# Mapping changes to consumer-mediated ecosystem function across African savannas

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# Abstract

This thesis seeks to clarify how humans are changing ecosystem function in consumer-controlled African savannas. As a framework, it adopts the theory of consumer control (Bond 2005), which argues that vegetation structure in savannas is controlled not only by plants' ability to fix solar energy, but also by fire and animals' ability to consume the energy plants fix. The corollary of consumer control is that fire and animals exercise far greater control over function—flows of energy and material—in savannas than in other biomes. As a methodology, this thesis examines two links between land use change and ecosystem function: changes to physical vegetation structure and changes to trophic energy flows from plants through animals. The theory of consumer control suggests that in savannas the first link, vegetation structure, is molded by the second, animal energy consumption. By investigating how global change is altering savannas' vegetation structure and trophic efficiency, this thesis clarifies how humans are changing ecosystem function and ultimately ecosystems' ability to support biodiversity and livelihoods.

The objective of the first article, entitled "**Energy flows reveal declining ecosystem functions by animals across Africa**", was to measure how changes to land use and biodiversity intactness have altered bird and mammal-mediated ecosystem functions across sub-Saharan Africa. Adopting an energetics framework, it found that the total food energy consumption by birds and mammals in sub-Saharan Africa has declined by over one third since ~1700. That decline included a ~75% decrease in functions performed by megafauna. The pattern of decreasing function varied by biome, driven by arboreal birds and primates in forests, terrestrial herbivores in grassy systems, and burrowing mammals in arid systems. Compared to other approaches, the article's energetics approach highlighted the functional importance of keystone species such as elephants and mole rats, and of smaller animals. The article concluded that approaches relating biodiversity intactness to energy and material flows can help advance efforts to integrate animal-driven functions into biosphere and earth system models, and possibly to identify regional or planetary boundaries for biodiversity.

The objective of the second article, entitled "**Extensive Woody Encroachment Altering Angolan Miombo Woodlands Despite Cropland Expansion and Frequent Fires**", was to

assess how changing land use and fire regimes have altered the vegetation structure of the Angolan miombo woodlands by driving and/or inhibiting woody encroachment. It found that from 2000 to 2020, the woody cover of the Angolan miombo woodlands increased by 8.3%, while open grassy ecosystems declined by 62%. Woody encroachment advanced rapidly even in areas experiencing extraordinarily high burn frequencies, and was concentrated far from the agricultural frontier, in remote areas with low population densities. These results challenge the hypothesis that human-altered fire regimes are the primary driver of woody encroachment in mesic savannas, and instead point to increased $CO_2$ concentrations. The large scale of changes to vegetation structure also indicates that woody encroachment is likely threatening open-ecosystem biodiversity as it transforms savannas' species composition and ecosystem function, a hypothesis I investigated in my third article.

The objective of the third article, entitled "**Woody Plant Encroachment Alters Bird Community Composition but not Ecological Function in a Zimbabwean Savanna**", was to quantify how fire suppression and resulting changes to savanna woody cover have altered bird-mediated ecosystem functions in a Zimbabwean savanna. It found that among 70 common savanna bird species, increasing woody cover caused the abundances of 27% of species to decrease and 34% to increase, with losing species distributed evenly across functional lifestyle, diet, and nesting categories. Although increasing woody cover dramatically shifted the bird community's structure, it did not change the absolute strength of bird-mediated ecosystem functions. These results highlight the risk that woody encroachment homogenizes bird communities across African savannas, threatening the diversity and conservation of open-habitat specialists. The results also suggest, however, that the high functional redundancy of savanna birds may make bird-mediated ecosystem functions resilient to woody encroachment, even as woody encroachment causes an overall decrease in consumer control of the ecosystem.

Together, the results of this thesis reveal two major consequences of the change transforming African savannas. First, African savannas are becoming less trophically efficient. As woody plants become more abundant in savannas, they lock up a greater proportion of the ecosystem's energy, leaving consumers—fire and animals—less able to alter vegetation structure and control ecosystem function. Second, savannas are becoming more homogenous. They are experiencing structural homogenization as woody vegetation encroaches into open areas; functional homogenization as human activity depletes unique megafauna-mediated functions; and taxonomic homogenization as communities of open-ecosystem animals are steadily replaced by closed-ecosystem specialists. Combined, these processes are making African savannas more like ecosystems elsewhere: more closed, more dominated by plants, and more devoid of the big animals that trample and devour vegetation and in doing so transform landscapes.

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# Table of Contents

# Thesis Overview

This thesis is article-based and presented according to the requirements for the University of Oxford’s DPhil degree in Geography and the Environment. The thesis is organized into seven chapters and an appendix. **Chapter 1** introduces the thesis and states its aims and research questions. **Chapter 2** contextualizes the thesis in the relevant literature and highlights the key gaps the thesis seeks to address. **Chapter 3** outlines the main methodological frameworks adopted by the thesis to pursue its research questions. **Chapters 4**, **5**, and **6** address the objectives of the thesis in three research articles. **Chapter 7** concludes by synthesizing from the results broader implications for the fields of savanna ecology and global change ecology. Finally, an **Appendix** presents a short letter to the editor of *Global Change Ecology*, published during the thesis, which summarizes a few key implications for science and conservation policy.

# 1. Introduction

## 1.1 Background

There is a growing effort to understand how human activity is changing ecosystems' physical structure and function (Hasan et al. 2020; Watson et al. 2019). One way humans alter ecosystems is by changing vegetation structure and composition (Ellis 2021). Agriculture, pollution, and natural resource extraction are all altering the balance of grasses, shrubs, and trees on a planetary scale (Malhi et al. 2014; Stevens et al. 2022). Another way is by changing the structure and composition of animal communities. Hunting, herding, and land clearing have replaced most wild animal populations with livestock, redistributing biomass and energy among animal trophic guilds (Duffy 2003; Estes et al. 2011; Ceballos, Ehrlich, and Dirzo 2017). Together, changes to plant and animal communities affect ecosystem function: the patterns and flows of energy and material in ecosystems. These functions include flows of food energy, heat, water, carbon, nutrients, and genetic material (Watson et al. 2019; Hooper et al. 2012). Changes to function are the means through which biodiversity loss harms people, as it degrades ecosystem services such as grazing, soil replenishment, freshwater provision, flood protection, and crop pollination (Mace, Norris, and Fitter 2012). To predict the consequences of biodiversity loss, it is therefore essential to understand how function is changing in increasingly human-modified ecosystems.

For nearly a century, ecologists understood ecosystem function to be controlled by plant communities and by the abiotic resources that constrain them (Polis 1999). Beginning in the early 20th century, ecologists understood intact ecosystems as stable climax communities of plants (Clements 1916; Clements 1936). Clearly the structure of these plant communities varied across biomes, as did stocks and flows of carbon and energy. This variation was understood to be caused by differences in abiotic resources, namely light, water, heat, and nutrients (Polis 1999). In 1978, the idea that ecosystems were resource-determined climax communities was complicated by the intermediate disturbance hypothesis, which proposed that only disturbance could maintain tropical ecosystems' high species diversity (Connell 1978). But disturbance was still not seen as fundamentally controlling stocks and flows of energy, carbon, and nutrients. The hypothesis that plants control ecosystem function seemed to be confirmed by most ecosystems' very low trophic efficiency: the proportion of fixed plant energy or net primary productivity (NPP) that is consumed by animals. Ecologists observed that in forests, deserts, grasslands, and tundra, animals consumed just 2% - 11% of NPP (Hairston and Hairston 1993). The higher trophic efficiency of savannas was viewed as an anomaly (Hairston and Hairston 1993). In general, animals appeared to just skim energy off the top of ecosystems without fundamentally shaping ecosystem function. Meanwhile fire, the other great potential energy consumer, was understood to be a human creation largely absent from intact natural ecosystems (Bond 2005).

Traditionally, the climax community concept has informed how ecologists assess ecosystem change, with most studies comparing human-transformed ecosystems to static, natural baselines. For example, ecologists assessing the Amazon's condition define degradation as any decrease in plant biomass whether caused by fire, timber extraction, or edge effects (Lapola et al. 2023). Assessments of global ecosystem carbon stocks, meanwhile, assume that ecosystems are degraded wherever abiotic conditions might allow trees to grow but trees are absent (Bastin et al. 2019). Ecologists have also used baselines to quantify biodiversity loss by determining the proportion of a once pristine landscape changed by cropland expansion or deforestation (Newbold 2018; Tilman et al. 2017; Scholes and Biggs 2005). These assessments of ecosystem condition have mostly assumed that any disturbance, whether logging, defaunation, or fire, is a harmful, degrading process. That assumption may hold true for forests, where function is largely controlled by plants and resources (Malhi et al. 2014). It does not hold true for savannas (Bond 2005).

Over the last 25 years, ecologists have learned that many of the world's open ecosystems, including African savannas, are structured by fire and herbivory rather than by resource limitations (Bond, Woodward, and Midgley 2005; Bond and Keeley 2005; Bakker et al. 2016; Pringle et al. 2023). A combination of dynamic global vegetation models and long-term fire and animal exclusion studies have led ecologists to observe that vegetation biomass is suppressed below its climatic maximum over at least a quarter of the world's land, largely in grasslands, shrublands, and savannas (Bond, Woodward, and Midgley 2005). In these consumer-controlled regions, the physical structure of vegetation is not determined by resource constraints. Instead, fire and herbivory indefinitely prevent trees and shrubs from growing into “climax communities” (Sankaran et al. 2005). In most savannas, then, fire or herbivory or both maintain the biome’s defining vegetation structure: a continuous grassy understory and a discontinuous layer of trees (Scholes and Archer 1997). Additional research has shown that fire and herbivory have maintained this structure for millions of years, indicating that savannas were open, consumer-controlled ecosystems long before humans began to shape ecology (Strömberg 2011; Maurin et al. 2014; He, Lamont, and Pausas 2019; Simon and Pennington 2012). Savanna plant biodiversity has adapted to this disturbance, evolving a unique suite of fire and herbivory-adapted functional traits (Charles-Dominique et al. 2018). Savanna animal have in turn adapted to these specialized plant communities, producing a distinctive savanna biota that is absent from other biomes and dependent on disturbance (Bond and Parr 2010).

