ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

DOCTORAL THESIS NO. 2022:45

Megaherbivores (> 1000 kg) can have strong influence on ecosystem and Earth system functioning. However, today's megaherbivores are increasingly threatened by poaching. This thesis investigated how the loss of the world's largest grass eating megaherbivore, white rhinoceros (Ceratotherium simum), affects crucial savanna processes in Hluhluwe-iMfolozi Park, South Africa. Rhino loss was associated with landscape-scale changes in vegetation and fire, with indirect implications on soil carbon dynamics. Importantly, poaching of rhino can have strong consequences on savanna functioning.

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Online publication of thesis summary: https://pub.epsilon.slu.se/

ISSN 1652-6880 ISBN (print version) 978-91-7760-965-0 ISBN (electronic version) 978-91-7760- 966-7 DOCTORAL THESIS NO. 2022:45 • Megaherbivores and Earth system functioning • Olli Hyvärinen

DOCTORAL THESIS NO 2022:45 FACULTY OF FOREST SCIENCES

Megaherbivores and Earth system functioning

Landscape-scale effects of white rhino loss on vegetation, fire and soil carbon dynamics

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Megaherbivores and Earth system functioning

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The Faculty of Forest Sciences Department of Wildlife, Fish and Environmental Studies Umeå



DOCTORAL THESIS

Umeå 2022

Acta Universitatis Agriculturae Sueciae 2022:45

Cover: Two Rhino and Savanna (Cover illustration: Petrus Louhio) ISSN 1652-6880 ISBN (print version) 978-91-7760- 965-0 ISBN (electronic version) 978-91-7760- 966-7 © 2022 Olli Hyvärinen, https://orcid.org/0000-0002-8988-1662 Swedish University of Agricultural Sciences, Department of Wildlife, Fish and Environmental Studies, Umeå, Sweden Print: Original Tryckeri, Umeå 2022 Megaherbivores and Earth system functioning: Landscape-scale effects of white rhino loss on vegetation, fire and soil carbon dynamics

Abstract

Megaherbivores (> 1000 kg) have been suggested to strongly influence ecosystem functioning with consequences potentially scaling up to the global climate. However, due to poaching, we may lose some of the most vulnerable species at functional densities in the wild in the coming decades. In this thesis, I investigated the consequences of white rhinoceros (Ceratotherium simum) loss on savanna functioning in Hluhluwe-iMfolozi Park, South Africa. I predicted that the loss of rhino leads to ecosystem-level changes in vegetation, particularly in terms of grass structure and grass-woody ratios, and fire patterns, and that these changes further affect climate drivers, more specifically, soil carbon dynamics. To start with a broader perspective, I conducted a systematic review which revealed major taxonomic, thematic and geographical biases and knowledge gaps in the empirical peer-reviewed literature on ecosystem and Earth system effects of extant megaherbivores. In a more in-depth study, I utilized a "natural experiment" and remote sensing imagery, which showed that rhino loss was associated with increased fire occurrence and, indirectly, a higher rate of woody encroachment. Moreover, grazing lawn, which has been previously linked to rhino presence, was associated with lower fire occurrence and, indirectly, lower rate of woody encroachment. Finally, through a field study I show that soil organic carbon (SOC) stocks or the size of functional SOC pools with varying persistence did not differ among grazing intensity contrasts even at the highest grazing intensities. Instead, I show that SOC stocks were higher in woody encroached grassland plots compared to not encroached reference plots for soils with low clay content but lower for soils with high clay content. Moreover, the least persistent SOC pool was smaller in the woody encroached plots compared to the reference plots in open grazing lawn habitat characterized by high grazing intensity. Instead, in hillslope grassland habitat characterized by low grazing intensity and high rainfall, both the least persistent and most persistent SOC pools were larger in the woody encroached plots than in the reference plots. These results support the hypothesis that white rhino loss leads to an increase in fire occurrence and thus indirectly an increase in woody encroachment. However, there was no evidence to support the hypothesis that white rhino grazing directly reduces SOC stocks, although the data suggest that rhino can influence soil carbon dynamics indirectly through limiting woody encroachment. I concur that white rhino are influential ecosystem-engineers and propose that their loss has meaningful landscape-scale consequences on savanna functioning where the dynamics of vegetation, fire and soil carbon are strongly coupled.

Keywords: Megaherbivore, white rhinoceros, ecosystem function, earth system function, savanna, grassland, woody encroachment, fire, soil carbon, soil carbon persistence, rewilding, nature-based climate solutions

Megaväxtätare och jordsystemets function: effecter i landskapskala av trubbnoshörning på vegetation, brand och markens koldynamic

Sammanfatning

Megaväxtätare (> 1000 kg) har föreslagits starkt påverka ekosystems funktion med konsekvenser som potentiellt skalar upp till det globala klimatet. Men på grund av tjuvjakt kan vi förlora några av de mest sårbara arterna vid funktionella tätheter i naturen under de kommande decennierna. I denna avhandling undersökte jag konsekvenserna av förlust av trubbnoshörning (Ceratotherium simum) på savannens funktion i Hluhluwe-iMfolozi Park, Sydafrika. Jag förväntade mig att förlusten av noshörning leder till förändringar på ekosystemnivå i vegetationen, särskilt när det gäller grässtruktur och förhållande mellan gräs och trä, och brand, och att dessa förändringar ytterligare påverkar klimatfaktorer som markens koldynamik. För att börja med ett bredare perspektiv genomförde jag en systematisk översikt som avslöjade stort bias och luckor i den vetenskapliga referentgranskade litteraturen om ekosystem- och jordsystemseffekter av befintliga megaväxtätare. I en mer djupgående studie använde jag ett "naturligt experiment" och fjärranalysbilder, som visade att förlust av noshörningar var förknippad med ökad brandförekomst och indirekt en högre grad av buskintrång. Betesgräsmattan, som tidigare har kopplats till noshörningsnärvaro, var dessutom förknippad med lägre brandförekomst och indirekt lägre frekvens av buskintrång. Genom en fältstudie visar jag att noshörningsbeteskontraster inte påverkade lagren av organiskt kol i marken (SOC) eller storleken på funktionella SOC-pooler med varierande beständighet även vid de högsta betesintensiteterna. Istället kontraster av buskintrång ökade SOC-bestånd med låg lerhalt i jorden och minskade SOC-bestånd med hög lerhalt i jorden. Kontraster i buskintrång minskade dessutom den minst ihållande SOC-poolen i öppen gräsmatta som kännetecknas av hög betesintensitet, samtidigt som de ökade både de minsta och mest ihållande SOC-poolerna i bergssluttningens habitat kännetecknas av låg betesintensitet och hög nederbörd. Dessa resultat stödjer hypotesen att förlust av trubbnoshörning leder till en ökning av brandförekomsten och därmed indirekt en ökning av buskintrång. Jag fann dock inga bevis för att stödja hypotesen att bete av trubbnoshörningar direkt minskar SOC-bestånden, även om data tyder på att de kan påverka markens koldynamik indirekt genom att begränsa buskintrång. Jag kan konstatera att trubbnoshörningar är inflytelserika ekosystemingenjörer och föreslår att deras förlust har betydelsefulla konsekvenser i landskapsskala på savannens funktion där dynamiken hos vegetation, brand och markkol är starkt kopplade.

Nyckelord: Megaväxtätare, trubbnoshörning, ekosystemsfunktion, jordsystemets funktion, savann, gräsmark, buskintrång, brand, markkol, naturbaserade klimatlösningar

Dedication

To mom and dad, whose continuous support and encouragement made it possible for me to climb this mountain, and to Elena, who was there for me every step of the way.

"There are times when I catch myself believing that there is such a thing as something, which is separate from something else."

- Gregory Bateson: An Ecology of Mind, Documentary

Preface

"The climate crisis and the biodiversity crisis are really, and truly, inextricably linked. We do not only need to solve the climate crisis in order to protect nature, we also must protect nature in order to solve the climate crisis."

- Al Gore, COP 26, Glasgow, November 2021

At the time of writing, I am sitting behind my desk looking at a photo glued onto a messy sheet of notes. In the photo, taken from Hluhluwe-iMfolozi Park (HiP), South Africa, lie columns of rhino skulls, each staring expressionless into the courtyard. I fix my eyes onto the photo and mark the chilling absence of horn in every skull. Looking at this scene, Al Gore's words quoted above resonate strongly. How would the loss of the world's largest terrestrial grazer, whose existence is weaved into the fabric of HiP's savanna, influence the complex patterns on the tapestry the fabric is part of? Let us place a part of this tapestry under the microscope and investigate how the ongoing loss of rhino affects the functioning of HiP's savanna.



Illustration: Olli Hyvärinen 2022

Contents

List o	f publ	ication	S	15
List o	of table	es		19
List o	of figur	es		21
Abbre	eviatio	ns		23
List o	of defir	nitions.		25
1.	Introd	duction	1	27
	1.1	Megah	erbivore as a functional definition	28
	1.2	Megag	razers drive savanna processes	29
	1.3	Savan	na processes and soil organic carbon stocks	30
	1.4	Persist	tence as a measure of long-term soil carbon storage	30
	1.5	Past a	nd present white rhino loss	32
	1.6	Aim ar	nd objectives	32
2.	Meth	ods		37
	2.1	Systen	natic review (Paper I)	37
	2.2	Study a	area (Papers II,III &IV)	38
	2.3	Experi	mental designs (Papers II,III & IV)	40
		2.3.1	Natural experiment (Paper II)	40
		2.3.2	Field study (Papers III & IV)	41
	2.4	Data c	ollection	44
		2.4.1	Megagrazer loss and savanna functioning (Paper II)	44
		2.4.2	Megagrazers, soil organic carbon stocks (Paper II	l) and
		soil ca	rbon persistence (Paper IV)	45
	2.5	Statisti	cal analyses	48

	 2.5.1 Megagrazer loss associations with vegetation and fire dynamics (Paper II)
3.	Results and discussion513.1Biases and gaps in the peer-reviewed literature (Paper I)3.2Associations between rhino loss, vegetation and fire dynamics(Paper II)533.3Associations between savanna processes and soil carbondynamics (Papers III & IV)563.4White rhino as a model for extant megagrazers623.5Synthesis of the results in relation to the overall thesis
4.	Conclusion65
5.	Future research67
Re	eferences
Po	opular science summary79
Po	opulärvetenskaplig sammanfattning81
Ad	knowledgements
Ap	opendix

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- Hyvarinen O, Te Beest M, le Roux E, Kerley K, de Groot E, Vinita R, Cromsigt J.P.G.M. (2021). Megaherbivore impacts on ecosystem and Earth system functioning: current state of the science. Ecography, vol 44 (11), pp. 1579-1594.
- II. Hyvarinen O, Te Beest M, le Roux E, Kerley K, Buitenwerf R, Druce D, Cromsigt J. P.G.M. Landscape scale associations between white rhino loss, vegetation and fire dynamics (manuscript).
- III. Hyvarinen O, Te Beest M, le Roux E, Kerley K, Schenkeveld W, Findlay N, Trouw V, Cromsigt J. P.G.M. Grazing in a megagrazer dominated savanna does not reduce soil carbon stocks even at high intensities (manuscript).
- IV. Hyvarinen O, Te Beest M, le Roux E, Kerley K, Kristensen J, Schenkeveld W, Findlay N, Trouw V, Cromsigt J. P.G.M. Soil carbon persistence along grazing and woody encroachment gradients in a megagrazer-dominated protected savanna (manuscript).

Paper I is reproduced with the permission of the publisher.

The contribution of Olli Hyvärinen to the papers included in this thesis was as follows:

- I. Lead author, co-designed the study, led the literature screening and data collection, carried out the analyses, led the write up and revisions.
- II. Lead author, co-designed the study, obtained the remote sensing data, carried out the statistical analysis and led the write-up.
- III. Lead author, co-design the study, led and carried out the data collection, sample processing, the statistical analyses and led the write-up.
- IV. Lead author, co-designed the study, led and carried out the data collection and laboratory analyses, statistical analyses and led the write up.

List of tables

Table 1. Summary of megaherbivore characteristics

Table 2. Outline of the laboratory analyses for each soil carbon pool per depth profile

Table 3. Summary of model structures for ecological effects of rhino loss

Table 4. Summary of model structures for grazing and woody encroachment effects on soil carbon dynamics

List of figures

Figure 1. Conceptual illustration outlining the structure of the thesis

Figure 2. Study area (Hluhluwe-iMfolozi Park, South Africa)

Figure 3. Temporal patterns of rhino loss in Hluhluwe-iMfolozi Park

Figure 4. Illustration of the field sampling design

Figure 5. Illustration of the grazing and woody encroachment contrast plots

Figure 6. Chord diagram showing biases in megaherbivore literature

Figure 7. Scatterplots showing the relationship between rhino loss and the vegetation- and fire parameters

Figure 8. Results of the pathway analysis through the piecewise Structural Equations Models

Figure 9. Boxplots showing the effects of grazing and woody encroachment contrasts on soil organic carbon stocks

Figure 10. Boxplots showing the effects of grazing and woody encroachment contrasts on the size of the functional soil organic carbon pools

Abbreviations

IC	Inorganic carbon
MAOC	Mineral associated organic carbon
OC	Organic carbon
oPOC	Particulate organic carbon occluded in soil aggregates
POC	Particulate organic carbon
PyroC	Pyrogenic carbon
SOC	Soil organic carbon
SPT	Sodium polytungstate

List of definitions

Defaunation - Functional loss of animal populations or species from ecological communities.

Earth system function -A process that is embedded in at least one of Earth's spheres (e.g. biosphere, atmosphere, hydrosphere) and that supports the structure and/or stability of the Earth system.

Ecosystem function – A process that controls the fluxes of energy, nutrients and organic matter through an ecosystem.

Megafauna – Large animals with an adult body size >45 kg.

Megagrazer – A grass eating terrestrial mammal with an adult body size >1000 kg. **Megaherbivore** – A plant eating terrestrial mammal with an adult body size >1000 kg.

Microbial carbon use efficiency – The proportion of organic carbon used by microbes and allocated for their growth.

Nature-based climate solution – A conservation or restoration action that promotes carbon storage or limits greenhouse gas emissions from ecosystems.

Soil carbon destabilization – A process that promotes the loss of organic carbon from an ecosystem.

Soil carbon persistence – The likelihood of soil organic carbon of remaining in the soil carbon pool.

Soil carbon saturation – A mechanism through which organic carbon accumulation in a functional soil organic carbon pool is limited by inherent physiochemical characteristic of the pool.

Soil carbon stabilization – A process that limits the loss of organic carbon from an ecosystem.

Soil carbon sequestration – A process through which CO_2 is removed from the atmosphere and transferred into the soil carbon pool.

Woody encroachment – An increase in density of woody plants at the expense of the herbaceous layer in savanna grasslands.

1. Introduction

The climate and biodiversity crises are arguably among the most urgent global challenges of the 21st century. There is an increasing recognition that both crises are strongly interlinked, calling for concerted efforts to identify synergies between biodiversity conservation/ restoration and climate change mitigation. In fact, recent research highlights that wild animals play important roles in global carbon cycling and thus are able to influence atmospheric carbon concentrations (also referred to as animating the carbon cycle, Schmitz et al. 2018). Their conservation and restoration (i.e. trophic rewilding) have therefore been suggested to contribute to the portfolio of climate change mitigation opportunities (Cromsigt et al. 2018; Schmitz et al. 2022).

In fact, studies on the prehistoric and historic dramatic loss of large fauna (i.e., defaunation) show us that their extinctions led to strong impacts on, e.g., the distribution of biomes (Gill 2014; Doughty et al. 2016b; Dantas and Pausas 2020), biodiversity (Gill 2014), carbon and nutrient cycling (Doughty et al. 2016b) and fire regimes (Gill et al. 2009; Rule et al. 2012). While these studies demonstrate the importance of prehistoric fauna on Earth system functioning, accumulating evidence reveals the importance of wild animals in more contemporary contexts. For example, a particularly severe rinderpest outbreak in the 1930's led to a dramatic decline in Serengeti's wildebeest population from 1.2 million to about 300 000 by the late 1950s. The resulting loss in grazing pressure led to an increase in grass biomass and fire fuel accumulation causing more fires across the area. This accelerated greenhouse gas emissions and caused the Serengeti to be a major source of atmospheric carbon. The recovery of the wildebeest population during the 1960s and 1970s, and their associated impacts on the fire regime and tree

cover, turned the Serengeti into a net carbon sink (Holdo et al. 2009). Despite the growing interest in the Earth system effects of wild herbivores, there is still large uncertainty about how today's largest terrestrial herbivores, i.e., megaherbivores (>1000 kg), influence ecosystem and Earth system functioning. Furthermore, only few areas remain globally where the impacts of megaherbivores, particularly of the most threatened species such as white rhinoceros (*Ceratotherium simum*), can be studied at functional population densities, highlighting the urgency to investigate their impacts where it is still possible.

1.1 Megaherbivore as a functional definition

Megaherbivores are plant-eating terrestrial mammals that weigh >1 000 kg as adults (Owen-Smith 1988) (see Table 1 for the characteristics of all extant megaherbivore species). It is important to highlight that the term "megaherbivore" differs from the widely-used term "megafauna", which is often used to refer to animals with an adult body mass >100 lbs (\sim 45 kg). While the latter is not based on a functional distinction (Moleón et al. 2020), megaherbivores are distinguished functionally from smaller species by their very large body size. Their large size makes megaherbivore adults nearimmune to non-human predation, and top-down population control by large carnivores. Therefore, megaherbivores are bottom-up limited by food resources, which exacerbates their impact on ecosystem processes (Caughley 1976). While megaherbivores require a large intake of forage, their low mass-specific metabolic rate allows them to tolerate low quality forage (Müller et al. 2013). Therefore, they can consume more fibrous plant material compared to smaller species, which leads to impacts on a larger variety of plant species and plant parts. Megaherbivores can also cover larger distances compared to smaller species, allowing them to move nutrients and seeds much further (Owen-Smith 1988, Doughty et al. 2016a). These functional differences have led to the proposition that megaherbivores can have disproportionately larger effects on ecosystems than their smaller counterparts (Owen-Smith 1988), thus potentially exerting stronger impacts on ecosystem- and Earth system functioning than smaller herbivore species, even when occurring at the same biomass density.

1.2 Megagrazers drive savanna processes

As the world's largest extant megagrazer (grass-eating megaherbivore), white rhino drive key ecosystem processes in areas where they occur at functional densities (Owen-Smith 1988; Waldram et al. 2008; Cromsigt and te Beest 2014). Pioneering work from Hluhluwe-iMfolozi Park (HiP) and Kruger National Park (KNP) in South Africa suggests that rhino can transform tall savanna grassland into functionally unique "grazing lawns" (Owen-Smith 1988; Waldram et al. 2008; Cromsigt and te Beest 2014). These grazing lawns are composed of a specific community of grazingtolerant, short-statured grass species that are outcompeted by taller caespitose grass species in the absence of grazing (Hempson et al. 2015). The nutritious quality and the openness of these lawns attract other short grass grazers that in turn deposit nutrients through dung and urine, further possibly increasing the grass' nutrient content (Hempson et al. 2015). Grazing lawns also act as natural fire breaks, limiting fire extent and intensity (Archibald et al. 2005). Grazing may also reduce grass biomass in the tall grassland adjacent to the lawns, further limiting fire fuel availability and decreasing the spread and intensity of fire surrounding the lawns (Waldram et al. 2008; Johnson et al. 2018). The openness of grazing lawns also attracts browsing herbivores, such as impala and nyala, that seek safety from predation, thereby increasing browsing pressure on the woody layer, consequently reducing woody plant recruitment and survival on and surrounding grazing lawns (Voysey et al. 2021). Furthermore, fire can either reduce or promote woody plant establishment such that intense fires can kill seedlings and saplings growing below the fire trap, while low intensity fires can temporarily reduce the grass cover, and therefore grass competition. When low intensity fires do not sufficiently harm woody seedlings and saplings, reduced grass competition will promote the establishment and growth of woody plants (Bond et al. 2017). This is particularly relevant in many South African savannas that, for at least 50-60 years, have experienced an increase in woody shrub cover in previously open savanna grasslands (O'Connor et al. 2014). This process is also referred to as "woody encroachment". While rhino have been previously linked to increased grazing lawn extent (Owen-Smith 1988; Waldram et al. 2008; Cromsigt and te Beest 2014), and grazing lawns have been shown to limit fire, woody recruitment and survival, we still lack a comprehensive understanding of how rhino, grazing lawn, fire and woody encroachment interact with each other through both direct and indirect links.

1.3 Savanna processes and soil organic carbon stocks

While the link between rhino and above ground savanna processes is getting clearer, we still know very little about how rhino influence below ground processes, particularly soil carbon dynamics (Hyvarinen et al. 2021). What we know from livestock systems, is that heavy to intermediate levels of grazing tend to reduce soil organic carbon (SOC), possibly due to the removal of above ground grass biomass and the stimulation of microbial decomposition of organic matter leading to an increase in soil respiration (McSherry and Ritchie 2013; Lai and Kumar 2020). However, low and intermediate levels of grazing may also increase SOC (McSherry and Ritchie 2013, Abdalla et al. 2018). There are multiple mechanisms through which grazing can positively influence SOC. For instance, grass defoliation can lead to the stimulation of root growth and root deposition into the soil (Wilson et al. 2018). By altering the grass community and cover (Sitters and Andriuzzi 2019) large grazers can influence how resources from photosynthesis are allocated into their below ground parts, while dung and urine deposition increases the availability of nutrients for plants and microbes (Sitters and Andriuzzi 2019). Additionally, depending on the rainfall context and the soil texture, woody encroachment can either increase or decrease SOC (Zhou et al. 2017). Woody encroachment tends to reduce SOC in higher rainfall and clay soils, and increase SOC with lower rainfall and sandy soils (Jackson et al. 2002; Li et al. 2016). Fires can also lead to CO² emissions and reduce SOC (Pellegrini et al. 2018; Li et al. 2021). Therefore, in addition to direct grazing impacts (i.e. defoliation, dunging), megagrazers may also strongly influence soil carbon storage indirectly through mediating woody plant cover and fire regimes.

1.4 Persistence as a measure of long-term soil carbon storage

Importantly, recent advances in soil science highlight that different SOC pools can cycle at vastly different rates, which is largely determined by their

biochemical recalcitrance and, crucially, the degree to which they are protected from microbial decomposition (Lehmann and Kleber 2015; Lavallee et al. 2020). This suggests that measures of total SOC stock changes alone may under- or overestimate the effect that a particular land use regime or driver, such as grazing, fire or woody encroachment has on soil carbon storage in the long-term. Typically, organic carbon in the soil can exist as particulate organic carbon (POC), which is freely available for microbes to be used, and therefore it turns over within years to decades. Moreover, organic carbon can be physically protected from microbial use by occlusion in soil aggregates (occluded particulate organic carbon, oPOC) or chemically protected by binding to mineral surfaces (mineral-associated organic carbon, MAOC). Due to the protection from microbial access, oPOC and MAOC turn over much slower, typically taking from decades to centuries (Lehmann and Kleber 2015; Lavallee et al. 2020).

In a recent perspective, Kristensen et al. (2022) suggest that large grazers can increase the fraction of organic carbon stored in the persistent MAOCpool through mediating the quality and quantity of litter- and rhizodeposits, microbial activity and carbon use efficiency, and through enhancing organic matter exposure to mineral surfaces (Fig. 1). Furthermore, bioturbation by large animals and soil fauna can mix organic matter from the surface soil, into deeper soil, where it is exposed to mineral surfaces and thus persists in longer (Wei et al. 2021; Tuomi et al. 2021). Alternatively, high levels of trampling may also break soil aggregates, destabilizing oPOC, as well as induce compaction, which in turn reduces soil moisture, microbial activity and hampers the mineral-stabilization of SOC (Schimel 2018). Furthermore, mychorrizal fungi associated with woody plant roots can promote soil aggregation. Therefore, woody encroachment of grassland may promote soil carbon persistence through facilitating the formation of aggregate occluded carbon (Ortiz et al. 2022; Agnihotri et al. 2022). Moreover, low intensity fires, and the resulting incomplete combustion of particularly woody biomass can facilitate the input of highly persistent pyrogenic carbon (PyroC) that has cycling times from centuries to millennia (Pellegrini et al. 2022). This means that, in addition to influencing SOC stocks, large grazers can either increase or decrease SOC persistence, through direct grazing related impacts and indirectly through mediating woody plant cover and fire.

