non-significant intercepts (Table 1, Fig. 2). The log response ratio of Thomson's gazelle shows an opposing result, where relative occurrence was higher in the village lands during the dry season compared to the wet season (LMM, Season effect, $F_{1,5} = 8.2$, $P = 0.035$). For both seasons, however, there is no significant effect of land use on the occurrence of Thomson's gazelle (Table 1, Fig. 2). Lastly, we found that elephants relatively occurred more in PAs during the dry season (Table 1). Log response ratios during the wet season were variable across sites, resulting in a non-significant effect of season and the absence of an effect of land use in the wet season.

The role of body weight and feeding guild

As a result of the low occurrences of browsers in this study (Table S1), we focused on comparing the grazers versus the mixed-feeder guild. The model with the lowest AIC value included both an effect of the covariate body weight (ANCOVA, $F_{1,7} = 14.03$, $P = 0.007$) and the factor feeding guild (ANCOVA, $F_{1,7} = 11.78$, $P = 0.011$) (Fig. 3A). Body weight had a negative effect on the log response ratio (so more preference for village land in smaller species) and species belonging to the grazers guild had a lower log response ratio (Fig. 3A). In this model, the leverage of the log response ratio value for elephants was found to surpass Cook's distance. However, excluding elephants does not change the results, with both body weight (ANCOVA, $F_{1,6} = 72.20$, $P < 0.001$) and feeding guild (ANCOVA, $F_{1,6} = 7.13$, $P = 0.037$) as significant predictors of log response ratio (Fig. 3B).

Table 1. Anova results for the effect of season (Season effect) on the log response ratios of different wildlife species used in linear mixed-effect models and the results of intercept-only models within each season (dry season and rain season).

Species	Dry season		Rain season		Season effect		
	$F_{1,3}$	P	$F_{1,3}$	P	df	F	P
Wilbebeest	40.86	0.008	2.46	0.215	1,8	25.03	0.001
Zebra*			6.51	0.084	1,8	824.29	<0.001
Impala	42.99	0.007	6.54	0.083	1,5	37.21	<0.001
Thomson's gazelle	6.96	0.078	0.27	0.654	1,5	8.2	0.035
Eland*			3.61	0.154	1,7	18.78	0.003
Hyena	11.56	0.043	9.17	0.056	1,7	19.77	0.003
Elephant	46.99	0.021	0.18	0.699	1,4	0.67	0.458

*Zebra and eland were absent from village lands during the dry season, hence intercept-only models were only constructed for the rain season.

Fig. 2. Log response ratios for seven wildlife species in the dry season and the wet season. Error bars represent confidence intervals. A negative ratio indicates a preference for the protected area, while a positive ratio indicates a preference for the village lands. The P-value gives the significance of the season effect.

Fig. 3. Fit of ANCOVA models describing the effect of body weight on the log response ratio for two guilds, grazers versus mixed-feeders including elephants (A) and without elephants (B). Ribbon signifies the 95% confidence interval of the fits for each guild (note that they overlap in both analysis). A negative ratio indicates a preference for the protected area, while a positive ratio indicates a preference for the village lands. Full species names for the codes can be found in Table S1.

Activity over the diel cycle of wildebeest and zebra

The activity of wildebeest and zebra was not equally distributed over the diel cycle, as indicated by the significant periodic components in the best models (Table 2). In addition, multiple interactions between periodic components and land use were included in the best models, implying that diel cycle patterns in activity are different across protected areas and village lands (Table 2). Activity over the diel cycle follows broadly the same pattern for the two species (Fig. 4). The mean predicted activity was higher in protected areas than in village lands during daytime (5:30 – 19:30) (Fig. 4). In the hour before night time (dusk), activity decreases more sharply in protected areas than in village lands and mean activity was higher in village lands until midnight. After midnight, zebra activity showed a peak between 1:00 and 2:00 in protected areas while activity remained constant in village lands until the hour before dawn. Wildebeest activity remained low after midnight in both protected area and village lands until the hour before dawn. The activity model for livestock revealed that Masai started to use the village lands between 7:00 and 8:00 in the morning and returned to their bomas around 17:00. Both these times coincide with respectively the decrease and increase of wildebeest and zebra activity in village

lands (Fig. 4). The best model for hyena activity over the diel cycle revealed a peak in activity between 4:00 and 5:00 and a smaller peak at 20:00. The best model did not include interactions between periodic components and land use implying that patterns over the diel cycle are comparable in village lands and protected areas (Table 2). Land use was a significant predictor in the best model describing Hyena activity, with overall higher abundances in village lands (Table 2, Fig. 4). The peaks in Hyena activity seemed to corresponds with the depressions in wildebeest and zebra abundance in both land-uses (Fig. 4). The stronger predicted peak in hyena activity in the early morning coincided with the strongest depression in predicted wildebeest activity, but not for zebra (Fig. 4).

Fig. 4. Mean predicted activity for village lands and adjacent protected area for wildebeest (upper panel) and zebra (bottom panel) over the diel cycle. Blue colour gradients represents the mean predicted activity of livestock (LS) in village lands and red colour gradients represents the mean predicted activity of hyena's (H) in village lands (VL, upper bar) and protected areas (PA, bottom bar). Vertical lines represent the switches from daytime (5:30 – 19:30) to night-time (19:30 – 5:30) based on the end and start of astronomic twilight in the study area.

Table 2. Zero-inflated generalized linear mixed model (ZIGLMM) estimates for wildebeest, zebra, hyena, and livestock describing the change in activity in relation to the diel cycle (fundamental 24h period: F; harmonics: H1 – H3) and land-use (LU).

Conditional model				
species	parameters	Estimates	<i>z</i>	<i>P</i>
Wildebeest	intercept	-3.015 ± 0.829	-3.64	<.001
	H1 cos	-0.476 ± 0.087	-5.49	<.001
	H1 sin	-0.288 ± 0.104	-2.77	0.006
	H3 cos	0.175 ± 0.084	2.08	0.037
	H3 sin	-0.085 ± 0.082	-1.04	0.299
	F cos * LU	0.720 ± 0.245	2.94	0.003
	F sin * LU	-0.020 ± 0.195	-0.10	0.92
	H2 cos * LU	-0.640 ± 0.176	-3.64	<.001
	H2 sin * LU	-0.533 ± 0.161	-3.31	<.001
Zebra	intercept	-1.840 ± 0.392	-4.7	<.001
Hyena	intercept	-0.486 ± 0.606	-0.8	0.423
Livestock	intercept	0.149 ± 0.425	0.35	0.727
	F cos	-3.957 ± 0.516	-7.67	<.001
	F sin	-1.186 ± 0.697	-1.7	0.089
	H1 cos	-1.978 ± 0.486	-4.07	<.001
	H1 sin	-1.788 ± 0.674	-2.66	0.008
	H2 cos	-0.380 ± 0.283	-1.34	0.18
	H2 sin	-0.864 ± 0.321	-2.69	0.007

Both the conditional model on the count portion of the data (negative binomial with log link) and the zero-inflation model (binomial with logit link) on the zero portion of the data is presented.

Zero-inflation model				
parameters	Estimates	z	P	
intercept	-0.457 ± 0.884	-0.52	0.605	
F cos	2.556 ± 0.388	6.60	0.043	
F sin	-0.539 ± 0.267	-2.02	<.001	
H1 cos * LU	0.817 ± 0.444	1.84	0.066	
H1 sin * LU	2.579 ± 0.547	4.71	<.001	
H2 cos * LU	-3.497 ± 0.998	-3.50	<.001	
H2 sin * LU	-1.654 ± 0.635	-2.60	0.009	
H3 cos * LU	1.257 ± 0.491	2.56	0.011	
H3 sin * LU	0.685 ± 0.481	1.43	0.154	
intercept	1.157 ± 0.378	3.06	0.002	
F cos * LU	-1.019 ± 0.253	-4.03	<.001	
F sin * LU	0.437 ± 0.228	1.92	0.055	
H1 cos * LU	0.552 ± 0.227	2.44	0.015	
H1 sin * LU	0.538 ± 0.239	2.25	0.024	
H2 cos * LU	0.355 ± 0.220	1.62	0.106	
H2 sin * LU	0.398 ± 0.231	1.72	0.085	
H3 cos * LU	0.112 ± 0.221	0.51	0.61	
H3 sin * LU	0.501 ± 0.221	2.26	0.024	
intercept	6.534 ± 0.969	6.74	<.001	
LU	-1.132 ± 0.376	-3.01	0.003	
F cos	-3.501 ± 0.967	-3.62	<.001	
F sin	-0.346 ± 0.312	-1.11	0.268	
H1 cos	1.774 ± 0.512	3.47	<.001	
H1 sin	0.121 ± 0.329	0.37	0.712	
intercept	3.396 ± 0.411	8.26	<.001	
H1 cos	-3.594 ± 0.524	-6.86	<.001	
H1 sin	-2.704 ± 0.428	-6.31	<.001	
H2 cos	-1.535 ± 0.327	-4.70	<.001	
H2 sin	-1.930 ± 0.384	-5.03	<.001	

The model with the lowest AIC is presented for each species. Estimates are presented as the estimate ± standard error. For the categorical predictor 'land use' (LU), village lands are the control.

Discussion

In this study, we showed that the boundary zone of a protected area and its adjacent pastoral village lands was hosting a diverse assemblage of wildlife, with likely frequent daily movement of wildlife across the conservation boundary. However, as expected and in agreement with other studies, not all species make the same use of human-occupied landscapes (Bhola *et al.* 2012). We show here that body size and feeding guild are important traits that determine the relative suitability of village grazing lands across seasons for different herbivore species. Averaged over both seasons, smaller sized herbivores and mixed-feeders occurred more in village lands than larger herbivores and grazers (Fig. 3). We did not have sufficient data to analyse the differences between season for each species, but the occurrence of herbivores in village lands relative to protected areas increased in the wet season across different body size classes, except for the smallest species, Thomson's gazelle. Wildebeest, zebra, impala, and eland all showed significant increases in occurrence in village lands in the wet season while they belong to different body size classes (Table 1).

The role of body weight and feeding guild in regulating spatial distribution across seasons

The role of body weight in predicting the occurrence of wild herbivores in village lands versus the protected area was expected to be due to a combined difference in forage quality and predation risks. Our finding however do not support the idea that fewer predators would be present the village lands (Table 1). In fact, the log response ratio of hyena occurrence was found to be marginal significantly higher than zero in the wet season, meaning that hyena occurrence may have actually been higher in village lands (Table 1). Positive effects in terms of safety from predation may therefore be more related to an increase in visibility which allows wild herbivore to spot predators in time, due to the shorter grass. The increase in occurrence of hyenas in village lands in the wet season may explain why Thomson's gazelle have lower occurrence in village lands in the wet season compared to the dry season (Fig. 2). This would imply a form of 'apparent competition' (Holt and Bonsall 2017), where the increase of multiple prey species (impala, wildebeest, and zebra) in village lands negatively impacts a fourth (and the smallest) prey species (Thomson's gazelle). The occurrence of Thomson's gazelle was found to be higher in pastoral ranches year-round in Bhola *et al.* (2012), which can be explained by sharper contrasts in the risk-resource landscape in the Mara reserve versus surrounding ranches. While the herbaceous layer is short and hence of higher quality in the village grazing lands

of Ololosokwan (Chapter 2, this thesis), high tree density may still allow for successful hunting by hyenas due to better stalking opportunities, a phenomenon observed for lions (Hopcraft *et al.* 2005). As habitat choice is expected to be the outcome of animals weighing predations risks (costs) to gains (resources) (Bakker *et al.* 2005, Preisser *et al.* 2005, Creel and Christianson 2008), costs for the smallest species may be higher during the wet season in these village lands.

The change in occurrence between seasons for Thomson's gazelle can also be explained by feeding strategy. Herbaceous plants generally senescent rapidly at the onset of the dry season, while many savanna trees can maintain productivity weeks into the dry season by extracting water from deeper soil layers (Scholes and Archer 1997). Mixed feeders tend to switch guilds on a seasonal basis, where they show a preference for fresh grass in the wet season while browse is a fall back option in the dry season (Jarman 1979, du Toit 2003). While access to high quality graze during the wet season in village lands may be limited due to predation risk constrains, Thomson's gazelle have ample browse opportunities and safety during the dry season in the village lands. The switch in diet of mixed feeders also explains the overall higher log response ratios of mixed feeders compared to grazers (Fig. 3). The use of village lands is restricted to the wet season for grazers while mixed feeders can potentially use village lands year-round. However, this explanation does not fit the seasonal habitat choices of eland as they were not scored in the village lands in the dry season. Despite its large body weight, eland was repeatedly observed in village lands during the wet season. Bhola *et al.* (2012) found an increased eland occurrence on pastoral ranches in the wet season as well, which they explained by a potentially higher density of (by eland) favoured nutritious forbs (Watson and Owen-Smith 2000).

While the generalization on the role of body size and feeding guild provides a useful framework, it is important to note that there are exceptions which can be explained by the specific ecology of individual species. For example, all species that were used in our analysis are more or less social/gregarious, with implications for strategies to escape from predation. While the low number of scorings for dik dik and grey duiker in this study prohibited us from including these species in the analysis, the fact that they were only captured in the National Park contrasts with the general patterns of body weight that was found for more abundant species. While gregarious species find safety in numbers (dilution effect, mutual warnings) (Lehtonen and Jaatinen 2016), dik dik and duiker live respectively in pairs or solitary and tend to avoid predation by crypsis (Jarman 1974). Predator avoidance by crypsis may be less effective in village lands where herbaceous

vegetation is short and hiding places for these elusive animals are scarce. Another example is provided by elephant, which in this study showed large variation between blocks in the wet season (Fig. 2) and did not fit well in the model describing the effect of body weight and feeding guild on relative use of village lands (Fig. 3A). An explanation may be that elephants select habitat based on finer scaled considerations (e.g. browse quality or fruits) than a contrast in land-use in the wet season. Furthermore, elephant was the only species in this analysis that feeds on large trees, a large unexploited food source in village lands as it is not consumed by livestock. Lastly, Elephants may be particularly attracted to park boundaries because of nearby croplands (Denninger Snyder *et al.* 2019)

Activity of wildlife and livestock across the diel cycle

Measured over the entire wet season, wildebeest and zebra occurrence was not different between protected area and village lands (Table 1, Fig. 2). Activity models over the diel cycle however revealed that the use of these contrasting land uses changed over the course of the day (Table 2, Fig. 4). Mean activity was predicted to be higher in village lands from the hour preceding dusk until midnight for both species (Fig. 4). This implies that village lands provide benefits to wildlife at these hours, but it cannot be directly inferred whether this is in the form of resources, safety from predation or a combination of the two. Wild herbivores are expected to continuously balance trade-offs in fitness between gains in resources, predation risk, as well as thermal constraints (Veldhuis *et al.* 2019a). Time allocation to different activities such as foraging or resting may be indicative of how animals make this trade off over the diel cycle. Owen-Smith & Goodall (2014) found depressions in activity (resting) during midday and pre-dawn for both buffalo and zebra. At the same time, activity (both foraging and travelling) peaked during the early morning and late afternoon (Owen-Smith and Goodall 2014). These schedules largely overlap with our activity models and may therefore reflect the same activities (Fig. 4). The lower activity of wildebeest and zebra in village lands compared to protected areas during daytime may be explained by the presence of Masai and livestock, while peaks in the late afternoon may reflect the onset of grazing activities.

The drop in activity after the peak in the late afternoon is deeper for both wildebeest and zebra in the PA (Fig. 4). Concurrently, the activity peak is predicted to be slightly later in village lands compared to the PA (Fig. 4). The drop coincides with increasing activity of hyenas in both village lands and protected area. Combined, these patterns may point towards rewards in the form of relieve from predation risk in village lands. Risk allocation theory predicts that animals should invest time in intense feeding efforts during pulses

of safety (Lima and Bednekoff 1999). In this case, the higher visibility in village lands may allow wildebeest to allocate time to foraging, explaining the higher abundance in the hours up until midnight (Fig. 4).

Hyenas showed a second (higher) peak in abundance during pre-dawn, which coincides with the lowest predicted activity of both wildebeest and zebra in both land uses. It may, however, be too simple to view the low activity of wildebeest and zebra as being the direct consequence of a higher hyena activity (Fig. 4). The pre-dawn depression in activity is alternatively explained by a sleeping period (Owen-Smith and Goodall 2014). A short sleeping / resting period has been recorded for several species around this time, including greater kudu (Owen-Smith 1998) and impala (Jarman and Jarman 1973). While it may seem counterintuitive that wild herbivores choose to sleep during a time with high activity of predators and low ambient temperatures, the net effect on fitness may be positive as the rest period clears the rumen space right before prime foraging hours in the morning (Owen-Smith 1988). This explains why the depression is more pronounced in wildebeest (ruminant) than in zebra (hindgut fermenters). Higher food intake requirements of hindgut fermenters additionally may explain why zebra activity show two more peaks during midday and between 1:00 and 2:00 during the night (Janis 1976). Zebras have to consume more food to meet their nutritional demands and a nightly feeding session during a temporary depression in hyena activity would be in line with risk allocation theory (Lima and Bednekoff 1999).

Conclusion

In this study we showed that body size and feeding guild are key traits in predicting the habitat use of pastoral village lands across seasons. Moreover, we showed how landscape changes due to persistent livestock grazing and human activity during the day time affect decision-making of wild herbivores on habitat use across the diel cycle. These results show that different species respond differently to anthropogenically modified landscapes, both through seasons and over the diel cycle. While monitoring and the characterization of diel activity of wildlife is challenging in areas where long-term conflicts over land use have created antagonism between authorities and local communities, this type of camera trapping will give important insight into future opportunities for continued coexistence of people and wildlife around protected areas in Africa.