Fire and herbivory affect ecosystem function in African savannas through a shared pathway: they both consume energy stored in vegetation (Pausas and Bond 2020). Together, fire and herbivory endow savannas with a unique trophic structure: compared to other biomes, in which most plant energy is ultimately consumed by detritivores, a far greater proportion of plant energy flows up the food chain into animals or out of the ecosystem via fire (Hairston and Hairston 1993; Pausas and Bond 2020). In parts of the Serengeti, for example, up to 40% of the annual energy fixed by plants (i.e. NPP) is consumed by herbivores (Sinclair and Norton-Griffiths 1979). In many other savannas, over 50% of NPP is consumed by fire (Beringer et al. 2007; Archibald and Hempson 2016). Fire and herbivores also shape ecosystem function through their pickiness, with fire limited by plant flammability, and herbivores limited by plant palatability and architecture. As they consume plants unevenly, fire and animals transform patterns of nutrients, carbon, and water, creating heterogenous ecosystems that support a richer biodiversity. Herbivores also perform other ecosystem functions, including seed dispersal, pollination, soil bioturbation, and trampling (Pringle et al. 2023). Meanwhile, non-herbivorous animals impact vegetation structure by controlling herbivore populations through carnivory and insectivory (Ripple et al. 2014). All of these animal-mediated activities ultimately impact the flows of energy and material through the landscape, as they have done for millions of years. Thus, to understand how human activity is affecting ecosystem function in savannas, we need to investigate how land use is altering the relationships between vegetation, fire, and animals. To do so, we need to find ways to translate changes in animal abundances and fire regimes into changes in ecosystem function.

This thesis helps to address these gaps in sub-Saharan Africa, a region where ecosystems remain uniquely consumer controlled (Andela et al. 2017; Archibald and Hempson 2016). Africa experiences the highest rate of natural disturbance in the modern world, in part because open savanna and grassland ecosystems cover ~70% of the continent (Lehmann et al. 2011). Africa accounts for ~65–70% world's burned area each year, despite covering just 22% of the world's ice-free land (Andela et al. 2017). Africa is also home to most remaining megafauna populations, including nearly all mega-herbivores (Faurby and Svenning 2015; Malhi et al. 2016). However, human activity has caused both fire prevalence and megafauna populations to decline across Africa over the last half century, threatening to alter ecosystem function in unpredictable ways (Moritz et al. 2012; Andela et al. 2017; Archibald and Hempson 2016). It is especially important to understand changes to disturbance in Africa's rangelands and near-natural lands, where ecosystems have been neither protected in parks nor converted to cropland. These lightly to moderately used ecosystems, shared by people and wildlife, cover 80% of the continent and host most of its remaining plant and animal populations (Clements, in review). Despite their importance, Africa's lightly and moderately used landscapes receive far less attention than the continent's protected areas and transformed croplands, in part because many have already lost their charismatic megafauna, and in part because the threats to biodiversity within them are subtler than the wholesale conversion of wildlands into croplands, plantations, and cities. A theme of this thesis is therefore to clarify how moderate human use, and associated changes to disturbance regimes, are altering ecosystem function in Africa's unprotected, unconverted savannas.

Over the last decade, ecologists have pulled together new methods to document consumer-mediated changes to African ecosystems. One major research agenda has used long-term plots and remote sensing to reveal a widespread increase in the cover of trees, bushes, and shrubs across sub-Saharan Africa at the expense of open grassy vegetation. Ecologists have shown that this woody plant encroachment is partly driven by decreases in burned area and changing herbivory regimes, particularly a collapse in elephant populations (Stevens et al. 2017; Venter, Cramer, and Hawkins 2018; McNicol, Ryan, and Mitchard 2018). Globally, megafauna extinctions have reduced the proportion of NPP that mammals consume by ~50% (Pedersen, Faurby, and Svenning 2023). Ecologists have less systematically explored the other ways that animals and land use combine to influence ecosystem function. Initial efforts, however, demonstrate that animals substantially shape ecosystems: for example, reductions in disturbance from elephants has been shown to reduce tree size, and thus carbon stocks, in African forests (Berzaghi et al. 2019); and extirpations of fossorial mammals have been shown to facilitate shifts from grasslands into shrublands (Eldridge and Soliveres 2023). What remains missing is a unified framework to incorporate various animal-mediated ecosystem functions into ecological models. Such a framework would need a common currency, capable of relating different functions to each other and to earth system processes, across regions, biomes, and land uses. In this thesis, I demonstrate that an energetics approach to ecology can provide such a framework.

## 1.2 Aim and Structure of Thesis

This primary aim of this thesis is to clarify how humans are changing ecosystem function in consumer-controlled African savannas. It focuses on two links between land use and function: changes to the physical structure of savanna vegetation, and changes to the trophic relationships between savanna plants and animals. Both sets of changes alter flows of materials, including the carbon, nutrients, and water consumed and dispersed by plants and animals. However, to grasp how savannas' physical and trophic structures are related, it is essential to also understand flows of energy. As a framework for analyzing energy flows in savannas, this thesis adopts the theory of consumer control, a theory now broadly accepted by savanna ecologists. According to the theory, savanna vegetation structure is controlled not only by the ability of plants to fix solar energy, but also by the ability of animals and fire to consume the energy that plants fix. I therefore investigate changes to savanna function using two metrics: changes to vegetation structure and changes to energy flow through animals. In ecosystems where vegetation is controlled by consumers, these metrics are now understood to be tightly linked.

To address this aim, the three articles of this thesis quantify changes to (1) animal-mediated ecosystem functions across sub-Saharan Africa, (2) consumer-mediated vegetation structure in an Angolan savanna, and (3) the relationship between changing vegetation structure and changing animal ecosystem functions in a Zimbabwean savanna. Throughout these articles, the thesis also pays attention to scale, with the geographical scope of the analysis narrowing from sub-Saharan Africa, to an ecoregion, and finally a landscape. Compared to a single-scale thesis, this multi-scale approach allowed me to learn a wider variety of ecological methods and frameworks. It also forced me to make connections between scales in order to arrive at a synthesized understanding of how global change is altering the animals, vegetation, and function of African savannas.

The first paper quantifies how land use change and associated changes in animal populations have altered animal-mediated ecosystem function at the scale of sub-Saharan Africa (22,000,000 $km^2$). It adopts an energetics approach to translate change in species abundances into function, quantifying how human land use has changed 23 animal-mediated ecosystem functions, carried out by ~3000 birds and mammals, across the region. Next, it breaks down changes to animal-mediated ecosystem function by biome, land use, and trophic guild, presenting a broad overview of how human activity has changed animal communities and functions across the continent. Finally, it explore how an energetics approach to ecosystem function can incorporate animal-mediated ecosystem functions into continental and global models of the earth system, which currently only model the functions performed by plants.

The second paper investigates how changes to land use and fire have altered the vegetation structure of a consumer-mediated savanna in Angola. It examines change at the scale of the ecoregion: the Angolan miombo woodlands (570,000 $km^2$). This paper addresses a key unresolved question in savanna ecology: what is causing woody cover to increase in the miombo woodlands, Africa's largest and most biodiverse savanna? (Frost 1996; SEOSAW 2020). An ecosystem-wide increase in woody cover would have substantial implications for biodiversity and ecosystem function, altering patterns of carbon, nutrients and water, and potentially decreasing the level of consumer control in affected savannas. However, ecologists still struggle to understand whether increases in woody cover within the miombo woodlands are driven by fire, cropland expansion, herbivore extirpations, or climatic factors such as rising temperature and $CO_2$. The paper helps to fill this gap by employing a remote sensing approach to investigate the drivers of woody encroachment in the little studied Angolan miombo woodlands. It provides evidence that nearly two thirds of the region's open grassy ecosystems have been replaced by woody vegetation and cropland, dramatically diminishing habitat for open ecosystem specialist biodiversity.

The third paper investigates how consumer-mediated changes to vegetation structure are affecting biodiversity and animal-mediated ecosystem function at the scale of the landscape (700km$^2$), and the plot (0.03 km$^2$). Drawing on months of fieldwork on a mixed-use cattle and wildlife ranch in Shangani, Zimbabwe, this paper investigates whether increasing woody cover is altering the species composition of savanna bird communities as well as the ecosystem functions the birds perform. To do so, the paper uses point count data and Bayesian species abundance modeling to estimate changes to the community composition of savanna birds. It then employs the energetics framework from the first paper to translate changes in bird abundances into changes in bird-mediated ecosystem functions such as invertivory, granivory, and frugivory. The results provide a first example of how an energetics approach can be applied to animal community survey data to reveal how global change is altering ecosystem function.

Finally, the conclusion synthesizes the results of each paper with the literature. It strives to advance the field of savanna ecology beyond the bounded conclusions of each article. To do so, it distills two overarching patterns of change encompassing the many human impacts on savannas. First, it argues that human activity has decreased the trophic efficiency of African ecosystems, meaning the proportion of fixed plant energy or NPP consumed by animals. Because African savannas have historically had uniquely high levels of consumer control, they have had greater trophic efficiency than other terrestrial ecosystems (Bond, Woodward, and Midgley 2005; Pausas and Bond 2020). A decline in trophic efficiency would mean that animals are exercising less control over savanna functions relative to plants, degrading a key process that differentiates African savannas from other biomes. Second, the conclusion argues that human activity is changing the diversity of African savannas by homogenizing the biome along three axes. Savannas are experiencing structural homogenization as woody vegetation encroaches on open areas; functional homogenization as unique megafauna-mediated functions disappear; and taxonomic homogenization as communities of open-ecosystem species are steadily replaced by communities of closed-ecosystem specialists. When viewed alongside the trend of declining consumer control, this homogenization paints a portrait of an African savanna that is converging with the world's other biomes and losing the unique consumer-controlled functions that have made savannas exceptional.