1.5 Past and present white rhino loss

We are currently facing a dramatic megaherbivore poaching crisis (Chase et al. 2016; Ferreira et al. 2018), potentially resulting in the loss of the most vulnerable megaherbivores at functional densities in the few areas where they still exist in the wild. For instance, white rhino used to occur across northeastern and southern Africa (Faurby et al. 2018), but historic hunting severely limited their distribution, resulting in the functional extinction of the northern subspecies (Callender 2021). However, conservation during the first half of the 20th century led to a strong increase in southern white rhino such that concerns were raised over the impacts of overgrazing on the grass cover and soils in HiP. To combat this, HiP management created artificial sink areas where rhino were regularly removed in an attempt to curb population growth and maintain stable rhino densities. The removed rhino were relocated elsewhere as part of wider range expansion efforts (Linklater and Shrader 2017). This management continued into the 2000s and led to substantial success in white rhino conservation across southern Africa (Leader-Williams 2014), including their recolonization of large parts of KNP (Pienaar et al. 1993). During the last decade, however, we have seen an upsurge in poaching on white rhino (Nhleko et al. 2022), where most of the surviving rhino are now limited to a few reserves in South Africa. Furthermore, poaching has already started to impact rhino numbers in the core areas where they remain such as KNP (Ferreira et al. 2018), and may decrease by another 35% within the next decade at current levels of poaching (Nhleko et al. 2022). This means that we may see a loss of white rhino at functional densities in the few areas where they still exist in the wild. This emphasizes that we must urgently increase our understanding of their ecological impacts where it is still possible.

1.6 Aim and objectives

In this thesis, I ask how the loss of white rhino influences crucial savanna processes i.e. grassland structure, grass/woody balance and fire dynamics and how these impacts further affect climate drivers, more specifically, soil carbon dynamics (Fig.1). I use the savannas of HiP as a model system to study these impacts. My general prediction is that rhino loss leads to

complex ecosystem-scale responses where vegetation, fire and soil carbon dynamics are strongly coupled. More specifically, I predict that (1) rhino loss leads to a decrease in grazing lawn cover, an increase in fire occurrence and woody encroachment, that (2) grazing lawns have smaller SOC stocks, but larger persistent SOC pools compared to adjacent tall grassland, that (3) woody encroachment either increases or decreases SOC stocks depending on the rainfall and soil texture contexts and increase the size of more persistent functional SOC pools. To test the general thesis and the more specific hypotheses, I used the following approaches. To place my research into a broader context, I conducted a systematic review to synthesize our current understanding of extant megaherbivore impacts on ecosystem and Earth system functioning, which allowed me to identify gaps and biases in the peerreviewed empirical literature (Paper I). In my further in-depth studies, I first tested my predictions on the effect of rhino loss on vegetation and fire dynamics through utilizing a landscape-scale "natural experiment", in which I related a spatial gradient in illegal and legal rhino removals in HiP to remotely sensed changes in vegetation and fire patterns (Paper II). Lastly, to test my predictions on the effects of rhino-driven changes in vegetation and fire on long-term soil carbon storage, I conducted a field study in which I compared SOC stocks (Paper III) and the size of the functional SOC pools with varying persistence in the soil (Paper IV) among grazing lawn and woody encroachment contrasts across rhino habitat use and along environmental gradients.

Thus, the specific objectives of this thesis are:

- 1. To identify biases and research gaps in the empirical peer reviewed literature on today's extant megaherbivore effects on ecosystem and Earth system functioning (Paper I).
- 2. To assess if and how the loss of white rhino is associated with predicted changes in vegetation and fire patterns (Paper II).
- To assess if and how white rhino-related vegetation and fire patterns (i.e. grazing lawn, grass/woody balance and fire frequency) affect SOC stocks (Paper III) and functional SOC pools with varying persistence in the soil (Paper IV) in predicted ways.

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Table 1	1 aUIV 1. 4	(Owen-Sr

Megaherbivore	Mass (kg)	Feeding	Gut	Status	Population
African savanna and forest elephants	2500-6000	Mixed feeder	Hind-gut fermenting	Vulnerable	415,000
Asian elephant	2720-5400	Mixed feeder	Hind-gut fermenting	Endangered	41,410–52,345
White rhino	1600-2300	Grazer	Hind-gut fermenting	Near threatened	17,212 -18,915
Black rhino	700-1300	Browser	Hind-gut fermenting	Critically endangered	5,630
Greater one-horned rhino	1600-2100	Grazer	Hind-gut fermenting	Vulnerable	3,588
Sumatran rhino	800	Browser	Hind-gut fermenting	Critically endangered	80
Javan rhino	1300	Browser	Hind-gut fermenting	Critically endangered	68
Giraffe	800-1200	Browser	Ruminant	Vulnerable	97,562
Hippopotamus	1365 - 2600	Grazer	Hind-gut fermenting	Vulnerable	115,000-130,000



Figure 1. Conceptual figure outlining the structure of my thesis on the impacts of white rhino loss on crucial savanna processes including vegetation, fire and soil carbon dynamics. To place my thesis into a broader context, I first synthesized our current understanding of megaherbivore effects on ecosystem and Earth system functioning using a systematic review (Paper I). In my in depth studies in Hluhluwe-iMfolozi Park, South Africa, I first utilized a "matural experiment" to test the prediction that white rhino loss leads to changes in grassland structure, grass/woody balance and fire occurrence (Paper II). In a further field study, I tested the prediction that rhino-associated changes in vegetation and fire dynamics influence soil organic carbon (SOC) stocks (Paper III) and the size of functional SOC pools that differ in turn-over rates and thus persistence in the soil (Paper Ξ.
2. Methods

2.1 Systematic review (Paper I)

To start my thesis with a broader perspective, I first performed a systematic review of our current understanding of the ecological impacts of megaherbivores, allowing me to identify knowledge gaps and biases. Using the PRISMA guidelines, I reviewed peer-reviewed empirical studies on extant megaherbivore effects on ecosystem and Earth system functioning published between 1945 and 1 July 2020 (Moher et al. 2009). I used a specified search string in Web of Science Core Collections containing the common and scientific names of all the extant megaherbivore species and terms for effect (e.g. impact, affect, influence etc.). I screened all studies based on predetermined relevance criteria, and categorized the remaining studies into Type I and Type II studies. Type I studies fit the criteria for formal quantitative meta-analyses and Type II were ineligible for quantitative meta-analyses.

I evaluated both Type I and Type II publications for taxonomic, thematic, geographic and environmental (temperature, precipitation and soil fertility) biases. For evaluating taxonomic and thematic biases I compared the number of studies published on the different megaherbivore species, and the different Earth system functions (e.g. vegetation structure, biodiversity, biogeochemistry and fire). For evaluating geographic bias, I mapped the publication study sites and evaluated their geographic locations relative to the current and historic distributions of each megaherbivore species. To analyse environmental bias, I plotted the study sites of the different species onto their respective climatic (rainfall and temperature) and soil fertility envelopes to identify areas of the envelopes that have not yet been studied.

2.2 Study area (Papers II,III &IV)

For my in-depth studies on white rhino impacts on vegetation, fire and soil carbon dynamics, I selected Hluhluwe-iMfolozi Park (HiP) in the province of KwaZulu-Natal, South Africa (28.44194°S, 32.22949°E), as a model system (Fig.2). HiP is an ideal system to study white rhino impacts, because it hosts among the highest densities of white rhino (~2/km2) that have persisted over multiple decades (Linklater and Shrader 2017). HiP covers \sim 960 km² and its elevation varies between 45 and 750 m above sea level. Mean annual rainfall in the park ranges between 550 and 1000 mm/year, most of which falls in the summer between October and March (Howison et al. 2017). Fire is an important part of the ecosystem, and it is actively managed through prescribed burning. The average fire return interval of 2-4 years, although spontaneous fires occur across the park regularly as well (Archibald et al. 2017). Increasing rainfall strongly predicts fire occurrence (i.e. burnt area and fire frequency), due to the higher accumulation of grass biomass and fire fuel with increasing rainfall. The underlying geology and soil types are heterogeneous, including strong variation in soil clay content (Howison et al. 2017). Afromontane forests and grasslands are found on the hillslopes and summits above 250-300 m, while the lower lying areas support savanna grasslands and woodlands with a varying degree of C3 tree and C4 grass cover (Staver et al. 2017). Grazing lawns occur throughout the park along soil texture gradient, and grazing lawn cover is more abundant in the lower rainfall areas of the center and south (Cromsigt et al. 2017a). HiP is among the few places globally that still supports near intact mega- and large herbivore and predator communities (Cromsigt et al. 2017b).



Figure 2. Study area (Hluhluwe-iMfolozi Park, South Africa), with the soil sampling sites (n=16) for my in depth field study Paper III & IV (Google Earth Pro Imagery, Landsat 8).

2.3 Experimental designs (Papers II, III & IV)

2.3.1 Natural experiment (Paper II)

In order to test my predictions on how rhino loss affects vegetation and fire dynamics, I used fine-scale spatial data on legal and illegal rhino removal during a 10-year period (2010-2019) in HiP (Fig.3) allowing me to link a rhino loss gradient to spatiotemporal patterns in vegetation and fire. I produced a 1x1 km grid over the park in QGIS, and overlaid it on the GPS rhino removal point data (see the section on data collection). I then derived the mean number of rhino individuals lost over the years for each grid cell. The spatial gradient in rhino loss provided conditions for a "natural experiment", where vegetation and fire parameters could be contrasted across spatial gradient in rhino loss. Because my questions focused on processes (i.e. fire and woody encroachment) that predominantly occur in relatively open grassland without closed canopy, I first masked all 1x1 km grid-cells that had >75% woody plant cover, which I removed from all further analyses.



Figure 3. Temporal (2010 to 2021) patterns of rhino loss in Hluhluwe-iMfolozi Park in South Africa, including management removals (legal) and poaching events (illegal).

2.3.2 Field study (Papers III & IV)

In order to test my predictions on how rhino grazing and associated impacts on woody recruitment and fire affect SOC stocks and the size of functional SOC pools, I utilized rhino-driven grazing lawns and other heavily grazed tall grassland patches in HiP, and used them as models for white rhino impacts. I selected 16 sites (Fig.4) along rainfall, fire frequency and soil clay content gradients in three different rhino habitats: open lawn (n=6), woodland lawn (n=5) and hillslope (n=5) habitats (Fig.5). To explore the effects of grazing on SOC stocks and functional SOC pools with varying persistence, I located natural grazing contrasts at each site. In the open lawn and woodland lawn habitats, I compared: (A) the center of the grazing lawn (the most grazed), (B) the edge of the grazing lawn (intermediately grazed) and (C) the tall grass outside the grazing lawn (the least grazed). The hill slope habitats only contained tall grass and I therefore based the grazing contrasts in this habitat on grass biomass and dung accumulation. I did not add a third contrast level in this habitat, as the grazing differences within this habitat type were already subtle (Fig.5). Thus, the open lawn and woodland lawn habitats contained three contrasts each and the hillslope habitat only two, providing relative, within-habitat contrasts. To explore the effects of woody encroachment on SOC stocks, I included an additional woodyencroached plot in the tall grassland at each site. I added this woody encroached plot only to the open lawn habitat sites and the hillslope habitat sites, since the woodland lawn habitat were naturally tree dense and not encroached by shrubs (plot D in Fig.4)



Figure 4. An illustration of the field sampling design for Papers III and IV.



Figure 5. An illustration of the combination of grazing and woody encroachment contrasts at each rhino habitat sampled, and the combinations of plots used for the different questions in Papers III and IV.

2.4 Data collection

2.4.1 Megagrazer loss and savanna functioning (Paper II)

I received the GPS coordinates for each management removal of rhino and poaching event between 2010-2019 from Ezemvelo KZN Wildlfe, which were recorded directly after each legal rhino removal and poaching event. I furthermore received yearly rhino counts (GPS locations of individual rhino or rhino herds, including the number of rhino in the herd) for the southern part of the park (iMfolozi), collected through fixed-wing aerial transects in the month of September for 2010-2019 by Ezemvelo KZN Wildlfe. I overlaid the 1x1 km grid over the rhino count GPS data, and calculated the mean rhino count as average number of rhino observations over the sampling years per grid cell. I furthermore calculated the rate of change in rhino density for each grid cell as the beta estimate of the linear model where rhino count was the response and year was the predictor.

Grazing lawn occurrence in the park was recorded in 2010, 2014, 2016 and 2019 on 23 fixed line transects, equally distributed throughout the park (but excluding the most southern part of the park, which is managed as a wilderness area) and representing all vegetation types and the different topographies found in the park. The transects were walked by teams of two people between March-July in 2010, July-September in 2014, October-November 2016 and between January and April in 2019, who recorded the presence/absence of grazing lawn within 5 m buffer on each side of the transect at each 5 m interval. I overlaid the 1x1 km grid over the transect lawn data and extracted the number of lawn observations per year for each grid cell that intersected with a transect (i.e., the number of 5m transect segments, where lawn was present). I further computed grazing lawn extent as the average number of lawn observations per grid cell across all the sampling years. I then normalized the values for the length of transect intersecting each grid cell. I also calculated the rate of change in grazing lawn extent over the years as the beta estimate for the linear model where grazing lawn extent was the response and year was the predictor.

I extracted percentage grass and bare-ground cover from Copernicus Global Land Cover Layers: CGLS-LC100 Collection 3 for each year between 2015-2019 at 100 m resolution using Google Earth Engine Java Script API (Gorelick et al. 2017). I used the grass cover estimates to create a proxy for woody plant cover, where woody cover was obtained by subtracting the grass cover from 100%. Here, I ignored bare-ground since bare ground cover turned out to be very low during all years (< 0.5%). For each 1x1 km grid cell, I computed the mean woody cover across the sampling years (2015-2019) and the rate of change in woody cover as the beta estimate of the linear model where woody cover is the response and year is the predictor. Hereon, I refer to the beta estimate for the rate of change in woody cover simply as "the rate of woody encroachment".

I extracted annual burned area for the park between 2010-2019 at 250 m resolution from MODIS Fire cci Burned Area Pixel Product, Version 5.1 using Google Earth Engine Java Script API (Gorelick et al. 2017). From this data, I derived the mean burnt area from 2010-2019 for each 1x1 km grid cell, and I also computed fire frequency for each grid cell as the number of years that a burnt pixel intersected the grid cell.

I acquired average rainfall data for park from Howison et al. (2017), who derived it through spatially extrapolating long-term average rainfall values between 1935 and 2010 across a number of recording stations in the park. I then computed the mean long-term rainfall per each 1x1 km grid cell by averaging rainfall values of all raster pixels within each cell.

2.4.2 Megagrazers, soil organic carbon stocks (Paper III) and soil carbon persistence (Paper IV)

In my 16 rhino habitat sites (Fig. 2), I sampled soil in plots differing in grazing intensity and woody encroachment. I first took a soil core of a known volume from three successive depths (i.e. 0-5 cm, 5-15 cm and 15-30 cm) at the center of each plot for the determination of bulk density per depth increment. I calculated bulk density as:

$$BD = \frac{DM - SM}{V}$$

where DM= dry mass of the sample, SM = total mass of stones in the sample and V= volume of the sample. Bulk density for the 0-30 cm profile was determined as the weighted mean of the three successive depths.

I then took a further soil cores using a Beater auger (4 cm diameter) from each three depths on each sampling plot (Fig. 4). Each sample was dried at 45°C to constant weight, crushed between rubber belts and sieved through 1 mm mesh. Subsamples that were analyzed for SOC stocks (Paper III) were kept separately per depth category per plot, while subsamples that were analyzed for the functional SOC pools (Paper IV) were aggregated across all depths per plot. Thus, for the SOC stock analyzes (Paper III) I was left with three depth samples (0-5, 5-15, 15-30 cm) per plot, while for functional SOC pool analyzes (Paper IV) I was left with one aggregate sample per plot (Table 2).

Total carbon (TC) content for Paper III analyses was quantified by the soil fertility laboratory of the KwaZulu-Natal Department of Agriculture & Rural Development Analytical Services in South Africa through the automated Dumas dry combustion method as described in Manson et al. (2020) using a LECO CNS analyzer at the lab in South Africa. Inorganic carbon for Paper III analyses was further quantified at Utrecht University Geolab using a LECO TGA701 thermogravimetric analyzer.

For Paper IV analyses, I first performed a density fractionation for the aggregate soil samples per plot, and thus separated soil organic matter into the following fractions: particulate organic matter, aggregate-occluded organic matter, and mineral associated organic matter for the 0-30 cm depth profile. I did this at Utrecht University Geolab following the protocol from Plaza et al. (2012) and Viret and Grand (2019). For all fraction samples, TC and δ^{13} C isotope ratios were analyzed in Utrecht using Thermo Scientific EA IsoLink IRMS CN-analyzer. Furthermore, for all fraction samples pyrogenic carbon (PyroC) and inorganic carbon IC were further quantified using a LECO TGA701 thermogravimetric analyzer (Edmondson et al. 2015).

I calculated TC and IC density for all Paper III and IV samples and PyroC density for all Paper IV samples by multiplying the percentage TC, IC and PyroC values by the bulk density. I further derived organic carbon (OC) density for each sample by subtracting IC density from TC density. I finally transformed the PyroC and OC density (kg/m³) into PyroC and OC stocks (tC/ha) for each sample and each fraction sample by:

$$(Pyr)OCs = \frac{(Pyr)OCdx \ D \ x \ 10 \ 000}{1000}$$

where (Pyr)OCd = pyrogenic carbon or organic carbon density (kg/m³) and D=depth increment (m). I used (Pyr)OC stock values (tC/ha) for all analyses.

To calculate the difference of C3 woody-originated carbon in each fraction between woody colonized plots and not encroached lightly grazed reference plots, I used methods described in Just et al. (2021). First, I determined the proportion of "additional" C4-derived carbon in the least grazed plots compared to woody encroached plots by:

$$FC4 = \frac{13C(LG) - 13C(WE)}{13C(C4 \text{ plant}) - 13C(WE)}$$

Where 13C(LG) is the δ^{13} C value for the least grazed plot, 13C(WE) is the δ^{13} C value for the woody encroached plot and 13C(C4 plant) is the δ^{13} C value for C4 grass, which I derived from Just et al. (2021) i.e. -12 ‰. Since FC4 signified the additional C4-derived carbon least-grazed plots compared to woody-encroached plots, it simultaneously represented the additional C3-derived carbon on woody-encroached plots compared to least grazed plots.

To determine a grazing intensity value to each of the grazing contrast plots (i.e. the most, intermediate and the least grazed), I used principal component analysis in base R to derive a composite variable for grazing intensity. I used the these parameters measured in the field to derive this composite variable: standing grass biomass, grass cover, percentage cover of stoloniferous grasses from total grass cover, forb cover and dung cover. I extracted the first principal component axis "PC1", which explained ~48% of the variation in the grazing proxies per sampling plot, and used it as an index for grazing intensity. This allowed me to include grazing intensity as a covariate with a single unique value per sampling plot in addition to my factorial grazing treatment.

Soil clay content for each site was estimated as the average soil clay content from all sampling plots within the particular site that was derived using the mid-infrared reflectance method in the lab in South Africa (Manson et al. 2020). Long-term rainfall values for each site (ranging between 519 - 769 mm/year) were obtained from Howison et al. (2017). I further extracted

medium-term fire (15 years) frequencies from MODIS burnt scar products for 2004-2018 from Google Earth Engine (Gorelick et al. 2017).

Table 2. The size (S) and isotope ratios (and $\delta 13C$) of each soil carbon pool per depth profile.

C pool	0-5 cm	5-15 cm	15-30 cm	0-30 cm	Paper
SOC	S	S	S	S	III
POC	-	-	-	S & 813C	IV
oPOC	-	-	-	S & 813C	IV
MAOC	-	-	-	S & 813C	IV
PyroC	-	-	-	S	IV

2.5 Statistical analyses

2.5.1 Megagrazer loss associations with vegetation and fire dynamics (Paper II)

Linear model approach

The same 1x1 km grid was used for all response variables consistently for all years. I used linear models (function lm) and generalized linear models (function glm) in base R (R team 2022) to test the relative effects of rhino loss and rainfall on mean rhino density and the rate of change in rhino density, grazing lawn extent and the rate of change in grazing lawn extent, mean woody cover and the rate of woody encroachment, mean burnt area, and fire frequency (Table 3).

Question	Model structure	Model type
Rhino count	Mean rhino count~Rhino_loss*Rainfall	glm()
Rhino count	Rate of change in rhino count ~Rhino_loss*Rainfall	lm()
Lawn	Mean grazing lawn extent ~Rhino_loss*Rainfall	glm()
Lawn	Rate of change in grazing lawn extent ~Rhino_loss*Rainfall	lm()
Fire	Mean burnt area~Rhino_loss*Rainfall	glm()
Fire	Fire frequency ~Rhino_loss*Rainfall	glm()
Woody	Mean woody cover ~Rhino_loss*Rainfall	lm()
Woody	Rate of change in woody cover ~Rhino_loss*Rainfall	glm()

Table 3. Summary of model structures for ecological effects of rhino loss (Paper II).

Pathway analysis

While the linear model approach allowed me to test the effect of rhino loss on each vegetation and fire parameter separately, it did not account for the multiple co-occurring links (i.e. direct and indirect associations) between these parameters. Thus, I augmented the linear model approach with a pathway analysis through piecewise Structural Equation Models (pSEM) in R (package: piecewiseSEM). Accordingly, I used pSEMs to test whether rhino loss influenced fire directly, or indirectly through its effects on grazing lawn, and whether rhino loss influenced the rate of woody encroachment directly, or indirectly through its effects on grazing lawn and/or fire.

2.5.2 SOC stocks (Paper III) and functional SOC pools (Paper IV) along grazing intensity and woody encroachment gradients

I had three main questions. In the first question, I used generalized linear models (function glm) in base R (R team 2022) to test whether SOC, POC, oPOC, MAOC and PyroC differed between the extreme grazing contrasts (i.e. within-site comparison of most vs. least grazed plots), woody encroachment (i.e. within-site comparison of woody-encroached vs. least grazed plots) and along a grazing intensity gradient (i.e. the PCA-derived grazing intensity index for the most, intermediately and the least grazed plots). Because of the unbalanced design, with some plot contrasts missing

from some habitats, each question only included the habitats that contained the plot contrasts relevant for the particular question (shown in Fig.5).

In the second question, I used linear models in base R (function lm) and generalized linear models (function lme) in the nlme package to ask whether and how rainfall, fire frequency and soil clay content explained the effect size and direction of grazing contrasts (lm), woody encroachment (lm) and grazing intensity (lme) on each response variable. For SOC, I first performed all analyses for the entire 0-30 cm profile, and then for each depth separately (0-5 cm, 5-15 cm and 15-30 cm). For POC, oPOC, MAOC and PyroC, I performed all analyses for the entire 0-30 cm profile only.

In the third question I used linear models in base R to test whether woody encroached plots had higher contribution of C3 woody-orgingated carbon in POC, oPOC and MAOC compared to least grazed plots in each habitat (Table 4).

Table 4. Summary of model structures and data inclusions (Papers III and IV). Refer to Fig.5 for plot ID explanations. SOCf indicates either SOC stocks or a particular functional SOC pool (i.e. POC, oPOC, MAOC, PyroC). Rainfall and fire frequency were tested in separate models due to co-linearity.

Question	Model structure	Data used	Model type
Grazing	SOCf ~ Contrast Plot *	Plots A & C from all three	lme
contrast	Habitat	habitats	
Woody	SOCf ~ Contrast Plot *	Plots C & D from the open lawn	lme
contrast	Habitat	and the hillslope habitats	
Grazing	SOCf ~ PCA-derived	Plots A, B & C from the open	lme
intensity	Grazing Intensity * Habitat	lawn and the woodland lawn	
		habitats	
Grazing	Δ SOCf ~ Rainfall (or fire	Plots A & C from all three	lm
contrast	frequency) * Clay content	habitats	
Woody	$\Delta SOCf \sim Rainfall$ (or fire	Plots C & D from the open lawn	lm
contrast	frequency) * Clay content	and the hillslope habitats	
Grazing	SOCf ~ Rainfall (or fire	Plots A, B & C from the open	lme
intensity	frequency) * PCA-derived	lawn and the woodland lawn	
	Grazing Intensity + Clay	habitats	
	content * PCA-derived		
	Grazing Intensity		
Woody	$\Delta C3a \sim Contrast$	Plots C & D from the open lawn	lm
contrast	plot*Habitat	and the hillslope habitats	

3. Results and discussion

3.1 Biases and gaps in the peer-reviewed literature (Paper I)

There were 11 977 peer-reviewed publications resulting from the specified search query, of which only 3% studied megaherbivore ecological impacts and thus were deemed relevant. Moreover, just 46% of this 3% deployed appropriate methodology and/or reporting to be eligible for a quantitative meta-analysis. Thus, I included 240 studies (144 Type I and 96 Type II studies) in this systematic review and decided against a quantitative metaanalysis due to too small sample size per megaherbivore species. The lack of studies on megaherbivore ecological impacts can be explained by the conservation status and generally low population sizes of most extant megaherbivore species, which promotes research on conservation management and re-introduction-related topics, such as reproduction, habitat suitability and movement ecology, instead of studies on their ecological impacts. Furthermore, many studies did not report effect contrast and/or effect sizes and measures of uncertainty, explaining the low inclusion rate of Type I studies. Many studies also did not distinguish megaherbivore impacts from the impacts of smaller large herbivores. For example, studies utilizing exclusion experiments often separated the impact of small and medium-sized herbivores from that of large herbivores but did not do so between large- and megaherbivores.