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Supporting Information

Table S1. Counts of scored individuals for each species in the rain season and the dry season

Species	code	Rain season		Dry season		Total
		PA	VL	PA	VL	
Wildebeest	WB	2209	1200	1069	4	4482
Zebra	ZE	954	464	575	0	1993
Impala	IM	38	116	113	4	271
Thomson's gazelle	TG	35	18	14	165	232
Eland	ELA	39	9	79	0	127
Hyena		25	66	24	4	119
Buffalo	BU	74	0	8	0	82
Topi	TO	5	2	43	0	50
Giraffe		0	8	0	20	28
Elephant	ELE	6	7	11	0	24
Hartebeest	HB	14	2	1	0	17
Duiker		9	0	4	0	13
Grant's gazelle	GG	0	4	6	0	10
Dik dik		2	0	2	0	4

Chapter 5

Camera traps enable the estimation of herbaceous ANPP of an African savanna at high temporal resolution

Inger K. de Jonge, Michiel P. Veldhuis, Anton Vrieling & Han Olff

Abstract

Determining the drivers of aboveground net primary production (ANPP), a key ecosystem process, is an important goal of ecosystems ecology. However, accurate measurement and estimation of ANPP across larger areas remains challenging, especially for savanna ecosystems characterized by high spatiotemporal heterogeneity in ANPP. Satellite remote sensing methods are frequently used to estimate productivity at the landscape scale, but generally lack the spatial and temporal resolution to understand the mechanisms and causes of productivity variation. This is especially challenging in grazed ecosystems where peak growing season standing crop is not a proxy for ANPP.

In this study, we developed and tested methods for estimating herbaceous productivity in grazed ecosystems as an alternative to labour-intensive repeated biomass clipping and caging of small plots. We compared time-integrated and temporal measures of two spectral greenness indices, normalized difference vegetation index (NDVI) and green chromatic coordinate (GCC), derived from Sentinel-2 (NDVIs), a handheld radiometer (NDVIg), and digital repeat cameras (GCC), and tested their relationship to biweekly field-measured herbaceous ANPP using movable exclosures.

We found that the sum of day to day increases in camera trap-derived vegetation greenness (tGCC) over the productivity measurement interval was a poor predictor of herbaceous ANPP when considered alone (explained deviance of 21%) and that time-integrated NDVIs in combination with a quadratic term for temporal changes in NDVIs (Δ NDVIs) is a better (stand-alone) predictor of productivity (explained deviance of 34%). However, the combination of these different measures (tGCC, NDVIs, and a quadratic term for Δ NDVIs) yielded the best model, explaining 48% of deviance. Furthermore, we found that the fine (daily) temporal resolution of GCC time series captured fast vegetation responses to rain events, that were missed by coarser resolution methods (>2 days).

These findings demonstrate the importance of fine temporal resolution in predicting herbaceous ANPP in savanna ecosystems. We conclude that digital repeat photography (camera traps) are promising in offering a reliable and cost-effective method to estimate productivity in savannas, that contributing to better understanding of ecosystem functioning and its drivers.

Introduction

Aboveground net primary production (ANPP) is considered a key aspect of ecosystem functioning, because of its defining influence on ecosystem structure and diversity (McNaughton *et al.* 1989, Cebrian 1999). Determining the causes of spatial and temporal variation in ANPP is therefore an important goal in ecosystem ecology, including the assessment of ecosystem services (Reid *et al.* 2006). The accurate measurement and estimation of ANPP at spatial and temporal resolutions that capture the relevant determinants of productivity in natural ecosystems remains challenging, especially in savanna ecosystems due to their inherent high level of variability. Short-term changes in ANPP in response to stochastic rainfall events are likely to be missed, for example because cloud cover during the rainy season can prevent optical satellite sensors to acquire cloud-free imagery and thus assess vegetation productivity at critical moments (Pettorelli *et al.* 2005). The challenge is further exacerbated by the disparity in magnitude and variability between various ANPP estimation methods which result from ignoring the effect of grazing (extra production may rapidly be removed), turn-over rates, and decomposition on ANPP (Scurlock *et al.* 2002, Ruppert and Linstädter 2014). To better understand the functioning of savanna ecosystems, it is crucial to improve and develop methods for efficient estimation of ANPP at relevant scales while using 'best practice' methods as benchmarks to evaluate these estimation methods (Ruppert and Linstädter 2014).

Traditionally, ANPP is estimated in the field using either clipping of peak standing biomass at the end of the growing season (so called 'peak methods'), or repeated clipping throughout the season ('incremental methods') (Byrne *et al.* 2011, Mbow *et al.* 2013). The majority of field-based herbaceous ANPP estimation methods rely on less labour intensive peak methods, which is inadequate in savannas as these are fast turnover ecosystems with high ANPP to biomass ratios (Sala and Austin 2000). Grazers also can affect productivity in multiple ways, e.g. by inducing compensatory growth in response to defoliation (Frank and McNaughton 1993) but also by reducing leaf area, reducing photosynthetic capacity. It is therefore 'best practice' to use incremental methods in combination with moveable exclosures in natural savanna ecosystems (McNaughton *et al.* 1996). Despite the advantage of relatively accurate ANPP measurements that are possible through repeated caging and clipping, the high labour intensity limits its applicability to landscape-scale investigations. However, these scale issues could potentially be solved when these labour intensive best-practice methods can be calibrated to methods that are less limited by time and resources.

The increasing availability of multispectral satellite imagery make satellite-derived vegetation indices (VI's), such as the Normalized Difference Vegetation Index (NDVI), a good candidate for such calibrations. Indeed, many ecological studies use NDVI as a proxy for vegetation productivity and phenology (Paruelo *et al.* 1997, Bonenfant *et al.* 2009, Pettorelli *et al.* 2011). At the basis of this relationship is the capability of NDVI to capture the contrast between strong absorption in the visible wavelengths and reflectance in the near-infrared wavelengths, which characterizes photosynthetically active vegetation (Tucker 1979). Important limitations of NDVI include its sensitivity to optical properties of the soil background (Huete *et al.* 1985), the quick saturation with increasing leaf area index (LAI) (Baret and Guyot 1991), and cloudiness (Pettorelli *et al.* 2005). Satellite-derived time series of NDVI with relatively short intervals between consecutive observations were until recently limited to spatial resolutions of approximately 250 to 1000m (e.g. the MODIS satellite program). The revisit frequency has also increased for other freely available data sources, with the Sentinel-2 mission now offering 10m resolution acquisitions every five days since 2016. However, due to cloud cover, particularly an issue during rainy seasons (the main growing season), no frequent observations of the vegetation can be made, thus limiting its potential to capture short-term vegetation responses to rain events. This is relevant as vegetation responses to rain occur rapidly in semi-arid ecosystems, especially for grasses (Williams *et al.* 1998, Xu *et al.* 2015). Methods that are only based on NDVI may therefore not fully capture patterns of primary production, but this is partially compensated by their excellent spatial coverage through remote sensing. Nevertheless, to accurately estimate ANPP in semi-arid ecosystems, we need improved methods that can capture these short-term vegetation responses, also during periods of prolonged cloud cover.

The use of digital repeat photography or 'near surface remote sensing' in the study of phenology is gaining popularity across a variety of ecosystems (Toomey *et al.* 2015, Alberton *et al.* 2017, Vrieling *et al.* 2018, Richardson 2019). The series of images taken by digital cameras allow the derivation of the green chromatic coordinate (GCC) which measures green reflection relative to the total reflection in the visible spectrum for vegetation within the camera field-of-view (Sonnentag *et al.* 2012, Richardson *et al.* 2013). This is done by employing cameras on the ground that take multiple images per day, providing a method that is insensitive to cloud cover. Digital repeat photography, possible with weather-proof, relatively cheap camera traps, can thus potentially capture fast vegetation responses to rain events. Unlike NDVI, absolute measures of GCC are less suitable for the estimation of biomass as the typical (and most practical) oblique mode of camera installation has consequences for the angle of view and thereby on the effect of non-photosynthetic parts, such as flowers and seeds, on measured GCC (Vrieling *et al.* 2018).

Although digital repeat photography has proven its usefulness for phenology studies (Vrieling *et al.* 2018), until present, to the best of our knowledge, no attempts exist to use time series of field photographs for estimating ANPP, supplemented with vegetation indices (VI's) from other data sources (remote and near-surface sensing). In this study, we compared temporal and integrated measures of two VI's (NDVI and GCC) derived from remote and near-surface sensing techniques and investigated their relationship with field-measured herbaceous ANPP using movable exclosures. Specifically, we examined the capacity of different combinations of sensing techniques, VI measures, and a field-measured proxy for aboveground standing biomass to predict short-term (14 days) herbaceous ANPP. Last, we explored the spatiotemporal responsiveness of GCC to rainfall events and assessed how the GCC's predictive capacity of ANPP was affected by stepwise reducing its temporal resolution.

Material and Methods

Study area and design

This study was conducted around Seronera in the centre of the Serengeti National Park (SNP), North-western Tanzania (Fig. S1). The SNP is part of the greater Serengeti-Mara ecosystem, one of the largest protected tropical savanna ecosystems in the world and home to abundant and diverse wildlife (Sinclair *et al.* 2008). Mean annual precipitation for Seronera is around 800 mm (Pellew 1983). Rainfall is highly stochastic, both in intensity and intermittency, but annual rainfall generally peaks during the short rain season in December – January and during the long rain season in March – May. Seronera is situated at the fringe of the Serengeti plains and is characterized by gently rolling pediplains on granitic rocks (Jager 1982). The vegetation is classified as Acacia woodlands, which is characterized by a continuous C4-grass dominated herbaceous layer intermixed with a discontinuous layer of (predominantly *Vachellia tortilis*) trees.

We set up cameras in the vicinity of the research station in Seronera over two study periods (April - June 2016 and April - September 2018) (Fig. S1). In 2016 we initiated the study with two cameras (I - J) for which we solely evaluated the relationship between camera-derived GCC and herbaceous ANPP. Since the launch of the Sentinel-2B satellite in March 2017, the Sentinel-2 mission allowed the use of open data at 10-60 m resolution every five days (instead of 10 days since the launch of the Sentinel-2A satellite in June 2015) (Drusch *et al.* 2012). Taking advantage of this increased temporal resolution of

the Sentinel-2 multispectral data imager (MSI) data, we set up an additional network of eight cameras (A – H) for which we evaluated the relationships between both camera derived GCC and Sentinel-2 derived NDVI (NDVIs) measures to herbaceous ANPP. We additionally measured NDVI on the ground (NDVIg) with a handheld radiometer every four days to be able to compare the predictive capacities of GCC and NDVI without being dependent on cloud-free images. The three VI's (GCC, NDVIs, and NDVIg) were thus simultaneously measured through time for each site, in one multi-scaled plot (Fig. 1A).

At the largest scale, NDVIs values were calculated for the pixel (10 m resolution) covering the centre of a 30 x 30 meters plot (NDVIs plot). The NDVIs plot is larger than the resolution to account for the reported geometric inaccuracy of the Sentinel-2 satellites (within 11 meters for 95.5% of the tiles; Claverie *et al.* 2018). To exclude NDVI signals from woody components, we selected sites without trees, shrubs, and saplings within and in the close vicinity of the NDVIs plot. The ~5 x 10 meters plot over which we calculated GCC values (GCC plot), is nested within the NDVIs plot (Fig. 1A). NDVIg and above-ground standing biomass (from now on biomass) were measured in 32 subplots of 1 m² covering both the NDVIs plot (N = 25) and GCC plot (N = 9). Within site variability was lower than between sites for measured VI's and biomass (Fig. S2).

While the most important green-up phase started at this location in March, we excluded this period because long periods of cloud cover prevent optical satellite sensors to acquire cloud-free imagery, which would make it impossible to compare the performance of digital repeat photography to satellite-based methods. Furthermore, evaluating the predictive capacity of VI's at later stages of the growing season (up until the dry season) offers the advantage of having independent spatial variation in biomass and vegetation greenness. Besides temporal variation in greenness, we introduced this spatial variation in greenness by placing cameras along the catenae sequence (sometimes described as hydrological linked hillslopes) (Fig. S1), which is associated with strong soil differentiation and thus drives a major local gradient in resource availability (Khomo *et al.* 2011, Borden *et al.* 2020). In addition, biomass can accumulate faster at lower catenae positions over the course of a growing season which introduces between-site variation in biomass during our study period, independent of phenological state (Fig. S2).

Fig. 1. A) Design of the multi-scaled plot for measurement of VI's. The blue polygon indicates the region of interest (ROI) for extracting the GCC time series using a digital camera (camera is indicated by the black rectangular). Sentinel-2 derived NDVI (NDVIs) was extracted for the pixel (10 x 10 meters resolution) covering the UTM coordinates of the red dot, at the centre of the red polygon (both in left figure). The red polygon indicates the area over which NDVI may have been calculated (due to geometric inaccuracy) and the grey area denotes a buffer-zone to exclude the influence of trees and disturbance by people and vehicles. Within both polygons, we measured NDVI in the field with a radiometer (NDVIg) and aboveground standing biomass with a disc pasture meter at every subplot (black dots). B) Sample photo of site A, showing the field of view of the plot used for GCC extraction (blue polygon) and a partial field-of-view of the 30 x 30 meters plot for NDVIs extraction.

Herbaceous aboveground net primary production

Herbaceous ANPP was measured using moveable exclosures following the protocol described by McNaughton *et al.* (1996). The exclosures were set up just outside the view of the camera in an area representative of the region of interest (ROI). Spatial variability in species composition, biomass and NDVI is limited at this scale (Fig. S2). At the onset of each interval, we clipped an area of 50 x 50 cm outside of the exclosure (t_0), with comparable aboveground standing biomass and species composition to that inside the exclosure. After 14 days, a 50 x 50 cm plot was clipped inside the exclosure (t_1). We set the measurement interval at 14 days because we want to have high temporal resolution while limiting the effect of clipping errors on biomass increment estimates. In one case (site I) we clipped T_1 after 18 days due to practical issues. Clipped biomass samples were oven-dried at the Seronera research station. Averaged daily herbaceous ANPP was then calculated as:

$$ANPP = \frac{Biomass_{t_1} - Biomass_{t_0}}{interval (days)} \quad (1)$$

Field camera time series

We used weather-proof Bushnell Trophy Cam Essential (model 119736) camera traps to collect 3-megapixel RGB photographs in JPG format every 15 minutes between 9:30 and 15:30 East Africa Time. Besides these repeated acquisitions, the cameras were also set to capture wildlife using the motion triggered (infrared) sensor, but those data are not used for this study. However, we complemented the image datasets with motion triggered images, although without animal presence, for days with low number of suitable images (due to under- or overexposure). Cameras were attached to trees, three meters above ground level, to maximize herbaceous canopy view and prevent damage by rubbing large animals (buffalo, elephant). Branches that obstructed the camera view were trimmed. The cameras faced either north or south to minimize overexposure as a result of incoming sunlight. The distance between the camera and the nearest edge of the GCC plot was 10 meters, resulting in vertical downward tilt of 16.7° (Fig. 1B). The depth of the GCC plot was limited to 10 meters, because the oblique mode of camera installation decreases herbaceous canopy view with distance and increases the contribution of non-photosynthetic elements such as flowers and seeds to GCC (Vrieling *et al.* 2018) (Fig. 1B). All cameras functioned as expected throughout the wet season, except for camera A, which was not operational between June 26th and July 7th due to unknown technical issues.

Camera imagery was processed using the R package *phenopix* (Filippa *et al.* 2016). Prior to processing, the images were manually filtered for wildlife presence disrupting the view on the vegetation, lens humidity caused by rainfall, and over- and underexposure. While the majority of over and underexposed images were filtered out by only including images between the set times of 9:30 – 15:30 EAT, we additionally limited the effect of brightness on GCC by only including images with an average digital number (DN) between 80 and 220 (Sonnentag *et al.* 2012). For each site, we delineated the pre-defined GCC plot as the region of interest (ROI) in the image (blue polygon, Fig. 1). For each image, the digital number of each colour layer of the RGB image (green, red and blue light in the visible spectrum: 400 – 700nm) within this ROI was extracted to yield a digital number triplet (G_{DN} , R_{DN} , B_{DN}), from which GCC can be calculated as follows:

$$GCC = \frac{G_{DN}}{R_{DN} + G_{DN} + B_{DN}} \quad (2)$$

GCC values were averaged for each ROI. To reduce noise, caused by between day variation in scene illumination, Sonnentag *et al.* (2012) suggests to calculate the 90th percentile of all averaged GCC values within non-overlapping three-day windows (GCC90). In this study, we tested both unsmoothed GCC90 values and smoothed GCC90 values using a moving (overlapping) three-day window to retain high temporal resolution. While moving windows may be adequate for the estimation of phenological relevant parameters such as the start or end of the season (SOS, EOS), vegetation responses to rainfall events occur at finer time scales and require temporally detailed GCC time series. In contrast to NDVI measures, such as the maximum NDVI or time integrated NDVI over a fixed period, absolute measures of GCC are not comparable in space due to differences in observation geometry and camera performance.

Instead, we summed the number of days on which GCC90 increases, for each site and measurement interval (see *Herbaceous ANPP*), as vegetation greenness, as well as productivity, is expected to vary on a daily basis due to changes in moisture availability caused by rainfall events. We calculated background variation in GCC90 during rainfall free periods for each site, so that day to day green up only counts when the increase is higher than the measured, site-specific standard deviation. Additionally, we considered time lags because production is expected to lag behind changes in greenness (Huxman *et al.* 2004). The used GCC measure to predict herbaceous ANPP was then calculated as follows:

$$GCC_{ij} = \sum_{t=0-l}^{13-l} \begin{cases} 1, & \text{if } GCC90_{t+1} - GCC90_t > SD\ GCC90_i \\ 0, & \text{otherwise} \end{cases} \quad (3)$$

Where GCC_{ij} is the GCC measure at the i_{th} site and the j_{th} measurement interval, GCC_t is the day within the measurement interval, and l is the number of 'lag' days ranging between zero and three days. For each GCC_{ij} we thus calculate four variables, based on the number of lag days. We did not consider lags beyond three days because an increased lag period additionally increases the time that herbivores may eat away material from the area that is used for the upcoming productivity measurements through caging.