## 1.3 Summary of Objectives and Research Questions

**Chapter 1**:

*Objective 1: Provide a quantitative estimate of how changes to land use and animal abundances have altered key bird and mammal-mediated ecosystem functions across sub-Saharan Africa.*

RQ 1.1 How has the human modification of land use changed the amount of energy flowing through bird and mammal trophic guilds and groups of birds and mammal performing key ecosystem functions?

RQ 1.2 To what extent are changes in energy flows through bird and mammal functional groups moderated by the different types of land use change and biomes?

RQ 1.3 How well do biodiversity intactness and species richness indices predict the intactness of energy flows through specific ecosystem functions, and through the whole community of birds and mammals?

RQ 1.4 What are the pros and cons of using ecosystem energy flows to translate changes in land use and biodiversity intactness into changes in animal-mediated ecosystem function?

**Chapter 2:**

*Objective 2: Assess how changing land use and fire regimes have altered the vegetation structure of the Angolan miombo woodlands by driving and/or inhibiting woody encroachment.*

RQ 2.1 What were the rate and extent of woody encroachment and land use change in the Angolan miombo woodlands ecoregion between 2000 and 2022?

RQ 2.2 To what extent have changes in woody cover in the ecoregion been driven by changes in land use cover, fire regime, and climatic variables (i.e. precipitation and temperature).

RQ 2.3 Over what area has woody encroachment altered the ecoregion's structure and function by converting open grassland into closed woodland?

**Chapter 3**:

*Objective 3: Quantify how fire suppression and resulting changes to savanna vegetation structure have altered bird-mediated ecosystem functions in a Zimbabwean savanna.*

RQ 3.1 How has woody encroachment, driven by fire suppression, changed bird abundances and bird-mediated ecosystem functions in a heavily encroached Zimbabwean savanna?

RQ 3.2 To what extent can the species winning and losing from woody encroachment be predicted based on their functional traits?

RQ 3.3 Can mapping energy flows through birds effectively be used to quantitatively link changes in woody cover to changes in animal-mediated ecosystem functions at a landscape scale?

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# 2. Literature Review

The primary aim of this thesis is to advance our understanding of how human activity is changing ecosystem function in consumer-controlled African savannas. To that end, this section reviews ecologists' evolving understanding of ecosystem function, a concept encompassing flows of material and energy through ecosystems, which serves as the conceptual link between biodiversity and human-facing ecosystem services. Historically, research on ecosystem function was biased in three ways. First, it emphasized how function is controlled by plants, rather than animals. Second, it highlighted flows of material, rather than energy. Third, it assumed ecosystems were static and resource-controlled rather than dynamic and consumer-controlled: an understanding suited to forests and deserts but not tropical savannas. After briefly reviewing early research on ecosystem function, I review these biases in turn. In particular, I examine how they are addressed by the growing sub-disciplines of animal functional ecology, ecological energetics, and savanna ecology. I then relate this theoretical discussions of function to the empirical processes changing African savannas: cropland conversion, fire regime change, woody encroachment, and defaunation. Finally, I highlight the gaps in our understanding of savanna function addressed by this thesis.

## 2.1 The Bases of Ecosystem Function

Ecosystems are more than static aggregations of life, rock, and air, of species, minerals, and gases. An ecosystem is also the way its parts move. All ecosystems are powered by energy, which comes overwhelmingly from the sun, although occasionally from the earth's core. This energy constantly rearranges ecosystems' matter by powering life and abiotic processes, such as erosion, tides, and weather. To describe these movements, ecologists use the term "function." IPBES, the global biodiversity authority, defines ecosystem function as "the flow of energy and materials through the biotic and abiotic components of an ecosystem [which] includes many processes such as biomass production, trophic transfer through plants and animals, nutrient cycling, water dynamics and heat transfer" (IPBES 2019). All these fluxes and more make up ecosystem function. In essence, though, ecosystem function describes the way ecosystems move.

Understanding ecosystem function is useful for assessing an ecosystem's condition, meaning its capacity to support biodiversity and people (Mace et al. 2014). That is because function is the link between biodiversity and people: functions are regulated by an ecosystem's species, and they in turn regulate human-facing ecosystem services, such as water regulation and provision, crops, and trees (Mace, Norris, and Fitter 2012). Because functional baselines differ across time and biomes, it is hard to predict which functional states will maximize an ecosystem's condition. The complexity of ecosystem function, including the way its constituent fluxes interact, makes prediction even harder. What is clear, however, is that major shifts in function often threaten biodiversity and ecosystem services (Díaz et al. 2019). Ecosystems that have experienced major shifts are therefore often classified as degraded (Brondizio et al. 2019). To alert societies to the dangers of biodiversity loss, it is therefore important to understand what makes an ecosystem functional and how functions can be measured.

As early as 1953, the renowned ecologist Charles Elton proposed that ecosystem function was supported by biodiversity: that higher diversity made ecosystems more stable, buffering them against invasion and disease (Elton 1953). At first, Elton's ideas were widely accepted. But then ecology transitioned for a few decades into being a more theoretical, mathematical discipline. Early mathematical models showed that ecosystems with more species were less stable and thus more prone to functional collapse (Tilman, Isbell, and Cowles 2014a). By the early 1990s, it became clear that the models did not match reality, drawing ecologists come back to the idea that biodiversity supports function. At a conference in 1993, ecologists launched a series of studies investigating flows of carbon, species, and nutrients, which showed that higher diversity systems were more productive, more resistant to invasion, and less prone to nutrient leaching (Tilman, Wedin, and Knops 1996; Hooper and Vitousek 1997). These studies initiated a major research agenda investigating the bases of function. Hundreds of empirical studies have since shown that ecosystems with high plant diversity are about twice as productive as monocultures and that the difference increase over time (Tilman, Isbell, and Cowles 2014b; Oliver et al. 2015). In drylands including savannas, plant species richness was found to account for 55% of the variation in key ecosystem functions (Maestre et al. 2012). A major meta-analysis, meanwhile, found that the effect of biodiversity loss on function was at least as great as the effect of herbivory, fire, drought, nitrogen addition, or elevated $CO_2$ (Tilman, Isbell, and Cowles 2014b).

Over the last decade, as ecology has focused on understanding global change, function-focused ecologists have sought to scale up their studies (Sage 2020). In particular, there has been a shift from field experiments investigating function at a local scale to analyses tracking function on continental and planetary scales (Sage 2020). To increase scale, ecologists have employed remote-sensing approaches, dynamic global vegetation models, and large networks of vegetation plots (see e.g. Brienen et al. 2015; Aguirre-Gutiérrez et al. 2025; Pavlick et al. 2013). These studies have tended to focus on a plant-related functions, predominantly changes to flows of carbon, forest canopy nutrients, photosynthetic capacity and associated plant functional traits (Pettorelli et al. 2018). This work has especially advanced ecologists’ ability to map how ecosystem functions are responding to human activity.

Even as a functional ecology research agenda took shape, however, three major biases skewed research into function-biodiversity relationships. First an overwhelming focus on plants obscured the functions performed by animals. Ecological research into animals tended to deal with populations and communities, rather than with flows of energy and material (Schmitz et al. 2018). Second, a focus on the material components of function, particularly carbon given its importance to climate change, caused ecologists to largely overlook flows of energy (Antunes et al. 2024). Research into energy flows through animals and animal-moderated functions were especially underexplored. Third, a longstanding bias toward work in temperate ecosystems and forests caused functional ecologists to underemphasize tropical open ecosystems. These biomes, which include savannas, function in distinctive ways due to their evolution as consumer-controlled ecosystems, dependent on animals and/or fire (Bond 2005; Bond and Parr 2010). The rest of this literature review addresses these biases in turn, reviewing ecologists’ growing efforts to right them, and outlining how this thesis advances those efforts.

## 2.2 Bringing Animals into Ecosystem Function

In 1988, John Terborgh became the first major modern ecologist to propose that large animals dramatically shaped ecosystem function. Terborgh hypothesized that in Amazonia, plants, the top predators, rather than plants, “held the key to ecosystem stability and to the maintenance of [Amazonia’s] extraordinary diversity of plants and animals” (Terborgh 1988). Predators, Terborgh suggested, propagated “perturbations through one or more levels in an ecosystem” that in turn impacted seed dispersal, nutrient dispersal, vegetation consumption by herbivores, vegetation recruitment, and ultimately carbon stocks (Terborgh 1988; Terborgh et al. 2001). For decades, however, faulty assumption caused ecologists to mostly ignore Terborgh’s hypotheses. Because flows of energy up the trophic chain are inefficient, herbivores and carnivores are orders of magnitude less abundant than plants (Bar-On, Phillips, and Milo 2018). Ecologists assumed that animals’ relative rarity prevented them from generating major feedback effects on plants and thus flows of carbon, energy, and nutrients (Schmitz et al. 2018). Another problem was that animal-mediated ecosystem functions were hard to test at scale: the loss or addition of species within an ecosystem can take decades or even centuries to meaningfully change function (Estes et al. 2011). As a result, until about 2010, few studies linked animal-focused community ecology to work concerning flows of energy and material (Schmitz et al. 2018). Over the last 15 years, however, advances in paleobiology have reemphasized the ecological importance of animals. These studies have sparked an effort to reintegrate animals into functional ecology and earth system science, as has growing concern about function’s role in sustaining ecosystem services (Svenning et al. 2024; Malhi et al. 2016). A new wave of animal-focused functional ecologists have sought to (1) identify the ecosystem functions moderated by animals, (2) directly test functions’ strength through exclosure and reintroduction experiments, (3) assess how megafaunal extinctions have changed ecosystem function long-term, and (4) model changes in ecosystem function strength over large spatial scales.