I identified major knowledge gaps and biases in the included studies. Approximately 70% of the included studies was on African savanna

elephants, followed by giraffe and hippo (10 % each), and white rhino (4 %). No studies were on Javan and Sumatran rhino. The remaining four megaherbivore species jointly made up only 6 % of studies (Fig.6), pointing at a very strong bias towards studying African megaherbivores relative to the Asian species. The most studied Earth system function categories were changes in vegetation structure and biodiversity, particularly for African savanna elephant (Fig.6). Only two studies focused on white rhino's role in nutrient transport (le Roux et al. 2018; Veldhuis et al. 2018) and on African savanna elephant's role in soil carbon storage (Sitters et al. 2020, Wigley et al. 2020). There were only three fire-related studies on white rhino, hippo and elephant (Waldram et al. 2008; Smit and Archibald 2019; Kimuyu et al. 2014). These taxonomic and thematic biases mean that our understanding of megaherbivore impacts is strongly biased towards mixed-feeder impacts on vegetation and biodiversity, and that we still have very limited empirical knowledge on megagrazer impacts, and particularly on how they influence fire and soil carbon dynamics, both of which are important for global carbon cycling.

There were also substantial geographic biases in the literature, such that almost half of Type I studies came from only five African areas, while a similar proportion of Type II studies came from ten areas including both African and Asian countries. Furthermore, the current study areas for all megaherbivore species only represent small parts of the climate and soil fertility envelopes of their current distribution ranges. The most studied areas, such as KNP, Addo Elephant National Park and HiP in South Africa and Mpala Research Centre in Kenya are internationally well known for their exceptional field research facilities, explaining the number of studies coming from these areas. Areas without such infrastructure are much more difficult and resource intensive to study. Moreover, some of the most vulnerable megaherbivore species such as white rhino only exist in a handful of areas at functional densities, strongly limiting opportunities to study their ecological impacts in a diversity of environmental conditions.



Figure 6. Chord diagram showing the proportion of studies published on the effects of the different megaherbivore species on each Earth system function category. The "other" category includes hydrology as well as soil and geomorphology.

3.2 Associations between rhino loss, vegetation and fire dynamics (Paper II)

Grazing lawn extent and the rate of change in grazing lawn extent did not differ among grid cells with varying degree of rhino loss (Fig.7a,b; Appendix Table S1). This was unexpected, because previous research from HiP and KNP suggests a central role for rhino in grazing lawn establishment and maintenance (Cromsigt and Olff 2006; Waldram et al. 2008; Cromsigt and

te Beest 2014). The lack of effect in my study can be partially explained by the fact that grid cells that lost more rhino had lower rate of change in rhino numbers but also higher overall rhino numbers. This means that despite management removals and poaching, rhino numbers probably remained functionally sufficient to maintain grazing lawns in grid cells that lost many rhino. Furthermore, grazing lawn cover, as measured in this thesis, is highly sensitive to changes in precipitation (i.e. higher biomass production and lower grazing lawn cover during wet season compared to dry season). It is likely that the strong seasonal differences in the timing for the grazing lawn surveys for the different years, and the drought that took place in HiP from 2014 to 2016 (Mbatha and Xulu 2018) obscured the effects of rhino loss on grazing lawn cover.

As expected, grid cells that lost more rhino had a larger extent of burnt area and higher fire frequency (Fig.7c,d; Appendix Table S1). There are two main mechanisms through which rhino can influence fire; (1) the creation and maintenance of grazing lawns, which act as natural fire breaks in the landscape (Hempson et al. 2015), and (2) the general reduction of tall grass biomass, and thus grass fuel for fire, by grazing (Cromsigt and te Beest 2014). I found support for the first mechanisms because grid cells with higher grazing lawn extent had lower burnt area and fire frequency across the rainfall gradient. This is corroborated by Archibald et al. (2005), who reported higher fire return intervals with increasing proportion of lawn grass cover in the same study system. Although I could not directly test whether rhino loss reduced grass biomass on the tall grassland specifically, evidence for this second mechanism comes from Waldram et al. (2008) who reported that legal rhino removal increased fire extent in both low and high rainfall areas of HiP, which was attributed to an increase in grass biomass accumulation following rhino removal.

Grid cells that lost more rhino had higher rates of woody encroachment (Fig.7e,f; Appendix Table S1). However, my pSEM analysis revealed that rhino loss was associated with higher rate of woody encroachment indirectly through its positive effects on burnt area and fire frequency (Fig.8). While intense fires tend to kill woody plants that grow below the fire trap (Mapiye et al. 2008; Smit et al. 2016), frequent low intensity fires can have the opposite effect. Low frequency fires that do not kill woody seedlings and saplings may on the other hand promote woody plant establishment and

recruitment to higher size classes due to reduced grass competition (Walters et al. 2004). Because increasing fire frequency is attributed to reduced accumulation of grass biomass thus reducing the abundance of fire fuel for each individual fire event (see Rodrigues et al. 2021, who show this for Brazilian Cerrado), I hypothesize that frequent fires in HiP burn relatively cool compared to less frequent fires. This would further explain why increasing fire frequency was associated with higher rate of woody encroachment in my study.

Another mechanism through which grazing lawns can reduce the rate of woody encroachment is through meso-browser visitation of grazing lawns. In fact, browser exclusion in HiP strongly limited the growth rates of woody plants in short grass habitat (Voysey et al. 2021). My pSEM analysis showed that instead of browser mediated impacts, grazing lawn extent was associated with lower rate of woody encroachment indirectly through its negative effects on fire. This highlights that grazing lawns play an important role in the functioning of HiP savanna system.

Although the pSEM analysis allowed me to test both direct and indirect associations between rhino loss and the vegetation and fire parameters, it is important to note that this does not necessarily confirm causality of the relations. In fact, the analysis here is based on spatial correlations and therefore it is important to consider whether the trends observed among the variables have alternative explanations. For instance, an alternative explanation for the relationship between grazing lawn and fire found in this study is that large frequent fires can also reduce grazing lawn extent. This is because nutritious postfire growth can attract large grazers away from grazing lawns, thus alleviating grazing pressure on the lawns, which in turn promotes tall grass growth and the loss of lawn cover (Archibald et al. 2005). Furthermore, the relationship between the rate of woody encroachment and fire found in this study can be alternatively explained by the active fire management in the park. In fact, management tends to burn more in areas that are highly encroached to control woody encroachment, (Archibald et al. 2017). Importantly, however, unplanned random fires occur in the park regularly, so management burning could provide only a partial explanation for why I found more frequent fires in grid cells with higher rate of woody encroachment. These alternative explanations do highlight that more research is needed. Future research can better entangle the spatial patterns of the relative importance for these two pathways for instance through a timeseries analysis that accounts for lag-effects.



Figure 7. Scatterplots showing the relationship between rhino loss and the vegetation- and fire parameters. The error bars indicate standard error.

3.3 Associations between savanna processes and soil carbon dynamics (Papers III & IV)

There were no significant differences in SOC between most intensely and least intensely grazed plots or along a grazing intensity gradient in any of the rhino habitats (Fig.9) (see Appendix Table S2 for the model outputs). Furthermore, soil clay content, rainfall or fire frequency were not significant



Figure 8. Results of the piecewise Structural Equation Models, testing the different pathways for the impact of rhino loss and grazing lawn extent on burnt area, fire frequency and woody encroachment. The dashed outlie for the boxes depicts that I specified a (quasi)poisson distribution. Green arrow describes a positive effect, and orange arrow a negative effect. Grey line describes no effect. Only, the estimates for pathways towards woody cover are standardized.

predictors of grazing effects on SOC (Appendix Table S3). Therefore, I found no evidence to support the hypothesis that wild grazing dominated by megagrazers hampers long-term soil carbon storage. This contrasts with other studies from African savannas, that reported that wild herbivores including megaherbivores either increase or decrease SOC. For instance, in a study in East Africa Sitters et al. (2020) found that the inclusion of African savanna elephant increased SOC stocks, while Wigley et al. (2020) showed that herbivore exclusion including elephants resulted in higher SOC stocks. This is interesting because these seemingly contradictory findings came from the same study area in Laikipia district, Kenya. In HiP, the intensely grazed grazing lawns have relatively little above ground biomass which probably limits the amount of carbon that is returned to the soil through litterfall. However, in productive grasslands, high grazing pressure can also stimulate productivity and root growth (Wilson et al. 2018), both of which will contribute to soil carbon storage. It is thus conceivable that these contrasting effects led to a net neutral SOC impact in my study.

There were no significant differences in the size of the different functional SOC pools (i.e. POC, oPOC, MAOC or PyroC) between most intensely and least intensely grazed plots or along a grazing intensity gradient in any of the rhino habitats (Fig.10; Appendix Table S4). Furthermore, soil clay content, rainfall or fire frequency were not significant predictors of grazing effects on any of the functional SOC pools (Appendix Table S5). This suggests that grazing in my study system does not clearly affect the size of the more persistent (MOAC, PyroC) or less resistant (POC) soil carbon pools, even at the highest grazing intensities. Despite the paucity of empirical studies, Kristensen et al. (2022) recently suggested that large grazers can promote MAOC formation through enhancing microbial carbon use efficiency. Grazer dung adds nutrients into the soil, which enables microbes to convert organic matter more efficiently into microbial biomass instead of leading to CO² production (Sinsabaugh et al. 2016). Because at least half of MAOC derives from microbial biomass (Angst et al. 2021), microbial carbon use efficiency plays an important role in MAOC formation. However, in nitrogen limited conditions, microbes may opt to mine nitrogen from organic matter that is associated with soil minerals. To do this, sufficient quantities of labile carbon needs to be available to power the production of enzymes that are

needed for breaking down organo-mineral bonds (Bailey et al. 2019). Thus, when nitrogen is limiting, grazing stimulated grass root exudation and rhizodeposition (i.e. labile carbon input) may in fact lead to MAOC destabilization (Hamilton et al. 2008). It is important to note that the grazer biomass in Hluhluwe-iMfolozi park amounts to ~8000 kg/km² which is comparable to the Serengeti system and twice more than in Kruger National Park (le Roux et al. 2017). Therefore, grazer biomass in HiP is high and is likely to exert a high grazing pressure overall and a particularly high grazing pressure on the heavily frequented grazing lawns. Despite this, I found no evidence of a loss in SOC stocks or a change in the size of functional SOC pools, even from these intensely used grazing lawns. However, it is important to note that I did not have a control that excluded large grazers completely. Thus, I was unable to compare grazing contrasts to the total absence of grazing

As expected, woody encroached plots had higher total SOC at coarser textured soils, and lower total SOC at finer textured soils, although only in the top 5 cm (Fig.9; Appendix Table S3). This is in line with the global meta-analysis by Li et al.'s (2016) that found woody encroachment to increase SOC content in sandy and sand loamy soils, and to decrease SOC in silty and clay soils. Woody encroached plots furthermore had higher POC than not encroached least grazed plots in hillslope habitat and lower POC in open lawn habitat (Fig.10; Appendix Table S4; Table S5). The negative impact of woody encroachment on POC in the open lawn habitat could be explained by the high visitation of this habitat by impala, kudu and nyala that browse woody leaves and directly feed on leaf litter in the dry season (Owen-Smith and Cooper 1985). It is thus possible that high levels of browsing leads to reduced litter fall, and thus burial into the soil. This together with the reduced grass competition and grass litter burial due to the shading effects of woody plant would explain the reduced POC. My isotope analysis confirmed this explanation (Appendix Table S6). I found that POC on woody encroached plots had similar concentrations of C3-woody originated carbon compared to least grazed plots in open lawn habitat. In hillslope habitat, however, where woody encroachment increased POC, woody encroached plots had ~40% more C3-woody originated carbon in POC compared to not encroached least grazed plots.

Woody encroached plots also had more oPOC and PyroC compared to least grazed plots but only in hillslope habitat (Fig.10; Appendix Table S4). This suggests that woody encroachment promotes SOC persistence through organic matter occlusion in soil aggregates and stimulates the production and burial of partially combusted above-ground biomass. This interpretation is supported by Ortiz et al. (2022) who found woody plants to promote soil aggregation due to their associations with mycorrhizal fungi, and the subsequent secretion of fungi-derived glycoproteins that act as effective binding agents for aggregate formation. The positive effect of woody encroachment on PyroC is also supported by past research showing that frequent fires can lead to the accumulation of partially combusted woody plant biomass (Pellegrini et al. 2022; Pingree and DeLuca 2017). However, it is important to note that climate change may lead to accelerated wetting/drying cycles (Fischer et al. 2021), and therefore promote the destabilization of soil aggregates (Schimel 2018). Therefore, there remains uncertainty on the long-term effects of woody encroachment on soil carbon persistence in these hillslope habitats.

My approach here was to use natural spatial contrasts in grazing intensity and woody encroachment to explore the impacts of rhinodominated grazing and woody encroachment on soil carbon dynamics. This approach is limited in its ability to make causative conclusions about the relationships between the drivers (grazing and woody encroachment) and soil carbon dynamics. An alternative approach is to exclude herbivores from an area and compare that to a control area where herbivores are not excluded. This would further allow to disentangle some of the direct (i.e. defoliation, dunging and trampling) and indirect effects (i.e. limiting woody encroachment) of grazing on soil carbon dynamics.



Figure 9. Boxplots showing the difference in soil organic carbon stocks (SOC) (tC/ha) between plot contrasts (most grazed vs. least grazed and woody encroached vs. least grazed) per habitat and soil depth.



Figure 10. Boxplots showing the difference in functional soil organic carbon (SOC) pools with varying persistence (tC/ha) between plot contrasts (most grazed vs. least grazed and woody encroached vs. least grazed) within the 0-30 cm soil depth profile per habitat

3.4 White rhino as a model for extant megagrazers

In this thesis, I focused my in-depth investigations on the ecosystem effects of a particular group of megaherbivores, i.e., megagrazers. In fact, I used white rhino as a model for megagrazer impacts. Other extant megagrazers include greater one-horned rhino and the common hippopotamus. Although the current population size of greater one-horned rhino is just ~3500 individuals (compared to ~18 000 white rhino) (Hyvarinen et al. 2021), they exist at relatively high densities at least in one park in Nepal, i.e. Subedi et al. (2013) reported a density of 1.0/km² for Royal Chitwan National Park (RCNP), while Dinerstein (1991) reported 1.7-3.2/km² for the same area two decades earlier. Other areas where greater one-horned rhino occur, although with much lower densities, include Bardia National Park (0.28/km²) and Suklaphanta Wildlife Reserve (0.1 /km²) (Subedi et al. 2013). Rhino density at RCNP is, at least at partly, comparable to HiP's average rhino density $\sim 2/km^2$ (Linklater and Shrader 2017), and therefore could be expected to exert similar grazing pressure on the grass layer. Despite the paucity of studies on their ecological impacts, there is some evidence to suggest that greater one-horned rhino have similar ecosystem impacts as white rhino, such as the creation and maintenance of grazing lawns (Owen-Smith 1988; Karki et al. 2000). It must be noted, however, that the available data on herbivory impacts on vegetation for the Nepalese areas is scarce compared to the relatively well-studied African areas such as HiP and KNP. Therefore, the extent to which the ecological impacts of white rhino and greater onehorned rhino compare to each other remain unclear.

Besides white rhino, hippo are the only extant megagrazer in African systems. Compared to greater one-horned rhino, there are more data available on the ecological impacts of hippo (Hyvarinen et al. 2021). Hippo have been shown to create and maintain grazing lawns that are also characterized by the dominance of grazing tolerant stoloniferous grass species and relatively high visitation by other short grass grazers (Verweij et al. 2006). However, because hippo spend most of their time in water bodies, their ecological impacts are also limited to adjacent rivers and pools (Owen-Smith 1988). Despite the scarcity of studies, hippo-driven grazing lawns may serve similar function in terms of limiting fire regimes and woody

encroachment in the landscape. This needs further testing however. Importantly, hippo have been recently shown to play important roles in nutrient cycling. Schoelynck et al. (2019) for instance, demonstrated that hippo were able to enhance the cycling of silicon by feeding on riverine grasslands and defecating in water bodies. The authors estimated that this "silicon pump" has potential cascading impacts on the silicon-limited estuarine diatoms. Despite, potentially similar ecological impacts on vegetation, it is important to highlight the differences in the spatial distribution of habitat and resource use between rhino and hippo. As such, more research is needed to assess generalities between extant megagrazer species.

3.5 Synthesis of the results in relation to the overall thesis

While prehistoric extinctions of large animals have been linked to changes in large-scale changes in ecosystem processes, there is still considerable uncertainty about megaherbivore impacts in contemporary contexts. To place my thesis into a broader context, I first conducted a systematic review, through which I show that there are substantial biases in our understanding of contemporary megaherbivore impacts on ecosystem and Earth system functioning, with only a handful of studies on the most vulnerable megagrazer species such as white rhino and only few studies on Earth system categories such as fire and biogeochemistry (Paper I). In my in-depth investigation on megagrazers, I asked how the loss of the world's largest megagrazer, white rhino, impacts crucial savanna patterns and processes such as grassland structure (i.e. grazing lawn cover), grass/woody balance and fire dynamics and how these impacts further affect climate drivers i.e. soil carbon dynamics. Using a landscape scale "natural experiment", I show that rhino loss in HiP was associated with higher fire frequencies and, indirectly, a higher rate of woody encroachment. Furthermore, grazing lawn extent, an increase in which has been previously linked to rhino presence, was associated with lower fire frequency and, indirectly, a lower rate of woody encroachment (Paper II). In my field study, I then looked at how changes in grazing intensity (i.e. grazing lawn contrasts), woody encroachment and fire could affect SOC stocks and functional SOC pools that vary in persistence. I show that rhino-dominated grazing in HiP did not directly reduce SOC stocks (Paper III) or alter functional SOC pools with

varying persistence (Paper IV) even at the highest grazing intensities. However, compared to not encroached reference plots, woody encroached plots had either higher or lower SOC stocks and lower levels of less persistent POC depending on the soil texture and habitat context, and higher levels of more persistent oPOC and PyroC pools but only in tall grassland hillslope habitat. These results thus support my general thesis that rhino loss leads to complex ecosystem-scale responses where vegetation, fire and soil carbon dynamics are tightly coupled. Moreover, these results support the specific hypotheses that rhino loss amplifies woody encroachment indirectly through increasing fire occurrence, and that grazing lawns that have been previously linked to rhino are important for savanna functioning. I did not find evidence that rhino loss resulted in a reduction in grazing lawn, although this link has been demonstrated before by (Waldram et al. 2008) in the same study area. There was also no evidence to suggest that grazing by rhino directly reduces SOC stocks or alters the size of functional SOC pools even at the highest grazing intensities. However, my results do suggest that rhino can indirectly limit the loss of soil carbon input through their negative effects on woody encroachment.

4. Conclusion

It is becoming increasingly clear that wild animals play crucial roles in ecosystem functioning, with an ability to influence climate drivers such as carbon cycling. However, there is still much uncertainty about how today's largest terrestrial herbivores i.e. megaherbivores influence ecosystem functioning. This is especially concerning because many megaherbivores are threatened by poaching, and we may thus lose them in the few places where they remain in the wild at functionally relevant densities. Based on the research presented in this thesis, I concur that white rhino, the world's largest extant megagrazer, are also important ecosystem engineers. I further propose that their loss can lead to complex consequences for the functioning of the HiP savanna system where the dynamics of vegetation, fire and soil carbon are tightly coupled. To more fully embrace this complexity, future assessments on megagrazer impacts on long-term soil carbon storage should factor in direct (i.e. defoliation, trampling and grazing) and indirect effects (i.e. limiting fire and woody encroachment) on both SOC stocks and persistence. I also encourage further experimental testing for instance through utilizing long-term exclosure set-ups.

5. Future research

"You look at where you're going and where you are and it never makes sense, but then you look back at where you've been and a pattern seems to emerge." — Robert M. Pirsig, Zen and the Art of Motorcycle Maintenance: An Inquiry Into Values

My systematic review revealed large biases in the empirical peer-reviewed literature on extant megaherbivore effects on ecosystem and Earth system functioning (Hyvarinen et al. 2021). In order to better understand how different megaherbivore species can contribute to ecosystem and Earth system functioning in different environmental contexts, we must substantially increase the taxonomic and geographic distribution of studies, and study a wider range of ecosystem and Earth system function categories beyond vegetation and biodiversity, and include categories such as nutrient and carbon cycling. A particularly interesting and relevant avenue for future research would be to study how megaherbivore effects on grass/woody balance and fire regimes influence surface-energy fluxes, and therefore Earth's energy balance. For instance, Dintwe et al. (2017) reported that savanna fires in sub-Saharan Africa and the subsequent dark burn scars resulted in a reduction in albedo, further increasing regional and global radiative forcing. Furthermore, Doughty et al. (2010) showed that megaherbivore extinctions and the subsequent alleviation in herbivore pressure in the Arctic steppe-ecosystems resulted in a biome-scale increase in shrub cover, which lowered the surface albedo, and increased temperatures in Siberia and Beringia on average by ~0.2°C. Because of the demonstrated impacts of extant megaherbivores on fire and woody plants (Waldram et al. 2008; Guldemond and Van Aarde 2008; Guldemond et al.

2017), we need more research on their potential in regulating local to regional temperatures through influencing surface albedo.

One of the outstanding hypotheses that I could not test with the available data in my systematic review was that megaherbivore impacts on ecosystems are disproportionate to those by smaller species. In order to test this hypothesis properly through meta-analyses, we need to first increase research output where relative densities of different taxa of large and megaherbivores are carefully quantified for example through areal census counts. A complementary approach would be to quantify herbivore visitation through dung counts and/or monitoring with camera trap technology (Sutherland et al. 2018). Importantly, studies must be also able to assign ecological impacts to correct herbivore species. While species-specific impacts may be logistically difficult to study, categorizing megaherbivores and smaller large herbivores into broader functional units (e.g. grazers, browsers and mix feeders) can help in reducing complexity and thus the research costs. Future exclusion studies, that aim to study the differential effects of megaherbivores and other large herbivores, could benefit from examples such as the Kenya Long-Term Exclosure Experiment (KLEE) at Mpala Research Centre (Young et al. 1997) and the exclosure design at Hluhluwe-iMfolozi Park which is no longer standing (Van der Plas et al. 2016).

Our understanding of grazing effects on SOC is strongly biased towards studies from livestock systems. Findings from this thesis however suggest that the effects of grazing can be very different in livestock and wild megagrazer dominated systems. Thus, extrapolating results from livestock systems can be problematic for animating the carbon cycle projects, as it can lead to under- or over estimation of the potential impacts of trophic rewilding on long-term carbon storage. For instance, where livestock studies show that intermediate grazing levels may increase SOC in C4 grasslands, my field study suggests that grazing dominated by megagrazers does not influence SOC storage even at the highest intensities. Therefore, basing the feasibility assessment of megagrazer rewildling contribution to climate change mitigation on data from livestock dominated systems would result in overestimating the effect of megagrazer rewilding on climate change mitigation. Although it is important to keep in mind that my field study did not enable the comparison of rhino-dominated grazing to the complete absence of grazing, this calls for more research identifying and testing the specific mechanisms responsible for the differential impacts of domestic vs. wild grazers on long-term soil carbon storage. This includes, but is not limited to, the difference in body plan diversity, digestive morphology, habitat and resource use in space and time.

One of the most interesting results from this thesis is the fact that wild grazing dominated by megagrazers did not directly influence the size of different functional SOC pools with varying persistence. While there are many possible explanations for this (see discussion), we still lack empirical support for most mechanisms proposed in this study. Future research can further disentangle the effects of megagrazers on MAOC (de)stabilization or the lack thereof through fraction specific nutrient analysis, more in depth characterization of organic matter composition and microbial community and biomass analyses. This is instrumental to our understanding of how soil microbial community responds to grazing, and how this response would further influence MAOC (de)stabilization. This is important for predicting where megagrazer rewilding can contribute to long-term soil carbon storage, and where it possibly hampers it.