Sentinel-2 and near-surface derived NDVI time series

Available satellite imagery between April and September 2018 were downloaded from the Copernicus Open Access Hub (<https://scihub.copernicus.eu/>). The images are acquired by two identical Sentinel-2 satellites, 2A and 2B, which each have a ten day repeat cycle, and together

provide a temporal resolution of five days. Prior to the retrieval of surface reflectance, we applied an atmospheric correction to all images using the Sen2cor toolbox (version 2.5.5) provided by the European Space Agency (Louis *et al.* 2016). Additionally, we used Sen2Cor's scene classification layer to discard pixel-level observations that were identified as clouds, cloud shadows and thin cirrus. Because we found that some smaller clouds and cloud shadows went undetected, to increase the confidence in the retained satellite observations, we manually masked observations on which we visually identified clouds or cloud shadows. From the 13 acquired spectral bands, we used band 4 (0.650 - 0.680 nm) and 8 (0.785 - 0.900 nm) at 10 meters resolution to calculate NDVIs as follows (Tucker 1979):

$$NDVIs = \frac{NIR - RED}{NIR + RED} \quad (4)$$

NDVI_g was measured using a pair of two-channel (RED: 636 – 673nm, NIR: 851 – 879nm) radiometric sensors (Model 1850, Skye Instruments LTD, Powys, UK). The upward pointing sensor measures the incident solar radiation while the second sensor measures upward reflectance from the herbaceous canopy. NDVI_g is obtained from measured incoming and reflected radiation as follows:

$$NDVI_g = \frac{\left(\frac{NIR_p}{NIR_\sigma}\right) - \left(\frac{RED_p}{RED_\sigma}\right)}{\left(\frac{NIR_p}{NIR_\sigma}\right) + \left(\frac{RED_p}{RED_\sigma}\right)} \quad (5)$$

where NIR_p and RED_p represent reflected quantum flux and NIR_σ and RED_σ represent incident quantum flux. The radiometric sensors were mounted on top of a handheld pole at 1.5 meters from the ground, which corresponds to a measured ground surface of 0.35 m². Every four days, two measurements were taken for each subplot inside the 30 x 30 meters grid (N = 25) and 5 x 10 meters grid (N = 9) (Fig 1.)

We temporally integrated NDVIs and NDVI_g by calculating the area under the curve (using R package *Desctools*, Signorell *et al.* 2016) through linear interpolation according to the composite trapezoid rule over the productivity measurement interval of 14 days +/- the lag days. We additionally considered temporal patterns of both NDVI time series as they relate to

phenological dynamics and phenostage (Fig. 2). The temporal measures of NDVIs (Δ NDVIs) and NDVIg (Δ NDVIg) were calculated as the difference between NDVI at the start of the productivity measurement interval (approximated by linear interpolation) and the time integrated NDVI measure. Positive values imply an increase in green biomass over the interval while negative values signify senescence. Similar to tGCC, we considered different time lags.

Aboveground standing biomass

We approximated aboveground standing biomass at the onset of each productivity measurement using a calibrated disc-pasture meter across a 30 x 30 m grid and a 10 x 5 m grid at each site, matching the spatial resolution of Sentinel-2 derived NDVI and field camera derived GCC, respectively. Disc-pasture meter measurements were averaged for each site before using a calibration equation ($R^2 = 0.83$) specific to the Serengeti to convert height (cm) of the disc into herbaceous biomass (kg ha^{-1}) (Unpublished data Smith *et al.*).

Rainfall

We used the 0.05° gridded rainfall dataset from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) (Funk *et al.* 2015), downloaded from <http://chg.geog.ucsb.edu/data/chirps/>, to assess the responsiveness of GCC to rain events. Additionally, we included visually observed rain events (through camera trap images) for days at which CHIRPS reported no rain to improve the accuracy.

Data analysis

The final dataset for predicting herbaceous ANPP from VI's consists of both time integrated and temporal measures of NDVIs and NDVIg, temporal measures of GCC, and field-approximated aboveground standing biomass (see Table 1 for an overview). Furthermore, quadratic terms for aboveground standing biomass and temporal measures of NDVIs and NDVIg are considered as we expect herbaceous ANPP to be highest at intermediate values of these predictors. Due to an increase in respiratory maintenance costs with higher and taller biomass (because of relative large amounts of stem tissue and increased self-shading) relatively less assimilated C can be allocated to growth (Coughenour *et al.* 1984) (Fig. 2). We consider models that combine VI's with biomass as well as models combining tGCC and NDVI and relate them to field-measured herbaceous ANPP.

The dataset used for exploring temporal responsiveness of GCC to rainfall consists of the number of sites that recorded green up for each day since the last rainfall event, for ten separate rainfall events during the 2018 study period. To establish the effect of

time since rain event, we only considered rainfall events which were followed by at least one day without rain. Finally, we assessed the importance of both temporal and spatial resolution through a (stepwise) reduction in resolution in both GCC and biomass. For GCC, we reduced temporal resolution from one day to two days by skipping one day in the dataset. For clarity, this yields two separate datasets where one GCC time series covers all the ‘even’ days (starting at day 1 of the study) and the second dataset covers all the uneven days (starting at day 2 of the study). An increase in GCC is then calculated in a similar way as in formula 3. We extended the reduction in resolution up to six days. At each resolution (1 – 6 days), we considered all possible ways of reducing the dataset, i.e. six models were tested at a temporal resolution of six days. Spatial resolution was reduced by using the recorded green ups of one particular site (GCC plot level, Fig. 1) and use that information for all the other sites (landscape resolution). In this way, we tested whether the effect of rainfall events on GCC change is uniform through space. This yielded eight different datasets, where for each dataset the counts of day to day GCC green ups (for every productivity measurement interval) for one particular site were used to predict the productivity in the other sites as well. The importance of resolution in biomass measurements was assessed in a similar way, where temporal resolution was stepwise reduced from two weeks (each productivity measurement interval) to 10 weeks with steps of two weeks.

We used generalized linear models (GLM) to predict herbaceous ANPP, with quasi-Poisson distributions to correct for overdispersion (Crawley 2012). We first constructed a maximal model including all predictors and then stepwise eliminated the most non-significant term at each step (based on p values) to yield a minimal adequate model (Crawley 2012). We used generalized linear mixed models (GLMMs) assuming a binomial error distribution with a logit link function, to model the number of sites that recorded green up (yes or no), weighted by the total number of sites for which the camera was functioning during the event. Because rain events vary in magnitude (which influences the chance that cameras may record a green-up) ‘rain event ID’ was included as a random factor.

Model fit was assessed using D^2 , the proportion of deviance explained by each model relative to the null model. Model consistency and predictive accuracy was evaluated using a jackknife evaluation procedure (Miller 1974). In this procedure, one single data point (one productivity measurement at one location) is taken out of the dataset at each iteration and predicted by a model based on remaining data points. We report the R^2 of the regression

between observed versus jackknife predicted values as a measure of consistency of the models. GLMs were fitted using the *base* package while GLMMs were conducted in the *lme4* package (Bates *et al.* 2011). All analyses were performed in the statistical environment R version (3.4.1) (R development Core Team 2017).

Fig. 2. Overview of the expected temporal behaviour of considered predictor variables over one growing season, beginning at the start of the season (SOS) to the end of season (EOS). A and B represent two different productivity measurement intervals, during two distinctive phenophases. Temporal measures of NDVI (Δ NDVI) and biomass are different between these two stages as NDVI generally increases during the weeks following the SOS (biomass accumulation) while NDVI decreases due to leaf senescence during the second stage of the growing season when the EOS approaches. The similar NDVI values during both A and B, reflects the hypothesis that time integrated NDVI alone may not be informative on phenophase as both the inclusion of bare ground during early phases and leaf senescence during later phases reduces NDVI. Furthermore, there may be spatial variation in NDVI (e.g. through catenae, here represented by the thinner, dashed lines) besides the temporal variation. The number of increases in GCC90 is an temporally independent predictor variable over the season. The colour gradient visualizes the expected effect of VI measures and biomass at different levels on herbaceous ANPP.

Table 1: Description of predictor variables and their expected effect on herbaceous ANPP

Predictor	Description	Effect
tGCC _x	The number of days with increases in GCC90 (> site specific SD) within the productivity measurement interval, with a lag of x days	Higher productivity with more days
NDVIg _x	Ground-based measure of NDVI averaged over the productivity measurement interval, with a lag of x days	Higher productivity with higher NDVI, which saturates or declines at the highest levels
ΔNDVIg	The difference between NDVI at the onset of each productivity measurement interval and NDVIg	Higher productivity with small positive values and low productivity with negative values
NDVIS _x	Sentinel-2 derived measure of NDVI averaged over the productivity measurement interval, with a lag of x days	Higher productivity with higher NDVI, which saturates or declines at the highest levels
ΔNDVIS	The difference between NDVI at the onset of each productivity measurement interval and NDVIS	Higher productivity with small positive values and low productivity with negative values
Biomass	Field approximated aboveground standing biomass using a disc pasture meter at the onset of each productivity measurement interval	Increase in productivity with higher biomass, which saturates or declines at the highest levels

Results

Prediction of ANPP

Herbaceous ANPP was best predicted by a combination of tGCC, NDVIS, and a quadratic term for ΔNDVIS (ANODEV, $D^2 = 0.48$, jackknife adj. $R^2 = 0.51$) (Table 2, Fig. 3) implying that both short- and long-term dynamics as well as an indicator for biomass are important predictors. When only ground-based methods were considered, herbaceous ANPP was predicted best by tGCC in combination with a quadratic term for disc-measured aboveground standing biomass (ANODEV; $D^2 = 0.43$, jackknife adj. $R^2 = 0.46$, Fig. S4) (Table 2). Both these models performed better than the best satellite-based model, where NDVIS in combination with a quadratic term for ΔNDVIS explained 34% of deviance (ANODEV; jackknife adj. $R^2 = 0.27$).

Considering single VI's, we found that tGCC explained more deviation ($D^2 = 21\%$) than NDVIg ($D^2 = 18\%$) and NDVIs ($D^2 = 16\%$). Biomass did not or only marginally improve model predictions when added to models including NDVIs or NDVIg (Table 2). For all NDVIs and NDVIg measures, a lag of zero days (no lag) consistently gave the best fit in all models (Table S2 and Table S3). For tGCC this was less consistent, e.g. a zero lag was best when tGCC was considered without any other predictors while a lag of three days was best when combined with biomass (Table S1, S4).

Fig. 3. Predicted herbaceous ANPP (grams dry weight m⁻² day⁻¹) (z-axis) based upon the best model, explaining 48% of total deviance (Table 2). The model includes the number of days with measurable increases in GCC90 (tGCC, y-axis), a quadratic term for ΔNDVIs (x-axis), and a time-integrated measure of NDVIs. The effect of NDVIs is here visualized through showing the predictive behaviour of the other predictors in the model at low NDVIs (< 0.500, left panel) and high NDVIs (> 0.500, right panel).

Time series of vegetation indices and temporal responsiveness to rain

The temporal profile of camera-derived GCC90 showed strong day to day fluctuation (Fig. 4). The profiles of NDVIg and NDVIs showed less fluctuations as a consequence of lower temporal resolution, where in some cases NDVIs time series were interrupted by observation gaps of up to 15 days. The importance of temporal resolution in relation to the predictive capacity of tGCC, is demonstrated by a strong decrease in the minimum adjusted R^2 (observed versus estimated values) of models with reduced temporal resolution (based on the best field-based model in Table 2) (Fig. 5A). Furthermore, the variation in adj. R^2 increased with decreasing resolution, where two models using a tGCC measure with reduced resolution (5 and 6 days) showed relatively high adj. R^2 (0.34 and 0.36). It appeared

that the GCC measurement moments of the reduced dataset that were used for these two models, often coincided with dates at which there was a rainfall event (Fig. 5A, see colour gradient). In other words, the results show that models that included tGCC at low resolution can have predictive capacity if the model by ‘chance’ captured influential rain events (by including a GCC measurement within one day after a rain event) while majority of the models using tGCC at the same temporal resolution (at different starting data) had no predictive capacity.

The defining role of rainfall events for ANPP is emphasized by the result that the proportion of sites that recorded a green-up in GCC was highest on the same day as the rain event and decreased with each following day (GLMM, $z = -5.893$, $P < 0.001$) (Fig. 6). The proportions dropped steeply after the first day, except for the rainfall event that occurred on the 19th of June 2018, which resulted in a green-up that was still detectable in three out of seven sites until the fifth day after the rain event (Fig. 6). At the same time, GCC did not increase in response to each estimated rain event in every site. While the sites are relatively close (< 5 kilometres), models with reduced spatial resolution (by using the green ups recorded by one particular site and using these moments for all the other sites) showed lower R^2 (Fig. 5C). The effect of reduced resolution in biomass on adj. R^2 was less important, where only the reduction in spatial resolution led to a notable decrease in adj. R^2 (Fig. 5B, D).

Fig. 4. Time series of field camera derived GCC90 (primary y-axis), satellite derived NDVI (NDVIs), and ground-based NDVI (NDVIg) (secondary y-axis) during the second study period (2018). Each panel is related to one site (A – H). Precipitation events are represented as a rug (blue vertical lines) at the bottom of each panel with a distinction between small (<5mm) and larger rainfall events (>5mm). The occurrence of a fire event is indicated by an arrow.

Fig. 5. The effect of temporal and spatial resolution of tGCC (A,C) and aboveground standing biomass (B, D) on the predictive capacity (given by the adjusted R^2) of the best field-based method (tGCC in combination with a quadratic term for aboveground standing biomass). Both temporal (A) and spatial resolution (C) are important for the predictive capacity of tGCC. The colour gradient in A reflects to what extent the dates of GCC measurements in the (reduced) time-series dataset coincided with dates at which there was a rainfall event. This extent is given as a proportion where ‘1’ means that each rain event was matched with a GCC measurement moment (which is only achieved when GCC is measured every day). The colour gradient in C reflects the mean biomass (measured at the onset of each productivity measurement interval) of the site of which the tGCC measure was used. The adj. R^2 was higher when information on tGCC from sites with higher biomass is projected to the entire landscape.

Fig. 6. Predicted relationship with 95% confidence interval between the proportion of instances of daily GCC increase beyond the set threshold and the day since last estimated (merged information from CHIRPS and visually observed on camera trap images) rainfall event. The proportion is calculated as the number of sites that recorded green up relative to the total number of sites and is given for ten separate rainfall events during the 2018 study period.

Table 2: Analysis of deviance table for generalized linear models with quasi-poisson errors considering measures of three vegetation indices (GCC, NDVIg, NDVis) and field-based measurements of aboveground standing biomass (Biomass). We present multiple models for the same VI, one with and one without including the biomass predictor. The minimal adequate model was obtained by elimination of non-significant terms from the full model. For each model, the adjusted R^2 of the regression between observed versus predicted values (Adj. R^2) and between observed versus jackknife predicted values (jk Adj. R^2) is presented.

	VI	Predictor	d.f.	Res. Deviance
tGCC		null		265.95
	tGCC	tGCC₀	1	211.3
	tGCC + Biomass	tGCC₃	1	226.67
		Biomass	1	176.74
		Biomass²	1	152.74
NDVI		null		244.81
	NDVIg	NDVIg₀	1	200.4
		Δ NDVIg	1	196
		Δ NDVIg ²	1	194.59
	NDVIg + Biomass	ΔNDVIg	1	222.16
		Biomass	1	195.25
		NDVIg ₀	1	189.88
		Biomass ²	1	187.7
		Δ NDVIg ²	1	179.66
	NDVis	NDVis₀	1	205.62
		Δ NDVis	1	204.29
		ΔNDVis²	1	159.39
	NDVis + Biomass	NDVis₀	1	205.62
		Δ NDVis	1	204.29
		ΔNDVis²	1	159.39
		Biomass	1	159.03
		Biomass ²	1	157.5

prop. Deviance	Resid d.f.	F	P	Adj R ² † / jk Adj. R ²
	49			
0.21	48	13.28	<0.001	0.17 / 0.07
0.15	48	12.81	<0.001	0.55 / 0.46
0.19	47	16.28	<0.001	
0.09	46	7.83	0.007	
	44			
0.18	43	9.84	0.003	0.18 / 0.09
0.02	42	0.97	0.330	
<0.01	41	0.31	0.580	
0.09	43	5.33	0.026	0.15 / 0.07
0.11	42	6.6	0.014	
0.02	41	1.29	0.263	
<0.01	40	0.53	0.473	
<0.01	39	1.94	0.172	
0.16	43	10.81	0.002	0.41 / 0.27
<0.01	42	0.37	0.547	
0.18	41	12.39	0.001	
0.16	43	10.37	0.003	0.41 / 0.27
<0.01	42	0.35	0.556	
0.18	41	11.88	0.001	
<0.01	40	0.1	0.758	
<0.01	39	0.4	0.529	

Table 2: Continued.

	VI	Predictor	d.f.	Res. Deviance
tGCC + NDVI	NDVI _{g₀}	null		238.64
		NDVI_g	1	182.22
		tGCC₃	1	164.24
		Δ NDVI _g	1	164.22
	NDVI _{s₀}	Δ NDVI _g ²	1	163.58
		ΔNDVI_s	1	238.58
		ΔNDVI_s²	1	203.37
		tGCC₁	1	135.38
		NDVI_s	1	123.06

The proportion deviance (prop. Deviance in table) is the proportional decrease in residual deviance relative to the null model. The ordering of predictors in the model is based on significance (p-value) in order to demonstrate the added importance (in terms of explained deviance) for each predictor. *† The reported adjusted R^2 is the degree to which the model predictions are correlated to observations.