Ecologists have determined that animals shape ecosystem functions through three processes (Svenning et al. 2024). First, animals transport matter, including nutrients, seeds, pollen, and other animals. Second, animals consume food, driving trophic processes that enforce top-down controls on other species, which in turn shape flows of material and energy. Third, animals physically engineer their environment, churning soil, trampling plants, and creating cavities, tunnels, and dams. This engineering directly moves matters and indirectly alters flows of matter, creating an enormous impact on the planet's geomorphology (Harvey et al. 2025). Within these primary categories, animals perform many functions. Systematically identify these has been a key goal of animal function ecologists. An early example of this work was a 2006 review of bird-moderated ecosystem functions, which sought to combat the "impression that birds have little influence on ecological processes" by cataloguing birds' pollination, invertivory, granivory, predation, cavity drilling, and nutrient transport (Sekercioglu 2006; see also Şekercioğlu and Buechley 2016). Other work has identified functions performed by megafauna (Pringle et al. 2023; Ripple et al. 2015; Malhi et al. 2016), apex carnivores (Ripple et al. 2015; Malhi et al. 2016), bats (Kunz et al. 2011), primates (Chapman et al. 2013), soil vertebrates (Eldridge and Soliveres 2023), digging animals (Fleming et al. 2014), and freshwater megafauna (He et al. 2024). Research has also identified functions performed by reptiles and amphibians (Cortéz-Gómez et al. 2015; Valencia-Aguilar, Cortés-Gómez, and Ruiz-Agudelo 2013; Hocking and Babbitt 2014). Finally, there has also been extensive work examining the functional contributions of invertebrates, which falls outside the scope of this thesis. For ecologists attempting to make sense of this throng of animal-mediated functions, one key insight is the exceptional importance of megaherbivores, meaning of species that way over 1000 kg. Megaherbivores impact ecosystems uniquely because their size shields them from predation (R. N. Owen-Smith 1988). Freed from top-down controls, megaherbivores can reach very high population densities and transform vegetation through widespread grazing and browsing. Today however, megaherbivores are rare: of 57 late Pleistocene megaherbivores, only 11 remain (3 elephants, 4 rhinos, the hippo, the giraffe, and two bovines), and even these remain functionally abundant in only few places, notably protected African savannas (N. Owen-Smith 1987; Svenning et al. 2024).

As ecologists have identified animal-mediated functions, they have sought to directly test the functions' strength. However, few functions have been quantified, because designing experiments to measure animal-mediated functions is logistically challenging and time consuming. Herbivory has been by far the most tested function, generally through exclosure experiments. There is now a wide literature measuring the direct local impacts of herbivores on vegetation, including work measuring elephant impacts on savanna vegetation (Asner and Levick 2012; Davies, Gaylard, and Asner 2018); reindeer impacts on tundra and boreal forest vegetation (Spiegel et al. 2023; Macias Fauria et al. 2008), and bison impacts on prairie vegetation (Towne, Hartnett, and Cochran 2005). Intriguing efforts to measure other animal-mediated ecosystem functions have been less systematic. For example, Lundgren et al., (2021), using camera traps, found that equids in North American deserts dig wells, changing patterns of surface water and vegetation structure, and increasing vertebrate richness. Other work has examined how seed dispersal links large animals to forest structure, finding that forest elephants disproportionately contribute to the dispersal of large-seeded trees and to forest carbon storage (Campos-Arceiz and Blake 2011; Bello et al. 2015). Work on carnivores, meanwhile, has focused on measuring the impacts of trophic cascades, either by quantifying how reintroduced carnivores change vegetation patterns (Fortin et al. 2005), or by assessing correlations between predator behavior, prey behavior, and herbivory patterns (Lundgren et al. 2022). While these local studies have identified how animals impact ecosystem function, they have been challenging to scale up across landscapes. Scaling problems have limited assessments of how animals shaped vegetation across biomes and continents. Large-scale studies are also needed to assess how animals affect the flows of material and energy that stabilize the earth system.

One solution has been to assess how the late Pleistocene megafauna extinctions impacted ecosystem structure and function. Paleoecologists determine when extinctions took place using paleorecords of a megafauna-dependent fungus *Sporormiella*, and then compare *Sporormiella* with records of charcoal and pollen (Rule et al. 2012). Many palaeoecological studies indicate that Pleistocene megafauna extinctions changed ecosystem function, although the nature of the changes varied across biomes and continents. In North America, palaeoecological evidence suggest that extinctions in prairies and forests increased fire and released hardwoods from herbivory (Gill et al. 2009). In Australian rainforests, extinctions also appear to have increased fire, causing sclerophyllous, fire-resistant vegetation to replace hardwoods (Rule et al. 2012). A global analysis of grassland charcoal records, meanwhile, found that extinctions of grazers, but not browsers, amplified fire in grassy ecosystems (Karp et al. 2021). Finally, e-DNA suggests that megafauna extinctions helped transform the forb- and grass-dominated mammoth steppe into a moss and shrub-dominated tundra (Murchie et al. 2021). Together, the palaeoecological record shows megafauna shaping biomes-scale patterns of vegetation and fire, which would in turn have shaped carbon and nutrient flows. Palaeoecological studies do not, however, illuminate how other, smaller animals affect ecosystem function. They have also been limited to a few biomes on a few continents and therefore cannot comprehensively analyze animal-function relationships.

Another way that functional ecologists have scaled up their analyses is by using predictive models to estimate how more species impact function over wide areas. In the most extensive spatially-explicit model of changes to animal-mediated ecosystem function, Hempson, Archibald, and Bond (2017) estimated how replacing large wild herbivores with livestock has impacted nutrient dispersal, methane emissions, and woody cover across sub-Saharan Africa. But even this study, the most extensive across space and species, assessed the functions of only ~8% of Africa's mammals, comprising 90 species. Other modeling studies, focused on South American biomes, have predicted large (29%) increases in savanna woody cover and astonishing (98%) decreases in forest nutrient dispersal as a result of megafaunal extinctions (Doughty, Wolf, and Malhi 2013; Doughty, Faurby, and Svenning 2016).

Together, the last fifteen years of research have shown that animals considerably impact ecosystem structure and function, emphasizing impacts on flows of carbon (in the form of vegetation) and nutrients. These these various lines of evidence were synthesized in a major meta-analysis of models and plot-based studies investigating "zoogeochemical processes" (Schmitz et al. 2018). It found that across all studies animals changed biogeochemical processes by a median value of 40% (Schmitz et al. 2018). It also noted that ecologists have been unable to model these changes across large spatial and taxonomic scales and across multiple functions (Schmitz et al. 2018). The creators of the Planetary Boundaries Framework identifed a similar problem, explaining that "the link of BII [biodiversity intactness indices] to Earth system functions remains poorly understood and BII cannot be directly linked to the planetary biogeochemical and energy flows relevant for establishing Earth system state" (Richardson et al. 2023). There is thus a need for a new approach to integrate animals into earth system science, one that can encompass thousands of species and dozens of functions on a continental or global scale. Such an approach will require a common currency for comparing species and functions.

By adopting the currency of energy to analyze all the birds and mammals of sub-Saharan Africa, this thesis's first article aims to fill that gap.

## 2.3 Ecosystem Function through an Energetics Lens

To address the question of animal-mediated ecosystem functions, this thesis adopts an energetics framework. Energetics approaches have a long history in ecology, dating to the foundation of the discipline (Lindeman 1942; Slobodkin 1962). The insight motivating energetic approaches is that nearly all ecosystems are powered by sunlight, which is captured by plants via photosynthesis, and flows up the trophic web as food energy. Energy thus serves as a common currency that can compare the activity of any species in any ecosystem, and can be quantitatively related to other measures of function such carbon and nutrient flows and even to geomorphological processes such as storms and erosion (Malhi et al. 2022; Harvey et al. 2025). Energetics approaches in ecology have mostly been used to quantify trophic relationships and to understand the structure of ecological communities (Moore and de Ruiter 2012; Hairston and Hairston 1993). However, as early as 1968, energy flows were proposed as a way to assess function, with Eugene Odum praising "the efficacy of rates of population energy flow as a measure of importance in community function" (Odum 1968). Of course, energy flow is also a component of ecosystem function itself. Even so, very few ecological studies since 1970 have used energetics to assess function, instead focusing on flows of nutrients, carbon, and genetic material. Energetics approaches have been particularly limited by their reliance on large species abundance datasets, which are hard to create (Malhi et al. 2022).

Energetics approaches have only reemerged over the last decade as a means to understand animal-mediated ecosystem functions. They address a key problem in ecology: the lack of a generalizable approach to relate animal biodiversity to function within complex, multi-trophic ecosystems (Antunes et al. 2024). As a metric of animal-mediated ecosystem function, energetics approaches have three advantages. First, energy is an ecologically meaningful common currency, which can be compared across all species and ecosystems. Second, energy flows can quantitatively relate animal-mediated functions to plant-mediated functions such as net primary productivity, and ultimately to earth system processes such as fire regimes and carbon sequestration. Third, energy flows capture an ecologically meaningful process, food consumption, providing energetics an advantage over other biodiversity metrics such as presence-absence data, abundance, or biomass. These advantages are explored in detail in the conclusion of Chapter 4.