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Popular science summary

Prehistoric losses of the world's largest animals are increasingly being linked to largescale changes in the functioning of the Earth. Grazing and trampling by extinct species such as mammoths and mastodons kept woody shrubs in check and reduced the incidence of fires, further influencing climate drivers such as soil's carbon storage. However, today's ecosystems are highly impoverished of large animals compared to prehistoric baselines, and there are still large uncertainties about how today's megaherbivores, the largest plant eating mammals, influence their surroundings in contemporary contexts. Furthermore, megaherbivores such as rhinos and elephants are experiencing a dramatic poaching crisis, and we may thus lose them in the coming decades in their last strongholds.

In this thesis, I investigated how the loss of world's largest megarazer (grass eating megaherbivore), white rhino, affected the savanna ecosystem in Hluhluwe-iMfolozi Park (HiP) in South Africa. Using GPS-locations for rhino poaching and management removals together with satellite-derived vegetation and fire maps, I found that rhino loss was associated with the expansion of shrubs onto the open grassland. The likely reason for this is that the reduction in grazing pressure by rhino resulting from poaching and management removals leads to the accumulation of grass biomass that acts as fire fuel. Frequent low intensity fires reduce the ability of grasses to compete against woody plant seedlings, and therefore result in the expansion of shrubs onto the open grassland.

Next, in my in-depth field study, I found that rhino grazing did not directly reduce soil carbon storage, which contrasts findings from previous research. However, the effects of shrub expansion on soil carbon storage were context dependent. Most importantly, shrub expansion was associated with reduced soil carbon input in areas characterized by high levels of rhino grazing, while increasing soil carbon persistence in areas that were less intensely utilized by rhino and experienced high rainfall. The story that emerges from these results is that rhino may be able to limit the loss of soil carbon input indirectly through hampering shrub expansion onto the open grassland, although more research based on long-term experiments is needed.

This leads me to propose that white rhino are influential ecosystem engineers whose future in HiP is tightly coupled with the future of HiP's savanna. Although today's ecosystems are highly impoverished of megaherbivores compared to prehistoric baselines, further loss of megaherbivores in the few areas where they remain in the wild can strongly impact how these ecosystems function. More importantly, however, megaherbivore rewilding could thus provide opportunities to restore ecosystem functioning in areas where they have been historically lost.

Populärvetenskaplig sammanfattning

Förhistoriska förluster av världens största djur kopplas alltmer till storskaliga förändringar i jordens funktion. Bete och trampning av utdöda arter som mammutar och mastodonter höll vedartade buskar i schack och minskade förekomsten av bränder, vilket ytterligare påverkade klimatfaktorer såsom markens kollagring. Men dagens ekosystem är mycket utarmade på stora djur jämfört med förhistoriska nivåer, och det finns fortfarande stora osäkerheter om hur dagens megaväxtätare, de största växtätande däggdjuren, påverkar sin omgivning i samtida sammanhang. Dessutom upplever megaväxtätare, som noshörningar och elefanter, en dramatisk tjuvjaktkris och vi kan därmed förlora dem under de kommande decennierna.

I den här avhandlingen undersökte jag hur tjuvjakten av världens största megabetar (gräsätande megaväxtätare) trubbnoshörning påverkade savannekosystemet i Hluhluwe-iMfolozi Park (HiP) i Sydafrika. Med hjälp av GPS-punkter för tjuvjakt av noshörningar tillsammans med satellitbaserade vegetations- och brandkartor, fann jag att noshörningsförlust var förknippad med trädens expansion på den öppna gräsmarken. Detta beror på att minskningen av noshörningsbetestrycket, till följd av tjuvjakt, leder till ackumulering av gräsbiomassa som fungerar som bränsle för bränder. Detta ökar förekomsten av frekventa lågintensiva bränder, vilket minskar gräsets förmåga att konkurrera med trädplantor, vilket i sin tur leder till att träden expanderar till den öppna gräsmarken.

I en ingående fältstudie fann jag att noshörningsbete inte direkt minskade markens kollagring, vilket kontrasterande fynd från tidigare forskning. Effekterna av trädexpansion på markens kollagring var dock beroende av sammanhanget. Viktigast av allt var att trädexpansion var förknippad med minskad koltillförsel till marken i områden som kännetecknas av höga nivåer av noshörningsbete, samtidigt som beständigheten av markens kol ökade i områden som utnyttjades mindre intensivt av noshörning. Slutsatsen av dessa resultat är att noshörningar kan begränsa förlusten av markens koltillförsel indirekt genom att hindra trädexpansionen på den öppna gräsmarken.

Jag förslår att trubbnoshörningar är inflytelserika ekosystemingenjörer vars öde är tätt kopplat till savannens. Även om dagens ekosystem är mycket utarmade på megaväxtätare jämfört med förhistoriska nivåer kan deras ytterligare förlust i de få områden där de finns kvar i naturen starkt påverka hur dessa ekosystem fungerar. Ännu viktigare är att återinförande av megaherbivorer kan förbättra ekosystemens funktion i områden där de historiskt har gått förlorade, med potentiella indirekta konsekvenser för klimatdrivande faktorer såsom på markens kollagring.

Acknowledgements

This thesis and the four years of work that went into it relied on the support of many dedicated people. First, I am very grateful to my main supervisor Joris Cromsigt for his excellent guidance and supervision throughout my thesis work, together with his encouragement through the good times and the bad. I hugely appreciate his unfaltering presence, insight and regular feedback in all the stages of my thesis work. I am equally grateful to all my other supervisors Mariska Te Beest, Elizabeth le Roux and Graham Kerley, who have given me their outstanding support and lent me their expertise during various parts of this thesis project. I cannot begin to express how lucky I feel to have been supervised by this incredible team of dedicated, enormously skilled and compassionate researchers and teachers. I thank you all for welcoming me into the fascinating world of megaherbivores and their importance in our rapidly changing world.

I feel privileged to have been part of SLU's Department for Wildlife, Fish and Environmental Studies, a dedicated bunch of people who do fascinating work across ecosystems in Sweden and abroad. I want to give special thanks to Göran Ericsson, Anders Alanära, Anne-Maarit Hekkala, and the departments past and present PhD communities. I am especially grateful to Emelie Fredriksson and Nannet Fabri, whose mental support in this process was crucial.

Although the Covid-19 pandemic had major influence on the course of my research, I was in many ways lucky that I managed to finish my fieldwork just one week before most countries across the world closed their borders and travelling became difficult if not impossible. Without the help of the remarkable team in the field, finishing my field work in time would not have been possible. Therefore, I am immensely grateful to our field technician Phumlani Zwane for lending his vast experience of the bush and giving his full commitment to helping me sample soils that sometimes felt tougher than concrete, while doing so in the scorching temperatures of Zululand's summer. Other people that I owe my gratitude to are Dlamini Falake and Eric Khumalo, whose excellent knowledge of the bush kept me and the other researchers safe. I want to specifically thank Dave Druce for his help and support in the field, and for all the staff at Dung Beetle Camp for the welcoming and scientifically stimulating atmosphere. I also thank all the friends and students who helped me during this physically and mentally demanding fieldwork including Emilia Malmström, Katharina Jüdt, Daniel Gambra, Maja Widell, Matti Meriläinen, Lawrence Steyn, Nathan Hayes, Kas Jansen, Tim Herkenrath, Phillip Otto and Alice Michel. It goes without saying that their help was imperative to the success of my field campaign.

Without much prior lab experience, I was lucky to spend altogether more than a year in two different labs, first at Cedara Soil Fertility & Analytical Services Laboratory in South Africa and then at the Geolab at Utrecth University in the Netherlands. My labwork year was an intense period of learning, which was facilitated by the help of the teams at Cedara including Nicola Findlay (who I have enormous gratitude towards for the help that I received from her), Alan Manson, Guy Thibaud, Rani Noel and Lucky Sithole, and at the Utrecht University Geolab including Katja Heister, Bernadette Marchand, Thom Claessen, Coen Mulder, Jan van Tongeren and Desmond Eefting. I am especially grateful to Victor Trouw, without whom my ambitious labwork plans would not have materialized the way they did. His exceptional commitment to helping me with the labwork was crucial. I also want to thank my colleagues Melanie Münch, Minkai Ma, Bayan Khojah, Olga Żygadłowska and Lawrence for welcoming me into the lab and encouraging me throughout.

This PhD project has been a large collaboration between researchers from South Africa and various countries in Europe, and therefore it provided me with a great opportunity to meet inspiring people across disciplines. I want to give a special thanks to all my co-authors that I have not mentioned yet, including Walter Schenkeveld, Jeppe Kristensen, Robert Buitenwerf, Rana Vinita and Esther de Groot. In addition, I want to thank Martin Wassen and the whole team at Copernicus Institute for Sustainable Development at Utrecht University, for welcoming me into such an inspiring atmosphere. Furthermore, Petrus Louhio deserves my full gratitude and a special acknowledgement for the beautiful cover art that he drew for this thesis.

The biggest toll for writing this PhD has been paid by the people closest to me. Therefore, I want to express my deepest gratitude to my partner Elena van Doorn, who not only helped me core soil samples and carry ~50 kg of soil across South Africa many times over, and endured a particularly resilient giardia infection with me, but also supported me unconditionally throughout the entire four years. I am grateful to you beyond words for your part in this, without which I am sure I would not be on top of this particular mountain. Furthermore, my mom, dad and my sister deserve a massive acknowledgement for their unfaltering and unquestioning support through these four years. I also want to thank Petra Rodewald for inspiring and encouraging me to follow my dreams and passions, and ultimately endeavour onto this life-changing PhD journey.

Finally, I want to acknowledge my humble little home town Kajaani and the country it resides in, Finland. Without the support from Finland, my academic journey from the beginning until here would have been much more difficult, if not unattainable.

This PhD research was funded by the Swedish Research Council for Sustainable Development, Formas, under the project acronym Megaclim (diary no. 2017-01000).

Appendix

Table S1 – Model output for Paper II

Table S2 – Model output for Paper III

Table S3 – Model output for Paper III

Table S4 – Model output for Paper IV

Table S5 – Model output for Paper IV

oignificant F values are in bola (<0.1)							
Response	Model type	Fixed effect	Estimate	Std.Estimate	S.E	t/z-value	p-value
Mean rhino count	glm("quasipoisson")	Rhino_loss	0.062	0.012	0.015	4.236	<0.001
		Rainfall	-0.001	-0.005	0.001	-1.460	0.145
Rate of change in rhino count	lm()	Rhino_loss	-0.001	-0.084	0.001	-2.061	0.040
Mean grazing lawn extent	glm("quasipoisson")	Rhino_loss	0.055	0.013	0.046	1.208	0.229
		Rainfall	0.000	-0.09	0.000	-7.435	<0.001
Rate of change in grazing lawn extent	lm()	Rainfall	0.007	0.364	0.001	5.146	<0.001
Mean burnt area	glm("quasipoisson")	Rhino_loss	0.081	0.009	0.011	7.271	<0.001
		Rainfall	0.007	0.033	0.000	23.686	<0.001
Fire frequency	glm("poisson")	Rhino_loss	0.487	0.052	0.110	4.427	<0.001
		Rainfall	0.007	0.287	0.000	24.599	<0.001
Mean woody cover	lm()	Rhino_loss	-1.734	-0.047	1.124	-1.543	0.123
		Rainfall	0.042	0.444	0.003	14.644	<0.001
Rate of change in woody cover	lm()	Rhino_loss	1.246	0.131	0.313	3.980	<0.001
		Rainfall	-0.005	-0.197	0.001	-5.999	<0.001
Rainfall	lm()	Rhino_loss	0.032	0.001	1.410	0.023	0.982

Table S1. Output for the best candidate models after step-wise elimination procedures from linear and generalized linear models testing the effects of rhino loss and rainfall on the different responses. Significant P values are in bold (<0.1)

Question	Response	Predictors	Depth	Model type	Fixed effect	Estimate	S.E	t-value	p-value
	SOC	Grazing contrast*Habitat	0- 30 cm	lme()	Most grazed plot*Open lawn	15.283	17.670	0.865	0.403
					Most grazed plot*Woodland lawn	-21.659	26.209	-0.826	0.424
					Most grazed plot*Hill slope	-29.739	26.209	-1.135	0.277
	SOC	Grazing contrast*Habitat	0-5 cm	lme()	Most grazed plot*Open lawn	2.679	2.268	1.181	0.268
					Most grazed plot*Woodland lawn	-5.138	3.246	-1.583	0.148
110					Most grazed plot*Hill slope	2.471	3.960	0.624	0.548
1.17	SOC	Grazing contrast*Habitat	5-15 cm	lme()	Most grazed plot*Open lawn	2.003	4.956	0.404	0.696
					Most grazed plot*Woodland lawn	-1.874	6.751	-0.278	0.788
					Most grazed plot*Hill slope	-5.176	7.639	-0.678	0.515
	SOC	Grazing contrast*Habitat	15-30 cm	lme()	Most grazed plot*Open lawn	7.553	19.568	0.386	0.708
					Most grazed plot*Woodland lawn	-11.598	28.259	-0.410	0.690
					Most grazed plot*Hill slope	-12.439	32.797	-0.379	0.712
	SOC	Woody contrast*Habitat	0-30 cm	lme()	Woody encroached plot*Open lawn	-12.890	14.519	-0.888	0.398
					Woody encroached plot*Hill slope	-0.979	21.535	-0.045	0.965
	SOC	Woody contrast*Habitat	0-5 cm	lme()	Woody encroached plot*Open lawn	-2.122	1.393	-1.523	0.179
C 10					Woody encroached plot*Hill slope	0.160	2.270	0.071	0.946
7.12	SOC	Woody contrast*Habitat	5-15 cm	lme()	Woody encroached plot*Open lawn	-6.008	5.774	-1.040	0.346
					Woody encroached plot*Hill slope	-0.849	11.953	-0.071	0.946
	SOC	Woody contrast*Habitat	15-30 cm	lme()	Woody encroached plot*Open lawn	-16.883	15.153	-1.114	0.346
					Woody encroached plot*Hill slope	23.782	23.879	0.996	0.393
	SOC	Grazing intensity*Habitat	0- 30 cm	lme()	Grazing intensity*Open lawn	10.314	6.022	1.713	0.102
					Grazing intensity*Woodland lawn	9.300	13.318	0.698	0.493
	SOC	Grazing intensity*Habitat	0-5 cm	lme()	Grazing intensity*Open lawn	-0.048	0.488	-0.097	0.924
					Grazing intensity*Woodland lawn	-0.658	1.865	-0.353	0.728
Q1.3	SOC	Grazing intensity*Habitat	5-15 cm	lme()	Grazing intensity*Open lawn	-0.187	1.665	-0.113	0.912
					Grazing intensity*Woodland lawn	5.609	3.852	1.456	0.163
	SOC	Grazing intensity*Habitat	15-30 cm	lme()	Grazing intensity*Open lawn	9.739	5.744	1.696	0.107
					Grazing intensity*Woodland lawn	-1 001	17877	-0.078	0 939

Γable S3. <i>Ot</i> ²-values (<6	utput from the stepwise 0.1) are marked in bola	; elimination on . L	the effect of the environmental v	variables on graz	ing contrasts ($Q2$.	1), woody effects (Q2.2) an	d grazing inte	msity (Q2.3)	on soil carbon s	tocks. Significanı
Question	Contrast	Response	Predictors full model	Depth	Model type	Remaining fixed effects	Estimate	S.E	t-value	p-value
	Grazing contrast	ASOC	Rainfall*Clay	0-30 cm	lm()	Clay	-0.284	0.752	-0.378	0.712
	Grazing contrast	ASOC	Fire*Clay	0-30 cm	lm()	Clay	-0.284	0.752	-0.378	0.712
	Grazing contrast	ASOC	Rainfall*Clay	0-5 cm	lm()	Clay	0.052	0.098	0.529	0.607
	Grazing contrast	ASOC	Fire*Clay	0-5 cm	lm()	Clay	0.052	0.098	0.529	0.607
	Grazing contrast	ASOC	Rainfall*Clay	5-15 cm	lm()	Clay	-0.483	0.331	-1.459	0.168
			5.		< -	į		1 200		0000

Question	Contrast	Response	Predictors full model	Depth	Model type	Remaining fixed effects	Estimate	S.E	t-value	p-value
	Grazing contrast	ASOC	Rainfall*Clay	0-30 cm	lm()	Clay	-0.284	0.752	-0.378	0.712
	Grazing contrast	ΔSOC	Fire*Clay	0-30 cm	lm()	Clay	-0.284	0.752	-0.378	0.712
	Grazing contrast	ASOC	Rainfall*Clay	0-5 cm	lm()	Clay	0.052	0.098	0.529	0.607
	Grazing contrast	ASOC	Fire*Clay	0-5 cm	lm()	Clay	0.052	0.098	0.529	0.607
	Grazing contrast	ΔSOC	Rainfall*Clay	5-15 cm	lm()	Clay	-0.483	0.331	-1.459	0.168
1.00	Grazing contrast	ASOC	Fire*Clay	5-15 cm	lm()	Fire	2.044	1.680	1.217	0.252
1.22						Clay	0.268	0.247	1.086	0.303
						Fire*Clay	-0.066	0.059	-1.123	0.287
	Grazing contrast	ASOC	Rainfall*Clay	15-30 cm	lm()	Clay	0.083	0.674	0.123	0.904
	Grazing contrast	ASOC	Fire*Clay	15-30 cm	lm()	Fire	2.044	1.680	1.217	0.252
						Clay	0.268	0.247	1.086	0.303
						Fire*Clay	-0.066	0.059	-1.123	0.287
	Woody contrast	ASOC	Rainfall*Clay	0-30 cm	lm()	Clay	-1.096	0.812	-1.349	0.214
	Woody contrast	ASOC	Fire*Clay	0-30 cm	lm()	Clay	-1.096	0.812	-1.349	0.214
	Woody contrast	ΔSOC	Rainfall*Clay	0-5 cm	lm()	Clay	-0.153	0.059	-2.603	0.032
00 2	Woody contrast	ΔSOC	Fire*Clay	0-5 cm	lm()	Clay	-0.153	0.059	-2.603	0.032
1.17	Woody contrast	ΔSOC	Rainfall*Clay	5-15 cm	lm()	Clay	-0.415	0.346	-1.199	0.270
	Woody contrast	ΔSOC	Fire*Clay	5-15 cm	lm()	Clay	-0.415	0.346	-1.199	0.270
	Woody contrast	ΔSOC	Rainfall*Clay	15-30 cm	lm()	Clay	-0.483	0.748	-0.646	0.536
	Woody contrast	ASOC	Fire*Clay	15-30 cm	lm()	Clay	-0.483	0.748	-0.646	0.536
	Grazing intensity	SOC	PC1*Rainfal1+PC1*Clay	0-30 cm	lme()	PC1	5.654	5.582	1.013	0.323
	Grazing intensity	SOC	PC1*Fire+PC1*Clay	0-30 cm	lme()	PC1	5.654	5.582	1.013	0.323
	Grazing intensity	SOC	PC1*Rainfall+PC1*Clay	0-5 cm	lme()				ı	
00 3	Grazing intensity	SOC	PC1*Fire+PC1*Clay	0-5 cm	lme()		ı	ı	ı	
	Grazing intensity	SOC	PC1*Rainfall+PC1*Clay	5-15 cm	lme()		ı	ı	ı	
	Grazing intensity	SOC	PC1*Fire+PC1*Clay	5-15 cm	lme()	PC1*Fire	1.102	1.394	0.791	0.438
	Grazing intensity	SOC	PC1*Rainfall+PC1*Clay	15-30 cm	lme()	PC1	5.940	5.360	1.108	0.281
	Grazing intensity	SOC	PC1*Fire+PC1*Clav	15-30 cm	lme()	PC1*Fire	5.274	5.389	0.979	0.340

Table S4. Ouput from the statistical analysis on the effect of habitat on grazing, grazing intensity and woody effects on the functional soil organic carbon pools stocks (POC, oPOC, MAOC, PyroC). Significant P values are in bold (<0.1)

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Response	Predictors	Model type	Fixed effect	Estimate	S.E	t-value	p-value
POC	Grazing contrast*Habitat	lme()	Grazing contrast*Open lawn	-0.502	0.569	-0.883	0.394
			Grazing contrast*Woodland lawn	-1.173	1.835	-0.639	0.534
			Grazing contrast*Hill slope	1.235	0.719	1.719	0.109
oPOC	Grazing contrast*Habitat	lme()	Grazing contrast*Open lawn	-0.637	0.481	-1.324	0.208
			Grazing contrast*Woodland lawn	1.095	0.714	1.535	0.149
			Grazing contrast*Hill slope	1.114	0.714	1.561	0.143
MAOC	Grazing contrast*Habitat	lme()	Grazing contrast*Open lawn	0.314	6.781	0.046	0.964
			Grazing contrast*Woodland lawn	-10.346	7.806	-1.325	0.208
			Grazing contrast*Hill slope	0.660	7.002	0.094	0.926
PyroC	Grazing contrast*Habitat	lme()	Grazing contrast*Open lawn	-0.616	0.344	-1.791	0.104
			Grazing contrast*Woodland lawn	0.152	0.515	0.294	0.775
			Grazing contrast*Hill slope	0.577	0.515	1.120	0.289
POC	Woody contrast*Habitat	lme()	Woody contrast*Open lawn	-1.126	0.507	-2.219	0.054
			Woody contrast*Hill slope	2.213	0.753	2.939	0.017
oPOC	Woody contrast*Habitat	lme()	Woody contrast*Open lawn	-0.760	0.523	-1.453	0.180
			Woody contrast*Hill slope	1.820	0.776	2.346	0.044
MAOC	Woody contrast*Habitat	lme()	Woody contrast*Open lawn	-8.646	8.807	-0.982	0.352
			Woody contrast*Hill slope	-6.293	13.063	-0.482	0.642
PyroC	Woody contrast*Habitat	lme()	Woody contrast*Open lawn	-0.238	0.148	-1.601	0.148
			Woody contrast*Hill slope	1.087	0.523	2.077	0.071
POC	Grazing intensity*Habitat	lme()	Grazing intensity*Open lawn	-0.027	0.293	-0.092	0.928
			Grazing intensity*Woodland lawn	1.946	0.693	2.807	0.110
oPOC	Grazing intensity*Habitat	lme()	Grazing intensity*Open lawn	0.075	0.213	0.353	0.728
			Grazing intensity*Woodland lawn	-0.136	0.518	-0.263	0.795
MAOC	Grazing intensity*Habitat	lme()	Grazing intensity*Open lawn	1.502	2.040	0.736	0.470
			Grazing intensity*Woodland lawn	4.355	4.953	0.879	0.390
PyroC	Grazing intensity*Habitat	lme()	Grazing intensity*Open lawn	0.181	0.120	1.505	0.150
			Grazing intensity*Woodland lawn	-0.010	0.294	-0.033	0.974

Table S5. Ouput from the stepwise elimination on the effect of the environmental variables on grazing contrasts (Q2.1), woody effects (Q2.2) and grazing intensity (Q2.3) on functional soil organic carbon pools (POC, oPOC, MAOC, PyroC). Significant P-values (<0.1) are marked in bold.