Discussion

We provided a first analysis on the capacity of camera derived GCC to improve estimates of herbaceous ANPP relative to satellite- or ground-based NDVI measures. The results show that day to day increases in GCC90 are related to CHIRPS-derived rainfall events (Fig. 6) and that the sum of these daily GCC increases (tGCC) enhance the predictive capacity of both a field-based model (+ 15% D^2) and a remote-sensing approach (+ 28% D^2) (Table 2). Both models provide new herbaceous ANPP estimation methods, with reported predictive accuracy of respectively $R^2 = 0.44$ and $R^2 = 0.51$. It should be noted that these R^2 values can be considered as high, as part of the unexplained variation results from clipping errors and variability of biomass inside GCC plots (Fig. S2).

The benefit of using camera derived GCC in predicting productivity lies in the increased temporal resolution that enables cameras to pick up rapid changes in vegetation greenness. While these increases could be caused by measurement errors due to variable incoming radiation between days, we are confident that the contribution of these errors has remained limited as we have both used a threshold (accounting for site-specific background variation) and applied the by Sonnentag *et al.* (2012) recommended calculation of GCC90. The 90th

prop. Deviance	Resid d.f.	F	P	Adj R ² † / jk Adj. R ²
	43			
0.24	42	13.1	<0.001	0.44 / 0.27
0.08	41	4.46	0.041	
<0.01	40	<.01	0.959	
<0.01	39	0.16	0.691	
<0.01	42	0.022	0.883	0.62 / 0.51
0.15	41	12.493	0.001	
0.28	40	24.122	<0.001	
0.05	39	4.369	0.043	

percentile has been shown to effectively suppress the effects of variable scene illumination (Sonnentag *et al.* 2012). The amplitude of daily fluctuations was variable between sites (Fig. 4), which may reflect vegetation responses in absolute ways and be informative of production, but it may also be driven by site specific conditions such as vegetation biomass, plant species composition, herbivore pressure, and camera performance. For example, as herbivores are generally attracted to short-statured lawns (McNaughton *et al.* 1997), grazers may exhaust green vegetation quicker in low biomass sites compared to high biomass sites and thereby limit measurable changes in GCC more in the former. Another possibility is that moisture driven green up is more easily observed in high biomass sites as more leaf material is present to respond to increased moisture availability. This could explain the positive effect of biomass on the explained variation of models at lower spatial resolutions in tGCC (Fig. 5C). In this study, we account for site-specific background noise (which is smallest in low biomass sites), but further investigation into the effects of biomass differences between sites on the behaviour of GCC time series may be a valuable point of consideration.

The study period mainly covered the reproductive and senescence phase of herbaceous vegetation. While we find strong relationships between (combinations of) measures of VI's and herbaceous ANPP, strategies on the allocation of resources can vary between

phenophases (Gu *et al.* 2003). Generally, the onset of flowering is associated with declines in nutrient uptake, which may make grasses relatively more water- than nutrient-limited towards the end of the growing season (Veresoglou and Fitter 1984). A tighter link between rainfall and production during later phenophases may explain why tGCC is a good predictor of ANPP in our study. In the tropics, however, we expect the effect of phenophase to be limited as tropical savanna grasses are known to use up water as quick as possible (Xu *et al.* 2015), which is thought to provide them a competitive advantage in environments characterized by unpredictable, but heavy rainfall events (Williams *et al.* 1998). Nevertheless, closer investigation of the relationship between tGCC and ANPP at the start of the growing season may yield additional insights on the use of time integrated and temporal measures of VI's to predict herbaceous ANPP.

Prediction of aboveground net primary productivity in natural ecosystems

All three considered VI's had limited predictive capacity of herbaceous ANPP when used alone, while combinations of tGCC with either NDVI's measures or disc-measured biomass perform well (Table 1). This implies that at least two forms of information are needed to predict herbaceous ANPP at high temporal resolution: a measure that describes vegetation state (which could be phenological or in terms of biomass) and a measure that captures vegetation responses to water inputs.

Several measures of NDVI, such as the maximum NDVI over a growing season and time integrated NDVI, have been suggested to be good predictors of annual ANPP (Hobbs 1995, Paruelo *et al.* 1997). Grassy biomes, such as grasslands and savannas, are believed to be suitable systems to derive estimates on annual ANPP from NDVI data due to the synchrony between the development of the canopy and photosynthetic activity (Paruelo *et al.* 1997). Using longer time scales, periods of temporary low productivity are averaged out and what remains is the gradual build-up of aboveground standing biomass in response to accumulative rainfall. We hypothesized that at shorter time scales, the integral of NDVI would become less informative due the alternation between productive and less productive periods during the same season as a result of the stochastic nature of rainfall in tropical savannas. Our study confirms that the temporal information extracted from NDVI's time series explains more variation in ANPP than time-integrated measures of NDVI's (Table 2). The change in NDVI's (Δ NDVI's) signifies increases or decreases in green biomass and could therefore have provided phenological context for the effects tGCC and NDVI's (Fig. 2). The fitted model predicts that productivity is lowest at the highest and at the lowest (negative) values of Δ NDVI's (Fig. 3). The highest values may reflect the earliest stages of biomass

accumulation post-fire (September 2018), where low biomass limits productivity. Negative values for ΔNDVIs were mostly associated to the end of the season where large fractions of green biomass turned brown. While short-term decreases can be caused by herbivores as well (in spatially explicit ways) (McNaughton *et al.* 1996), their effect on the dynamics of NDVIs time series over the course of a growing season within sites is expected to be limited.

The best field-based model, which included tGCC and a quadratic term for disc-measured biomass, had slightly lower predictive capacity compared to the overall best model that combined ground-based and satellite-based methods (Table 2). The field-based model at least partly misses the aforementioned phenological context as disc pasture meters cannot distinguish between green and dead biomass. An explanation for the predictive capacity of this 'simpler' model (in terms of the number of predictor variables) is that it captures the effect of both spatial and temporal variation in biomass and thus the generally positive effects of biomass on herbaceous ANPP as more can be produced when there is more photosynthetic active plant material.

Spatiotemporal resolution and responsiveness to rain events

The use of automated field cameras allows for GCC time series with high temporal resolution and therefore detailed information on productive periods. The clear responses of GCC to rainfall events (Fig. 6), support the idea that subtropical savanna vegetation respond in a more immediate manner to rainfall compared to arid and semi-arid vegetation (Williams *et al.* 1998, Schwinning and Sala 2004, Moreno-de las Heras *et al.* 2012) and that these responses can be used to predict herbaceous ANPP. That vegetation sometimes failed to respond to rainfall (Fig. 6) may be due to that the rain events were not actually measured at each camera location but estimated from cloud cover and density using the CHIRPS procedure. The absence of green up could therefore have resulted from spatial variability in rainfall, where one subarea received no or less rainfall than another subarea. Besides the temporal component, the spatial resolution of tGCC may thus play an important role as well (Fig. 5C). The predictive capacity of disc-measured biomass is less affected by reduced spatial resolution (Fig. 5D) than tGCC and only minimally affected when considering temporal resolution (Fig. 5B). The minimal effect of reduced temporal resolution implies that this model based on field-based methods indeed captures only little phenological information compared to a model that includes ΔNDVIs . The availability of cloud-free satellite imagery may be restricted during the start of the season which hinders the estimation ΔNDVIs . In this case, the field-based method could potentially benefit from other indicators that provide phenological context (such as flowering).

Applications and conclusion

Accurate estimates of herbaceous ANPP serve a wide variety of ecological applications. Here, we have presented a new method that improves the temporal resolution of such estimates. The added value of methods that allow the estimation of short-term productivity is due to its role for a range of other ecological processes. For example, short term productivity is closely synchronized to grazing activity (Bonnet *et al.* 2010). A network of cameras that spans an ecosystem may therefor assist in predicting the movement of herbivores.

An advantage of using field camera's to estimate ANPP is the fact that digital repeat imagery is an ubiquitous, multi-purpose tool with applications in for example the study of phenology and monitoring of wildlife. Phenology plays important roles in key ecosystem functions and processes such as competitive interactions, trophic dynamics, primary production and nutrient cycling (Cleland *et al.* 2007, Morisette *et al.* 2009). Using field cameras enables researchers to characterize the entire seasonal trajectory of herbaceous canopy greenness and the spatiotemporal distribution of herbivores, while at the same time having good estimates of ANPP when combined with either field-approximated biomass (in space) or temporal and time integrated measures of satellite derived NDVI.

The results of this study highlight that the key to successfully estimating herbaceous ANPP at short time intervals is to catch the spatial and temporal variability in responses to rain. While a model using field approximated biomass oversimplifies the dynamics of phenology, this model provides the best available estimation method when long periods of cloud cover prevent sensors to acquire cloud-free imagery (Pettorelli *et al.* 2005). While in need for further calibration in other phenophases and study systems, we conclude that field cameras can offer a reliable and cost-effective method to quantify herbaceous ANPP.

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Supporting Information

Fig. S1. Study area and location of sites (A-J) across a topographical gradient. The red colours in the figure on the right reflect a high catenae position, while the light green colours reflect a low catena position. Landform classes are determined using a modified (De Reu *et al.* 2013), multiscale (600 and 2400m neighbourhood sizes) topographic position index algorithm by Weiss (2001), based on a digital elevation model (DEM), derived from global C-band shuttle radar topographic mission (SRTM), with 30 m pixel resolution.

Fig. S2. Near surface NDVIg measurements (A) and biomass (disc pasture meter) measurements (B) for sites A – H for the 3th of May 2018 (peak of season) across multiple scales: Sentinel plot (30 x 30 m), GCC plot (10 x 5 m), and the measurement near the cage (1 x 1 m).

Table S1. Analysis of deviance table for generalized linear models with quasi-poisson errors considering different lags of tGCC measures (tGCCm: moving windows approach) and aboveground standing biomass (Biomass). The minimal adequate model was obtained by elimination of non-significant terms, beginning from the maximal model. For each model, the Adj. R^2 of the regression between observed versus predicted values is presented. The best model (based on D^2) is shaded in grey.

	lag	Predictor	d.f.	Res. Deviance
tGCC	-	null		265.95
	0	tGCC	1	211.3
	1	tGCC	1	214.82
	2	tGCC	1	220.97
	3	tGCC	1	226.67
	0	tGCCm	1	265.64
	1	tGCCm	1	264.2
	2	tGCCm	1	261.86
	3	tGCCm	1	264
tGCC + Biomass		tGCC	1	211.3
	0	Biomass	1	184.32
		Biomass²	1	170.38
		tGCC	1	214.82
	1	Biomass	1	177.35
		Biomass²	1	159.51
		tGCC	1	220.97
	2	Biomass	1	172.95
		Biomass²	1	153.73
		tGCC	1	226.67
	3	Biomass	1	176.74
		Biomass²	1	152.74

The proportion deviance (prop. Deviance in table) is the proportional decrease in residual deviance relative to the null model. The ordering of predictors in the model is based on significance (p-value) in order to demonstrate the added importance (in terms of explained deviance) for each predictor. $P < 0.1$, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. † The reported adjusted R^2 is the degree to which the model predictions are correlated to observations.

prop. Deviance	Resid d.f.	F	P	Adj R2†
	49			
0.21	48	13.28	<0.001***	0.17
0.19	48	12.09	0.001**	0.16
0.17	48	10.34	0.002**	0.15
0.15	48	9.046	0.004**	0.13
<0.01	48	0.052	0.821	< 0
0.01	48	0.296	0.589	< 0
0.02	48	0.707	0.405	< 0
0.01	48	0.338	0.564	< 0
0.21	48	16.512	<0.001***	
0.1	47	8.151	0.006**	0.38
0.05	46	4.209	0.046*	
0.19	48	16.088	<0.001***	
0.14	47	11.791	0.001**	0.44
0.07	46	5.614	0.022*	
0.17	48	14.128	<0.001***	
0.18	47	15.083	<0.001***	0.53
0.07	46	6.038	0.018*	
0.15	48	12.812	>0.001***	
0.19	47	16.282	>0.001***	0.55
0.09	46	7.83	0.007**	

Table S2. Analysis of deviance table for generalized linear models with quasi-poisson errors considering different lags of both temporal and time integrated measures of near surface NDVI (NDVIg) and aboveground standing biomass (Biomass). The minimal adequate model was obtained by elimination of non-significant terms, beginning from the maximal model. For each model, the Adj. R^2 of the regression between observed versus predicted values is presented. The best model (based on D^2) is shaded in grey.

	lag	Predictor	d.f.	Res. Deviance
NDVIg	-	null		244.81
	0	NDVIg	1	200.4
		Δ NDVIg	1	196
		Δ NDVIg ²	1	194.59
	1	NDVIg	1	200.91
		Δ NDVIg	1	198.62
		Δ NDVIg ²	1	196.56
	2	NDVIg	1	201.6
		Δ NDVIg	1	200.8
		Δ NDVIg ²	1	198.72
	3	NDVIg	1	202.53
		Δ NDVIg	1	202.32
		Δ NDVIg ²	1	200.27
NDVIg + Biomass	0	ΔNDVIg	1	222.159
		Biomass	1	195.25
		NDVIg	1	189.88
		Biomass ²	1	187.7
		Δ NDVIg ²	1	179.66
	1	Biomass	1	222.03
		ΔNDVIg	1	197.06
		Biomass ²	1	192.71
		NDVIg	1	189.68
		Δ NDVIg ²	1	179.48
		Biomass	1	222.03
		ΔNDVIg	1	201.93
	2	Biomass ²	1	195.75
		NDVIg	1	192.31
		Δ NDVIg ²	1	189.84

prop. Deviance	Resid d.f.	F	P	Adj R2†
	44			
0.18	43	9.839	0.003**	
0.02	42	0.974	0.33	0.18
<0.01	41	0.312	0.58	
0.18	43	9.869	0.003**	
<0.01	42	0.515	0.477	0.18
<0.01	41	0.461	0.501	
0.18	43	9.555	0.003**	
<0.01	42	0.178	0.676	0.18
<0.01	41	0.459	0.502	
0.17	43	9.221	0.004**	
<0.01	42	0.046	0.832	0.18
<0.01	41	0.448	0.507	
0.09	43	5.334	0.026*	
0.11	42	6.596	0.014*	
0.02	41	1.291	0.263	0.18
<0.01	40	0.525	0.473	
<0.01	39	1.936	0.172	
0.09	43	5.651	0.022*	
0.1	42	6.196	0.017*	
0.02	41	1.079	0.305	0.15
<0.01	40	0.752	0.391	
0.01	39	2.532	0.12	
0.09	43	5.327	0.026*	
0.08	42	4.7	0.036*	
0.03	41	1.446	0.236	0.13
0.01	40	0.804	0.376	
0.01	39	0.578	0.452	

Table S2. Continued

	lag	Predictor	d.f.	Res. Deviance
NDVlg + Biomass (Continued)	3	NDVlg	1	202.53
		Biomass	1	201.16
		Biomass ²	1	197.16
		Δ NDVlg	1	194.48
		Δ NDVlg ²	1	192.16

The proportion deviance (prop. Deviance in table) is the proportional decrease in residual deviance relative to the null model. The ordering of predictors in the model is based on significance (p-value) in order to demonstrate the added importance (in terms of explained deviance) for each predictor. · $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. † The reported adjusted R^2 is the degree to which the model predictions are correlated to observations.

Table S3. Analysis of deviance table for generalized linear models with quasi-poisson errors considering different lags of both temporal and time integrated measures of sentinel derived NDVI (NDVIs) and aboveground standing biomass (Biomass). The minimal adequate model was obtained by elimination of non-significant terms, beginning from the maximal model. For each model, the Adj. R^2 of the regression between observed versus predicted values is presented. The best model (based on D^2) is shaded in grey.

	lag	Predictor	d.f.	Res. Deviance
NDVIs	-	null		244.81
	0	NDVIs	1	205.62
		Δ NDVIs	1	204.29
		ΔNDVIs²	1	159.39
	1	NDVIs	1	205.14
		Δ NDVIs	1	203.91
		ΔNDVIs²	1	163.31
	2	NDVIs	1	204.69
		Δ NDVIs	1	203
		ΔNDVIs²	1	170.93
	3	NDVIs	1	204.18
		Δ NDVIs	1	201.58
		ΔNDVIs²	1	177.55

prop. Deviance	Resid d.f.	F	P	Adj R2 [†]
0.17	43	9.753	0.003**	
<0.01	42	0.317	0.577	
0.02	41	0.922	0.343	0.18
0.01	40	0.616	0.437	
<0.01	39	0.535	0.469	

prop. Deviance	Resid d.f.	F	P	Adj R2 [†]
	44			
0.16	43	10.8118	0.002**	
<0.01	42	0.3679	0.547	0.41
0.18	41	12.3899	0.001**	
0.16	43	10.395	0.002**	
<0.01	42	0.324	0.572	0.4
0.17	41	10.638	0.002**	
0.16	43	9.931	0.003**	
<0.01	42	0.417	0.522	0.36
0.13	41	7.938	0.007**	
0.17	43	9.953	0.003**	
0.01	42	0.637	0.429	0.32
0.1	41	5.887	0.02*	

Table S3. Continued.

	lag	Predictor	d.f.	Res. Deviance
NDVIs + Biomass	0	NDVIs	1	205.62
		Δ NDVIs	1	204.29
		ΔNDVIs²	1	159.39
		Biomass	1	159.027
		Biomass ²	1	157.504

The proportion deviance (prop. Deviance in table) is the proportional decrease in residual deviance relative to the null model. The ordering of predictors in the model is based on significance (p-value) in order to demonstrate the added importance (in terms of explained deviance) for each predictor. · $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. † The reported adjusted R^2 is the degree to which the model predictions are correlated to observations.