Despite these advantages, the new functional energetics agenda is only just emerging. A 2018 review of energetics approaches described its untapped potential: “Although the concept of energy flux in food webs is not novel, its application to BEF [biodiversity-ecosystem function] research remains virtually untapped, providing a framework to foster new discoveries into the determinants of ecosystem functioning in complex systems” (Barnes et al. 2018). So far, existing efforts have used two strategies. The first is to use aggregate energy flow as a metric of an ecosystem’s overall functionality or health (Barnes et al. 2018). This category of approaches was pioneered in a study of insect energy consumption across a land use gradient in Borneo. Adopting an energetics approach revealed that ecosystems lose energetic intactness and thus functionality long before they lose species (Barnes et al. 2014). A problem with this strategy, however, is that ecosystem function is not solely dependent on the amount of energy flowing through a system. The distribution of energy among animal species and functional groups also matters. When an increase in energy is dominated by just a few species, as for example in an algal bloom, increased energy flow can indicate degradation rather than vibrancy. To address this problem, another study in Borneo integrated changes in the magnitude of energy flows with changes in the evenness of energy flows, using a Shannon diversity index (Malhi et al. 2022).

The second strategy is to quantify changes in energy flows through individual animal-mediated ecosystem functions, rather than to assess the aggregate functionality of ecosystems. It is very new research agenda: when I began working on this thesis, I was aware of no previous study that had used energy flows to map changes to multiple individual ecosystem functions over large spatial scales. Since I began, Antunes et al., (2024) have provided a useful theoretical framework for how this approach can work, describing how energy flows can be used to relate biodiversity change to ecosystem functions and ecosystem services. The authors also provide a proof of concept by mapping energy flows through carnivores across Europe to assess predator control of an agricultural pest, the common vole (*Microtus arvalis*). An earlier study, by Hempson and Archibald (2017), also used energy flows through large herbivores to estimate change in herbivory, although the authors did not make their energetic approach explicit. Both studies, however, have investigated only a single function, and energetics approach have not yet been applied to multiple functions over large geographical areas. Chapter 4 of this thesis addresses this gap, dramatically upscaling previous energetics analyses to estimate energy flows through all the wild birds and mammals inhabiting sub-Saharan Africa, and to assess the strength of key bird- and mammal- performed functions, such as pollination, herbivory, carnivory, and seed dispersal. Chapter 6 also takes an energetics approach to understanding function, investigating how a global change process, woody encroachment, has affected bird-mediated functions in savannas. My hope is that together, these papers can advance a research agenda that uses energetics approaches to clarify how human are changing animal-mediated ecosystem functions.

## 2.4 Ecosystem Function in Savannas

If integrating animals and energy flows represents the first two major shifts in the study of ecosystem function, incorporating disturbance, particularly the positive roles of fire and herbivory, marks a third. Ecologists' understanding of disturbance has been transformed by the sub-discipline of savanna ecology, which has revealed how fire and animals shape the structure and function of savannas as consumers of vegetation(William J. Bond 2019; 2005; Strömberg and Staver 2022).

Savannas are defined as ecosystems co-dominated by a continuous layer of grass and a discontinuous layer of trees (Scholes and Archer 1997). Tree cover in healthy savannas ranges from 10% to ~40%, making savannas neither pure grasslands nor forests. Alongside grasslands, where tree cover is <10%, savannas make up the broader category of open or grassy ecosystems (UNESCO 1973; William J. Bond 2019). For centuries, historians and policymakers believed savannas to be degraded forests, in which clearing and human-ignited fires prevented succession (William J. Bond and Parr 2010). Ecologists assumed that savannas had degraded ecosystem function, with too much energy and carbon released by fire, and too little carbon and energy stored in trees. To improve savanna ecosystem function, ecologists and decisionmakers proposed schemes to plant trees and suppress fire on public and private lands (Bastin et al. 2019; William J. Bond 2019; Frost 1999). Such schemes are still often proposed today, despite research showing that tree planting and fire suppression in fact threaten savanna biodiversity and degrade function (Parr, Te Beest, and Stevens 2024; Djiofack et al. 2024; Loft et al. 2024; Veldman et al. 2019).

### *2.4.1 Disturbance in Savannas*

Two lines of evidence have overturned the assumption that savannas are degraded ecosystems, and shown that savannas have in fact been shaped by disturbance for millions of years. First, ecologists investigating the processes maintaining savannas have revealed that savannas are controlled by consumers and thus dependent on disturbance, but not necessarily on human-created disturbance. Second, ecologists investigating the paleobiology and evolutionary history of savannas have shown that savannas arose millions of years before humans controlled fire.

To explain savanna's structure and distribution, ecologists have developed a theory of disturbance-dependence and consumer control. In a seminal article on savannas, Scholes and Archer (1997) showed that the coexistence of trees and grasses in savannas could not be explained by resource partitioning based on rooting depth. Reviewing hundreds of articles on the determinants of savanna vegetation structure, the authors concluded that tree-grass codominance could only be explained by disturbance, namely herbivory and fire. In another seminal article, Bond, Woodward, and Midgely (2005) showed that fire and herbivory suppress tree cover below its climatic maximum across the world's open ecosystems, including savannas. Their work upended the understanding of ecosystems as resource-determined climax communities, instead revealing savanna vegetation as controlled by consumers, namely herbivory and fire (William J. Bond 2005; Pausas and Bond 2020). Further research indicated that fire and herbivory maintain savannas through positive feedback loops (Beerling and Osborne 2006; Staver, Archibald, and Levin 2011). Below about 45% tree cover, enough sunlight reaches the ground to support palatable and flammable grass, which feeds herbivores and fuels fire (Beerling and Osborne 2006; Staver et al. 2021). Fires and herbivores in turn consume saplings, limiting tree cover, and allowing sunlight to reach the grassy layer. Above about 45% tree cover, however, the closed canopy increases humidity and stops sunlight from reaching grasses, limiting fuel for fire and forage for herbivores (Oliveras and Malhi 2016). Canopy closure establishes a positive feedback loop, with diminished disturbance further increasing tree cover, which in turn further limits grassy fuel, and thus further suppresses disturbance (Staver, Archibald, and Levin 2011; Huntley and Walker 2012). For many savannas to remain savannas, then, they must burn or be eaten regularly.

Studies on the distribution of savannas provide further evidence that savannas are disturbance-dependent. Using vegetation plots and climate models, these studies show that climate and soil alone cannot predict the distribution of savannas, particularly at the savanna-forest boundary (Bond 2005; Sankaran et al. 2005). Some proportion of land is always “not savanna over the whole range of climates and soils in which savannas exist,” (Lehmann et al. 2011). The distribution of mesic savannas in particular—which occur where mean annual precipitation exceeds 650mm—is best explained by fire-driven feedback loops (Staver, Archibald, and Levin 2011). In many mesic savannas, frequent lightning and a long dry season make annual or biennial fire inevitable even without human ignitions (Archibald et al. 2009). On the arid end of the savanna distribution, meanwhile, herbivory limits shrub encroachment, allowing megafaunal African savannas to extend into more arid climates than demegafaunated South American and Australian savannas (Lehmann et al. 2011). Nutrient-poor soils in savannas also play a role in arresting succession into forests (Veenendaal et al. 2018), but models that include soil type and disturbance suggest soil type alone is highly unlikely to explain savannas’ distribution (Sally Archibald and Hempson 2016). Together, this research overwhelmingly indicates that savannas are consumer-controlled biomes with a structure dependent on disturbance.

Two lines of evidence, palaeobiological records and species endemism, show that disturbance in savannas is ancient and natural. Pollen and carbon records indicate that frequently-burning, grass-dominated African savannas evolved between 5 and 10 MA, long predating human mastery of fire (Strömberg 2011; Strömberg and Staver 2022). Palaeobiological records of charcoal, fire biomarkers, and stable carbon isotopes also show that fire has occurred regularly in African savannas for at least seven million years (Hoetzel et al. 2013; Stevens et al. 2022).

Moreover, spatially-explicit fire propagation models suggest that burned area in African savannas peaked at least 4,000 years ago before declining until today (Archibald, Staver, and Levin 2012; Andela et al. 2017). Floristic evidence, meanwhile, shows that distinct communities of savanna specialist tree species grow within mesic savannas but not in adjacent arid savannas or forests (Aleman et al. 2020; F. White 1983). Principles of evolutionary biology indicate that such a diverse and specialized flora could not have evolved in the short period after humans mastered fire (Maurin et al. 2014). This floristic and palaeoecological evidence thus overwhelmingly suggests that the disturbance shaping savannas is ancient, and that changes to savanna disturbance regimes would degrade ecosystem function and endanger savannas' disturbance-dependent biodiversity (Veldman 2016; Parr, Gray, and Bond 2012).

Because savannas depend on disturbance, they function differently from static, resource-controlled ecosystems. Flows of energy and material in intact savannas should therefore not be assessed based on patterns and baselines from better studied biomes, such as forests deserts, and wetlands. In forests, for example, increased outflows of carbon and energy caused by fire are considered degradation. In savannas, however, fire and herbivory cause large natural flows of energy and carbon to move through vegetation annually (Grace et al. 2006). These carbon outflows constitute natural ecosystem function, while increases in carbon stocks caused by woody encroachment can constitute degradation (William J. Bond 2019; Buisson et al. 2019). Because of this complexity, savanna ecologists increasingly argue that efforts to assess degradation in savannas must assess changes to both function and biodiversity (Veldman 2016). In particular, these efforts should assess whether structural changes in savannas threaten savannas' endemic, disturbance-dependent species (Veldman 2016; Veldman et al. 2015).