Contrast	Response	Predictors full model	Model type	Remaining fixed effect	Estimate	S.E	t-value	p-value
Grazing contrast	APOC	Rainfall*Clay	lm()	Clay	0.043	0.040	1.087	0.297
		Fire*Clay	lm()	Clay	0.043	0.040	1.087	0.297
	ΔοΡΟϹ	Rainfall*Clay	1m()			ı	,	ı
		Fire*Clay	1m()			ı	,	
	AMAOC	Rainfall*Clay	lm()	Clay	0.1973	0.209	0.944	0.363
		Fire*Clay	lm()	Clay	0.1973	0.209	0.944	0.363
	$\Delta PyroC$	Rainfall*Clay	1m()			ı		
		Fire*Clay	lm()			ı	ı	
Woody contrast	APOC	Rainfall*Clay	lm()	Rainfall	0.012171	0.004437	2.743	0.0227
		Fire*Clay	lm()	Fire	0.3015	0.1136	2.653	0.0263
	ΔoPOC	Rainfall*Clay	lm()			ı	ı	ı
		Fire*Clay	1m()			ı		
	AMAOC	Rainfall*Clay	lm()	Clay	-0.8296	0.4546	-1.825	0.105
		Fire*Clay	1m()	Clay	-0.8296	0.4546	-1.825	0.105
	APyroC	Rainfall*Clay	lm()			ı	ı	ı
		Fire*Clay	1m()			ī	ı	
Grazing intensity	POC	PC1*Rainfall+PC1*Clay	lme()			ī	ı	ı
		PC1*Fire+PC1*Clay	lme()			ī	ı	
	oPOC	PC1*Rainfall+PC1*Clay	lme()			i	ı	I
		PC1*Fire+PC1*Clay	lme()			ı		ı
	MAOC	PC1*Rainfall+PC1*Clay	lme()			ī	ı	I
		PC1*Fire+PC1*Clay	lme()	PC1*Fire	2.84505	1.680851	1.692624	0.106
	PyroC	PC1*Rainfall+PC1*Clay	lme()			ī	ı	I
		PC1*Fire+PC1*Clay	lme()					

carbon in the	functional SOC pools (i.e. P.	<i>OC, ₀POC</i>	and MAOC). Significant P values a	ıre in bold ((<0.1)		
Response	Predictors	Model type	Fixed effect	Estimate	S.E	t-value	p-value
C3 POC	Woody contrast*Habitat	lme()	Woody contrast*Open lawn	0.002	0.099	0.017	0.987
			Woody contrast*Hill slope	0.307	0.122	2.519	0.066
C3 oPOC	Woody contrast*Habitat	lme()	Woody contrast*Open lawn	0.007	0.032	0.215	0.838
			Woody contrast*Hill slope	0.191	0.095	2.015	0.114
C3 MAOC	Woody contrast*Habitat	lme()	Woody contrast*Open lawn	-0.016	0.178	-0.088	0.933

Table S6. Output from the statistical analysis on the effect woody contrast on the additional C3 woody derived organic

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Review and Synthesis

Megaherbivore impacts on ecosystem and Earth system functioning: the current state of the science

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Ecography 44: 1579-1594, 2021 doi: 10.1111/ecog.05703

Subject Editor: Kate Lyons Editor-in-Chief: Miguel Araújo Accepted 2 August 2021





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Megaherbivores (adult body mass > 1000 kg) are suggested to disproportionately shape ecosystem and Earth system functioning. We systematically reviewed the empirical basis for this general thesis and for the more specific hypotheses that 1) megaherbivores have disproportionately larger effects on Earth system functioning than their smaller counterparts, 2) this is true for all extant megaherbivore species and 3) their effects vary along environmental gradients. We furthermore explored possible biases in our understanding of megaherbivore impacts. We found that there are too few studies to quantitatively evaluate the general thesis or any of the hypotheses for all but the African savanna elephant. Following this finding, we performed a qualitative vote counting analysis. Our synthesis of this analysis suggests that megaherbivores can elicit strong impacts on, for example, vegetation structure and biodiversity, and all the elephant species promote seed dispersal. We were, however, unable to evaluate whether these effects are disproportionate to smaller large herbivores. Although environmental conditions can mediate megaherbivore impact, few studies quantified the effect of rainfall or soil fertility on megaherbivore impacts, precluding prediction of megaherbivore effects on the Earth system, particularly under future climates. Moreover, our review highlights major taxonomic, thematic and geographic biases in our understanding of megaherbivore effects. Most of the studies focused on African savanna elephant impacts on vegetation structure and biodiversity, with other megaherbivores and Earth system functions comparatively neglected. Studies were also biased towards semi-arid and relatively fertile systems, with the arid, high-rainfall and/or nutrient-poor parts of the megaherbivores' distribution ranges largely unrepresented. Our findings highlight that the empirical basis of our understanding of the ecological effects of extant megaherbivores is still limited for all species, except the African savanna elephant, and that our current understanding is biased towards certain environmental and geographic areas. We further outline a detailed, urgently needed avenue for future research.

Keywords: Earth system functioning, ecosystem functioning, herbivore impact, megaherbivore

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Introduction

Large-bodied animals and Earth system functioning

The global climate and biodiversity crises highlight the growing urgency to better understand the connections and interactions between the different parts of the Earth system. The Earth system consists of different spheres, such as the atmosphere, geosphere, hydrosphere and biosphere, that are all interlinked by dynamic and complex processes (Kerényi and McIntosh 2020, Steffen et al. 2020). A major disruption in the processes within one sphere can influence processes in other spheres and, therefore, affect the entire Earth system. Here, we define 'Earth system function' as any process that is embedded in at least one of these spheres and that supports the structure and/or stability of the Earth system.

The Earth's biosphere has shaped the atmosphere and hydrosphere for at least 2.5 billion years, that is, since the Great Oxidation Event (Pufahl and Hiatt 2012). Largebodied animals are increasingly recognized as playing important roles in the functioning of the biosphere and thus the Earth system (Cromsigt et al. 2018, Schmitz et al. 2018). Their prehistoric and historic dramatic loss (i.e. defaunation) has, therefore, been proposed as an underestimated driver of global change (Estes et al. 2011). A growing body of literature explores the effects of Pleistocene defaunation on various Earth system functions (Brault et al. 2013), including the distribution of biomes (Gill 2014, Doughty et al. 2016c, Dantas and Pausas 2020), biodiversity (Gill 2014), biogeochemistry (Doughty et al. 2016c), seed dispersal (Pires et al. 2018), fire regimes (Gill et al. 2009, Rule et al. 2012), surface energy fluxes (Doughty et al. 2010, Brault et al. 2013) and pathogen dispersal (Doughty et al. 2020). Simultaneously, there is an increasing interest in the ongoing effects of extant large-bodied animals on Earth system functioning (Smith et al. 2016, Cromsigt et al. 2018, Schmitz et al. 2018). For example, mammals, as prime dispersers of seeds of certain hardwood tree species, importantly contribute to the carbon sequestration potential of tropical forests (Bello et al. 2015). Thus, a disruption in seed dispersal (a biosphere process) by defaunation can lead to changes in carbon sequestration (a process that intersects the atmosphere, biosphere and geosphere). Other recent examples of how extant large-bodied animals shape Earth system functioning include reindeer Rangifer tarandus grazing and trampling reducing shrub cover in the arctic tundra, thereby increasing surface albedo (Te Beest et al. 2016) and beavers (Castor spp.) changing watershed chemistry and hydrology (Rosell et al. 2005, Nummi et al. 2018).

Environmental conditions shape the magnitude and direction of herbivore effects

Environmental conditions are known to mediate the magnitude and direction of the ecological impacts of large herbivores on, for example, vegetation structure, soil processes and fire regimes. For instance, Augustine and McNaughton (2006) found that the impacts of wild grazers on primary productivity varied along rainfall and soil fertility gradients. They reported that increasing rainfall improved the aboveground productivity on relatively fertile soils while suppressing it on nutrient-poor soils, leading to different grazing impacts. Similarly, Waldram et al. (2008) found that white rhino *Ceratotherium simum* impact on grassland structure and fire regimes was more pronounced in the higher rainfall areas of their study area compared to the lower rainfall areas.

Megaherbivore effects on Earth system functioning

Megaherbivores, as defined by Owen-Smith (1988) are planteating mammals that weigh > 1000 kg as adults. The term 'megaherbivore' differs from the increasingly popular term 'megafauna', which often refers to animals with adult body mass > 100 lbs (-45 kg), but the latter is not based on a functional distinction (Moleón et al. 2020). In contrast, their very large body size distinguishes megaherbivores functionally from smaller species. First, it renders them near-immune to non-human predation and top-down population control by large carnivores. Consequently, megaherbivores are bottomup limited by food resources, exacerbating their impact on the environment (Caughley 1976). Second, owing to their size, megaherbivores require a large intake of forage, but their low mass-specific metabolic rate allows them to tolerate low-quality forage (Müller et al. 2013). As a result, they can consume more fibrous plant material than smaller species, which leads to impacts on a wider range of plant species and plant parts and potentially more homogenous space use. Third, their size enables megaherbivores to cover greater distances than smaller species, allowing them to move nutrients and seeds much further (Owen-Smith 1988, Doughty et al. 2016a). Because of these functional differences, megaherbivores are hypothesized to have disproportionately larger effects on ecosystems than their smaller counterparts (Owen-Smith 1988), thus eliciting stronger effects on ecosystem and Earth system functioning than smaller herbivore species, even when occurring at the same biomass density (Fig. 1).

Aims and scope of the study

Here, we systematically review published, peer-reviewed studies that presented empirical data on contemporary megaherbivore effects on ecosystem and Earth system functioning. While traditional reviews can be useful in summarizing the state of a scientific discourse, systematic reviews may reveal and reduce publication and selection bias by deploying a strict methodology that promotes transparency, objectivity and repeatability (Haddaway et al. 2015). We are unaware of any studies that have systematically reviewed the literature on the ecological and Earth system effects specifically of extant megaherbivore species. Our main aim was to evaluate the empirical basis for ecological impacts of megaherbivore species and for the thesis that megaherbivores shape the functioning of the biosphere (i.e. ecosystems) and the Earth system as a whole. We also test the more specific, generally assumed hypotheses that 1) megaherbivores have disproportionately



Figure 1. (A–C) Illustration of potential megaherbivore impacts on various aspects of Earth system functioning: (A) white rhino impact on vegetation structure, terrestrial biodiversity and fire, (B) hippo impact on vegetation structure, terrestrial biodiversity, biogeochemistry, hydrology and aquatic biodiversity and (C) African savanna elephant impact on seed dispersal, vegetation structure, terrestrial biodiversity and fire.

larger effects on Earth system functioning than their smaller counterparts, that 2) this is true for all megaherbivore species and that 3) their effects vary along environmental gradients. Our second aim was to synthesize the current-state-of-the-art of our understanding of megaherbivore impacts on the Earth system and to explore possible biases in our understanding. We evaluated studies that used megaherbivore density or presence/absence contrasts (hereafter 'effect contrasts') and that report effect sizes (therefore being eligible to be used in a quantitative meta-analysis) (here classified as type I studies). We also included more descriptive studies that did not meet the criteria for a formal quantitative meta-analysis, such as the reporting of effect sizes and confidence intervals (here classified as type II studies) (Supporting information). Following Owen-Smith's (1988) definition, extant terrestrial megaherbivore species include African savanna elephant Loxodonta africana, African forest elephant Loxodonta cyclotis, Asian elephant Elephas maximus, white rhinoceros, black rhinoceros Diceros bicornis, greater one-horned rhinoceros Rhinoceros unicornis, Javan rhinoceros Rhinoceros sondaicus, common hippopotamus Hippopotamus amphibius as well as giraffe Giraffa camelopardalis and Sumatran rhinoceros Dicerorhinus sumatrensis. The latter two species marginally fit the definition as only some adult individuals exceed the 1000 kg threshold (Table 1).

Material and methods

Study design

We systematically reviewed peer-reviewed empirical studies on megaherbivore effects on ecosystem and Earth system functioning published between 1945 and 1 July 2020 following the widely used PRISMA guidelines. These guidelines describe the routines and criteria for systematic reviews and meta-analyses (Moher et al. 2009). We included all extant megaherbivores in this review (Table 1). We conducted the literature search 1 May 2019 on the Web of Science core collections database and updated the search 1 July 2020. The search string consisted of the common and scientific names of all the megaherbivore species and terms for effect (Supporting information).

Screening process

First, the search was narrowed by excluding studies not published in peer-reviewed journals and those not written in English. All the remaining studies were filtered through a stepwise screening based on pre-defined relevance and inclusion criteria (steps 1-3) and quality criteria (step 4) (Supporting information). Figure 2 gives more details on the criteria. In step 1, the titles of the publications were evaluated against criteria set 1, and all the titles deemed irrelevant were excluded from further analysis. Step 2 exclusions were based on abstracts evaluated against criteria set 2, and step 3 exclusions were based on the full-text evaluated against criteria set 3. In step 4, we categorized the remaining publications into type I and type II based on the reported methods and results, which we evaluated against criteria set 4. Type I publications consisted of studies that fit the criteria for formal quantitative meta-analyses (i.e. those that deployed effect contrasts, tested significance and reported measures of uncertainty) while type II publications did not have an effect contrast and/or did not test significance or report measures of uncertainty (i.e. type II publications were ineligible for quantitative meta-analyses). For steps 1-3, all studies were evaluated by two assessors independently. The lead author, O H, screened through all the search outputs while co-authors E D and R V each screened half of the search outputs for steps 1-3. The first half of the search output consisted of publications on the three elephant species, while the second half included the rest of the studied species. In case of a disagreement, all three afore-mentioned authors discussed the publication in question until an agreement about its inclusion or exclusion was reached. Step 4 was carried out solely by O H.

Data collection

For each publication that passed the full-text screening (both type I and type II studies), we recorded the authors, journal, year of publishing, study location(s), mean annual temperature, mean annual precipitation, a measure of soil fertility (cation exchange capacity), each megaherbivore species studied and each Earth system function studied. For type I studies, we further recorded the effect contrast type for each response variable at the detail reported in the study (i.e.

Table 1. Summary of megaherbivore characteristics. Adult body weight, feeding strategy and gut morphology are extracted from Owen-Smith (1988), while conservation status and population number are extracted from the IUCN red list ('The IUCN Red List of Threatened Species').

Megaherbivore	Adult body weight (kg)	Feeding strategy	Gut morphology	Conservation status	Population number
African savanna and forest elephants	2500-6000	mixed feeder	hind-gut fermenting	vulnerable	415 000
Asian elephant	2720-5400	mixed feeder	hind-gut fermenting	endangered	41 410–52 345
White rhino	1600-2300	grazer	hind-gut fermenting	near threatened	17 212-18 915
Black rhino	700-1300	browser	hind-gut fermenting	critically endangered	5630
Greater one-horned rhino	1600-2100	grazer	hind-gut fermenting	vulnerable	3588
Sumatran rhino	800	browser	hind-gut fermenting	critically endangered	80
Javan rhino	1300	browser	hind-gut fermenting	critically endangered	68
Giraffe	800-1200	browser	ruminant	vulnerable	97 562
Hippopotamus	1365-2600	grazer	hind-gut fermenting	vulnerable	115 000-130 000



Figure 2. Prisma flow diagram of the systematic review process including identification, screening eligibility and inclusion of publications. Reasons for exclusion in each step and the characteristics of type I and type II papers are described in the yellow column on the right.

level 1 in Fig. 3, e.g. mortality of *Vachellia tortillis* < 2 m or concentration of total phosphorus in soil, etc.), whether the effect was significant or not based on p-values (significance cut-off < 0.05) and/or confidence intervals and the direction of the effect (whether increasing or decreasing) (Fig. 3, Supporting information). If the effect on the response variable was not significant, it was reported as such (i.e. 'no significant effect'). For type II studies, we further recorded each measured response variable, but in slightly coarser categories than for type I studies (i.e. Level 2 in Fig. 3) (e.g. woody cover or nutrient concentration etc.), and the direction of effect if applicable. If there was no observed effect, it was reported as such (i.e. 'no effect') (Fig. 3).

Analysis of potential biases

We evaluated both type I and type II publications for taxonomic, thematic, geographic and environmental (temperature, precipitation and soil fertility) biases. For evaluating taxonomic and thematic biases, we compared the number of studies published on the different megaherbivore species and the different Earth system functions. For this purpose, we grouped all selected articles into the following seven general Earth system function categories: vegetation structure, biodiversity, biogeochemistry, seed dispersal, fire, hydrology as well as soil and geomorphology. For evaluating geographic bias, we first extracted the current and prehistoric distributions for



Figure 3. A schematic overview of the levels of data collection and analysis. For type I publications, we extracted each unique response variable at the finest level (level 1) and further categorized them into a general response variable category (level 2). For type II publications, we extracted response variables directly at level 2. We finally assigned each response from type I and type II publications into an Earth system function category at level 3. We performed our qualitative synthesis at level 2, and our analysis of biases at level 3.

each megaherbivore species from the Phylacine database (prehistoric distributions called 'present natural' in the database of origin (Faurby et al. 2020)). For current distributions, we only used records that were corroborated by the distribution estimates reported in Wilson and Reeder (2005) (Supporting information). We then mapped the publication study sites and evaluated their geographic locations relative to the current and prehistoric distributions of each megaherbivore species. To analyze environmental bias, we first extracted the climate (mean annual precipitation, mean annual temperature) and elevation data from WorldClim database at 10 min resolution (Fick and Hijmans 2017). We further derived the soil fertility data from ISRIC as mean soil cation exchange capacity at pH 7, 0-5 cm depth at 250 m spatial resolution (Hengl et al. 2015). We derived the climatic and soil fertility envelopes for the current distribution of each megaherbivore species by extracting values for mean annual precipitation, mean annual temperature and cation exchange capacity from 1000 random points throughout their current distribution ranges. We then plotted the study sites of the different species onto their respective climatic and soil fertility envelopes to identify areas of the envelopes that had not been studied. Early in our analysis, we noticed unusually high rainfall values for some of the random points on the Asian elephant, African savanna elephant and white and black rhinos current distribution ranges. Due to the low spatial resolution (96.5 km by 96.5 km at 30° north and 30° south) of the Phylacine data, high-altitude areas, potentially outside of the species' current distribution ranges, overestimated the averaged values per pixel included in our analysis. While elephants have been recorded at high altitude (Yalden et al. 1986), they are unlikely to spend a significant amount of time at high altitude (Choudhury 1999), and thus we felt it justified to mask areas above 2000 m from the current distribution ranges in order to minimize this distortion due to high-elevation outlier rainfall and temperature values. This excluded part of the Himalayas as well as Ethiopian and Lesotho highlands. We finally analyzed the temporal trends in the publications per Earth system function studied and citation bias (citation counts extracted from Google Scholar on 20 July 2020) by evaluating the relative contribution of the different study sites to our understanding of the Earth system effects of each megaherbivore species separately.

Synthesis

With the initial intention of doing a quantitative meta-analysis of type I publications, we identified all relevant response variables within each type I publication at the finest level (level 1 in Fig. 3) and recorded the direction of effect per megaherbivore species, that is, 'increasing', 'decreasing' or 'no significant' effect. For a more inclusive qualitative analysis within which we could include both type I and type II publications, we further classified each response variable in each type I and type II study into a more general response variable category (level 2 in Fig. 3) and recorded the direction of effect at that level per megaherbivore species, that is, 'increasing', 'decreasing' or 'no' effect. We then qualitatively synthesized the reported megaherbivore effects on the level 2 response categories, across all type I and type II studies using the so-called 'vote counting' method. Using this method, we counted the number of statistically significant 'increasing' and 'decreasing' as well as 'no (significant)' effects per response category in order to evaluate the overall effect on that particular category (Vogel et al. 2021, Stewart 2010) (Fig. 3).

Results

Literature identification and screening

By specifying the publication type and language in Web of Science core collections, we first omitted 3202 symposium presentations, abstracts, newsletters, books and book chapters, postgraduate theses, reports and other grey literature as well as 622 peer-reviewed publications that were not written in English, before running the search. Our specified search query led to 11 977 peer-reviewed publications for the period from 1945 to 1 July 2020. We excluded 11 016 publications in the relevance screening of titles (step 1), 415 in the relevance screening of abstracts (step 2) and 306 in the relevance screening of full-text (step 3). After full text screening, 240 publications remained, which we subjected to a critical appraisal (step 4) during which we categorized each remaining study as either type I (144) or type II (96). In other words, only 3% of the 11 977 studies from the initial search were deemed relevant (i.e. studied megaherbivore ecological impacts). Moreover, just 46% of this 3% deployed appropriate methodology and/or reporting (i.e. use of effect contrasts, reporting of effect sizes and measures of uncertainty) to be eligible for a quantitative meta-analysis.

In the full-text screening (step 3), the most common reasons for exclusion were that the publication was not specifically focused on megaherbivore ecological impacts (82% of 306 excluded studies), megaherbivore impacts could not be distinguished from the impact of other herbivores and/ or environmental variables (11% of 306 excluded studies), or that the publication was a review (5% of 306 excluded studies). In the critical appraisal (step 4), the most common reasons for classifying publications as type II (instead of type I) were the absence of effect contrast (61% of 96 type II studies), the absence of required test statistics (23% of 96 type II studies), insufficient quantitative data (11% of 96 type II studies) or that the publication was based on modelling without yielding novel data (5% of 96 type II studies) (Supporting information for a full list of excluded papers in step 3 with reasons for exclusion).

Characteristics of the peer-reviewed publications

The number of both type I and II studies increased strongly over the years and appeared in a wide diversity of journals (Supporting information). The vast majority of studies (70%) was on African savanna elephants, followed by giraffe and hippo. The other seven species jointly made up about 10% of studies (Fig. 4). Studies on Asian megaherbivores were particularly rare, with only 16 on Asian elephant, one on the greater one-horned rhino and none on the other two rhino species. Only 10% (14) of the included type I publications and 7% (7) of type II publications looked at the effects of two or more megaherbivores in the same system, of which just one quantified the relative effect sizes for each species separately. From these initial results, we concluded that we could not perform rigorous formal quantitative meta-analyses for any of the species and Earth system functions, except for African savanna elephant effects on vegetation structure and biodiversity. The sample sizes for the other species were too small (<5 studies) to meaningfully perform a similar quantitative analysis for all species. Quantitative meta-analyses for African savanna elephant effects on vegetation structure and biodiversity have already been completed (Guldemond and Van Aarde 2008, Guldemond et al. 2017). Hence, instead of duplicating these studies on the savanna elephant, we focused our efforts on qualitative analyses where we were able to include more studies and all extant megaherbivore species. In terms of the Earth system functions, the vast majority of studies looked at vegetation structure (~65%) and biodiversity (~20%), with relatively few studies on biogeochemistry and seed dispersal and only a handful on the other Earth system functions (Fig. 4).

Geographic distribution of studies and potential environmental biases

The included type I and type II studies originated from 26 different countries (Supporting information) and 105 different study areas (Supporting information). The number of type I and type II publications per country ranged between 1 and 88, whereas the number of publications per study area ranged between 1 and 31 (Supporting information). Almost half of type I studies (40%) came from only five areas in three countries: Kruger National Park in South Africa (20), Mpala Research Centre in Kenya (18), Addo Elephant National Park in South Africa (9), Hluhluwe-iMfolozi Park in South Africa (8) and Hwange National Park in Zimbabwe (5), while the same proportion of type II studies (41%) came from ten areas in seven countries (Supporting information). Major parts of the extant distribution ranges of all megaherbivore species lacked any studies on their ecological impacts (Supporting information).

Collectively, the study sites represented only a fraction of the climate and soil fertility envelopes of the current distribution ranges of these megaherbivore species (Supporting information). Studies on African savanna elephant were strongly biased towards the arid and semi-arid parts of their distribution range, with 83% of the studies in areas that are below their distribution range's median rainfall (Supporting information). In contrast, Asian elephant studies were biased



Figure 4. Chord diagram showing the proportion of studies published on the effects of the different megaherbivore species on each Earth system function category. The 'other' category includes hydrology as well as soil and geomorphology.

towards the mesic and very wet parts of their range (all studies coming from areas with mean annual precipitation > 1500 mm (Supporting information). White rhino effects were studied in only three locations, under semi-arid and mesic conditions, limited to the parts of their range with relatively high soil fertility (Supporting information). Studies on black rhino and giraffe were heavily biased towards relatively cool (17-18°C and 17-22°C, respectively) (Supporting information) and relatively fertile areas (Supporting information). All black rhino studies were performed under relatively similar rainfall conditions (mean annual precipitation of 506-760 mm), despite black rhinos occurring over a wide range of rainfall (Supporting information). Studies on hippo were concentrated in the drier and relatively more fertile parts of their range (Supporting information). One outlier study site was present at the high rainfall end of the hippo's range (at 2607 mm year⁻¹) but comes from outside of their natural distribution range (from South America where they were introduced) (Shurin et al. 2020).

Synthesis

We extracted 1259 and 99 responses at level 2 of data collection from type I and type II publications, respectively (Supporting information for a detailed overview per study), and further classified them into 26 vegetation structure categories, 47 biodiversity, 10 biogeochemistry, 4 seed dispersal and 4 other categories (Fig. 5).

1. Vegetation structure

Most studies dealt with the effects of African savanna elephants on woody species, in general concluding that they open up the landscape by either increasing woody damage or mortality or decreasing woody cover, density. Effects of the African forest and the Asian elephant species on woody communities were more mixed (votes more spread among 'increasing', 'decreasing' and/or 'no' effects), with much fewer response categories studied. Similar to the African savanna elephant, several studies on the browsers, black rhino and giraffe, found that they generally have negative effects on woody vegetation, with increased woody damage or mortality or reduced reproduction, height and abundance. Giraffes were often reported to have negligible effects on many woody response categories, therefore suggesting a lack of consensus on the direction of effect. The majority of studies on the grazers, hippo and white rhino, found them to increase grassland heterogeneity although the direction of their effects on herbaceous structure was less clear.