Table S4. Analysis of deviance table for generalized linear models with quasi-poisson errors considering temporal and time integrated measures of sentinel derived NDVI (NDVIs) and near surface NDVI (NDVIg) with a lag of zero days, in combination with (different lags of) tGCC. The minimal adequate model was obtained by elimination of non-significant terms, beginning from the maximal model. For each model, the Adj. R^2 of the regression between observed versus predicted values is presented. The best model (based on D^2) is shaded in grey.

	GCC lag	Predictor	d.f.	Res. Deviance
NDVIs	-	null		238.64
	0	ΔNDVIs	1	238.58
		ΔNDVIs²	1	203.37
		GCC	1	137.37
		NDVIs	1	126.27
	1	ΔNDVIs	1	238.58
		ΔNDVIs²	1	203.37
		GCC	1	135.38
		NDVIs	1	123.06
	2	ΔNDVIs	1	238.58
		ΔNDVIs²	1	203.37
		NDVIs	1	143.57
		GCC	1	127.66

prop. Deviance	Resid d.f.	F	P	Adj R2 [†]
0.16	43	10.368	0.003**	0.41
<0.01	42	0.353	0.556	
0.18	41	11.882	0.001**	
<0.01	40	0.096	0.758	
<0.01	39	0.403	0.529	

prop. Deviance	Resid d.f.	F	P	Adj R2 [†]
	43			0.54
<0.01	42	0.021	0.885	
0.15	41	12.1	0.001**	
0.28	40	22.56	<0.001***	
0.05	39	3.931	0.054	
<0.01	42	0.022	0.883	0.62
0.15	41	12.493	0.001**	
0.28	40	24.122	<0.001***	
0.05	39	4.369	0.043*	
<0.01	42	0.021	0.885	
0.15	41	12.25	0.001**	0.6
0.25	40	20.8	<0.001***	
0.07	39	5.538	0.024*	

Table S4. Continued.

	GCC lag	Predictor	d.f.	Res. Deviance
NDVis (Continued)	3	Δ NDVis	1	238.58
		ΔNDVis²	1	203.37
		NDVis	1	143.57
		GCC	1	132.56
NDVlg	0	NDVlg	1	182.22
		GCC	1	167.85
		Δ NDVlg	1	167.55
		Δ NDVlg ²	1	165.66
	1	NDVlg	1	182.22
		GCC	1	166.82
		Δ NDVlg	1	166.42
		Δ NDVlg ²	1	165.3
	2	NDVlg	1	182.22
		GCC	1	166.55
		Δ NDVlg	1	166.41
		Δ NDVlg ²	1	165.81
	3	NDVlg	1	182.22
		GCC	1	164.24
		Δ NDVlg	1	164.22
		Δ NDVlg ²	1	163.58

The proportion deviance (prop. Deviance in table) is the proportional decrease in residual deviance relative to the null model. The ordering of predictors in the model is based on significance (p-value) in order to demonstrate the added importance (in terms of explained deviance) for each predictor. · $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. † The reported adjusted R^2 is the degree to which the model predictions are correlated to observations.

prop. Deviance	Resid d.f.	F	P	Adj R2†
<0.01	42	0.021	0.887	0.47
0.15	41	11.847	0.001**	
0.25	40	20.116	<0.001***	
0.05	39	3.707	0.062	
0.24	42	14.619	<0.001***	0.18
0.06	41	3.723	0.061	
<0.01	40	0.079	0.78	
<0.01	39	0.49	0.488	
0.24	42	14.433	<0.001***	0.18
0.06	41	3.94	0.054	
<0.01	40	0.103	0.75	
<0.01	39	0.286	0.596	
0.24	42	14.065	<0.001***	0.18
0.07	41	3.907	0.055	
<0.01	40	0.036	0.851	
<0.01	39	0.15	0.701	
0.24	42	13.996	<0.001***	0.44
0.08	41	4.462	0.041*	
<0.01	40	0.003	0.959	
<0.01	39	0.16	0.691

Fig. S3. Observed versus Jackknife predicted regression plots for the best model, combining tGCC, NDVIs and a quadratic term for Δ NDVIs (A) and for the best field-based model, combining tGCC and a quadratic term for aboveground standing biomass (B). Regression model and parameters are shown in the graph.

Chapter 6

Synthesis

Inger K. de Jonge

Introduction

The aim of this thesis was to improve the understanding of anthropogenic impacts on the functioning of savanna ecosystems. Human population growth associated land-cover conversion and fragmentation, and growing livestock numbers increasingly threaten the few remaining intact savanna ecosystems. Longer and more frequent droughts due to changing rainfall regimes form additional threats to the ecological integrity of these ecosystems. Therefore, I aimed through this work to understand the mechanisms behind savanna ecosystem responses to anthropogenic change and to identify practices that ensure the resilience of ecosystems functions and services to both people and wildlife. In this thesis, I showed how components of 'resilience' can be used to study these highly dynamic, heterogeneous ecosystems and how we may use them to predict the outcome of human pressure on savanna function and structure (**Chapter 2 and 3**). Then, I quantified how and when edge areas bordering protected areas facilitate or exclude wildlife to further ideas on how edge areas may be best managed to preserve both biodiversity and human livelihoods (**Chapter 4**). Lastly, I showed in **Chapter 5** how camera traps can be used as 'phenocams' to track vegetation response to water inputs and how that may improve the estimation of Aboveground net primary productivity (ANPP), a key ecosystem function. Here, I will integrate and synthesize the key findings of this research.

Regime shifts in savannas

The increase in livestock grazing, both inside protected areas, and in adjacent edge area, is a major driver of vegetation change, both structurally (woody versus grassy, tall grass versus short grass) and compositional (species, traits). Livestock consume grass and thereby compete with other 'consumers' of living plant biomass and litter (fire and native grazers), thereby changing the disturbance regime. Disturbance in the form of fire has been shown to maintain open savannas and closed forests as alternative states in both the Neotropics and Afrotropics (Dantas *et al.* 2016), while fire in drier savannas (those that do not support closed forest) may additionally maintain *grazing-lawn* savannas and *fire-grass* savannas as alternative states (Hempson *et al.* 2019). Dense woodlands that arise through fire suppression in drier savannas are less often seen as alternative states as the flammable grass layer is hardly completely excluded. However, the negative effect of woody plants on the herbaceous layer through shading and retaining a moist microclimate and thereby the spread of fire, is part of a feedback loop which may give rise to an alternative regime, sustaining dense woody vegetation.

Through impacts on fire frequency and intensity, livestock grazing interacts with both of these feedback loops in and around the GSME (Fig 1.). Outside protected areas, high intensity grazing has turned many pastoral lands into grazing-lawn savannas, while the slightly lower intensity (just enough to suppress fire) in margin areas of protected area mainly interacts with the feedback between woody plants, shade and grass suppression (Fig. 1, chapter 3). In some edge areas, such as the Ololosokwan village lands, both of these alternative feedback loops have influenced the current vegetation structure over the past 10 to 20 years with increased woody cover and increased lawn formation (Fig. 3). Both regime shifts involve the reduction of 'pulse disturbance' (in fire *and* in herbivory), which reduces the competitive advantage of species or lifeforms with traits that allow fast 'recovery'. The increase in 'press disturbance' (chronic grazing and browsing regimes) are alternatively promoting typical resistance traits. This switch is well illustrated by the widely reported invasion of the prickly *Opuntia* sp. in rangelands within the savanna biome (Mlilo and Lyaruu 2008). As members of the Cactaceae, *Opuntias* are among the most drought-resistant plants and as such they thrive in arid regions. Due to low palatability, they may invade human-modified savannas and replace palatable native grasses. Being 'resistant' to both drought and herbivory, they appear to be a typical indicator of resistant systems. Alternatively, their low growth rates and hence low 'recovery' rates from fire, limits their success in protected areas (Bukombe *et al.* 2018). In chapter 2, I experimentally showed how livestock grazing decreased the recovery potential but may have improved resistance to drought of the herbaceous vegetation. Additionally, one could argue that the widely observed woody plant encroachment in response to human-induced fire suppression (Chapter 3) represents a similar switch, as woody plants (those that have escaped the fire-trap) are more resistant than grasses. **Together, this suggests that one of the major implications of human impacts in savannas is the general replacement of 'recoverable' elements with 'resistant' ones, which can be observed at the level of communities, species, and traits.**

Fig. 1. Alternative dynamic regimes in the GSME maintained by fire (promoting fire grass), grazing (promoting lawn grass), and fire suppression (promoting trees). The intensity of livestock grazing plays important roles in regime shifts through imposing drought conditions (A) and through suppression of fire (B).

The role of plant functional types and traits

Not all areas with increased livestock grazing in and around the GSME experienced regime shift-associated changes in vegetation composition and structure. This raises questions on what biotic and abiotic factors control the strength of these alternative positive feedback loops. The results of Chapter 3 showed that transitions from open savannas to encroached woodlands were slowest on sandy soils and at the high end of the rainfall gradient. This was partly explained by indirect effect of these environmental conditions on plant functional strategy, where sandy soils and higher rainfall promote erect trees (T) rather than ‘trees that can grow as shrubs’ (SST). There is a large functional distinction between these two *growth forms* (Zizka *et al.* 2014) in a range of traits and life history strategy. Sapling densities of woody species that identify as SST’s were generally higher than of woody species that identify as T’s. In addition, the time needed to reach maturity is shorter for SST’s (Zizka *et al.* 2014) and SST’s are generally shorter in height when maturity is reached. Further, T’s are more conservative in water use (Zizka *et al.* 2014), implying a stress-resistance strategy rather than being ‘wasteful’. These differences all imply shorter and thus faster life cycles, with plants being less conservative in resource use (basal resprouting, rather than re-growing from surviving

stems). The fact that landscapes with high proportions of SST's in the tree community showed the highest encroachment rates might thus reflect a 'recovery' strategy of the woody component (both through densities and a wasteful strategy enabling fast life cycles).

The differences between *growth forms* in resource acquisition and utilization strategies could be viewed in terms of physiological trade-offs. Woody plants that identify as T's, may be thus be more 'resistant' and conservative under stressful conditions while SST's invest more in resource acquisition and thus faster growth and 'recovery' (Fig. 2). As plant functional strategy is the outcome of both resources and disturbance regimes (Pianka 1970, Grime 1977, Tilman 1990), high soil fertility may therefore not necessarily promote fast recovery. Landscapes with high soil fertility that are relatively flat and far away from rivers (and hence safe) can attract large amounts of grazers (grazing hotspots) (Anderson *et al.* 2010). The negative impacts associated with trampling and bulk feeding on woody saplings may promote resistance strategies and thus a more conservative use of resources. The dominant woody species on both the Dutwa plains and in the Mara triangle, typical grazing hotspots in the GSME, is *Balanites aegyptiaca* which is characterized by early bark growth, late height investment and is a typical 'T' (chapter 3).

An important remaining question is what specific traits associated to T's versus SST's mediated encroachment in margins areas of the GSME. Not all SST's are encroachers, and some T's in this study can locally encroach as well (e.g. *Combretum molle*, *Senegalia polyacantha*). Is it better to summarize encroaching ability by considering a full vector of traits (e.g. short stature, early maturity, early height growth, thin bark, root suckering) (Fig. 2)? Typical encroachers of semi-arid African savannas such as *Vachellia drepanolobium* (Dalle *et al.* 2006, Belay and Kebede 2010) and *Dichrostachys cinerea* (Moleele *et al.* 2002, Wakeling and Bond 2007) seem to fit that idea as they are among the species with lowest *early bark investment*, the highest *height investment*, and are considered SST's (Chapter 3). In a two dimensional trait space with *growth form* on one axis and the trade-off between *height investment* and *early bark investment* (Chapter 3) on the other axis, these two species would be close to each other (Fig. 2). Other species, such as *Kigelia Africana* (which had both the highest bark investment and slowest height investment of the measured species in chapter 3) would end up at the other end of this trait space (Fig. 2). In between, there may be species that have only a subset of traits that allow them to encroach areas only under certain conditions. *Senegalia polyacantha*, a tall riverine tree with high abundance along for example the Grumeti river (Sharam *et al.* 2009), can locally

heavily encroach as a result of fire suppression (pers. observation). *Commiphora trothea*, a woody plant that occurs as both a tree and shrub-like *growth forms*, is encroaching on slopy areas (mid-catenae and ridges) in stretches of Maswa Game Reserve.

Fig. 2. Two-dimensional trait space with the functional distinction between 'Trees' and 'Trees that are sometimes shrubs' on the x-axis and the trade-off between early bark investment and height investment on the y-axis. Species codes reflect the following species: Kigafr - *Kigelia Africana*; Comtro - *Commiphora trothea*; Senpol - *Senegalia polyacantha*; Vacdre - *Vachellia drepanolobium*; Diccin - *Dichrostachys cinerea*.

Consequences for higher trophic levels and future human – wildlife coexistence

The consequences of regime shifts in edge areas along the GSME to higher trophic levels are complex as these regime shifts influence both resource quantity and quality, and perceived predation risks by herbivores. Persistent high intensity grazing by livestock has resulted in, and maintains, short swards of high-quality forage in village lands (Fig. 1). On the other hand, populations of larger grazers, such as buffalo, are more regulated by forage quantity (Hopcraft *et al.* 2010) and should therefore profit more from 'recoverable' landscapes where grass biomass can recover fast (Fig. 1, chapter 2). The switch to 'resistant'

species or ecotypes and growth-forms (woody plants) limits forage quantity and thereby the largest grazers (Chapter 4). A similar effect of body size can be observed from long-term survey data in Kenyan rangelands for different livestock species (Ogutu *et al.* 2016). Apparently, the switch from ‘recoverable’ to ‘resistant’ landscapes similarly affects pastoral systems, where grazing cattle is increasingly replaced by sheep and goats (Ogutu *et al.* 2016).

Long term fire suppression (> 15 years) in the pastoral village lands of Ololosokwan gave rise to a cohort of predominantly tall *Vachellia gerrardii* trees that now dominate the landscape and locally form dense woody patches (Fig. 3A). Across landscapes in the GSME and beyond, *V. gerrardii* has variable growth-form and occurs as both single-stemmed trees and multi-stemmed shrubs (Zizka *et al.* 2014). In Ololosokwan, *V. gerrardii* predominantly grows as tall, relatively sparsely distributed single-stemmed trees with important consequences for both visibility for herbivores (Riginos 2015) and the potential for positive tree-grass interactions (Blaser *et al.* 2013) (Fig. 3B). Besides the positive effect of trees on the recovery of the herbaceous vegetation underneath their canopy (Chapter 2), trees may additionally improve forage quality to both wildlife and livestock (Treydte *et al.* 2007, Bernardi *et al.* 2016). However, the lack of recruitment of these trees under intense livestock grazing can make this a temporary state, transforming to open and short grassland when the trees reach their maximum age, are pushed over by elephants, or are harvested for timber and firewood by people, as is currently happening across the Loliondo village lands.

Fig. 3. Contrast between (A) the Serengeti National Park without livestock in the back (yellow tall grass) and village lands of Ololosokwan in front, where long-term fire suppression has promoted woody cover, and resulted in short green grass (Photo credit: Han Olff, near Klein's gate). The dominant species in these village lands is *V. gerrardii*, that predominantly grows as single-stemmed tree allowing herbaceous vegetation to grow underneath its canopy (B) (Photo credit: Inger de Jonge).

At least under the current situation in the Ololosokwan village lands, I showed in chapter 4 that not all consequences of regime shifts are per se negative and that some may be perceived as beneficial. However, one might ask how general this situation is and whether other edge areas can be managed in similar ways. Moreover, the ongoing debate over land rights and best natural resource management in this part of LGCA has resulted in the removal of bomas in some parts of the landscape. Given the dynamic nature of savanna landscapes and their quick responses to human-induced alterations in disturbance regimes (Chapter 3) and current benefits of spatial coexistence during the wet season (Chapter 4), an important question for future work is what interventions can alleviate spatial decompression, benefit people, and promote landscape heterogeneity all at once.

The combination of short grazed lawns with the specific growth-form of *V. gerrardii* trees provides high quality forage with still good visibility for grazers while offering relatively safe habitat during dangerous times of the day (Chapter 4). The removal of livestock practices from this landscape, which is intended to be done along a 5-15 km wide buffer zone along the eastern border of the Serengeti National Park, between Ngorongoro Conservation Area and the Kenya border, may decrease these benefits for especially smaller herbivores in a couple of years as 'fire grasses', or ecotypes adapted to fire, eventually outcompete lateral growing lawn grasses by overshadowing them (Fig. 1, regime shift A). Vertical, erect growth of the herbaceous layer in a time frame of just a couple of months (Personal observation) during the temporary eviction of Masai initiated in August 2017 (Mittal and Fraser 2018), implies that the potential for a flammable herbaceous layer may be achieved rather quick as these traits are associated to fire-adapted grasses. This needs however further testing.

The consequences of the distortion in the size-class distribution of the woody component for future vegetation structure may be harder to predict. Heavy browsing by goats have reversed patches of older saplings (*Vachellia hockii* and *Vachellia gerrardii*) and are in a chronic browse trap (Staver and Bond 2014). Mature trees, that by age have become resistant to fire (Fig. 1, regime shift B), form the major size class which means that the reintroduction of fire may not be enough to decrease woody cover in most areas while release from the browse trap allows older saplings, close to the Gulliver stage, to escape from the fire trap. The release from livestock pressure may additionally improve tree recruitment and establishment opportunities as herbivore pressure has strong negative effects at the earliest recruitment phases (Morrison *et al.* 2019). Lastly, reduced human disturbance may increase the occurrence of native large herbivores with potential positive effects on seed viability and germination. Through ingestion of seeds in the dry season,

large mammalian herbivores mitigate the negative effects of larval infestation by bruchid beetles, a serious threat to the viability of seeds (Or and Ward 2003). The positive effects of ingestion by herbivores is suggested to increase with body mass because they swallow larger percentages of unchewed pods (Miller 1995). A reduction in livestock and increase in larger bodied wildlife may therefore improve overall recruitment.