### *2.4.2 Global Change in Savannas*

Efforts to track biodiversity and function in savannas have intensified as humans transform the biome. Perhaps the most visible form of global change in savannas is conversion to cropland. Globally, a greater proportion of savannas has been converted than of any other tropical biome, although the proportion lost in Africa is lower than on other continents (Ellis 2021; Potapov et al. 2022). In the last two decades, however, cropland conversion in African savannas has accelerated (Potapov et al. 2022). By 2060, agriculture is projected to clear another 430 million ha of natural vegetation in Africa, equal to 18% of the continent's land (Tilman et al. 2017). Analysist expect future conversion to be concentrated in Africa's mesic savannas, particularly the miombo woodlands of South-Central Africa (Eigenbrod et al. 2020; Tilman et al. 2017). Cropland conversion dramatically changes savannas' ecosystem function, decreasing aboveground and belowground carbon, depleting soil nutrients, and dramatically reducing biodiversity (Clements et al. 2024; Osborne et al. 2018; Veldman 2016). Cropland expansion also fragments landscapes, a process that prevents fires from spread and amplifies direct threats to wildlife such as hunting, logging, and charcoal gathering (Sally Archibald et al. 2009; Carvalho, De Marco, and Ferreira 2009; Zorrilla-Miras et al. 2018). Despite the scale of these changes, the complex interactions in savannas between land use change, fire, and vegetation structure are not very well understood (SEOSAW 2020). Chapter 5 of this thesis aims to address that gap in one of the world's least studied savannas, the Angolan miombo woodlands.

Besides driving cropland expansion, human activity is also affecting savanna structure and function by changing fire regimes. Historically, fires in savannas and grasslands have been distinct from fires in other biomes; they have been cooler, smaller, more grass-burning, and less likely to burn tree crowns (Archibald et al. 2013). Today, Africa still has by far the greatest annual burned area of any continent (Andela et al. 2017). Two mesic African savannas, the miombo woodlands and the Sudano-Guinean woodlands experience the planet's highest burn frequencies (Archibald et al. 2013; Andela et al. 2017). However, fire models suggest burned area in Africa has decreased over millennia, and remote sensing confirms a decrease in the frequency and size of fires over the last twenty years (Andela et al. 2017; Archibald, Staver, and Levin 2012). These change have been driven by human agricultural activity, including cropland expansion, as well as hunting, and herding, which change how much fuel animals consume (Archibald, Staver, and Levin 2012).

Changes to fire regimes in savanna alter ecosystem function, including patterns of nutrients, carbon, and biodiversity. For example, frequent fires significantly decrease soil nitrogen, although they do not impact soil phosphorus (Pellegrini et al. 2015; Strydom et al. 2019). These changes in soil nutrient concentrations do not alter savanna vegetation stoichiometry, however, suggesting that vegetation in savannas is uniquely adapted to fire-driven nutrient losses (Pellegrini et al. 2015). In fact, fire may even improve forage for grazers, by concentrating nutrients in new growth (Van de Vijver, Poot, and Prins 1999). In terms of carbon, fire suppression appears to be increasing aboveground woody cover, although its impacts are hard to disentangle from other drivers of woody encroachment, a problem explored in the next section (Venter, Cramer, and Hawkins 2018; Archer et al. 2017). In mesic savannas, fire may also prevent encroachment by limiting soil nitrogen, which more severely constrains forest species than fire-adapted savanna species (Pellegrini 2016). These large increase in woody cover do not seem to proportionately increase carbon stocks, however. A 60-year fire exclusion experiment in South Africa reported that 79% increase in tree cover only increased carbon storage by 35%, a discrepancy caused by savannas' substantial belowground carbon stores, which are generated by grass rather than woody vegetation (Zhou et al. 2023). Changing fire regimes also change biodiversity; 28% of threatened species in savannas are threatened in part by changing fire regimes, the highest proportion of any biome (Kelly et al. 2020). These relationship between fire and biodiversity are often mediated by changes to habitat structure, particularly changes in the balance between trees, shrubs, and grasses (Archer et al. 2017; Clélia Sirami et al. 2009).

Another symptom of global change in unconverted savannas is widespread woody plant encroachment, defined as a unidirectional increase in woody plant cover (William J. Bond and Midgley 2000; Archer et al. 2017). A remote sensing analysis of Africa's grassy ecosystems reported an 8% increase in continent-wide woody cover between 1986 and 2016, and a 14% increase in Angola and Zimbabwe, the countries analyzed in Chapters 5 and 6 of this thesis (Venter, Cramer, and Hawkins 2018). Moreover, woody encroachment in Africa appears to be accelerating (Stevens et al. 2017). The reported drivers of woody encroachment include both local and global factors, including fire suppression, elevated $CO_2$, changing herbivory patterns, and changes to temperature and precipitation (William J. Bond and Midgley 2000; Buitenwerf et al. 2012; Venter, Cramer, and Hawkins 2018; Archer et al. 2017). The importance of these drivers probably differs between mesic and arid savannas. Woody plant encroachment is much better understood in arid savannas, where it manifests as increasing bush and shrub cover and is at least partially regulated by disturbance. In South African arid savannas, woody cover in increasing in all landscapes except those retaining both fire and elephants (Stevens et al. 2016).

By contrast, the drivers and character of woody plant encroachment are less well understood in mesic savannas, where it is unclear whether shrubs, savanna trees, or forest trees behind greening trends (SEOSAW 2020). There is some evidence that miombo trees in savannas may be more sensitive to carbon emissions due to their root morphology, elevating $CO_2$'s importance as a driver (Wakeling and Bond 2007).

Woody encroachment profoundly impacts savanna ecosystem function beyond simply increasing tree and shrub cover. Rising woody cover fundamentally changes patterns of carbon, water, forage, habitat, and ultimately biodiversity, in what has been termed a socioecological regime shift (Luvuno et al. 2018). In some savannas, trees and shrubs use more water than grasses, increasing transpiration, and leaving less surface water available for animals (Huxman et al. 2005). In other savannas, increased shade can decrease evaporation and thus conserve soil moisture (Archer et al. 2017). Woody encroachment also generally eliminates forage for grazers and livestock, as palatable grass is replaced with less palatable woody vegetation (Luvuno et al. 2018). Fire, too, is impacted as more shade, more moisture and less grassy fuel makes ecosystems less flammable (Staver, Archibald, and Levin 2011). Finally, there is a growing literature showing that woody plant encroachment has driven large changes in animal communities in savannas and grasslands, including in North America, Africa, and Brazil (Abreu et al. 2017; Smit and Prins 2015; Andersen and Steidl 2019; Sirami et al. 2009; J. D. M. White et al. 2024). The effects of these changes on trophic energy flows remain unexplored, however, and it is unclear if decreases in flows through mammalian grazers are offset by increases through leaf-eating species, such as mammalian browsers and folivorous insects. It also remains unclear whether winning and losing species can be predicted based on their traits or habitat preferences. Yet another gap is whether changes in species composition impact plot-level biodiversity, although at least one study shows species diversity peaking at moderate levels of woody cover (Sirami and Monadjem 2012). Broad-scale biodiversity is likely falling, though, if the same open-ecosystem species are declining everywhere due to the widespread replacement of grassy ecosystems with shrub-dominated ones (Parr, Gray, and Bond 2012).

A final feature of global change in African savannas is a widespread decline in animal populations. Human-driven extinctions began in the late Pleistocene, with the loss of hundreds of large mammals, including 80% of megaherbivores globally (Svenning et al. 2024). Although Africa was less affected than other continents, it did experience some large mammal extinctions in the late Pleistocene. And there is increasing evidence that pre-human hominids restructured the size-biomass distribution of African animals, by causing substantial megafauna extinctions in Africa in the early and mid-Pleistocene, beginning 700,000 years ago (Bibi and Cantalapiedra 2023). It is unclear what effect these extinctions would have had on herbivory. On the one hand, large animals are more metabolically efficient than small ones, so a faunal downsizing may have increased herbivory by hungry small animals. On the other hand, large animals are less vulnerable to top-down predator control, so a faunal downsizing may decreased herbivory by amplifying predators' ability to control herbivore populations.

Over the last century, biodiversity loss in Africa has accelerated, and a number of continental and planetary indices track modern declines in species richness and abundance (Newbold et al. 2016; Watson et al. 2019; Almond, Grooten, and Peterson 2020; Clements et al. 2024). These indices reveal two broad patterns. First, declines in animal abundances have been substantial in Africa, with populations falling by at least 20% if not much more. The Living Planet Index, which tracks animal abundances, found that 1100 populations of terrestrial and freshwater Afrotropical species declined by 56% between 1970 and 2014 (Almond, Grooten, and Peterson 2020). The biodiversity intactness index for Africa, which extrapolates changes to animal abundances from expert estimates and land use maps, estimated that mammals have declined by 34% since ~1700 (Clements et al., In review). Second, human activity has most severely affected large herbivores and apex carnivores, groups which have unique and outsized impacts on ecosystem function. For example, the biodiversity intactness index estimated that large mammals declined by 74%, versus a 29% decline among all terrestrial vertebrates (Clements et al., In review). Globally, 47% of animal species weighing >10kg and 60% of the world's largest herbivores are threatened with extinction, compared to just 28% of total assessed species (IUCN 2025; Ripple et al. 2015). Another approach to tracking animal declines has been to track the populations of apex predators as proxy for intact savannas, as apex predators require the largest tracts of intact habitat among animal species. Taking this approach, a study found that lions occupy just 25% of their historic range in African savannas, suggesting that 75% of African savannas are no longer trophically intact, and are thus missing key animal-mediated ecosystem functions (Riggio et al. 2013). Avian predators have also experienced pervasive declines in savannas, with 69% of African savanna raptors declining by at least 30% since the 1980s (Shaw et al. 2024). Over the same period, Africa experienced large increases in livestock populations, and while overall biomass has decreased substantially, livestock biomass now exceeds historical herbivore biomass in many arid savannas (Hempson, Archibald, and Bond 2017). However, livestock are much less functionally diverse than wild herbivores, and provide only a simplified suite of functions in comparison (Hempson, Archibald, and Bond 2017).