2. Biodiversity

Again, most studies on biodiversity impacts dealt with African savanna elephant impacts, suggesting that they have variable effects on most plant groups except succulents, for which there is a voting bias towards them decreasing species richness. Their impact on the diversity of other organisms varied widely, with most votes going to 'increasing' or 'no' effects. Notable exceptions are the vertebrate foraging behavior as well as presence and richness indices, where the vote balance leaned towards 'decreasing' and 'no' effects. Studies on the biodiversity impacts of hippo also varied widely with a relatively equal spread of votes among 'increasing', 'decreasing' and 'no' effects or too low number of votes to draw meaningful conclusions about the direction of their effects. The number of votes for the biodiversity-related variables studied in the context of the other megaherbivore species were too few to make any general conclusions.

3. Biogeochemsitry

Most publications on biogeochemistry studied hippo effects on nutrient content and concentration of water bodies, predominantly suggesting nutrient addition, that is, responses collectively leaning towards 'no' and 'increasing' effects (yet with substantial variation among studies and elements). Collectively, only three studies dealt with biogeochemical effects of white rhino and African savanna elephant, mostly showing them to promote soil carbon and lateral nutrient transport (most responses exhibiting 'no' and/or 'positive' effects). No studies were done on the effects on biogeochemistry by the other species.

4. Seed dispersal

Most studies on megaherbivore effects of seed dispersal have been done on elephants, particularly on African forest elephant and Asian elephant. Overall, these studies show elephants to increase germination success and decrease germination time (although a large proportion of studies did not find (significant) effects). For the three elephant species combined, there is a vote bias towards positive effects on seed dispersal.

5. Other

Only a handful of studies dealt with other response categories. African savanna elephants, white rhino and hippo reduced fire-related variables (five votes in total), and hippo reduced soil pore space while increasing geomorphology and hydrology-related variables (only one vote each).

Discussion

We concluded that the number of peer-reviewed, empirical, studies is still too small (<5 studies) to run formal quantitative meta-analyses for any of the megaherbivore species and Earth system functions, except for African savanna elephant impacts on vegetation structure and biodiversity. However, our qualitative synthesis suggests that megaherbivores can have a wide variety of impacts on the different Earth system functions. Yet, the empirical support for this varies substantially across ecosystem processes, species and systems, suggesting considerable contextual complexity that remains unexplored. Only a few studies directly quantified the effect of rainfall or soil fertility on megaherbivore impacts. Given the paucity of studies, we could not quantify the extent to which surviving megaherbivore species shape contemporary

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Figure 5. (A–C) Summary of the results of the vote counting per megaherbivore species. Green columns indicate increasing effect, yellow columns no (significant) effect and red columns decreasing effect. The intensity of the colour signifies the number of responses in that category, but does not necessarily reflect the number of studies in that category.

ecosystems and Earth system functioning or how this varies across environmental gradients. There was also insufficient evidence to evaluate one of the core hypotheses that megaherbivore effects are disproportionate to those of smaller herbivores. Moreover, almost half of all type I studies suitable for future meta-analyses, originated from only three study areas in South Africa, one in Kenya and one in Zimbabwe potentially leading to major environmental biases in our current understanding.

Low inclusion rates

Most published research on non-elephant megaherbivore species focused on conservation-oriented topics, such as

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Figure 5. (Continued).

reproduction, habitat suitability and movement ecology rather than their ecological impacts. This may be a consequence of the conservation status and generally low population sizes of most of these species (Table 1), which promotes conservation management such as re-introduction and range expansion. As a result, research on these species focuses on aspects of their ecology that support these conservation actions. A second reason for the low inclusion rate of type I studies was methodological and reporting issues such as the lack of effect contrasts and/or missing effect sizes and measures of uncertainty. Therefore, we encourage researchers working on megaherbivore effects to invest in studies that use a comparative approach (effect contrasts) and to report the essential statistics for inclusion in future quantitative metaanalyses. Relocation and range expansion programs provide fruitful opportunities to study megaherbivore impacts as they have clear 'effect contrasts' i.e. before versus after reintroduction or range expansion (Landman et al. 2014).

Many studies also failed to (or did not aim to) distinguish megaherbivore impacts from the impacts of smaller large herbivores. For example, exclusion experiment studies often separated the impact of small and medium-sized herbivores from that of large herbivores, while making no distinction between large- and megaherbivores (Dharani et al. 2009, Cassidy et al. 2013) (but see Ogada et al. 2008 and Charles et al. 2017). Future exclusion experiments, aimed specifically at discerning the impact of megaherbivores from the impact of other large herbivores, could benefit from examples, such as the Kenya Long-Term Exclosure Experiment (KLEE) at Mpala Research Centre (Young et al. 1997) and the, no longer standing, exclosure design at Hluhluwe-iMfolozi Park (Van der Plas et al. 2016). The studies that do discern impacts of megaherbivores from those of other large herbivores suggest that these two groups can elicit vastly different effects on vegetation structure (Van der Plas et al. 2016) and biodiversity (Ogada et al. 2008). If, in addition, the intention is to assess the disproportionality of megaherbivore impact, measures of biomass density must also be included (Van der Plas et al. 2016). Another approach is to carefully quantify the relative density of the different taxa and use statistical models to quantify their relative effects (Smit and Archibald 2019).

Taxonomic bias

We found strong taxonomic bias towards the African savanna elephant, with a complete absence of qualifying studies on Asian rhino species (apart from one type II study on greater one-horned rhino). This bias can be partly explained by the growing conservation management concerns about the impacts of confined, growing, African savanna elephant populations on vegetation structure and biodiversity, prompting research in these directions (Guldemond et al. 2017). When studies are solely motivated by concerns of extremely high or low megaherbivore population densities, their impacts may not be studied across their entire density range, but only at the extremes. This presents another potential bias. Most of the studies that report decreasing impacts of African savanna elephant on woody cover (Guldemond and Van Aarde 2008), for example, come from confined fenced areas with relatively high elephant population numbers. Although these findings robustly show that high densities of elephants can decrease woody cover, they do not necessarily demonstrate that such impacts are universal across population densities and environmental gradients (Guldemond and Van Aarde 2008, Guldemond et al. 2017 for extensive discussions).

The impact of megaherbivores other than African savanna elephant has generated less management concern, which may translate into less research focus on ecological impacts of these species (although see Heilmann et al. (2006) and Luske et al. (2009) for the discussion on the impact of black rhino on euphorbia trees). The lack of studies on ecological impacts by Asian rhino species may at least partly be explained by their extremely low population sizes and restricted ranges (and possibly by the English language restriction on this study). Management of these species is thus focused on enhancing their conservation status, stimulating research in directions such as population ecology and habitat selection, rather than ecological impacts. Furthermore, ecological impacts of a species occurring at extremely low population densities are difficult to study, and results of such studies would likely suffer from type II error (false negative). In other words,

megaherbivore effects studied at extremely low population densities do not necessarily reflect the effects they would elicit at higher densities. This point is particularly relevant for the Javan and Sumatran rhino. Asian elephant and greater onehorned rhino do occur in several areas in Asia at densities that would allow for studies on how they shape Earth system functions. We strongly encourage such studies and comparative work between Asian and African megaherbivores. Comparisons between African forest versus Asian elephant and white rhino versus the greater one-horned rhino seem to be particularly relevant as they seem functionally similar.

Only 10% of type I studies included in our systematic review dealt with more than one megaherbivore species in the same landscape, and only one of them was able to differentiate the relative impacts of the different species (Smit and Archibald 2019). Many studies for instance recorded herbivore damage on woody plants and associated the damage to a particular megaherbivore based on the physical attributes of the damage. Certain megaherbivore species, such as black rhino and savanna elephant, leave a unique fingerprint on the damage, making it relatively easy for the researcher to identify which species caused it. Such studies, however, often did not quantify the respective megaherbivore visitation rate, population density nor employ any other effect contrast (Birkett 2002, Muboko 2015). Exclusion studies, on the other hand, often combined different megaherbivore species as part of the same treatment, although without quantifying the relative species-specific impacts. For example, Charles et al. (2017) studied the impact of different groups of herbivores on various aspects of vegetation structure. While African savanna elephant and giraffe were both studied, they were included in the same treatment as 'megaherbivores' without teasing apart their relative impacts. Given this inability to compare between the impacts of different megaherbivore species and the taxonomic bias in studies mentioned above, extra caution should be taken when generalizing 'megaherbivore impact' across species. This is particularly relevant given the likely differences between the ecological impacts of grazers, such as white rhino and hippo, and browsers, such as black rhino and giraffe (Owen-Smith 1988).

Thematic (Earth system function) bias

Our analysis revealed clear thematic biases in the literature. Changes in vegetation structure and biodiversity were the most studied Earth system function response categories, particularly for African savanna elephant, with more emphasis placed on their impact on woody plants than on the herbaceous layer, despite a large proportion of their diet consisting of grasses (Codron et al. 2011). Strikingly, very few studies addressed the impact of megaherbivores on soils and soil microbes, even though their foraging, trampling and other disturbances are expected to have a large impact on them (Sitters and Andriuzzi 2019). Our understanding of how megaherbivores influence biogeochemistry is very limited, and most of our knowledge comes from studies on hippo's role in nutrient transport in riverine systems (Stears et al.
2018, Schoelynck et al. 2019). Although megaherbivores have been also suggested to play major roles in terrestrial lateral nutrient transport and ecosystem carbon dynamics (Doughty et al. 2016a), very few have studied this for extant megaherbivore species (but see le Roux et al. (2018) and Veldhuis et al. (2018) for white rhino's role in nutrient transport, as well as Sitters et al. (2020), Wigley et al. (2020) for African savanna elephant's role in soil carbon storage). Megaherbivore effects on seed dispersal have only been studied in the context of the three elephant species, particularly for African forest elephant and Asian elephant (Babweteera et al. 2007, Granados et al. 2017) (although see Dinerstein (1991) for a description of the potential of greater one-horned rhino for seed dispersal). Giraffes might have an important role in pollination and seed dispersal, although their effects have been largely overlooked in the literature (but see Fleming et al. 2006). Although megaherbivores are frequently said to shape fire regimes (Gill et al. 2009, Rule et al. 2012), we found only three fire-related studies coming from Hluhluwe-iMfolozi Park (on white rhino (Waldram et al. 2008)), Kruger National Park (on African savanna elephant and hippo (Smit and Archibald 2019)) and Mpala Research Centre (on African savanna elephant (Kimuyu et al. 2014)). Furthermore, we found only one type I study on megaherbivore impacts on ecosystem hydrology (Dutton et al. 2018), and two type II studies on soil and geomorphology. No studies were found on surface energy fluxes, pathogen dispersal or any other Earth system function (although see Keesing et al. 2013).

Our findings reveal mismatches between literature on the Earth system effects of Pleistocene megaherbivore extinctions and the studies on modern effects of extant megaherbivores. First, the Pleistocene literature links megaherbivore extinctions to increases in fire extent and frequency (Gill et al. 2009, Rule et al. 2012), decreases in surface reflectance (Doughty et al. 2010, Brault et al. 2013) and pathogen dispersal (Doughty et al. 2020) as well as changes in lateral nutrient diffusion and carbon dynamics (Doughty et al. 2016b). These connections have not been solidly tested for the extant megaherbivores, although changes in surface energy fluxes (Te Beest et al. 2016) and pathogen dispersal (Berggoetz et al. 2014) have been linked to other large herbivores. Surviving megaherbivores, in turn, have been well linked to changes in vegetation structure, aspects of biodiversity and seed dispersal, with much weaker understanding of their effects on other aspects of earth system function, such as biogeochemistry, hyrdrology and fire. Second, the Pleistocene literature often upscales their findings to the biome or global scale, while studies on modern effects of extant megaherbivores mostly remain at the local to landscape scale. Few studies, however, have modelled the impact of other large-bodied herbivores on processes such as carbon emissions (Hempson et al. 2017) and surface energy fluxes (Te Beest et al. 2016) at a biome or global scale. Bridging these thematic and scale mismatches will strengthen the basis for our understanding of megaherbivore effects on Earth system functioning.

Geographic and environmental biases

We also found substantial geographic bias in the literature on megaherbivore effects with almost half of type I studies coming from only five African areas (i.e. Kruger National Park, Addo Elephant National Park and Hluhluwe-iMfolozi Park in South Africa and Mpala Research Centre, Kenya and Hwange National Park, Zimbabwe). These areas are internationally well-known for their excellent field research facilities, exemplifying the importance of governments and the private sector continuing to invest in long-term field facilities. Without the presence of such facilities in these five areas, our understanding of megaherbivore impacts would undoubtedly be much poorer. In contrast, a similar proportion of type II studies came from ten areas, including both African and Asian countries, demonstrating slightly smaller geographic bias compared to type I studies.

This enormous overall geographic bias, however, potentially leads to further environmental biases in our understanding of megaherbivore impacts. Our findings reveal, for all megaherbivores species, that current study areas only represent small parts of the climate and soil fertility envelopes of their current distribution ranges. Both type I and type II studies are generally biased towards semi-arid and relatively fertile systems, with a near absence of studies under arid, high rainfall and nutrient-poor conditions. Furthermore, less than a handful of studies directly quantified the effect of rainfall or soil fertility on megaherbivore impacts (Waldram et al. 2008, Goheen et al. 2013, Smit and Archibald 2019). Therefore, we do not know how megaherbivores shape ecosystems and Earth system processes for particularly the drier and wetter parts of their ranges, or how environmental drivers influence the direction and strength of their effects. The few studies that we have on megaherbivores and those on other large herbivores, however, suggest that environmental drivers do mediate herbivore impacts (Waldram et al. 2008). These limitations hinder our efforts to predict how future climates may influence the Earth system effects of megaherbivores.

Emerging trends in megaherbivore impact research

Although much of the research on modern megaherbivore impacts focus independently on either vegetation structure or biodiversity, some have recently studied their interactive effects on both vegetation structure and biodiversity (Ogada et al. 2008), therefore, incorporating a focus on ecological cascades. Although very few studies, in general, were on megaherbivore impacts on ecosystem biogeochemistry, two recent publications reported on the impact of white rhino on lateral nutrient transport, demonstrating their ability to move nutrients against fear-driven gradients (le Roux et al. 2018, Veldhuis et al. 2018). There is an increasing interest in the role of hippos on allochthonous nutrient transport, and their further effects on aquatic primary productivity and biodiversity. Schoelynck et al. (2019), for instance, demonstrated that hippos can significantly contribute to the global cycling of silicon by feeding on riverine

grasslands and defecating in water bodies, with potential cascading impacts on the silicon-limited estuarine diatoms. Recent studies have also linked African savanna elephants to changes in above- and below-ground carbon, paving the way to an exciting research avenue on megaherbivore impacts on global carbon cycling and carbon sequestration. Interestingly Sitters et al. (2020) and Wigley et al. (2020) found contrasting impacts of African savanna elephant on soil carbon in the same system, the former showing an increase and the latter a decrease in total organic carbon. In addition to investigating total organic carbon, future research should look at megaherbivore effects on the different soil carbon fractions (Lehmann and Kleber 2015) to better understand how they influence soil carbon stabilization processes and therefore carbon residence times. An exciting, although nearly untouched, area of research is the impact of megaherbivores on terrestrial and aquatic microorganisms. Our knowledge is limited to but a few studies that investigated for instance the impact of African savanna elephant dung on mycorrhizal colonization of plants (Paugy et al. 2004) and the impact of hippo dung on biofilm productivity and respiration (Subalusky et al. 2018).

Study limitations

We acknowledge that our focus on English language peerreviewed journals may have limited our sample size. With this systematic review, however, we specifically aimed to assess the state of the empirical peer-reviewed literature and explicitly excluded non-peer-reviewed studies. To identify a possible language bias in our results, we did a posthoc assessment using Web of Science core collections database (15 October 2020), which revealed that the total number of studies on megaherbivores published in other major language peerreviewed journals, that is, French, Spanish and Portuguese, was 342. In this assessment, we ran the search for the scientific names and the common names of the megaherbivore species in each language, excluding the term of effect, therefore making our estimate conservative. Using the 3% inclusion rate based on relevance and the 46% inclusion rate based on quality (the rates that we found for our original screening of articles in English), we estimated that we may have missed five type I and five type II studies published in French, Spanish or Portuguese language peer-reviewed journals that would qualify for inclusion in our analysis. This gives us confidence that our systematic review captured a representative sample of the current global scientific discourse (that is based on peer -reviewed empirical literature) on the extant megaherbivore effects on ecosystem and Earth system functioning.

The small number of qualifying studies that reported the impacts of a megaherbivore species on a particular response category (apart from African savanna elephant impact on some aspects of vegetation structure and biodiversity) prevented us from running a full quantitative meta-analysis. Instead, we synthesized the literature through a qualitative 'meta-analysis' using the vote-counting method. Although vote-counting is used widely in the field of applied ecology, it has been criticized for ignoring sample size and effect magnitude. Researchers who use vote-counting often synthesize unweighted averages of effect sizes, when only study estimates but not variances are available (Stewart 2010). This can lead to bias, because it ignores the different volumes of information coming from studies of different size and quality (Stewart 2010). In contrast, we used vote-counting to qualitatively synthesize the impacts of the different megaherbivore species on a given response category (level 2). Instead of synthesizing unweighted effect sizes, we simply looked at the direction of the effect (increasing, decreasing, no effect). While this approach still ignores the size and quality of the study, it avoids the pitfall of using unweighted effect sizes. Despite these shortcomings, vote-counting allowed us to synthesize the overall impacts of the different megaherbivore species on a given response category, through identifying areas of agreement and dispute.

Concluding remarks

Our systematic review revealed that the empirical support for the thesis that extant megaherbivores (>1000 kg) shape ecosystem and Earth system functioning relies on very few, localized, studies and suffers from major taxonomic, thematic, geographic and environmental biases. This prevented us from running a strictly quantitative meta-analysis for any other species than the African savanna elephant. Therefore, we could not evaluate our follow-up hypotheses and thus it remains largely unclear whether 1) megaherbivores have disproportionately larger effects on Earth system functioning compared to their smaller counterparts, and how effects may vary among 2) species and 3) environmental gradients. Despite these shortcomings, our qualitative 'meta-analysis' revealed widely varying, context and species-dependent impacts of megaherbivores on the different response categories. Furthermore, interesting research avenues are gradually opening on the cascading effects of megaherbivores connecting different Earth system functions, and a few studies already report on megaherbivore effects on micro-organisms, nutrient transport and carbon cycling. Future research should, however, considerably increase the number of empirical studies on the ecological and Earth system effects of the different non-African savanna elephant megaherbivore species such as African rhino spp and hippo, and test the net effects of possible interactions among sympatric megaherbivore species. Furthermore, we must strategically expand the geographic distribution of studies across environmental gradients. Finally, we call for more, creative, studies that aim at differentiating megaherbivore effects from those of smaller large herbivores.

Acknowledgement – We thank Dr Kees Rookmaker for his advice regarding Asian rhino literature.

Funding – This research project was funded by the Swedish Research Council for Sustainable Development, Formas, under the project acronym Megaclim (diary no. 2017-01000). EL was funded by the Claude Leon Foundation and through a Royal Society Newton International Fellowship.

Conflicts of interest – All the authors declare that they have no competing interests.

Author contributions

Olli Hyvarinen: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Resources (lead); Software (lead); Validation (lead); Visualization (lead); Writing - original draft (lead); Writing - review and editing (lead). Mariska te Beest: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (equal); Resources (equal); Supervision (equal); Visualization (supporting); Writing - original draft (equal); Writing - review and editing (equal). Liza Roux: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing original draft (equal); Writing – review and editing (equal). Graham I. H. Kerley: Conceptualization (supporting); Data curation (supporting); Investigation (equal); Methodology (equal); Supervision (equal); Validation (equal); Writing original draft (equal); Writing - review and editing (equal). Esther de Groot: Data curation (equal); Methodology (supporting). Rana Vinita: Data curation (equal); Methodology (supporting). Joris P. G. M. Cromsigt: Conceptualization (lead); Data curation (supporting); Formal analysis (supporting); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (equal); Software (equal); Supervision (lead); Validation (equal); Visualization (supporting); Writing original draft (equal); Writing – review and editing (equal).

Transparent Peer Review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.05703>.

Data availability statement

Data are available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.2z34tmpn4> (Hyvarinen et al. 2021).

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Supplementary Material A

1. Search term in Web of Science Core Collections:

TS = ("megaherbivor*" OR "rhino" OR "rhinos" OR "hippo" OR "hippos" OR "elephant" OR "elephants" OR "african elephant*" OR "african savanna elephant*" OR "african bush elephant*" OR "loxodonta africana" OR "african forest elephant*" OR "loxodonta cyclotis" OR "asian elephant*" OR "elephas maximus" OR "white rhino*" OR "ceratotherium simum" OR "black rhino*" OR "diceros bicornis" OR "greater one-horned rhino*" OR "indian rhino*" OR "rhinoceros unicornis" OR "javan rhino*" OR "rhinoceros sondaicus" OR "sumatran rhino*" OR "dicerorhinus sumatrensis" OR "hippopotam*" OR "hippopotams" OR "hippopotams" OR "greater" OR "greater"

AND TS = ("add*" OR "giv*" OR "suppl*" OR "reduc*" OR "transform*" OR "accelerat*" OR "enrich*" OR "alleviat*" OR "agent*" OR "creat*" OR "affect*" OR "modif*" OR "transport*" OR "engineer*" OR "keystone*" OR "transport*" OR "damag*" OR "damag*" OR "maintain*" OR "restor*" OR "impact*" OR "effect*" OR "influence*" OR "chang*" OR "facilitat*" OR "increas*" OR "decreas*" OR "limit*" OR "promot*" OR "dispers*" OR "deposit*" OR "improv*" OR "hinder*" OR "prevent*" OR "induc*" OR "shap*" OR "graz*" OR "brows*" OR "alter*" OR "relax*" OR "driv*")

- 2. Relevance and quality criteria
- Relevance and quality criteria
- Step 1 Title screening (Criteria set 1)
 - (a) The title had to refer to a mammalian terrestrial herbivore or mammalian terrestrial herbivory in general. This largely excluded titles that were about medicine, astronomy and marine mammals.
 - (b) The title had to indicate that the study had a link to terrestrial mammalian herbivore ecology or their interaction with any earth system function. This largely excluded titles that were about mammalian reproduction and/ or veterinary medicine.
- Step 2 Abstract screening (Criteria set 2)
 - (a) The abstract had to confirm that the study was about terrestrial mammalian herbivores and/or herbivory in general, and that the study had a link to terrestrial mammalian herbivore ecology.
 - (b) The abstract had to indicate that the study reported new empirical results and was not purely based on simulations and/or modelling. If it was not fully clear from reading the abstract that the study was based on simulations or modelling or not, it was included for the next step.
- Step 3 Full-text screening (Criteria set 3)
 - (a) The full text had to present new empirical results and not results purely derived from simulations and/or other forms of theoretical modelling. Reviews and meta-analyses were also excluded.
 - (b) The full text had to present results for at least one of the extant megaherbivore species. This excluded studies on herbivores other than megaherbivores.
 - (c) The full text had to present results of a megaherbivore effect on any earth system function as defined above. This excluded pure behavioral studies and those focusing only on megaherbivore movement, home range, feeding choice, habitat selection or habitat suitability.
 - (d) Studies on captive animals and in zoological gardens were excluded.
 - (e) Studies on megaherbivore utilization of crops were excluded.

Step 4 - Quality appraisal (Criteria set 4)

- (a) The study design had to be adequately described:
 - (i) Response and explanatory variables had to be reported (Type I publications).
 - (ii) The contrast over which megaherbivore effect was evaluated (here termed "effect contrast") had to be reported e.g. megaherbivore exclusion vs. inclusion, contrasts in megaherbivore density, time after introduction etc. Furthermore, studies that deployed an exclusion experiment had to describe which species the experiment excluded. Studies that tested megaherbivore density effects on a response variable had to explicitly report the low and high megaherbivore density or the full range. Studies with designs that did not allow for separating megaherbivore effects from the effects of other large herbivores were thus excluded. For instance, studies that solely used distance from water points as a proxy of elephant utilization intensity were excluded, because elephant impact could not be reliably distinguished from the impact of other herbivores. Furthermore, studies that compared full herbivore exclusion to control areas were also excluded on the same grounds (Type I publications).
- (b) As a minimum, each study had to report the p-value, confidence interval or any other measure of uncertainty as well as the estimate of the effect for at least one response variable (Type I publications).
- (c) If data were re-used, the most recently published study was included (Type I and II publications).