Clearly, there are different 'pathways' for the response of the vegetation to livestock removal and the outcome will depend on the relative development of herbaceous layer (both in terms of biomass/fuel and composition) versus trees and elephant presence (that may reduce woody cover across all size classes). While the restoration of this landscape to a fire-controlled system with seasonally migrant herbivores may 'decompress' the ecosystem in favour of wildlife populations, there are thus some important considerations for future work: 1) Fire spread may be limited due to local high density of trees, potentially driving further encroachment; 2) the facilitative effect of livestock grazing on wildlife through the maintenance of grazing lawns will be reduced, especially for smaller wildlife, while for larger species (buffalo, wildebeest) more food will be available; 3) people are losing valuable grazing lands, potentially furthering antagonism between people and conservation goals and; 4) moving up the border of core protected areas more eastwards will still maintain a potentially sharp spatial shift between fire and grazing controlled regimes, which limits local plant structural heterogeneity needed to maintain diverse assemblages (rather than just smaller-bodied herbivores, Chapter 4).

In Chapter 4, I have shown that the activity of two dominant herbivore species (wildebeest and zebra) in the village lands is lowest during the day time when livestock is present. This implies that Human – wildlife coexistence may potentially benefit from management interventions that promote further spatial coexistence, while limiting temporal coexistence. Facilitative effects of pastoral lands for wild ungulates were highest in the wet season (Chapter 4) meaning that reserving human-induced grazing lawns during this season would increase coexistence. Temporal segregation may additionally limit disease transmission (Fynn *et al.* 2016) and reduce any negative impacts of higher predator abundances that follow wildlife to human-occupied areas (Chapter 4). Interventions may include a dynamic border, giving wildlife access to human-modified landscapes at specific times of the year while limiting livestock access during that period. However, such management interventions need much further investigation. While temporally 'variable' use of the landscape between livestock and wildlife is applied in some Kenyan conservancies (Tyrrell *et al.* 2017), its success remains questionable considering the fact that wildlife numbers are experiencing a dramatic decline in Kenya (Ogutu *et al.* 2016).

Appendix

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Appendix

Summary

Introduction

Human impacts increasingly threaten Earth's natural ecosystems. The rise in human population over the past century is taking its toll on the environment as people need land and resources to sustain their livelihood. Moreover, the increase in the human population is closely related to carbon emissions and therefore one of the lead causes of climate change. These anthropogenic pressures are and will be most severe in sub-Saharan Africa, where the human population continues to grow exponentially and is projected to quadruple by the year 2100. In recent decades, increasing resource demand has led to the conversion of natural habitats to agricultural fields and pastoral rangelands. This has recently reached a point where even the largest protected areas are under great pressure, with people increasingly migrating to the borders of these parks. In addition to the aggravation of human-wildlife conflicts and increasing antagonism between people and conservation objectives, this trend has led to a new set of ecological challenges as we still have little understanding of the impact of human activities in and around protected areas on the functioning of savannas.

Human impacts in African savannas

Natural savanna ecosystems provide a wealth of ecosystem services to people, including water, food, fuel and animal feed. The abundant and unique wildlife populations characteristic of savannas furthermore support tourism and thereby the economies of many African countries. However, these services are not unlimited and different objectives may compete for the same ecosystem service. Livestock and native herbivore assemblages both need fresh graze and browse, so they must share these resources in savanna ecosystems. While wild herbivore populations are generally constrained by a limiting or regulating factor in a specific area, supplemental feed and water combined with protection from predators at night (e.g. inside animal shelters called 'bomas') release those constraints for livestock populations. These 'advantages' have set in motion a rapid and ongoing replacement of native herbivores with livestock across the African continent at present day.

In addition to the direct effect of exclusion through resource competition, intensifying livestock grazing regimes are indirectly affecting wildlife population through the modification of the landscape. Chronic grazing regimes often lead to changes in the herbaceous plant community, with either positive or negative effects on forage quality.

Moreover, higher grazing intensity may prevent the build-up of herbaceous biomass at the end of the growing season which in turn precludes fire from the landscape. Depending on other environmental conditions, such as rainfall and soil properties, long-term fire suppression can cause a substantial increase in woody plants. This process, often referred to as 'woody plant encroachment', can have profound effects on a number of ecosystem functions and services, including the productivity of the herbaceous layer.

The concerns about reductions in forage (exclusion of wildlife), changes in vegetation composition (e.g. less desirable grasses) and structure (increase of woody plants) and their consequences for wildlife in savanna ecosystems have increased in recent decades. Strict protection of areas has become increasingly important for the conservation of biodiversity and is now critical for the conservation of natural processes in African savannas. However, as suitable areas for human settlements are running out elsewhere, human activities in edge areas (areas directly adjacent to protected areas) are intensifying and are now threatening the ecological integrity of natural ecosystems. The intensification and expansion of small agricultural fields along the western boundary of the GSME have led to a 'sharp' conservation border zone from which wildlife is largely excluded. In order to provide livestock with sufficient food, several human communities have been found to graze their livestock within protected areas, leading to an increase in the overall grazing intensity in the park, which is altering a variety of other ecological processes, including the fire regime. There are also reports of livestock grazing in protected areas along the southern and eastern borders of the GSME.

The magnitude and speed of vegetation changes, caused by the alteration in disturbance regimes, is highly variable within the ecosystem. In this thesis I try to find general explanations for the variation in responses of landscapes and their plant communities (chapters 2 and 3) and wild herbivore assemblages (chapter 4) to human impacts in savannas. Second, since our understanding of the response of savanna ecosystems to anthropogenic pressures is still limited by the availability of relevant data, I have developed and tested several time- and cost-effective methods to estimate the productivity of the herbaceous layer (Chapter 5), as well as a new way to experimentally manipulate water availability at landscape level (Chapter 2).

The effect of disturbance regimes on plant communities and functional traits

Herbivory and fire are key ecological processes that regulate the abundance, distribution, and functional composition of plant communities in savannas. Because some plant species are better able to withstand repeated defoliation or frequent fire than others, their abundance may increase in an area that is subject to alterations in these disturbance regimes. The increase in livestock grazing and the associated decrease in fire in edge areas of the GSME is therefore expected to lead to a directional shift in vegetation composition. The plant species in this shifted community can be characterized by a set of morphological, physiological, or biochemical traits (commonly referred to as functional traits) that improve performance under these 'new' human-induced conditions. When considering the impact of people on ecosystem functioning, some of these functional traits are of particular interest because they are related not only to a plant's response to its environment, but also because they have a strong effect on the ecosystem and its functioning.

For plants, there is no single best way to persist in environments with disturbances from herbivores or fire. Under certain conditions, 'avoiding' stress can be most adaptive: plants can become less palatable to herbivores (biochemical trait) and thereby prevent being eaten. In other situations, 'tolerating' or 'resisting' stress can increase plant performance the most: many grasses tolerate herbivores by quickly producing new plant material (physiological trait) and possibly sacrificing stems for leaves (morphological trait). The best 'strategy' for dealing with herbivory will depend on the entire context. Intensive grazing regimes often lead to drier conditions due to the increase in soil temperature and evaporation rates. Functional traits that increase performance during drought as well as under intense grazing may be most beneficial to the plant in those situations.

Climate change is expected to lead to more frequent, intense and prolonged drought in East Africa in the future. The question is whether the properties of the plant community in edge areas cause a change in the functioning of the entire landscape during ecological perturbations such as extreme drought. Prolonged exposure to drier soils through intensive grazing is expected to make the landscape more drought '*resistant*' compared to natural savannas with lower grazing pressures. However, 'Darwin's demon' makes ecologists believe that no organism on Earth can perfectly withstand all forms of disturbance or abiotic stress because otherwise it would outperform any other 'imperfect' organism. Improving one trait (drought resistance) must therefore come at the expense of another trait which results

in a 'trade-off' at the plant level. In natural protected savannas, grazing pressure is lower and there may be enough biomass to promote fire towards the end of the growing season. In addition, grasses will overshadow each other over time, which has consequences for the degree of light competition. The traits that enable plants to '*recover*' quickly after fire disturbance (so that an individual can escape light competition), are therefore expected to be more important in protected areas and thus contrast with the traits that are presumably more adaptive in the edge areas.

The resilience of ecosystem functions and services to perturbation

In Chapter 2, I test the above expectations using a landscape-wide experiment. I measured both the recovery potential from and the resistance to perturbation of the herbaceous plant community in a protected area and an adjacent edge area that is used as grazing land by local Masai. In order to measure recovery potential, colleagues and I removed all aboveground biomass in small plots of one square meter and then assessed the increase in newly produced plant material over time with a hand-held greenness radiometer. Resistance of the vegetation to perturbation has been measured using a newly developed method, in which drought is created in large plots of 40 by 40 meters by draining rainwater away from the plot using gullies. The resistance of the vegetation can be determined by measuring vegetation greenness after a year in the 'drought' plot and comparing it with a 'control' plot in the same landscape. Savannas are heterogeneous ecosystems and are characterized by the simultaneous occurrence of trees and grasses, which can influence each other both positively and negatively. To include the influence of trees in this experiment, we measured the greenness of the herb layer both underneath the canopy of trees and beyond the zone of influence of the tree.

The results of this experiment seem to be largely in line with the expectations: pastoral edge areas are drought resistant, while protected areas show fast recovery. These results are supported by differences in functional traits between the plant communities in these two areas. Interestingly, the herbaceous layer underneath tree canopies in the pastoral grazing lands is both drought resistant and has high recovery potential. A possible explanation for this is that the micro-habitat underneath tree canopies offers higher resource availability and thus facilitates a 'tolerance' strategy characterized by rapid growth of new leaves. The resilience of ecosystem functions, an important indicator of stability, is determined

by both the resistance to and the recovery from perturbation, where high resilience can arise through high resistance or rapid recovery. Since these processes are both relatively high underneath tree canopies, an important conclusion of this experiment in terms of management is that trees make a very valuable contribution in edge areas to the resilience of ecosystem functions and services.

In Chapter 3, I extend the expectation of plant-level ‘trade-offs’ to the entire ecosystem and apply it to a very common problem in African savannas; the strong increase in woody plants. Certain grasses promote fire in savannas and have special adaptations that promote their own persistence under a frequent fire regime. This applies to a lesser extent to woody plants; until a certain height or trunk diameter, a tree will burn after which it will have to resprout. From that moment on, a new race against time applies to the woody plant where a certain ‘escape height’ must be reached before the next fire takes place. As with the herb layer in Chapter 2, a woody plant can use different strategies to cope with this pressure. The plant can ‘resist’ fire by developing a thick layer of bark fairly quickly; this protects cambium from the heat. Rapid *recovery* can also be a successful strategy; trees that invest in rapid growth try to place their canopy above the flame zone as soon as possible before the next fire. Another trade-off which plants can make involves the ‘pace of life’; how fast does an organism complete a life cycle? Plants with a ‘slow’ strategy increase allocation to traits related to longevity and a decrease in population turnover (i.e. more generation time) at the expense of ‘*rapid growth*’ and production of new recruits. In fire prone landscapes, it can be advantageous to quickly go through the life cycle before a new fire event takes place. When considering the rapid increase in woody plants as a result of fire suppression in boundary zones of the GSME, ‘fast’ strategies (*fast recovery* or *fast life cycle*) could be relevant in explaining the magnitude of encroachment.

In an ecosystem-wide study, I investigated whether areas with plant communities characterized by ‘fast’ strategies show a higher increase in woody plants due to human-induced fire suppression than ‘slow’ strategies. This was done by measuring the increase in woody plants in boundary zones that are experiencing fire suppression. At the same time, tree species composition was recorded so that the increase can be linked to plant strategies. The results of this study show that the increase in woody plants was highest in areas with lower soil fertility, finer soil structure, and at the lower rainfall end. The model that statistically fits the data best shows that this can be partly explained by ‘fast’ strategies that are more common in the plant communities on clayey soils and in areas with relatively little rainfall. The ‘fast-slow’ trade-off was approached in this study by the

functional distinction that can be made between ‘trees’ and woody plants that have both a tree and a shrub growth form. For the latter category, it has been established that they reach the reproductive stage faster and are less conservative in the use of water compared to ‘trees’. This explains why the fast strategy is more dominant on clayey soils: in general, plants tend to be more ‘conservative’ in terms of resource consumption in stressful environments where resources are scarce, while plants in nutrient-rich environments tend to be more ‘acquisitive’.

Alternative dynamic regimes in savannas and the importance of adequate experiments and monitoring

In chapter 6 I reflect on the results of chapters 2 and 3 and discuss possible general implications of human influences on savanna ecosystem functioning. In both studies, the trade-off between plant traits that maximize recovery and rapid growth at the expense of traits that make a plant more resistant to stress appears to be translatable to the functioning of an entire landscape. This may ultimately have consequences for the flow of ecosystem services because the landscape ends up in a different ‘dynamic’. Through a combination of functional traits such as ‘high flammability’ and rapid recovery, grasses promote their own success in fire-prone savannas, leading to a positive feedback loop. On the other hand, the short vegetation in edge areas may attract more herbivores because grasses here become more palatable due to the decrease in stem / leaf ratio. This is what makes many savannas special; under the same environmental variables, multiple ‘alternative dynamic regimes’ are possible that can maintain landscape and its vegetation into a certain configuration.

Savannas, prairies, and other grassy ecosystems are known to be sensitive to both too much and too little grazing. Many arid and semi-arid ecosystems are on the verge of too much grazing and are often described as ‘degraded’ due to soil erosion or the establishment of invasive species. However, descriptions such as degradation are not informative about the mechanisms that cause the ecosystem to function differently and as such they are not helpful when the effects of human impacts need to be monitored. The two-part process of resilience, consisting of resistance and recovery, can potentially solve this issue. Resistance is a continuous variable and can be measured at multiple locations in the landscape using a simple experimental design. Although grazing pressure in the pastoral edge area is homogeneously distributed in chapter 2, different responses are visible in the landscape. Outside of the tree’s influence, vegetation is poorly able to recover

and certain strategies to conserve water seem to be increasing in the plant community. As the grazing pressure increases, the pressure can become so high that tasty grazes are no longer able to maintain a positive carbon balance. Cactus species like *Opuntia sp.* are often used as indicator species for vegetation change, however these are pre-eminently those that are 'resistant' to herbivores and drought. By measuring resistance and recovery after perturbation experimentally on a continuous scale, a quantitative analysis can therefore be carried out in which an estimate can be made of the effectiveness of management interventions (e.g. forbidding the cutting of trees in edge areas).

A future experiment in which both indicators of resilience are measured across important environmental gradients in rainfall and soil properties is a possible next step. Under what circumstances are landscapes most vulnerable to a shift to an alternative dynamic regime? Such experiments are logistically challenging, especially in tropical savanna ecosystems where recovery of the herbaceous layer can proceed quickly. This calls for the development of new methods that can accurately estimate important ecosystem functions, such as productivity, with a high temporal resolution as well as a large spatial extent.

In Chapter 5, I explore the possibilities of estimating aboveground productivity of the herbaceous layer using camera traps. This type of field camera is normally used to map the distribution of wild herbivores, but when the camera has a good view of the herb layer, they can also be used to track changes in greenness over time. Since plant greenness is generally strongly related to productivity, my expectation is that an increase in day-to-day greenness, measured as the difference in 'green pixels' on two consecutive camera images, is indicative of productivity. I tested this expectation in a small-scale field study around the field station in the GSME. Together with colleagues, I used movable cages (the benchmark) of one square meter to measure productivity of the herbaceous layer over a two-week interval in ten different locations. Cameras were installed at the same locations to take pictures of the herb layer during the day. The results of this study show that the sum of the number of days on which there is a significant increase in greenness on the camera images is predictive of the productivity measured with the cages. This prediction becomes even better when the information from the cameras is combined with data from satellite imagery. This data consists of estimates on aboveground standing biomass and the phenological status of the vegetation, both very important predictors of aboveground productivity. The conclusion of this work is that the use of cameras is a promising method for estimating productivity, certainly in addition to the methods that only use satellite data, as prolonged cloud cover during the rainy season lowers temporal resolution.

Human – wildlife coexistence in edge areas

Although the landscape and vegetation composition can change greatly under the influence of humans (chapters 2 and 3), this does not necessarily have to be disadvantageous for all native species occurring in the GSME. The decline in food availability in pastoral edge areas suggests that wild herbivores are adversely affected by livestock, but grass quality often increases when its grazed. Another possible positive effect is the redistribution of soil nutrients in pastoral areas through the use of bomas by the Masai resulting in the concentration of large amounts of manure and urine in small areas. Abandoned bomas can persist for decades and attract (nursing) native herbivores because they provide grass of high nutritional quality. Also, the presence of humans can keep predators away and thus make the landscape safer for wild herbivores. Finally, the short grazed herb layer increases the visibility of the landscape, which may make edge areas more attractive to prey animals. Animals weigh predation risk (fear) against gains (quality of food items), which means that herbivore populations are regulated both by direct predation but also by an ‘intimidation’ or ‘perceived’ predation risk.

In chapter 4, I investigate how a human-modified landscape influences the spatial and temporal distribution of wild herbivores compared to an adjacent protected area. Since food quality and predation risk mainly regulate the population of smaller herbivores while food abundance is mainly limiting for larger herbivores, I expect body size to be an important predictor of the presence of wild herbivores in edge areas. I tested this expectation by installing camera traps, which recorded animals in both areas over a period of six weeks, of which three weeks in the wet season and three weeks in the dry season. The results confirm the expectation that small herbivores such as Thomson’s gazelle and impala make relatively more use of pastoral areas than large herbivores such as buffalo and eland. This cannot be explained by a discouraging effect of humans on predators; there seem to be more Hyenas in the pastoral areas, although this data is only marginally significant. For this reason, it is more likely that positive effects are associated with increased visibility that allow wild herbivores to see predators in time. A further analysis of the data, examining the activity of wildebeest and zebra over a 24-hour cycle, shows that the depression in activity during sunset is less deep in the pastoral edge areas than in the protected area. This is usually the ‘most dangerous’ time of the day for prey species, which is corroborated by the spike in hyena activity around this time. While wild herbivores seem to prefer the park during the day, presumably because of the activity of humans and livestock, they seem to take advantage of the safety that the pastoral landscape offers them in the evening.