The widespread decline in animal populations is almost certainly changing savanna function, but our understanding of these changes remains limited. Because the impacts of large mammals are most well understood, I focus on them here, although Chapters 4 and 6 also investigate changes to functions performed by small mammals and birds. (Insects also impact ecosystem function in profound ways, but our ability to track their declines in Africa remains extremely limited, and our ability to track changes to their functions remains nearly nonexistent). A synthesis of plot-based studies across mostly arid African savannas found that herbivory decreased grass abundance by 57% and tree abundance by 31% (Staver et al. 2021). The absence of elephants in particular was found to drive woody plant encroachment, as saplings were released from predation (Stevens et al. 2016). Ecologists also hypothesize that introducing high density livestock into arid systems is eroding soil and depleting plant biomass, although these relationships have not been tested at a regional or continental scale (Hempson, Archibald, and Bond 2017). Finally, the collapse of migratory herbivore populations, coupled with the fragmentation of remaining natural landscapes, has caused lateral nutrient transport to fall by over 95%, even as herbivore methane emissions have doubled (Hempson, Archibald, and Bond 2017).

Severe declines in large carnivores also influence ecosystem function, although their impacts on African savannas are even less well understood than those of herbivores. In theory, large carnivores extirpations can unleash trophic cascades that increase large herbivore populations, release meso-predators from competition, and suppress small herbivores (Ripple et al. 2014). Historically, however, even apex carnivores have not managed to limit megaherbivore populations. Carnivores may therefore not be able to affect total vegetation biomass in landscapes that contain elephants and rhinos (R. N. Owen-Smith 1988). This theory is supported by empirical evidence showing that African lion reintroductions shift herbivore communities toward larger species, but do not change total herbivore biomass (Le Roux et al. 2019). As such, the major impact of predator extirpations in landscapes with mega-herbivores is likely not to increase herbivory but to redistribute it, in accordance with changing landscapes of fear. This redistribution is in turn likely to repattern carbon and nutrient flows, as herbivores move and eat in different places. The examples of how large herbivores and carnivores impact savannas show that (1) animal activity is a major determinant of ecosystem function (2) animal effects on function can be complex and surprising, and (3) animal effects are only beginning to be assessed and understood. This thesis attempts to contribute to that growing understanding.

## 2.5 Synthesis and Research Gaps

The aim of this thesis is to advancing our understanding of ecosystem function in changing, fire- and animal-shaped African savannas. This review shows that fire, woody plant encroachment, and cropland expansion are major drivers of change to ecosystem function in African savannas. It also show that the role of animals in mediating global change is only beginning to be understood.

Chapter four of this thesis develops a metric, energy flows, to assess how animal-mediated functions have changed across Africa in response to global change. While a review of the literature presents consistent evidence that global change has caused African wildlife populations to decline, ecologists have been unable to translate those declines into changing ecosystem function beyond the well-studied large herbivore guilds. Chapter four estimates how animal-mediated functions have responded to human activity by quantifying continent-wide changes to bird and mammal food energy consumption. Chapter five addresses a different gap: the poorly mapped relationships between the key drivers of global change in savannas, which include cropland expansion, fire regime alteration, and woody plant encroachment. To address that gap, chapter five investigates how these three global change processes have combined to alter vegetation in an African mesic savanna, the Angolan miombo woodlands. Finally, chapter six addresses the problem of feedbacks between animal-mediated changes to savanna function and disturbance-mediated changes to savanna function, the subjects of chapters four and five. Observing that global change processes such as fire suppression and woody encroachment are altering savannas' animal communities, this chapter explores how changing animal communities in turn alter the ecosystem functions that mediate global change.

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# 3. Methodological Overview

The aim of this thesis, as outlined in Chapter 1, is to advance understanding of how human activity affects consumer-mediated ecosystem function in African savannas. For each of this thesis's three articles, I approach this question from a distinct scale and using distinct methods. In chapter 4, I take a macro-ecological approach to analyze animal-mediated ecosystem function at the scale of sub-Saharan Africa (24,000,000 $km^2$). In Chapter 5, I employ a remote sensing approach to assess consumer-mediated changes to vegetation structure at the scale of an ecoregion (570,000 $km^2$). In Chapter 6, I combine field data with Bayesian modeling approach to assess the relationship between fire-mediated vegetation structure animal-mediated function at the scale of the landscape (700 $km^2$) and the plot (0.03$km^2$).

I varied the methods within my DPhil in an effort to broaden my understanding of how ecologists think about global change. Clearly, the processes changing the planet's ecosystems, are extraordinarily complex. Climate change, land use conversion, and defaunation generate countless feedback loops and interactions. To understand how these processes change ecosystem function, analysts will therefore need to integrate data from across scales, using all the methods humans can devise. During my PhD, I have therefore tried to surveys these scales and methods, investigating the ways that humans are changing function in fire and animal-shaped savannas from different viewpoints using different tools. In this section, I outline the key approaches and methodologies that have driven this thesis. More detailed, reproducible methods are recorded in the methods section of each chapter, and, where necessary, in the supplementary materials.

## 3.1 Macroecological Methodology

Chapter 4 takes a macroecological approach. Macroecology is the investigation of "the patterns of ecological systems that emerge at large spatial or temporal scales" (Beck et al. 2012). Its goal is to use methodological "macroscopes," (as opposed to microscopes), to step away from raw data on individual species or landscapes and discern the general patterns that emerge from large datasets (Beck et al. 2012). The premise of macroecology is that a broad macroscopic lens can help ecologists see past the many forms of contingency that obscure patterns in local studies (McGill 2019). An ecologist investigating the trophic ecology of a savanna, for example, can never account for all the factors that make a given savanna unrepresentative of savannas generally. He might not account for a savanna's unusual soils, or a year's unusual rainfall, or the lingering impact of a decades-old disease outbreak or poaching epidemic. Macro-ecologists hope that these local effects will cancel each other out in the aggregate, allowing the analyst to reveal the broad underlying processes that shape the Earth's ecological patterns. In macro-ecology, there are three dimensions to be large on: space, time, and taxonomy (Beck et al. 2012). My first article goes large on all three, estimating energy flows through ~3,000 animal species across ~22 million km$^2$, over ~250 years.

To undertake the article's analysis, I linked together data from six different continental and global datasets, some of which were themselves aggregations of multiple datasets. To relate all this data, I used both spatial and mathematical relationships. I used GIS software to determine the species composition, land uses, and historical species population densities in each of 317,000 grid cells. I then multiplied population densities by species response values to land use, as provided by an expert-elicited biodiversity intactness index (Clements et al. 2024). Next, I used allometric equations and species trait data to translate species abundances into metrics of species-level energy consumption (Nagy, Girard, and Brown 1999; Malhi et al. 2022). Finally, I summed energy consumption across species performing the same ecosystem function, and then averaged values across land uses and biomes, to produce the mean energy flow values driving the study. To estimate uncertainty across these various datasets, I ran 10,000 simulations of the study using values drawn from parameter distributions rather than mean values. I then used the 10,000 values of each output variable to calculate 95% credibility intervals. The synthesis of all this data are spatially explicit maps that show how energy flows through various animal guilds vary across sub-Saharan Africa, as well as how energy flows have declined over time. These maps allow ecologists to identify broad ecological patterns, which can advance both our fundamental understanding of ecology and our knowledge of global change. The uncertainty intervals associated with the outputs give ecologists a range of reasonable values across broad scales. However, these results have not been ground-truthed against plot- and transect-level survey data, a common drawback to macroecological studies.

## 3.2 Remote Sensing Methodology

Chapter 5 takes a remote sensing approach to ecology, using spectral data from satellite imagery to assess ecological change. Remote sensing methods have helped ecologists overcome a key limitation with field data: despite its abundance, it cannot be reliably scaled up over large areas (Pettorelli et al. 2018). In contrast to field data, remote sensing is “the only methodology currently able to provide global coverage and continuous measures across space at relatively high spatial and temporal resolutions” (Pettorelli et al. 2018). Remote sensing approaches can be used to measure a wide variety of essential variables related to biodiversity and ecosystem function (Pereira et al. 2013; Nagendra et al. 2013). They are especially useful for measuring changes to vegetation, with ecologists developing a suite of remotely-sensed vegetation indices that track vegetation traits such as canopy structure and photosynthetic capacity by relating different wavelengths of optical imagery (Zeng et al. 2022). Vegetation indices can be used to track landscape-wide vegetation gradients such as woody encroachment (Rosan et al. 2019). They can also be combined with other optical data and machine learning technique to classify landscapes into discrete land use categories, such as grassland, woodland, and cropland (Khatami, Mountrakis, and Stehman 2016). These approaches let ecologists track ecological trends in landscapes where access is difficult either due to remoteness, politics, or conflict. For example, there is almost no plot-level data available for the Angolan miombo woodlands, the subject of Chapter 5, and a landscape that is expensive and difficult to access.

To investigate how global change processes are altering Angolan savannas, I combined optical, remotely sensed satellite imagery, spanning visual and near-infrared light bands, with vegetation indices and burned area indices. All the datasets used are freely available on Google Earth Engine. I used vegetation indices to track continuous change in woody cover. I used burned area indices to classify the landscape into categories based on how frequently grid cells burned. I also employed a random forest algorithm, a commonly-used machine learning algorithm, to classify the ecoregion into four land use categories: grassland, savanna woodland, unvegetated land, and cropland. By combining these three metrics of global change, I was able to track rates of woody encroachment across burn frequency and land use categories. This process allowed me to quantify correlative relationships between cropland expansion, fire regimes, and canopy greenness, a proxy for woody cover and a key determinant of savanna ecosystem function. By analyzing these correlative relationships, I was able to better understand how global change affects ecosystem function in savannas, particularly the flows of carbon into vegetation. While the results are correlative rather than mechanistic, their wide scope allows ecologist to prioritize sites and relationships that should be further investigated using fieldwork.