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Supplementary Material B

Figure S1. Number of extracted Type I and Type II studies per year.



Type I studies Type II studies

Figure S2. Number of extracted Type I and Type II studies per journal.



Figure S3. Number of extracted Type I and Type II studies per country





Figure S4. Number of extracted Type I and Type II studies per location.



Figure S5. Number of publications per megaherbivore species and earth system function. The total number of Type I and Type II publications included in this systematic review per megaherbivore species (African savanna elephant, African forest elephant, Asian elephant, white rhino, black rhino, greater one-horned rhino, Javan rhino, Sumatran rhino, Giraffe and Hippo) and earth system function category (vegetation structure, biodiversity, seed dispersal, fire, hydrology and soil and geomorphology). The left number inside the black megaherbivore figure represents the total number of Type I publications and the right bracketed number represents the total number of Type II publications for that particular species.



Figure S6A. Study locations of African savanna elephant. The square symbol represents Type I studies and the oval symbol represents Type II studies. The colour gradient of the symbol represents the average number of citations, and the size of the symbol represents the number of studies for that particular location. The light green fill depicts African savanna elephant's prehistoric, and the dark green its current distribution.



Figure S6B. Study locations of African forest elephant. The square symbol represents Type I studies and the oval symbol represents Type II studies. The colour gradient of the symbol represents the average number of citations, and the size of the symbol represents the number of studies for that particular location. The light green fill depicts African forest elephant's prehistoric, and the dark green its current distribution.



Figure S6C. Study locations of Asian elephant. The square symbol represents Type I studies and the oval symbol represents Type II studies. The colour gradient of the symbol represents the average number of citations, and the size of the symbol represents the number of studies for that particular location. The light green fill depicts Asian elephant's prehistoric, and the dark green its current distribution.



Figure S6D. Study locations of white rhino. The square symbol represents Type I studies and the oval symbol represents Type II studies. The colour gradient of the symbol represents the average number of citations, and the size of the symbol represents the number of studies for that particular location. The light green fill depicts white rhino's prehistoric, and the dark green its current distribution.



Figure S6E. Study locations of black rhino. The square symbol represents Type I studies and the oval symbol represents Type II studies. The colour gradient of the symbol represents the average number of citations, and the size of the symbol represents the number of studies for that particular location. The light green fill depicts black rhino's prehistoric, and the dark green its current distribution.



Figure S6F. Study locations of greater one-horned rhino. The square symbol represents Type I studies and the oval symbol represents Type II studies. The colour gradient of the symbol represents the average number of citations, and the size of the symbol represents the number of studies for that particular location. The light green fill depicts greater one-horned rhino's prehistoric, and the dark green its current distribution.



Figure S6G. Study locations of Javan rhino. The square symbol represents Type I studies and the oval symbol represents Type II studies. The colour gradient of the symbol represents the average number of citations, and the size of the symbol represents the number of studies for that particular location. The light green fill depicts Javan rhino's prehistoric, and the dark green its current distribution.



Figure S6H. Study locations of Sumatran rhino. The square symbol represents Type I studies and the oval symbol represents Type II studies. The colour gradient of the symbol represents the average number of citations, and the size of the symbol represents the number of studies for that particular location. The light green fill depicts Sumatran rhino's prehistoric, and the dark green its current distribution.



Figure S6I. Study locations of giraffe. The square symbol represents Type I studies and the oval symbol represents Type II studies. The colour gradient of the symbol represents the average number of citations, and the size of the symbol represents the number of studies for that particular location. The light green fill depicts giraffe's prehistoric, and the dark green its current distribution.



Figure S6J. Study locations of hippo. The square symbol represents Type I studies and the oval symbol represents Type II studies. The colour gradient of the symbol represents the average number of citations, and the size of the symbol represents the number of studies for that particular location. The light green fill depicts hippo's prehistoric, and the dark green its current distribution.



Figure S7A. The climate and soil fertility envelopes of African savanna elephant study locations of in relation to the envelopes recorded from 1 000 random points from their current distributions. The density plots for the X-axes represent the density of Type I, Type II and current distribution points at any given value of temperature and cation exchange capacity respectively. The density plot for the Y-axis represents the density of Type I, Type II and current distribution to the density of Type I, Type II and current distribution points at any given value of rainfall.



Figure S7B. The climate and soil fertility envelopes of African forest elephant study locations of in relation to the envelopes recorded from 1 000 random points from their current distributions. The density plots for the X-axes represent the density of Type I, Type II and current distribution points at any given value of temperature and cation exchange capacity respectively. The density plot for the Y-axis represents the density of Type I, Type II and current distribution points at any given value of Type I, Type II and current distribution points at any given value of Type I, Type II and current distribution points at any given value of the X-axis represents the density of Type I, Type II and current distribution points at any given value of the X-axis represents the density of Type I, Type II and current distribution points at any given value of the X-axis represents the density of Type I, Type II and current distribution points at any given value of the X-axis represents the density of Type I, Type II and current distribution points at any given value of the X-axis represents the density of Type I, Type II and current distribution points at any given value of the X-axis represents the density of Type I, Type II and current distribution points at any given value of the X-axis represents the density plot for the X-axis represents the density of Type I, Type II and current distribution points at any given value of the X-axis represents the density plot for the X-axis represents the density plot for the X-axis represents the density of Type I.



Figure S7C. The climate and soil fertility envelopes of Asian elephant study locations of in relation to the envelopes recorded from 1 000 random points from their current distributions. The density plots for the X-axes represent the density of Type I, Type II and current distribution points at any given value of temperature and cation exchange capacity respectively. The density plot for the Y-axis represents the density of Type I, Type II and current distribution points at any given value of the temperature and cation exchange capacity respectively. The density plot for the Y-axis represents the density of Type I, Type II and current distribution points at any given value of rainfall.



Figure S7D. The climate and soil fertility envelopes of white rhino study locations of in relation to the envelopes recorded from 1 000 random points from their current distributions. The density plots for the X-axes represent the density of Type I, Type II and current distribution points at any given value of temperature and cation exchange capacity respectively. The density plot for the Y-axis represents the density of Type I, Type II and current distribution points at any given value of the temperature and cation exchange capacity respectively. The density plot for the Y-axis represents the density of Type I, Type II and current distribution points at any given value of rainfall.



Figure S7E. The climate and soil fertility envelopes of black rhino study locations of in relation to the envelopes recorded from 1 000 random points from their current distributions. The density plots for the X-axes represent the density of Type I, Type II and current distribution points at any given value of temperature and cation exchange capacity respectively. The density plot for the Y-axis represents the density of Type I, Type II and current distribution points at any given value of the density of Type I, Type II and current distribution points at any given value of the type I, Type II and current distribution points at any given value of the type I, Type II and current distribution points at any given value of rainfall.



Figure S7F. The climate and soil fertility envelopes of giraffe study locations of in relation to the envelopes recorded from 1 000 random points from their current distributions. The density plots for the X-axes represent the density of Type I, Type II and current distribution points at any given value of temperature and cation exchange capacity respectively. The density plot for the Y-axis represents the density of Type I, Type II and current distribution points at any given value of the temperature and cation exchange capacity respectively. The density plot for the Y-axis represents the density of Type I, Type II and current distribution points at any given value of rainfall.



Figure S7G. The climate and soil fertility envelopes of hippo study locations of in relation to the envelopes recorded from 1 000 random points from their current distributions. The density plots for the X-axes represent the density of Type I, Type II and current distribution points at any given value of temperature and cation exchange capacity respectively. The density plot for the Y-axis represents the density of Type I, Type II and current distribution points at any given value of the density of Type I, Type II and current distribution points at any given value of the density of Type I, Type II and current distribution points at any given value of the density of Type I, Type II and current distribution points at any given value of rainfall.

Figure S8 (A-I). Phylacine & Wilson and Reeder data for the prehistoric distributions of the different megaherbivore species.

We extracted prehistoric distributions for the study species from the Phylacine database (primarily used in Figure S6A-J), which were corroborated with those described by Wilson and Reeder (2005). Below are the original Phylacine maps for the prehistoric distributions together with the description of the prehistoric distribution by Wilson and Reeder for all the megaherbivore species.



Figure S8A. Prehistoric distributions of African savanna and forest elephants extracted from the Phylacine database.

Wilson and Reeder:

"Sub-Saharan, except C and W coast of Africa, including 30 countries from Senegal in the west to Somalia in the east."

Areas north of the southern edge of Sahara including Morocco, Algeria, Tunis, Libya, Egypt, N Mauritania, N Mali, N Niger, N Chad and N Sudan were excluded from African savanna elephant's prehistoric distributions.



Figure S8B. Prehistoric distribution of Asian elephant extracted from the Phylacine database.

Thirteen countries in SE Asia from India in the west to Borneo in the east.

The Phylacine prehistoric Asian elephant distribution remained unchanged.



Figure S8C. Prehistoric distribution of white rhino extracted from the Phylacine database.

Wilson and Reeder:

Formerly north of Equator in S Chad, Central African Republic, S Sudan, NE Dem. Rep. Congo, and Uganda. Southern Africa in SE Angola, Botswana, NE Namibia, S Mozambique, South Africa (north of Orange-Vaal Rivers and in KwaZulu-Natal), Swaziland, Zimbabwe, and possibly also SW Zambia. Now much restricted in distribution; in south of range, extinct except in E KwaZulu-Natal (South Africa), but reintroduced into other parts of South Africa (KwaZulu-Natal, Limpopo Prov., Mpumalanga, Free State), Namibia, Swaziland, Mozambique, Zimbabwe, and Botswana; introduced into Zambia and Kenya. In north of range, now confined to NE Dem. Rep. Congo.

The Phylacine prehistoric white rhino distribution remained unchanged.



Figure S8D. Prehistoric distribution of black rhino extracted from the Phylacine database.

Formerly in S Angola, Botswana, Burundi, N Cameroon, Central African Republic, S Dem. Rep. Congo, S Chad, N Eritrea, Ethiopia, Kenya, Malawi, Mozambique, Namibia, SE Niger, Nigeria, Rwanda, Somalia, South Africa, Sudan, Swaziland, Tanzania, Uganda, Zambia, and Zimbabwe; possibly more widespread in Niger, extending to Benin and Côte d'Ivoire, within historic times (Blancou, 1960; Sayer and Green, 1984). Very much reduced in numbers, particularly in recent decades of 20th century, and probably now extinct in many countries which it formerly occupied. Survives in reserves in Kenya, Tanzania, Namibia, Zambia, Zimbabwe and KwaZulu-Natal (South Africa), and possibly still in Cameroon, Chad, Central African Republic, Sudan, Rwanda, Malawi, Mozambique, Angola, and Botswana; widely reintroduced into parts of South Africa (Cumming et al., 1990).

Mali, Guinea, Liberia, Burkina Faso and Sierra-Leone were excluded from Phylacine prehistoric black rhino distribution.



Figure S8E. Prehistoric distribution of greater one-horned rhino extracted from the Phylacine database.

Within the present millennium, Indus Valley (Pakistan) east in N India to Assam and N Burma. Survives in India (Assam, West Bengal), Nepal, and possibly N Burma.

Part of northern Myanmar was included for the prehistoric distribution of greater one-horned rhino



Figure S8F. Prehistoric distribution of Javan rhino extracted from the Phylacine database.

Formerly Bangladesh, Burma, Thailand, Laos, Cambodia, Vietnam, and probably S China through peninsular Malaya to Sumatra and Java. Survives in Ujung Kulon (W Java) and in Vietnam; perhaps in small areas of Burma, Thailand, Laos, and Cambodia.

Bhutan and India were excluded for the prehistoric distribution of Javan rhino,


Figure S8G. Prehistoric distribution of Sumatran rhino extracted from the Phylacine database.

Wilson and Reeder:

Formerly Bangladesh (Chittagong Hills), Borneo, Burma, India (Assam), Laos, Malaysia (peninsular Malaya), Mergui Isl, Sumatra, Thailand, and Vietnam; probably also S China, and Cambodia. Survives in Tenasserim Range (Thailand-Burma), Petchabun Range (Thailand), and other scattered localities in Burma, peninsular Malaya, Sumatra, and Borneo.

China was excluded from the prehistoric distribution of Sumatran rhino apart from the southern-most parts of the country.



Figure S8H. Prehistoric distribution of giraffe extracted from the Phylacine database.

Wilson and Reeder:

Disjunct; W and C Africa in Burkina Faso (vagrant), N Cameroon, Central African Republic, S Chad, NE Dem. Rep. Congo, Eritrea (extinct), W and S Ethiopia, Gambia (extinct), Kenya, Mali (extinct), SE Mauritania (extinct), Niger, Nigeria (extinct, now a vagrant), Senegal (extinct), S Somalia, Sudan, Tanzania and Uganda; no reliable records from Ghana, Guinea, and Togo; may have occurred in Benin; introduced into Rwanda; S Africa in S Angola (extinct?), Botswana, Mozambique (extinct), Namibia, South Africa (originally mostly N of Orange River), Swaziland (extinct, reintroduced), Zambia (SW and Luangwa Valley), and Zimbabwe. Distribution now much restricted; in W Africa still present in Niger, and N Cameroon but extinct in Mali according to Ciofolo and Le Pendu (2002), apparently very recently; in southern Africa, now naturally distributed no farther south than N Namibia, Botswana and NE South Africa (E Limpopo and E Mpumalanga Provs.). Introduced beyond its former range in South Africa, including KwaZulu-Natal.

Guinea-bissau, Malawi, South Eastern DRC and Burundi were excluded and parts of Eritrea were added to the Phylacine prehistoric distribution of Giraffe.



Figure S8I. Prehistoric distribution of hippo extracted from the Phylacine database.

Wilson and Reeder:

Rivers of savanna zone of Africa, and main rivers of forest zone in C Africa, in Angola, Benin, N Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, S Chad, Côte d'Ivoire, Dem. Rep. Congo, Egypt (extinct; formerly along Nile to its Delta), N Eritrea, Ethiopia, Equatorial Guinea (Mbini), Gabon, Gambia, Ghana, Guinea, Guinea Bissau, Kenya, Liberia (only 2 records), Rwanda, Senegal, Sierra Leone, Somalia, Sudan, Swaziland, Malawi, Mozambique, Namibia (Caprivi Strip, Okavango River), Niger, Nigeria, Republic of Congo, Sierra Leone, South Africa (now only in N and E Limpopo Prov. and E Mpumalanga Prov., and N KwaZulu-Natal), Tanzania, Togo, Uganda, Zambia, and Zimbabwe.

Mauritania, Morocco, Algeria, Mali and all countries outside of the African continent were excluded for the Phylacine prehistoric distribution of hippo

Landscape-scale associations between white rhino loss, vegetation and fire dynamics

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Abstract

Prehistoric extinctions of large fauna have been linked to changes in vegetation and fire dynamics. However, we lack data on the ecosystem effects of modern defaunation, particularly for megaherbivore species (plant-eating mammals with adult size > 1000 kg) that are highly vulnerable to poaching and habitat loss. Megaherbivores are suggested to have disproportionately strong effects on ecosystems due to their very large body size. The rapid increase in illegal hunting of African rhino for their horn in the past decade has raised concerns about their future viability. If rhino loss continues at the current rate, we may lose these species from African ecosystems at functionally relevant densities in the coming decades. We used an ecosystem-scale "natural experiment" to assess what the loss of white rhinoceros (Ceratotherium simum), a megagrazer and ecosystem engineer, means for the functioning of savanna grasslands. Fine-scale spatial data on legal and illegal rhino removal during a 10-year period in Hluhluwe-iMfolozi Park allowed us to link a rhino loss gradient to vegetation and fire dynamics. Our study shows that burnt area, fire frequency and the rate of woody encroachment were higher in areas that lost more rhino and lower in areas with higher grazing lawn extent. Furthermore, our piecewise structural equations model revealed that instead of direct effects, rhino loss was associated with higher rate of woody encroachment indirectly through its positive effects on fire, and that grazing lawn was associated with lower rate of woody encroachment indirectly through its negative effects on fire. These findings support our hypotheses that (1) rhino loss increases the rate of woody encroachment through its effects on fire, and that (2) grazing lawns, which have previously been associated with rhino, play an important role in regulating fire regimes and thus woody encroachment in the landscape. Importantly, our study demonstrates that the loss of the world's largest terrestrial grazer may have meaningful ecosystem-scale consequences for savanna functioning.

Keywords: Defaunation, megagrazer, white rhinoceros, poaching, grazing lawn, vegetation, woody encroachment, fire, ecosystem impact, ecosystem functioning

Introduction

The ongoing defaunation and trophic downgrading of ecosystems for the past ~50 000 years has resulted in dramatic changes to the functioning of ecosystems globally (Estes et al. 2011; Brault et al. 2013). It is now established that the Pleistocene extinctions of large fauna led to biome-scale changes in, for example, vegetation structure and fire regimes (Gill 2014; Dantas and Pausas 2020; Gill et al. 2009; (Karp et al. 2021). Yet, despite

ongoing and rapid defaunation, we still do not understand the full ecosystem consequences of current mammal loss (Dirzo et al. 2014). Megaherbivores, plant-eating mammals weighing > 1000 kg as adults, such as the world's elephants and rhinos (Owen-Smith 1988), are particularly vulnerable to illegal hunting and habitat loss (Williams et al. 2022) and they are hypothesized to have disproportionate effects on ecosystem functioning (Owen-Smith 1988). We are currently facing a dramatic (Owen-Smith 1988). We are currently facing a dramatic Ferreira et al. 2018), and need to urgently increase our understanding of how their loss may impact key ecosystem processes (Hyvarinen et al. 2021). Such improved understanding is particularly important for informing recent suggestions that megaherbivore rewilding can contribute solutions for climate change mitigation (Cromsigt et al. 2018; Mahli et al. 2022; Schmitz et al. 2022).

White rhino are iconic megarazers that used to be widespread across northeastern and southern Africa (Faurby et al. 2018), but historic illegal hunting severely reduced their distribution and has already led to the functional extinction of the northern subspecies (Callender 2021). Furthermore, the last decade has seen an upsurge in illegal hunting on the southern white rhino (Nhleko et al. 2022). The majority of surviving rhino are now limited to a few core areas in South Africa, but poaching has already started to significantly affect their numbers in these remaining core areas. The Kruger National Park (KNP) for instance hosted about half of South Africa's rhino up to recently, but rhino numbers in the park have declined significantly (Ferreira et al. 2018) and may decrease by another 35% within the next decade at current levels of poaching (Nhleko et al. 2022). This means that, within the next decade, we may see a loss of functionally relevant densities (i.e. high enough densities to maintain their particular ecological function) in the few areas where rhino remain. Here, we ask what the consequences of this loss could mean for the functioning of African savannas.

In fact, past research demonstrates that rhino drive key ecosystem processes in areas where they occur at functional densities (Owen-Smith 1988; Waldram et al. 2008; Cromsigt and te Beest 2014). Their very large body size necessitates high food intake, and their low mass-specific metabolic rate allows them to tolerate low quality forage (Owen-Smith 1988). Their size furthermore renders rhino relatively immune to population control by non-human large carnivores (Owen-Smith 1988). These characteristics are thought to allow rhino to exert disproportionately larger impacts on vegetation and ecosystem processes compared to smaller large grazers at similar population biomass, and to use habitat and resources with relatively little regard for predation risk (Owen-Smith 1988; le Roux et al. 2018). This allows rhino to transform tall savanna grassland into functionally unique "grazing lawns" (Waldram et al. 2008; Cromsigt and te Beest 2014) that consist of a specific community of grazing-tolerant, short-statured grass species that are outcompeted by more tall-statured grasses in the absence of grazing. These lawns are further characterized by relatively high levels of visitation and utilization by other short grass grazers (Hempson et al. 2015)

Moreover, grazing lawns act as natural fire breaks, limiting fire extent and intensity (Archibald et al. 2005). More generally, the reduction of grass biomass by rhino grazing also limits fire fuel availability, therefore decreasing the spread and intensity of fire in the tall grassland surrounding the lawns (Waldram et al. 2008; Johnson et al. 2018). The openness of grazing lawns further attracts large browsers that seek safety from predation, thereby increasing browsing pressure on the woody layer, consequently reducing woody plant recruitment and survival on and surrounding grazing lawns (Voysey et al. 2021). Fire on the other hand can either reduce or promote woody plant establishment. An intense fire may kill seedlings and saplings that are still growing below the fire trap, while low intensity fires may temporarily reduce the grass cover without sufficiently harming woody seedlings and saplings (Bond et al. 2017). Therefore, low intensity fires can reduce grass competition and thus promote the establishment and growth of woody plants. Thus, through the creation and maintenance of grazing lawns, rhino may be able to indirectly influence savanna fire dynamics and patterns in tree/grass ratios. This functional role of rhino may become even more pronounced in areas with high rainfall. Studying changes in grass sward height and fire extents following the legal removal of rhino, Waldram et al. (2008) found that other herbivores were able to compensate for the reduced grazing pressure caused by rhino loss only where rainfall and grass biomass production were low. In areas with higher rainfall and more rapid grass growth, the loss of rhino also led to an increase in grass sward height and to increased fire extent.

Here, we test the effects of rhino loss on ecosystem processes and savanna functioning in Hluhluwe iMfolozi Park in South Africa (HiP). More specifically, we use a 10-year record of high-resolution spatial data of legal and illegal rhino removal to investigate the changes in vegetation and fire dynamics across a rhino loss gradient. Based on the above, we predict that rhino loss over the past decade in HiP has led to complex ecosystem-scale responses, where the dynamics of grazing lawns, fire and woody encroachment are tightly coupled. More specifically, we expect lower grazing lawn extent and rate of change in grazing lawn extent but higher burnt area, fire frequency and the rate of woody encroachment with more rhino loss. We also predict the effects of rhino loss on all the responses to be stronger in areas with higher rainfall. Furthermore, we expect rhino loss to be associated with burnt area and fire frequency directly (through reduced consumption of grassy fuel) and indirectly (through its negative effects on grazing lawn extent). Finally, we expect rhino loss to be associated with woody encroachment indirectly through negative effects on grazing lawn extent and the resulting positive effects on fire frequency and extent of low of intensity fires (Fig. 1).

Methods

Study area

HiP (28.44194°S, 32.22949°E) is situated in north-eastern South Africa, and covers \sim 960 km² of protected



Figure 1. Conceptual figure on the effects of rhino loss on ecosystem processes such as vegetation dynamics and fire. We hypothesize that rhino loss leads to reduction in grazing lawn cover and fire frequency. We also expected the reduction in grazing lawn cover and increase in fire frequency to further promote woody encroachment. A solid arrow indicates that we found evidence, and dashed line indicates no support for the particular pathway.

area, with elevation varying between 45 and 750 m above sea level. The area receives summer rainfall (ranging from an average of 550 mm/year in the drier southwestern parts to 1,000 mm/year in the more hilly northern parts) (Howison et al. 2017). However, the area experienced a severe drought between 2014 and 2016, followed by particularly high rainfall for the next few years (Mbatha and Xulu 2018). Fire is actively managed in the park through prescribed burning, with an average fire return interval of 2-4 years (Archibald et al. 2017). However, despite this fire management, spontaneous fires occur regularly, and the extent and intensity of fire are influenced by natural drivers such as rainfall and grazing pressure by rhino and other grazers (Waldram et al. 2008). Rainfall and fire in the park are strongly correlated, with high rainfall areas burning more frequently (Archibald et al. 2017). Large parts of the park are dominated by savanna grassland and woodlands with a varying degree of tree and grass cover, with patches of heavily utilized "grazing lawns" distributed across the park (Cromsigt et al. 2017). For at least four decades, the park has experienced strong woody plant encroachment, where large, woody shrubs encroach and replace open grass patches (Wigley et al. 2010, Staver et al. 2017). The park is among the very few places globally that still hosts a near intact mega- and large herbivore and predator communities.

Rhino removals in HiP

HiP has among the world's highest rhino densities $(\sim 2/km^2)$ that have persisted over several decades

(Linklater and Shrader 2017). Hunting by European colonial hunters led to the near extinction of the southern white rhino by the late 1800s, and during the early 1900s there were only 100 -200 remaining in parts of what is now known as HiP (Brooks 2006). Conservation during the first half of the 20th century led to a strong increase in rhino numbers reaching ~1500 individuals in HiP by the late 1960s (Linklater and Shrader 2017). During the 1960s, this early rhino conservation success led to concerns over the impacts of overgrazing on the grass cover and soils. To combat this, HiP management attempted to curb population growth by creating artificial sink areas where rhino were regularly removed to maintain stable rhino densities. The removed rhino were relocated elsewhere as part of wider range expansion efforts (Linklater and Shrader 2017). This management continued into the 2000s and led to substantial success in white rhino conservation across southern Africa (Leader-Williams 2014). Since 2013, however, poaching of rhino rapidly increased in the park. Consequently, the management removal of rhino was halted in 2016, but the illegal removal continues (Fig. 2).