Conclusion

In this thesis I have shown that human influences on the functioning of savanna ecosystems are predictable based on the interplay between the history of the landscape, abiotic environmental variables, and the resulting traits of the vegetation. The increase in grazing pressure in and around the GSME has led to a change in disturbance regime where typical 'pulse' perturbations such as fire and intense but short-term grazing events by migrating herbivores have given way to chronic stressors such as drought and livestock grazing. My research suggests that one of the main implications of these human effects is the replacement of 'recoverable' elements with 'resistant' elements, which can be observed at the level of landscapes, species, and functional strategies.

In pastoral grazing areas, these insights can potentially be used to investigate which forms of management increase resilience to perturbation. In addition, this concept sheds new light on the general increase in woody plants in savannas; encroachment can also be seen as an increase in 'resistance'. As woody plants attain a certain height and thickness they become resistant to fire (unlike grasses). Moreover, fire will be completely suppressed when woody plants have reached a certain threshold in cover which will make a 'return' to an open, grassy landscape difficult: an example of unhelpful resilience.

The above conclusions regarding the shift from 'recovery' to 'resistance' are not automatically detrimental to wildlife populations. For the time being, edge areas in the GSME provide habitat for native animals, which can be linked to a form of security against predators that these areas offer. As the pressure on savanna ecosystems increases, the need for solutions and strategies that promote coexistence of people and wildlife will increase. Insights into the choices that wild herbivores make in edge areas, such as the night time use of pastoral grazing areas, will help develop solutions that benefit both people and wildlife.

Appendix

Samenvatting

Introductie

Menselijke invloeden vormen een steeds grotere bedreiging voor natuurlijke ecosystemen op aarde. De bevolkingsgroei van de afgelopen eeuw eist zijn tol op het milieu omdat mensen steeds meer land en middelen nodig hebben om in hun levensonderhoud te voorzien. De toename van de menselijke bevolking hangt bovendien nauw samen met CO₂-uitstoot en is daarmee een van de belangrijkste oorzaken van klimaatverandering. Deze antropogene druk is en zal het grootst zijn in sub-Sahara Afrika, waar de menselijke bevolking nog steeds exponentieel toeneemt en naar verwachting zal verviervoudigen tegen het jaar 2100. In de afgelopen decennia heeft de toenemende vraag naar hulpbronnen geleid tot de conversie van natuurlijke habitats naar landbouwgebieden en pastorale weilanden. Dit heeft onlangs een punt bereikt waarop zelfs de grootste beschermde gebieden onder grote druk staan, aangezien mensen steeds meer naar de grenzen van deze parken migreren. Naast de verergering van conflicten tussen mens en natuur en toenemende antagonisme tussen mensen en natuurbeschermingsdoelstellingen, heeft deze trend geleid tot een nieuwe reeks ecologische uitdagingen, omdat we nog steeds weinig inzicht hebben in de impact van menselijke activiteiten in en rondom beschermde gebieden op het functioneren van savannes.

Menselijke invloeden in Afrikaanse savannes

Natuurlijke savanne-ecosystemen bieden een schat aan ecosysteemdiensten aan mensen, waaronder water, voedsel, brandstof en veevoer. De overvloedige en unieke natuurpopulaties die kenmerkend zijn voor savannes, ondersteunen bovendien het toerisme en daarmee de economie van veel Afrikaanse landen. Deze diensten zijn echter niet onbeperkt en verschillende doelstellingen kunnen concurreren om dezelfde ecosysteemdienst. Vee en inheemse herbivoor assemblages hebben beide vers gras en/of bladeren nodig en moeten deze bronnen dus met elkaar delen in savanne-ecosystemen. Terwijl wilde herbivoorpopulaties over het algemeen worden beperkt door een limiterende of regulerende factor in een specifiek gebied, zorgen aanvullende voeding en water in combinatie met bescherming tegen roofdieren 's nachts (bijv. in dierenverblijven genaamd 'bomas') ervoor dat deze beperkingen voor vee worden opgeheven. Deze 'voordelen' hebben geleid tot een snelle en voortdurende vervanging van inheemse herbivoren door vee op het Afrikaanse continent.

Naast het directe effect van uitsluiting door concurrentie, heeft de intensivering van begrazing indirecte gevolgen voor de populatie van wilde dieren door de aanpassing van het landschap. Chronische beweidingsregimes leiden vaak tot veranderingen in de gemeenschap van kruidachtige planten, met positieve of negatieve effecten op de kwaliteit als voer. Bovendien kan een hogere begrazingsintensiteit de opbouw van kruidachtige biomassa aan het einde van het groeiseizoen voorkomen, wat op zijn beurt vuur uitsluit. Afhankelijk van andere omgevingsomstandigheden, zoals regenval en bodemeigenschappen, kan langdurige onderdrukking van brand een aanzienlijke toename van houtige planten veroorzaken. Dit proces kan ingrijpende effecten hebben op een aantal ecosysteefuncties en -diensten, waaronder de productiviteit van de kruidachtige laag.

De zorgen over veranderingen in vegetatiesamenstelling (bijv. minder wenselijke grassen) en structuur (toename van houtige planten) en de gevolgen daarvan voor wilde dieren in savanne-ecosystemen zijn de afgelopen decennia toegenomen. Het strikt beschermen van gebieden is steeds belangrijker geworden voor het behoud van biodiversiteit en is nu van cruciaal belang voor het behoud van natuurlijke processen in Afrikaanse savannes. Echter, omdat geschikte gebieden voor menselijke nederzettingen elders opraken, worden de menselijke activiteiten in randgebieden (gebieden direct grenzend aan beschermde gebieden) geïntensiveerd en breiden ze zich nu steeds meer uit tot in het park, waardoor de ecologische integriteit van natuurlijke ecosystemen wordt bedreigd. De intensivering en uitbreiding van kleine landbouwvelden langs de westelijke grens van het groter Serengeti-Mara ecosysteem (GSME) hebben geleid tot een 'scherp' grensgebied waarvandaan wilde dieren nu grotendeels zijn uitgesloten. Om vee van voldoende voedsel te voorzien, blijkt dat verschillende gemeenschappen hun vee binnen beschermde gebieden laten grazen, wat leidt tot een toename van de algehele begrazingsintensiteit in het park waardoor allerlei andere ecologische processen, waaronder het brandregime, veranderen. Ook langs de zuidelijke en oostelijke grenzen van de GSME zijn er meldingen van begrazing van vee in beschermd gebied.

De omvang en snelheid van vegetatieveranderingen, veroorzaakt door de verandering in verstoringsregimes, is zeer variabel binnen het ecosysteem. In dit proefschrift probeer ik algemene verklaringen te vinden voor de variatie aan responsen van landschappen en hun plantengemeenschappen (hoofdstuk 2 en 3) en wilde herbivoren assemblages (hoofdstuk 4) op menselijke invloeden in savannes. Ten tweede, aangezien ons begrip van de reactie van savanne-ecosystemen op antropogene druk nog steeds beperkt is door de beschikbaarheid van relevante data, heb ik verschillende tijd- en kosteneffectieve

methoden ontwikkeld en getest om de productiviteit van de kruid laag te schatten (hoofdstuk 5), evenals een nieuwe manier om water beschikbaarheid experimenteel te manipuleren op landschapsniveau (hoofdstuk 2).

Het effect van verstoringsregimes op planten-gemeenschappen en functionele eigenschappen

Herbivorie en vuur zijn belangrijke ecologische processen die de abundantie, distributie en functionele samenstelling van plantengemeenschappen in savannes reguleren. Omdat sommige plantensoorten beter bestand zijn tegen herhaalde ontbladering of veelvuldig vuur dan andere, kan hun abundantie toenemen in een gebied dat onderhevig is aan veranderingen in deze verstoringsregimes. De toename van begrazing door vee en daarmee samenhangende afname van brand in randgebieden van de GSME zal dus naar verwachting leiden tot een gerichte verschuiving in vegetatiesamenstelling. De plantensoorten in deze verschoven gemeenschap kunnen worden gekenmerkt door een reeks morfologische, fysiologische, of biochemische eigenschappen (gewoonlijk functionele eigenschappen genoemd) die de prestaties verbeteren onder deze 'nieuwe' door mensen veroorzaakte omstandigheden. Als we kijken naar de impact van mensen op het functioneren van ecosystemen, zijn sommige van deze functionele eigenschappen van bijzonder belang omdat ze niet alleen verband houden met de *reactie* van een plant op zijn omgeving, maar ook omdat ze een sterk *effect* hebben op het ecosysteem en zijn werking.

Voor planten is er niet één beste manier om te overleven in omgevingen met verstoring door herbivoren of vuur. Onder bepaalde omstandigheden kan het 'vermijden' van stress het meest adaptief zijn: planten kunnen minder smakelijk worden voor herbivoren (biochemische eigenschap) en daardoor voorkomen dat ze worden gegeten. In andere situaties kan 'tolereren' of 'weerstaan' van de stress de prestatie van planten het meest verhogen: veel grassen tolereren herbivoren door snel nieuw plant materiaal te produceren (fysiologische eigenschap) en eventueel stengels op te offeren voor bladeren (morfologische eigenschap). De uiteindelijk beste 'strategie' om met herbivorie om te gaan, zal afhangen van de gehele context. Intensieve begrazingsregimes leiden vaak tot drogere omstandigheden door de verhoging van de bodemtemperatuur en verdampingssnelheden. Functionele eigenschappen die zowel de prestaties gedurende droogte als onder intense begrazing verhogen, kunnen in die extremere situaties het meest voordelig zijn voor de plant.

Klimaatverandering zal naar verwachting in de toekomst leiden tot meer frequente, intense en langere droogte in oost-Afrika. De vraag is of de eigenschappen van de planten gemeenschap in randgebieden zorgen voor een verandering in functioneren van het hele landschap ten tijde van ecologische perturbaties zoals extreme droogte. De verwachting is dat de langdurige blootstelling aan een drogere bodem door intensieve begrazing, het landschap ‘*bestendiger*’ heeft gemaakt tegen droogte in vergelijking met natuurlijke savannes met een lagere begrazingsdruk. Echter, ‘Darwins demon’ doet ecologen veronderstellen dat geen enkel organisme op aarde perfect bestand kan zijn tegen alle vormen van verstoring of abiotische stress omdat dit organisme anders uiteindelijk ieder ander ‘imperfect’ organisme zou overtreffen. Het verbeteren van een eigenschap (bestendigheid tegen droogte) moet dus ten koste gaan van een andere eigenschap; wat een ‘compromis’ op plant niveau oplevert. In natuurlijke, beschermde savannes ligt de begrazingsdruk lager en kan er tegen het einde van het groeiseizoen genoeg biomassa staan om een brand te voeden. Daarnaast zullen grassen elkaar hier na verloop van tijd overschaduwen, wat consequenties heeft voor de mate van lichtcompetitie. De eigenschappen om snel te kunnen ‘*herstellen*’ na een vuur verstoring, zodat een individu o.a. aan lichtcompetitie kan ontkomen, zijn daardoor naar verwachting belangrijker in beschermde gebieden en vormen zo een contrast met de eigenschappen die vermoedelijk meer adaptief zijn in de randgebieden.

De weerbaarheid van ecosysteemfuncties en -diensten tegen verstoringen

In hoofdstuk 2 test ik bovenstaande verwachtingen met behulp van een landschapsbreed experiment. Zowel het *herstellend vermogen* van de kruidachtige plantengemeenschap, als de *bestendigheid* tegen perturbatie heb ik tegelijkertijd gemeten in een beschermd gebied en een naastgelegen randgebied welke door lokale Masai als begrazingsgebied word gebruikt. Om het herstellend vermogen te meten, heb ik samen met collega’s alle bovengrondse biomassa verwijderd in kleine plots van een vierkante meter om vervolgens door de tijd heen toename in nieuw geproduceerd planten materiaal te bepalen met een daarvoor bestemde ‘groenheid’ monitor. Bestendigheid van de vegetatie tegen perturbatie is gemeten met behulp van een nieuw ontwikkelde methode, waarbij droogte word gecreëerd in grote plots van 40 bij 40 meter door regenwater weg te voeren van de plot met behulp van geulen. De bestendigheid van de vegetatie kan hier worden bepaald door de groenheid te meten na een jaar tijd in de ‘droogte’ plot en deze te vergelijken

met een 'controle' plot in hetzelfde landschap. Savannes zijn heterogene ecosystemen en worden gekenmerkt door het gelijktijdig voorkomen van bomen en grassen, die elkaar zowel positief als negatief kunnen beïnvloeden. Om de invloed van bomen mee te nemen in dit experiment, meten we de groenheid van de kruid laag zowel onder de kroon van bomen als ver buiten de invloedssfeer van de boom.

De resultaten van dit experiment lijken grotendeels in overeenstemming te zijn met de verwachting: pastorale randgebieden zijn *bestand* tegen droogte terwijl het beschermde landschap een groot *herstellend* vermogen heeft. Deze resultaten worden ondersteund door verschillen in functionele eigenschappen tussen de plant gemeenschappen in deze twee gebieden. Interessant is dat de kruid laag onder boomtoppen in het pastorale randgebied zowel bestendig is tegen de droogte, als een goed herstellend vermogen heeft. Een mogelijke verklaring hiervoor is dat het microhabitat onder een boomtop een hogere beschikbaarheid van hulpbronnen biedt en zo een 'tolerantie' strategie faciliteert welke gekenmerkt wordt door snelle groei van nieuwe bladeren. De weerbaarheid van ecosysteem functies, een belangrijke indicator van stabiliteit, wordt bepaald door zowel de 'bestendigheid' als het 'herstellend vermogen' tegen perturbatie waar hoge weerbaarheid kan ontstaan door een hoge bestendigheid of een snel herstel. Aangezien deze processen beiden relatief hoog zijn onder de boomtop in randgebieden, is een belangrijke conclusie van dit experiment op het gebied van management daarom dat bomen een zeer waardevolle bijdrage leveren in randgebieden aan de weerbaarheid van ecosysteem functies en services.

In hoofdstuk 3 trek ik de verwachting omtrent de 'compromissen' op plantniveau door naar het hele ecosysteem en pas ik dit toe op een zeer algemeen probleem in Afrikaanse savannes; de sterke toename in houtige planten. Bepaalde grassoorten stimuleren vuur in savannes en hebben speciale aanpassingen die hen eigen persistentie bevorderen onder een frequent vuur regime. Dit geldt in mindere mate voor houtige planten; tot een bepaalde hoogte of stam diameter zal een boom bovengronds verbranden waarna deze opnieuw moet ontspruiten. Vanaf dat moment geldt een nieuwe race tegen de klok voor de houtige plant waar er een bepaalde 'ontsnappingshoogte' moet worden behaald voordat de volgende brand plaatsvindt. Net zoals bij de kruid laag in hoofdstuk 2, kan een houtige plant verschillende strategieën inzetten om met deze druk om te gaan. De plant kan '*bestendig*' zijn tegen vuur door vrij snel een dikke laag schors te ontwikkelen; op deze manier wordt o.a. het cambium beschermt tegen de hitte. Maar ook *snel herstel* kan een succesvolle strategie zijn; bomen die investeren in snelle groei proberen hun

bladerdak zo snel mogelijk boven de vlamzone te plaatsen voor de volgende brand. Een ander 'compromis' welke planten kunnen maken heeft te maken met 'levenstempo'; hoe snel rond een organisme een levenscyclus af? Planten met een '*langzame*' strategie verhogen hun allocatie aan eigenschappen die verband houden met levensduur en een afname van de populatieomzet (d.w.z. meer generatietijd) ten kost van '*snelle groei*' en productie van nieuwe rekruten. In een landschap dat regelmatig in vuur en vlam staat, kan het voordelig zijn om de levenscyclus snel te doorlopen voor een nieuw vuur event. Juist die snelle groei (*snel herstel* of *snelle levenscyclus*) kan erg relevant zijn voor een snelle toename van houtige planten ten gevolge van vuur suppressie in grensgebieden van de GSME.

In een ecosysteem brede studie heb ik onderzocht of gebieden met planten gemeenschappen die worden gekenmerkt door 'snelle' strategieën een hogere toename in houtige planten laten zien ten gevolge van vuur suppressie dan 'langzame' strategieën. Dit heb ik gedaan door samen met collega's de toename in houtige planten te meten in grensgebieden die te maken hebben met vuur suppressie. Door tegelijkertijd de soortensamenstelling vast te stellen in deze gebieden, kan de toename gelinkt worden aan plant strategieën. De resultaten van deze studie laten zien dat de toename in houtige planten het hoogst was in gebieden met een lagere bodem fertiliteit, een fijnere bodem textuur, en lagere regenval. Het model dat statistisch gezien het beste bij de data past, laat zien dat dit deels verklaart kan worden door 'snelle' strategieën die vaker voorkomen in de planten gemeenschap op kleiachtige bodems en in gebieden met relatief weinig regenval. Het 'snel-langzaam' compromis werd in deze studie benaderd door het functionele onderscheid dat gemaakt kan worden tussen 'bomen' en houtige planten in savannes die zowel een boom als een struik groeivorm hebben. Voor deze laatste categorie is vastgelegd dat ze o.a. sneller het reproductieve stadium behalen en minder conservatief zijn in het gebruik van water ten opzichte van 'bomen'. Dit verklaart waarom de snelle strategie dominant is op kleiachtige bodems: over het algemeen geldt dat planten 'conservatiever' zijn in termen van hulpbronnen verbruik in stressvolle omgevingen waar hulpbronnen schaars zijn, terwijl planten in omgevingen waar nutriënten overvloedig aanwezig zijn vaker 'acquisitief' zijn.