Figure 2. Temporal (2010 to 2021) patterns of rhino loss in Hluhluwe-iMfolozi Park in South Africa, including management removals (legal) and poaching events (illegal).

Experimental design

We assessed changes in vegetation and fire dynamics along a gradient of rhino removal, including legal and illegal removals. To determine this gradient, we obtained a permission to use the GPS coordinates for each management removal and poaching event between 2010-2019 from Ezemvelo KZN Wildlife. We overlaid these locations with a 1x1 km grid. We then calculated the total number of individuals lost for each grid cell over the 10-year period. This provided us with a parkwide gradient in the total number of rhino lost by management removals and poaching. Because of the sensitivity around rhino poaching, we could not display any spatial information regarding the rhino removals in this report. Our focus was on impacts of rhino on ecological processes (i.e. fire, lawn extent and woody encroachment) in savanna grassland areas. Therefore, we first masked all 1x1 km grid-cells that had >75% woody



Figure 3. The spatial patterns of grazing lawn extent, woody plant cover, woody encroachment, mean burnt area and fire frequency in Hluhluwe-iMfolozi Park in South Africa in 1 x 1 km grid cells with <75% woody cover.

plant cover and removed those from all further analyses (Fig.3a). The same grid was used for all response variables consistently for all years.

Data collection

In addition to the removal data, we received annual rhino counts and distribution data for the southern part of the park (iMfolozi). These data were collected by Ezemvelo KZN Wildlife from 2010-2019 through annual fixed-wing aerial transects in the month of September, where for each individual or herd of rhino the observer noted down the GPS location of the rhino and, if a herd, the number of individuals in the herd. The transects were bordering each other and as such covered the full extent of iMfolozi. We overlaid the same 1x1 km grid as used for the removals data over the rhino count locations and calculated the mean rhino count as the average number of rhino observed per 1km² grid cell across the sampling years. We also calculated average rate of change in rhino count across the 10 years as the beta estimate of the linear model for each grid cell, where rhino count was the response and year was the only predictor.

in 2010, 2014, 2016 and 2019 along 23 fixed line transects, equally distributed through ~70% of the park and representing all vegetation types and the different topographies found in the park. The remaining 30% is wilderness area, the most southern part of the park, where research is more restricted, and was thus excluded from the lawn monitoring. The length of the transects varied between 3.9 and 10.4 km with an average of 7.9 km. The transects were walked by teams of two people between March-July in 2010, July-October in 2014, October-November 2016 and January-April in 2019), during which they recorded the presence/absence of grazing lawn at 5 m intervals directly on and within 5 m buffer on each side of the transect. We defined grazing lawn as present when very shortly grazed ($\leq 3 \text{ cm tall}$) prostrate growing, or other short-statured, grazing lawn species dominated ($\geq 75\%$ of grass cover) the 5 by 10m plots on the transects (see Cromsigt et al. 2009 for more details about the set-up of the transect count protocol). We overlaid the same 1x1 km grid as used for the rhino data with the transect lawn data and extracted the number of lawn observations (i.e. the number of 5 by 10m plots on a transect with lawn present) per year for each grid cell that

Grazing lawn extent in the park was recorded on foot

intersected with a transect. We then calculated the mean number of lawn observations per grid cell across all the sampling years and corrected for the length of transect intersecting each grid cell. i.e. we determined the proportion of transect intersecting a grid cell that was covered by grazing lawn (referred to as grazing lawn extent in the remainder of the text) (Fig 3b). We also calculated the average rate of change in grazing lawn extent across the sampling years for each grid cell as the beta estimate of the linear model, where grazing lawn extent was the response and year was the only predictor.

We extracted the percentage grass and bare-ground cover from Copernicus Global Land Cover Layers: CGLS-LC100 Collection 3 for each year between 2015-2019 at 100 m resolution using Google Earth Engine Java Script API (Buchhorn et al. 2020; Gorelick et al. 2017). Bare ground cover averaged ~0.5% of the total park area across the sampling years, and the changes in bare ground cover over the years were minimal (average increase of 0.8 % per year). Bare ground cover was thus excluded from the analyses. We used the grass cover estimates to create a proxy for woody plant cover, where woody cover was obtained by subtracting the grass cover from 100%. For each 1x1 km grid cell, we then computed the mean woody cover across the sampling years (2015-2019) and the rate of change in woody cover as the beta estimate of the linear model with woody cover as the response and year as the predictor. In the remainder of the text, we refer to the latter as "the rate of woody encroachment" (Fig 3c,d).

We extracted burnt area for the entire park for each year between 2010-2019 at 250 m resolution from the MODIS Fire cci Burned Area Pixel Product, Version 5.1 using Google Earth Engine Java Script API (Padilla 2018; Gorelick et al. 2017). From this data, we then computed the mean burnt area for each 1x1 km grid cell over the years from 2010 to 2019. Finally, we calculated the fire frequency for each grid cell as the number of years that at least one burnt pixel (250 m) intersected the grid cell (Fig. 3e,f).

We obtained average rainfall data (at 180 m resolution) for the entire park from Howison et al. (2017), which was derived through spatially extrapolating longterm average rainfall values between 1935 and 2010 across various recording stations in the Park using elevation as a covariate. From this, we estimated the mean long-term rainfall per 1x1 km grid cell by averaging rainfall values of all 180 m raster pixels within each cell.

Data analysis

First, we used linear models (function lm) and generalized linear models (function glm) in base R (R team 2022) to test the relative effects of rhino loss and rainfall on (Q1.1) mean rhino count and (Q1.2) the rate of change in rhino count, (Q2.1) grazing lawn extent and (Q2.2) the rate of change in grazing lawn extent, (Q3.1) mean woody cover and (Q3.2) the rate of woody encroachment, and (Q4.1) mean burnt area and (Q4.2) fire frequency. We also tested the relationship between rainfall and rhino loss (Q5). Because the rhino count data was only available for iMfolozi, Q1 was limited to this region. For Q2 we excluded all grid cells that did not intersect with a transect. For Q3, Q4 and Q5 we included all grid cells (see Supplementary Material Table S1 for full model structures).

For each question, we performed a step-wise elimination procedure, where the predictors of the full model were the rhino loss, rainfall and their interaction. We selected the best candidate model based on the AICc criterion. The model for Q3 fulfilled the OLS assumptions for normality and were modelled linearly. Because the responses for Q1, Q2, Q4 followed a Poisson distribution, we used glm, and specified "poisson" family. When overdispersion was present, we specified "quasipoisson" family. For all models where heteroscedasticity was present, we applied weights. See Supplementary Material for the full model structures.

While linear models allowed us to test the effect of rhino loss on each vegetation and fire parameter separately, it did not allow us to account for potential indirect relations between the variables. To test for these relations, we built piecewise structural equations models (pSEM) in R (package: piecewiseSEM). Accordingly, we used pSEMs to test whether rhino loss was associated to fire directly, or indirectly through its effects on grazing lawn extent, and whether rhino loss was associated with the rate of woody encroachment directly, or indirectly through its effects on grazing lawn extent and/or fire. We first excluded all grid cells that did not intersect a grazing lawn transect. We first identified all the variables to be included in the model, the interactions between the variables and the directions of the interactions based on our original hypotheses. This led us to build two separate models, one with fire frequency and one with burnt area. For the sub-models within the pSEMs, where grazing lawn extent, total burnt area and fire frequency were response variables, we specified "poisson" or "quasipoisson" family, which was informed by our lm and glm analyses. Because of this, we could not derive the standardized estimates for any of the pathways except those leading to woody encroachment (with gaussian distribution). This limited our ability to assess the relative importance of the different pathways for the other responses.

Results

Rhino loss

The number of rhino counted increased from 783 in 2010 to 885 in 2012, and decreased to 493 by 2019. The number of management removals of rhino increased from 8 in 2010 to 75 in 2016, while the number of rhino poached increased from 19 in 2013 to 106 in 2019 (Fig.2).

Grazing lawn, fire and woody cover

The number of grazing lawn observations across the park (including all grid cells from 0 to 100% woody cover) increased from 1608 in 2010 to 2434 in 2014 and 2433 in 2016 dropping to 846 in 2019. More grazing lawns were found in the south and central parts of the park compared to the north (Fig. 3c). Woody plant cover in the park varied between 30 and 100% with a grid cell median ranging between 47-61%. Woody encroachment (positive rate of change in woody cover) took place in nearly all grid cells that had <75% woody cover, with the beta estimate ranging between -1.4 and 11.8 with a mean of 6.58. The mean burnt area over the years per grid cell for the Park varied between 0 to 62 ha with a mean of 16 ha and the fire frequency varied from 0 to 7 times with a mean of 2 times within the 10 year period. However, there were no fires in the Park from 2015 to 2017, which is attributable to the drought between 2014-2016 leading to constrained grass biomass and thus fire fuel build-up.

The effects of rhino loss on rhino numbers, vegetation, fire dynamics and rainfall

Grid cells that lost more rhino had lower rate of change in rhino count, but higher mean rhino count overall. Rainfall was not a significant predictor of either response (Fig. 4,5; Table 1). Grid cells with more rhino loss and less rainfall had higher mean burnt area and fire frequency. Grid cells with more rhino loss and less rainfall had higher rate of woody encroachment. Rhino loss was not a significant predictor of grazing lawn extent, the rate of change in lawn extent or mean woody cover (Fig. 4,5; Table 1). Finally, rainfall was not a significant predictor of rhino loss (Table 1).

Pathway analysis and ecological cascades

Our pSEMs (Fig.6) furthermore indicated that grid cells with higher grazing lawn extent had lower burnt area and fire frequency, and that cells with higher burnt area and fire frequency had higher rate of woody encroachment. Furthermore, the pSEMs revealed that instead of direct associations, rhino loss was associated with higher rate of woody encroachment indirectly through its positive effects on burnt area and fire frequency. Similarly, grazing lawn extent was not directly associated with lower rate of woody encroachment, but instead indirectly through its positive effects on burnt area and fire frequency (Fig. 6).

Discussion

We found evidence that rhino loss in HiP led to landscape-scale responses in crucial savanna processes between 2010 and 2019. More specifically, we found a higher burnt area, fire frequency and rates of woody encroachment in grid cells that lost more rhino. However, rhino loss was not a significant predictor of grazing lawn extent. Despite this, grid cells with higher grazing lawn extent had a lower extent of burnt area, fire frequency and rates of woody encroachment. Furthermore, our pathway analysis revealed that instead of direct effects, rhino loss was associated with higher rate of woody encroachment indirectly through its positive effects on fire, and that grazing lawn extent was associated with lower rate of woody encroachment indirectly through its negative effects on fire. These findings support the hypotheses that (1) rhino loss amplifies woody encroachment through its effects on fire, and that (2) grazing lawns, which have been previously associated with rhino, play an important role in regulating fire regimes and thus woody encroachment in the landscape. Importantly, our study suggests that poaching of the world's largest terrestrial grazer impacts savanna functioning at the scale of a protected area.



Figure 4. Scatterplots showing the relationship between rhino loss and rhino density-, vegetation- and fire parameters. The error bars indicate standard error.



Figure 5. Scatterplots showing the relationship between rainfall and the rhino density, vegetation and fire parameters.

As expected, the rate of change in rhino count was lower in grid cells that lost more rhino. Despite this, we found that grid cells with more rhino loss also had higher mean rhino count. This suggests that both management removals and poachers target areas with more rhino, although for different reasons. Management targets rhino hotspots because of objectives to create artificial population sinks (Linklater and Shrader 2017), whereas poaching may focus on these areas because of the relative ease of locating suitable targets. Thus, the effects of rhino loss on vegetation and fire dynamics may be partially obscured by the relatively high numbers of rhino in areas with high levels of rhino loss. Because of this, our results represent conservative estimates for the impacts of rhino loss on vegetation and fire dynamics. Although we found no effect of rainfall on the rate of change in rhino count, Nkhelo et al. (2021) showed that the effects of poaching on the rhino population in KNP were amplified under low rainfall.

Response	Model type	Fixed effect	Estimate	Std.Estimate	S.E	t/z-value	p-value
Mean rhino count	glm("quasipoisson")	Rhino_loss	0.062	0.012	0.015	4.236	<0.001
		Rainfall	-0.001	-0.005	0.001	-1.460	0.145
Rate of change in rhino count	lm()	Rhino_loss	-0.001	-0.084	0.001	-2.061	0.040
Mean grazing lawn extent	glm("quasipoisson")	Rhino_loss	0.055	0.013	0.046	1.208	0.229
		Rainfall	0.000	-0.099	0.000	-7.435	< 0.001
Rate of change in grazing lawn extent	lm()	Rainfall	0.007	0.364	0.001	5.146	<0.001
Mean burnt area	glm("quasipoisson")	Rhino_loss	0.081	0.009	0.011	7.271	< 0.001
		Rainfall	0.007	0.033	0.000	23.686	< 0.001
Fire frequency	glm("poisson")	Rhino_loss	0.487	0.052	0.110	4.427	< 0.001
		Rainfall	0.007	0.287	0.000	24.599	< 0.001
Mean woody cover	lm()	Rhino_loss	-1.734	-0.047	1.124	-1.543	0.123
		Rainfall	0.042	0.444	0.003	14.644	< 0.001
Rate of change in woody cover	lm()	Rhino_loss	1.246	0.131	0.313	3.980	< 0.001
		Rainfall	-0.005	-0.197	0.001	-5.999	< 0.001
Rainfall	lm()	Rhino loss	0.032	0.001	1.410	0.023	0.982

Table 1. Output for the best candidate models after step-wise elimination procedures from linear and generalized linear models testing the effects of rhino loss and rainfall on the different responses.

Rhino loss and grazing lawn cover

In contrast to our expectations, grazing lawn extent and the rate of change in grazing lawn extent did not differ among grid cells with varying degree of rhino loss. This is surprising because previous research from HiP (Cromsigt and Olff 2006, Waldram et al. 2008) and KNP (Cromsigt and te Beest 2014) suggests a central role for rhino in grazing lawn establishment and maintenance. Owen-Smith's (1988) pioneering work on rhino in HiP already established the link between rhino densities and grazing lawn cover, while Cromsigt and te Beest (2014) demonstrated that recolonization of KNP by rhino led to an increase in the number of grazing lawns and extent of short grass. Furthermore, Waldram et al. (2008) showed that management removals of rhino in HiP led to an increase in grass sward height nearby rhino wallows, but only at high rainfall areas. This was due to the high grass productivity associated with high rainfall, and the subsequent inability of other short grass grazers to compensate for the loss in overall grazing pressure resulting from rhino loss. This discrepancy can be partially explained by our conservative approach discussed above i.e. grids cells that lost more rhino had lower rate of change in rhino count but also higher overall rhino count. Accordingly, despite management removals and poaching, rhino numbers may have remained at functionally sufficient level to maintain grazing lawns particularly in the lower rainfall areas. However, this does not fully explain the seemingly different results by us and Walram et al. (2008) in the high rainfall areas. A probable reason for this relates to the sensitivity of grazing lawn cover, as defined by the dominance of stoloniferous grass species that have been maintained in a short-statured form ≤ 3 cm by grazing, to changes in precipitation (i.e. higher biomass production and lower grazing lawn cover during wet season compared to dry season). It is likely that the strong seasonal differences in the timing for the grazing lawn measurements in the different years (see the section on data collection), and the severe drought experienced in HiP from 2014 to 2016 (Mbatha and Xulu 2018), at least partly obscured the effects of rhino loss on grazing lawn in areas that normally experience relatively high rainfall.

Rhino loss and fire regimes

As expected, grid cells that lost more rhino had higher burnt area and fire frequency across the Park's rainfall gradient. One mechanism through which rhino influence fire is the creation and maintenance of grazing lawns, which act as natural fire breaks in the landscape (Hempson et al. 2015). In fact, we did find lower burnt area and fire frequency in grid cells with higher grazing lawn extent across the rainfall gradient. This is in line with Archibald et al. 2005, who reported higher fire return intervals with increasing proportion of lawn grass cover in the same study system. Another mechanism beyond grazing lawns, is the general reduction of tall grass biomass, and thus grass fuel for fire, by grazing (Johnson et al. 2018). Recent studies support the hypothesis that rhino, and other large grazers, limit the accumulation of fire fuel (Johnson et al. 2018). Staver and Bond (2014)

for instance reported that the exclusion of large grazers in HiP led to an increase in grass biomass, and that grass biomass decreased rapidly again after the reintroduction of grazers. Similarly, Cromsigt and te Beest (2014) showed how the extent of short grass was almost twice as high in areas in Kruger that rhino had colonized early on versus areas that they recolonized more recently. Furthermore, Waldram et al. (2008), found that legal rhino removal increased fire extent in both low and high rainfall areas of HiP, which was attributed to an increase in grass biomass accumulation following rhino removal. In the present study, we could not directly test whether rhino loss reduced grass biomass on the tall grassland specifically. However, because rhino loss was associated with higher burnt area and fire frequency consistently across the park, including high rainfall areas with extremely low grazing lawn cover, our results do suggest that rhino loss promoted fire by reducing grass biomass on the tall grassland.

An alternative interpretation for the relationship between grazing lawn and fire found in this study is that large frequent fires can also reduce grazing lawn extent. This is because nutritious postfire growth can attract large grazers away from grazing lawns, thus alleviating grazing pressure on the lawns, which in turn promotes tall grass growth and the loss of lawn cover (Archibald et al. 2005). Increasing number of small, patchy fires can however have the opposite effect. Small burnt patches can concentrate large grazers in spatially more confined areas leading to high localized grazing pressure that further promotes lawn formation (Archibald et al. 2005).

Rhino loss and woody encroachment

As expected, we found higher rates of woody encroachment in grid cells that lost more rhino. More specifically, instead of direct impacts, our pSEMs revealed that rhino loss was associated to woody encroachment indirectly through its positive effects on burnt area and fire frequency. While intense fires are commonly linked to increased mortality of woody plants growing below the fire trap (Mapiye et al. 2008; Smit et al. 2016), frequent low intensity fires that are not able to kill woody seedlings may in fact promote woody plant establishment and recruitment to higher size classes by temporarily reducing grass competition (Walters et al. 2004). While we were unable to specifically test the effect of fire intensity, a recent study from the Brazilian Cerrado linked increasing fire frequency to decreasing fire intensity (Rodrigues et al. 2021). This was attributed to reduced accumulation of grass biomass, thus reducing the abundance of fire fuel for each individual fire event. This leads us to propose that frequent fires in our study area burn relatively cool compared to less frequent fires, which would further support why increasing fire frequency seemed to amplify woody encroachment in our study. An alternative explanation for the relationship between the rate of woody encroachment and fire found in this study has to do with fire management in the park. With an aim to control woody encroachment, management tends to burn more in areas that are highly encroached (Archibald et al. 2017). It is important to note that unplanned random fires do take place in the park regularly, but this could provide a partial reason why we found more frequent fires in grid cells with higher rate of woody encroachment.



Figure 6. Results of the pathway analysis through the piecewise Structural Equation Models, testing the different pathways for the impact of rhino loss and grazing lawn extent on burnt area, fire frequency and woody encroachment. The dashed outline for the boxes depicts that we specified a (quasi)poisson distribution. Green arrow describes a positive effect, and orange arrow a negative effect. Grey line describes no effect. Only, the estimates for pathways towards woody cover are standardized.

Furthermore, this relates to the seemingly high overall increases in woody cover we found in in the park (averaging ~6% increase per year). While Wigley et al. (2010) also found dramatic increases in woody cover in the park, namely 19% increase in shrub cover and 66% increase in tree cover over a 67-year period, our estimate amounts to an average increase of ~30% in total woody cover over the 5-year period. Although this trend seems extremely high, it can be partly attributed to the severe drought experienced in the park from 2014 to 2016 leading to reduced grass biomass built up and a virtual absence of fire during 2015-2017. The absence of fire may have allowed a large percentage of woody encroachers of 0.5-2 m in height to grow and recruit to size classes above 2.5 m, making them nearly immune to top-kill by fire (see Bond et al. 2017). Additionally, the drought may have distorted the proportion of woody cover identified by the satellite-derived land cover product, and thus influenced our estimates for the rate of change in woody cover. In fact, the first two years of our analysis (2015-2016) coincided with the drought such that the vegetation greenness (measured as NDVI) was extremely low in those years (Mbatha and Xulu 2018). This may have led to an underestimation of woody cover for those years, and a subsequent overestimation of the rate of woody encroachment across the study period. A closer inspection reveals that the effects of the drought on vegetation greenness in HiP strongly correlated with the spatial variation in mean annual rainfall i.e. areas with the lowest mean annual rainfall were the most affected, and areas with the highest mean annual rainfall were the least affected (Mbatha and Xulu 2018). Because grid cells with varying degrees of rhino loss did not differ in terms of rainfall (Table 1), this gives us confidence that the possible drought-induced distortion in woody cover estimates did not systematically influence the relative differences in the rate of woody encroachment among grid cells with varying degree of rhino loss.

Another mechanism through which grazing lawns can reduce the rate of woody encroachment is through meso-browser visitation of the lawns. In fact, Voysey et al. (2021) showed in HiP that the exclusion of browsers strongly modified the growth rates of woody plants in short grass habitat. Furthermore, the authors found that browser visitation of grazing lawns decreased with browser body size, suggesting that meso-browsers visit lawns because of the openness that helps them avoid predation. Our pSEM showed that the rate of woody encroachment decreased with grazing lawn cover. However, instead of browser driven impacts as suggested by Voysey et al. (2021), our analysis confirmed that grazing lawn extent was associated with lower rate of woody encroachment indirectly through its negative effects on fire. While the reason for the lack of browser driven effects in our study remains unclear, these findings highlight the import role of grazing lawns in the functioning of HiP savanna system.

Concluding remarks

While Pleistocene defaunation has been linked to changes in ecosystem functioning, including processes such as vegetation and fire dynamics (Gill 2014; Dantas and Pausas 2020; Karp et al. 2021), we still do not understand the full consequences of contemporary defaunation, particularly of megaherbivores that are the most vulnerable to poaching and habitat loss. White rhino are the world's largest extant megagrazers, that have been previously shown to drive grassland structure and fire dynamics (Waldram et al. 2008; Cromsigt and te Beest 2014). However, they are facing a severe poaching crisis where their numbers are drastically declining in the core areas where they still remain (Nhleko et al. 2022). With the current rates of poaching, we might lose this species at functional densities in the coming decades, with potentially far-reaching consequences on savanna functioning. Our study supports this notion and suggests that the loss of rhino in HiP between 2010 and 2019 led to an increase in fire occurrence, which in turn promoted woody encroachment. Furthermore, our study supports the role of grazing lawns, which have been previously linked to rhino, in regulating fire and woody encroachment in the landscape. It is thus becoming increasingly clear that rhino are influential ecosystem engineers that drive processes that are crucial for savanna functioning.

Supplementary Material:

Supplementary Material Paper II - MS word document

Acknowledgements

We want to acknowledge the crucial contribution of Ezemvelo KZN Wildlife including Dave Druce by granting us access to the rhino removal and count data for the purpose of this research. This research project was funded by the Swedish Research Council for Sustainable Development, Formas, under the project acronym Megaclim (diary no. 2017-01000).

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Hyvarinen O, Te Beest M, le Roux E, Kerley K, Buitenwerf R, Druce D, Cromsigt J. P.G.M. Landscape scale associations between white rhino loss, vegetation and fire dynamics (manuscript).

Supplementary Material

Question	Model structure	Model type
Q1.1	Mean rhino count~Rhino_loss*Rainfall	glm()
Q1.2	Rate of change in rhino count ~Rhino_loss*Rainfall	lm()
Q2.1	Mean grazing lawn extent ~Rhino_loss*Rainfall	glm()
Q2.2	Rate of change in grazing lawn extent ~Rhino_loss*Rainfall	lm()
Q3.1	Mean burnt area~Rhino_loss*Rainfall	glm()
Q3.2	Fire frequency ~Rhino_loss*Rainfall	glm()
Q4.1	Mean woody cover ~Rhino_loss*Rainfall	lm()
Q4.2	Rate of change in woody cover ~Rhino_loss*Rainfall	glm()
Q5	Rainfall~Rhino_loss	lm()

Table S1. Model structures for the analysis