Alternatieve dynamische regimes in savannes en het belang van adequate experimenten en monitoring

In hoofdstuk 6 reflecteer ik op de resultaten van hoofdstukken 2 en 3 en bespreek ik mogelijke algemene implicaties van menselijke invloeden op savanne ecosystemen. In beide studies lijkt het 'compromis' tussen plant eigenschappen die *herstellend vermogen* en *snelle groei* maximaliseren ten koste van eigenschappen die een plant bestendiger maken tegen stress, vertaalbaar te zijn naar het functioneren van een geheel landschap. Dit kan uiteindelijk gevolgen hebben voor de stroom van ecosysteem diensten omdat het landschap in een andere 'dynamiek' terecht komt. Door middel van een combinatie aan functionele eigenschappen zoals 'hoge ontvlambaarheid' en snel herstel, bevorderen grassen hen eigen succes in vuurgevoelige savannes wat leidt tot een positieve terugkoppeling. Anderzijds, kan de korte vegetatie in randgebieden juist meer herbivoren aantrekken omdat de grassen smakelijker worden door de afname in stengel / blad ratio. Dit is wat veel savannes bijzonder maakt; onder dezelfde omgevingsvariabelen zijn er meerdere 'alternatieve dynamische regimes' mogelijk die een landschap en diens vegetatie in zijn greep houdt.

Van savannes, prairies, en andere met gras begroeide ecosystemen is bekend dat zowel teveel als te weinig begrazing problemen geeft. Veel aride en half aride ecosystemen balanceren op het randje van teveel begrazing en worden dikwijls beschreven als 'gedegradeerd' vanwege bodem erosie of de vestiging van invasieve soorten. Een beschrijving als degradatie is echter niet informatief over de mechanismes waardoor het ecosysteem anders functioneert en daardoor niet behulpzaam wanneer de effecten van menselijk handelen gemonitord moeten worden. Het tweedelige proces van weerbaarheid, bestaande uit bestendigheid en herstel kan daar potentieel bij helpen. Bestendigheid is een continue variabele en kan met behulp van een simpele experimentele opzet op meerdere plekken in het landschap gemeten worden. Hoewel de begrazingsdruk in het pastorale randgebied in hoofdstuk 2 homogeen verdeeld is, zijn er verschillende responses in het landschap zichtbaar. Buiten de invloed van de boom is de vegetatie slecht in staat te herstellen en lijken bepaalde strategieën om water te besparen in de planten gemeenschap toe te nemen. Wanneer de begrazingsdruk toeneemt kan de druk zo hoog worden dat smakelijke grazen niet meer in staat zijn een positieve koolstof balans te onderhouden. Cactus soorten als *Opuntia* sp. worden vaak gebruikt als indicator soorten voor vegetatie verandering, echter zijn dit bij uitstek de soorten die 'bestendig' zijn tegen herbivoren en droogte. Door bestendigheid en

herstel na perturbatie experimenteel op een continue schaal te meten kan er dus een kwantitatieve analyse uitgevoerd worden waarbij een inschatting gemaakt kan worden omtrent de effectiviteit van beheer interventies (bijv. het verbieden van de kap van bomen).

Een toekomstig experiment waarin beide indicatoren van weerbaarheid worden gemeten over belangrijke omgevingsgradiënten in regenval en bodemeigenschappen is een mogelijk volgende stap. Onder welke omstandigheden zijn landschappen het meest kwetsbaar voor een verschuiving naar een alternatief dynamisch regime? Dergelijke experimenten zijn logistiek uitdagend, zeker in tropische savanne ecosystemen waar herstel van de kruidlaag snel kan verlopen. Dit vraagt om de ontwikkeling van nieuwe methoden die nauwkeurige schattingen kunnen verrichten aan belangrijke ecosysteem functies met zowel een hoge temporele resolutie als een grote ruimtelijke omvang.

In hoofdstuk 5 verken ik de mogelijkheden om bovengrondse productiviteit van de kruid laag te schatten met behulp van camera vallen. Dit soort veld camera's wordt normaliter ingezet om de distributie van wilde herbivoren in kaart te brengen maar wanneer de camera goed zicht heeft op de kruid laag kunnen ze ook gebruikt worden om veranderingen in groenheid vast te leggen door de tijd heen. Omdat groenheid van planten over het algemeen sterk gerelateerd is aan productiviteit, is mijn verwachting dat een toename in groenheid van dag tot dag, gemeten als het verschil in 'groene pixels' op twee achtereenvolgende camerabeelden, indicatief is voor productiviteit. Deze verwachting heb ik getest in een kleinschalige veldstudie rondom het veld station in de GSME. Samen met collega's heb ik verplaatsbare kooien van een vierkante meter gebruikt om productiviteit van de kruid laag te meten (De goudenstandaardmethode) over een tweeweekse interval op tien verschillende locaties. Op dezelfde locaties zijn camera's geïnstalleerd die gedurende de dag foto's maken van de kruid laag. De resultaten van deze studie laten zien dat de som van het aantal dagen waarop er een sterke toename is in groenheid op de camerabeelden voorspellend is voor de productiviteit die met de kooien is gemeten. Deze voorspelling wordt nog beter wanneer de informatie vanuit de camera's word gecombineerd met satelliet data. Deze satelliet data bestaat uit gegevens die de staande biomassa en de fenologische toestand van de vegetatie schat, beiden zeer belangrijke factoren voor bovengrondse productiviteit. De conclusie van dit werk is dat het gebruik van camera's een veelbelovende methode is om productiviteit te schatten, zeker als aanvulling op de methoden die enkel satelliet data gebruiken aangezien langdurige bewolking gedurende het regenseizoen de temporele resolutie verlaagt.

Het samen leven van mens en wilde natuur in randgebieden

Hoewel het landschap en de vegetatie samenstelling sterk kan veranderen onder invloed van de mens (hoofdstuk 2 en 3), hoeft dit niet perse nadelig te zijn voor alle inheemse diersoorten die de GSME rijk is. De afname in voedsel beschikbaarheid in pastorale randgebieden doet in eerste instantie vermoeden dat wilde herbivoren nadelig worden beïnvloed door vee, maar vaak neemt de kwaliteit van het gras toe. Een ander mogelijk positief effect is de herverdeling van bodemvoedingsstoffen in pastorale gebieden door het gebruik van bomas door de Masai wat resulteert in de concentratie van grote hoeveelheden mest en urine in kleine gebieden. Verlaten bomas kunnen tientallen jaren blijven bestaan en (zogende) inheemse herbivoren aantrekken omdat ze gras van hoge voedingskwaliteit bieden. Ook kan de aanwezigheid van de mens er voor zorgen dat roofdieren wegblijven en zo het landschap veiliger maken voor wilde herbivoren. Tenslotte verhoogt de korte begraasde kruid laag de zichtbaarheid van het landschap wat randgebieden mogelijk aantrekkelijker maakt voor prooidieren. Dieren wegen predatierisico (angst) af tegen winsten (kwalitatief voedsel), wat betekent dat herbivoorpopulaties zowel worden gereguleerd door directe predatie maar ook door een 'intimidatie' of 'waargenomen' predatie risico.

In hoofdstuk 4 onderzoek ik hoe een door mensen gemodificeerd landschap de ruimtelijke en temporele verspreiding van wilde herbivoren beïnvloed ten opzichte van een naastgelegen beschermd gebied. Omdat voedselkwaliteit en predatierisico voornamelijk de populatie van kleinere herbivoren reguleert en voedsel abundantie vooral limiterend is voor grotere herbivoren, verwacht ik dat lichaamsgrootte een belangrijke voorspeller is voor de aanwezigheid van wilde herbivoren in randgebieden. Deze verwachting heb ik getest door camera vallen op te hangen, die alle voorbij trekkende dieren hebben geregistreerd over een periode van zes weken waarvan drie weken in het natte seizoen en drie weken in het droge seizoen. De resultaten bevestigen de verwachting dat kleine herbivoren zoals Thomson's gazelle en impala relatief gezien meer gebruik maken van pastorale gebieden dan grote herbivoren zoals buffels en elanden. Dit kan niet worden verklaard door een ontmoedigend effect van mensen op roofdieren; er lijken meer Hyena's in de pastorale gebieden voor te komen hoewel deze data enkel marginaal significant is. Om die reden is het waarschijnlijker dat positieve effecten op het gebied van veiligheid tegen predatie verband houden met een toename van de zichtbaarheid waardoor wilde herbivoren roofdieren op tijd kunnen zien. Een verdere analyse van de data waarbij er gekeken is naar de activiteit van wildebeest en zebra over een 24-uurs cyclus laat zien dat de depressie in activiteit gedurende zonsondergang en de uren hierna minder

diep is in de pastorale randgebieden dan in het beschermde gebied. Dit is gewoonlijk het 'gevaarlijkste' moment van de dag voor prooi soorten en ook in deze studie is er rond deze tijd een piek in hyena activiteit te zien. Terwijl wilde herbivoren overdag kiezen voor het park, vermoedelijk vanwege de activiteit van mens en vee, lijken ze 's avonds en 's nachts gebruik te maken van de veiligheid die het pastorale landschap ze biedt.

Conclusie

In dit proefschrift heb ik laten zien dat menselijke invloeden op het functioneren van savanne ecosystemen voorspelbaar zijn aan de hand van het samenspel tussen de historie van het landschap, abiotische omgevingsvariabelen, en de daaruit vloeiende functionele eigenschappen van de vegetatie. De toename in begrazingsdruk in en rondom de GSME heeft geleid tot een verandering in het verstoringsregime waarin typische 'pulse' verstoringen zoals vuur en intens, maar kort durende begrazingsevents door migrerende herbivoren hebben plaats gemaakt voor chronische stressoren zoals droogte en vee begrazing. Mijn onderzoek suggereert dat een van de belangrijkste implicaties van deze menselijke effecten de vervanging is van 'herstelbare' elementen door 'bestendige' elementen, die kunnen worden waargenomen op het niveau van landschappen, soorten, en functionele strategieën.

In pastorale begrazingsgebieden kunnen deze inzichten potentieel gebruikt worden om te onderzoeken welke vormen van management de weerbaarheid tegen verstoringen vergroten. Daarnaast werpt dit concept nieuw licht op de algemene toename van houtige planten in savannes; ook dit is een trend die gezien kan worden als de toename in 'bestendigheid'. Na een aantal jaar zullen houtige planten vanwege toegenomen hoogte en dikte vanzelf bestendig worden en bij een bepaalde bedekkingsgraad van houtige planten zal vuur in zijn geheel worden uitgesloten.

Bovenstaande conclusies aangaande de verschuiving van 'herstel' naar 'bestendigheid' zijn niet automatisch nadelig voor populaties van wilde dieren. Randgebieden in de GSME bieden vooralsnog habitat aan inheemse dieren wat gelinkt kan worden aan een vorm van veiligheid tegen roofdieren. Naarmate de druk op savanne ecosystemen toeneemt, zal de behoefte aan oplossingen en strategieën die co-existentie van mens en natuur bevorderen groter worden. Inzichten in de keuzes die wilde herbivoren maken in randgebieden, zoals het nachtelijk gebruik van pastorale begrazingsgebieden, dragen bij aan de vorming van oplossingen waar zowel mensen als dieren in het wild van profiteren.

Appendix

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Dankwoord / Acknowledgments

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While the village of Ololosokwan was vibrant and welcoming, coming back to Soitsambu after long days of fieldwork really felt as coming home. I want to thank Issaya and his family for the care and the extraordinary wali na maharage and chapatis. I gained a kilo after each fieldtrip, which not only increased my performance in the field, but also my approval rating in the community. Thanks to village elder Michael for the nice talks and sharing your books with me.

There was one person that accompanied me on almost all of my field journeys. 'Almost' is an important detail here, because things tended to go sideways when he was not around (I once 'parked' a Land rover inside the wall of a building). I don't think there are many people around that understand more about the Serengeti than Emilian Mayemba. I want to thank you for the great field campaigns and your lessons and stories, whether it be about recognizing different grass species or your past adventures in the Serengeti. Perhaps, one day, you will tell future students about that time you had to spend a night in a tree because a student 'needed' to see the most remote area of the Serengeti. Teddy, thank you for the great care and making the research station and the research house a happy place.

Tegen het einde van mijn master programma bos en natuurbeheer wist ik nog niet of nauwelijks wat ik wilde doen na mijn opleiding. Alles leek me leuk, zolang ik maar niet in de regen op de slufteur hoefde te werken. In eerste instantie geloofde ik dat een promotieonderzoek niets voor mij was, maar ik nam toch de stap om te reageren op een plek die werd aangeboden in Groningen. Een onderzoek in de Afrikaanse savanne,

dat kon ik onmogelijk aan me voorbij laten gaan. Ik wil bij deze mijn promotor Han en copromotor Michiel bedanken voor deze kans en de begeleiding de afgelopen jaren. Jullie hebben me wegwijs gemaakt in zowel de savanne als in de wereld van het academisch onderzoek. Daarnaast wil ik jullie bedanken voor de vrijheid die ik heb gekregen, zowel in het onderzoek als in het indelen van mijn tijd. Mijn onderzoeksinteresse waren nogal breed en ik vind het bijzonder dat ik (bijna) alles heb mogen 'najagen' van jullie. Ook op persoonlijk vlak heb ik onze samenwerking als zeer prettig ervaren. De kilimanjaro's konden rijkelijk vloeien! Ik vind het fantastisch dat deze samenwerking nog een aantal jaar voort mag duren.

Hoewel ik moeite had te aarden in het hoge noorden, heb ik een fijne tijd gehad aan de RUG wat mede komt door de leuke groep collega's binnen de onderzoeksgroep. Ten eerste gaat mijn dank uit naar Ingeborg, Joyce, Corine, Joke, Jacob, Jan, Nelly, en Paul. Van ieder van jullie heb ik ondersteuning gehad, ofwel in mentale vorm toen ik het even niet meer zag zitten, ofwel administratief en praktisch. In het bijzonder wil ik Ingeborg bedanken. Ik werd soms radeloos door de vergunningsperikelen, maar jij wist altijd alles te regelen.

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I would also like to thank the Serengeti community for all the great moments. Sonja, Anna C, Ryan, Neha, Thomas, Peter, Suzanna, Stuart, Louis, Jason D., Dennis, Stan, Grant, Mike, Mark, Anna E, George, Anna T, Carole and Donald, The balloon guys João, Jason A., Shawn,

thank you for all the nice sundowners on the rock, campfires, Sunday brunches, safaris, barbeques, and much more which made my time in the Geti and Arusha even better. Sonja and Anna C, I admire your hard and continuous work in and around the Serengeti and I am grateful for your friendship. João, thank you for the epic flight over the Serengeti. It was truly a life time experience.

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Papa, jouw interesse in mijn werk is ongeëvenaard. Je staat altijd klaar en denkt met me mee. Je gaf me boeken over Afrika, bracht me weg naar schiphol en haalde me ook weer op om mijn verhalen aan te horen. Dankje voor alles. Margot, ook jou wil ik bedanken voor je support en aanmoediging.

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Matteo, we met a month before I went on a fieldwork campaign of almost three months. The first couple of weeks were challenging, and I cursed the airtel tower in Ololosokwan many times for not sending my messages through to you. Luckily, you have supported me tremendously in my research right from the start and less than six months later we travelled to Lake Natron and the Ol Doinyo Lengai together. It is my most precious memory. It brings me great joy that you have developed an interest in the wildlife of the African savanna and your talent for photography is clearly visible in this thesis. Thank you for pushing me and being by my side always, I could not have finished this thesis without you. I adore you.

Appendix

Curriculum Vitae

Curriculum Vitae

Inger Kirsten de Jonge werd op 26 januari 1990 geboren te Zeewolde. In 2008 behaalde zij haar atheneum diploma aan het Christelijk College Nassau Veluwe te Harderwijk. In het jaar hierop volgend ging zij biologie studeren aan de Universiteit Utrecht met als hoofdzakelijke studie richting Ecologie en natuurbeheer. Na deze bachelor opleiding studie afgerond te hebben in 2013, vervolgde zij deze met een masteropleiding Forest and Nature Conservation aan de Wageningen universiteit. Tijdens deze studie verrichtte zij twee wetenschappelijke stages. Onder begeleiding van dr. M. Holmgren en dr. R. E. Bernardi rondde zij een masters project af met een scriptie getiteld 'Forest-Grassland Transitions in Subtropical South America: Tree recruitment patterns at the ecotone between riverine forests and grasslands'. Uit het tweede project, onder begeleiding van dr. S. E. van Wieren en dr. M.J.A. Weterings, volgde een tweede scriptie getiteld 'The reactive and predictive response of the European brown hare (*Lepus europeaus*) to the Red fox (*Vulpes vulpes*) in terms of spatial habitat use'. In Juni 2015 studeerde zij cum laude af.

In September 2015 begon zij bij de vakgroep Conservation Ecology (ConsEco), onderdeel van Groningen Institute for Evolutionary Life Sciences (GELIFES) van de Rijksuniversiteit Groningen (RUG), aan het promotietraject dat leidde tot dit proefschrift, onder begeleiding van prof. dr. H. Olff en dr. M.P. Veldhuis. Dit promotieonderzoek is onderdeel van het AfricanBioServices project: een groot, interdisciplinair onderzoek naar ecosysteemdiensten in het groter Serengeti-Mara ecosysteem in Oost Afrika.

Vanaf 1 december 2019 is Inger werkzaam als post-doc onderzoeker bij de Systeem ecologie groep aan de Vrije Universiteit Amsterdam.