## 3.3 Field Ecology Methodology

Chapter 6 employs field ecology methods, specifically plot-based biodiversity surveys and vegetation assessments. Ecology was founded as field-based discipline, with ecologists physically observing species and ecosystems in order to identity ecological patterns and processes. Ecologists have refined field methods over centuries to better account for variation and uncertainty. I primarily collected the data for this chapter using plot-based bird surveys and rapid vegetation assessments along a woody encroachment gradient in a Zimbabwean savanna. Together, a research assistant and I identified birds visually and by sound, a process that involved me memorizing the calls of over 100 species of savanna bird. I combined this field data with a satellite imagery analysis of woody cover in each plot, which allowed me to more accurately quantify woody cover in encroached plots, where thick, thorny vegetation hindered in-person assessment. Through fieldwork, I gained a rich knowledge of central Zimbabwean savannas, including a species-level knowledge of the ecosystem that is impossible to glean from macroecological analysis or remotely sensed imagery.

For the analysis, I used a hierarchical Bayesian model to predict species abundances from point counts, and to estimate how species abundances varied in response to woody encroachment. The Bayesian model estimated abundances and environmental covariate effects for each species by combining prior knowledge with observed data in a probabilistic framework that updates uncertainty through Bayes' theorem (McElreath 2018). Bayesian ecological models are rapidly improving, with the models I used to predict bird abundances released only in 2024 (Doser et al. 2024). This new model not only measures how environmental factors affect abundance, but also measures how environmental factors affect detection probability, accounting for how variables such as temperature, wind speed, cloudiness, time of day, and plot visibility impact an observer's ability to detect birds. Once the species abundances were modeled, I used an ecosystem energetics framework to estimate how woody plant encroachment changed the strength of trophic ecological functions, such as insectivory, granivory, and frugivory. To do so, I used allometric equations to calculate the food energy consumption of each species based on its modeled population density and trait data. I modeled how the energy consumption of each species varied across the woody encroachment gradient. I then summed energy consumption across the species performing each function to understand how function strength varied. Most functions were performed by many species and thus varied independently from the abundance of any single contributing species.

A key benefit of this field data and modeling approach is that it produces detailed, granular results. In this case, I was able to meaningfully estimate how individual species respond to woody encroachment. This outcome contrasts with that of the first, macroecological paper, which estimated how groups of dozens or hundreds of species respond to land use change, but which was unable to meaningfully predict individual species responses, due to high uncertainty. Field ecology thus remains absolutely necessary for generating high quality data on individual species, data that is essential to species conservation.

## 3.4 Energetics Framework

Chapters 4 and 6 both employ an ecosystem energetics approach to measure ecosystem function. The core value of energetics approaches are that they quantitatively estimates how species are affecting an ecosystem through their food consumption. Energetics approaches measure the amount of kilojoules (i.e. calories) each species consumes per unit area per year (kJ $m^{-2}$ $yr^{-1}$). The result is a physically meaningful metric of ecosystem function that quantifies how much grazing, browsing, carnivory, granivory, or insectivory each species does in an ecosystem, in a unit transferable between any species and landscape. Knowing the magnitude of these functions allows ecologists to quantify how species impact vegetation, trophic structure, nutrient dispersal, and other ecosystem processes. Ecologists can also compare energy flows through animals to energy flows through plants (net primary productivity), or to energy conserved in fossil fuels, or to the total energy that reaches the Earth from the Sun, allowing ecologists to estimate animals' relative impact on earth system processes. By contrast, when ecologists estimate changes using species biodiversity and density alone, they produce a non-fungible metric, which cannot be quantitatively compared to other ecosystem processes. While these metrics can tell ecologists about species biomass or diversity, it is unclear what aspect of ecosystem function these metrics capture if any.

Compared to approaches based on scaling population densities or functional diversity metrics, an energetics approach incorporates more information, which results in a much better approximation of how species actually impact ecosystems. The energetics approach not only scales up population densities, but also weights individuals of each species based on their food consumption, which is itself a function of each individual's body mass and diet composition, as well as the digestibility of diet components, and the assimilation efficiency of each species' digestive system. Scaling approaches that ignore this additional data provide misleading results. For example, a scaling approach that weighted species based on their population density, would dramatically overstate the ecological importance of high-density, small-bodied species such as rodents and passerines. To account for this issue, one could instead scale up species based on their biomass, by multiplying population densities by body mass. But this would create the opposite problem, overrating the importance of large species, because it would not account for smaller species' lower energetic efficiency, which causes them to consume more food per unit mass. In addition, neither of the aforementioned approaches would account for the important differences in food assimilation efficiency between food types and animal digestive systems, factors that dramatically impact the total amount of energy a species consumes in an ecosystem, and thus a species' impacts on an ecosystem's vegetation and trophic structure.

Elephants, Africa's most energy-consuming wild mammal, provide a clarifying example. Elephants consume almost entirely leaves, from trees, shrubs, and grass. On average, leaves have a much lower assimilation efficiency (~40%) than other food sources (70-90%). But this assimilation efficiency varies widely based on herbivores' digestive systems: ruminants assimilate ~60-70% of leaf energy, perissodactyls and small herbivores (e.g. rabbits) around 40%, and elephants, which are highly inefficient digesters, just 20%! If elephant energy consumption was estimated via a simple scaling process, without accounting for elephants' anomalously low digestion efficiency and the low digestibility of leaves, it would lead to a three-to-fourfold underestimate in elephants' total energy consumption. Such a result would dramatically underrate elephants' contribution to ecosystem function through their grazing, browsing, and nutrient dispersal, and ultimately understate the impact of elephants (and of their extirpation) on landscapes, biomes, and the earth system.

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# 4. Energy flows reveal declining ecosystem functions by animals across Africa

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## 4.1 Chapter Statement

This chapter uses an energetics approach to estimate how the strength of key animal-mediated ecosystem functions have changed across sub-Saharan Africa since the 1700s. It also breaks down energy flows through animal guilds by biome and land use to distill insights that can inform the conservation of African ecosystems. It contributes to the broader goal of assessing changes to consumer-mediated ecosystem functions by assessing changes to a key set of consumer-mediated functions: those mediated by birds and mammals.

As of May 14, 2025, this paper is accepted in principle in *Nature*. Its full acceptance is contingent upon reviewer responses to an underlying data paper, which is currently also under review at *Nature*: “Sub-Saharan Africa’s biodiversity intactness assessed with place-based knowledge”.

This paper is structured in the *Nature* paper format, with a main text followed by references, a methods section, additional methods references, a series of 7 extended data figures, and finally a supplementary materials section with additional discussion, figures, and tables.

The ideas and research questions, study design, methods, data collection, data analysis, and writing presented in this chapter are the work of the first author, Ty Loft. These activities also benefited greatly from the contributions of Yadvinder Malhi, Imma Oliveras Menor, Nicola Stevens, , and Joseph Tobias, who also made substantial contributions to the writing of the manuscript. Luca Santini, Robert Beyer, and Hayley Clements provided key underlying datasets, while Seth Thomas contributed expertise on animal-mediated ecosystem functions. All these authors also provided constructive comments during the writing of the manuscript.

## 4.2 Summary Paragraph

A key challenge for ecological science is to understand how biodiversity loss is changing ecosystem structure and function at scales relevant for policy[1]. Almost all biodiversity metrics are challenging to disaggregate into animal-mediated ecosystem functions such as pollination, seed and nutrient dispersal, and predation. Here, we adopt an ecosystem energetics approach[2] as a physically meaningful method of translating animal species composition into a suite of ecosystem functions. Drawing on new datasets estimating biodiversity intactness and species population densities[3–5], we quantify historical changes to energy flows through mammal- and bird-mediated ecosystem functions across sub-Saharan Africa. In total, trophic energy flows have decreased by over one-third. The pattern of decreasing function varies by historical biome, driven by arboreal birds and primates in forests, terrestrial herbivores in grassy systems, and burrowing mammals in arid systems. Functions performed by megafauna in particular have collapsed outside protected areas. Compared to other biodiversity metrics, an energetics approach highlights the ecological importance of smaller animals and keystone species. The results can help practitioners conserve and restore functionally diverse, energetically intact ecosystems across land uses and biomes. By relating biodiversity intactness to energy and material flows, ecosystem energetics can also advance efforts to integrate animal-driven functions into biosphere and earth system models, helping to understand possible regional or planetary boundaries[6] for biodiversity.

## 4.3 Introduction

Ecologists have devised numerous metrics to track species loss and recovery,[7–9] but alone they can be poor indicators of changes in ecological function[10]. The influence of a species on its ecosystem depends on the species' abundance and on the specific functions it performs[11]. To assess how changing biodiversity affects ecosystem function at large scales, ecologists must develop consistent methodologies that account for species' changing abundances and their diverse impacts on ecosystems. Doing so is central to predicting how biodiversity change affects the ability of ecosystems to provide services, such as storing carbon, supporting food production and buffering natural disasters[12].

Many ecosystem functions are moderated by animals, yet most ecosystem function literature addressing regional or larger scales focuses exclusively on vegetation functions such as carbon storage or water cycle modification. Animals perform multiple functions including herbivory, seed and nutrient dispersal, and predation[13,14], which shape ecosystems by controlling species abundances and flows and patterns of carbon, nutrients and water[15,16]. Since the pre-industrial Holocene, animal populations have declined as intensively human-modified landscapes have expanded fivefold[8,17]. Tracking how biodiversity loss alters animal-moderated ecosystem functions is challenging because species respond unevenly to land use change depending on their traits[18]. For example, agricultural conversion depletes populations of large or frugivorous animals faster than small and omnivorous ones[18,19]. These asymmetric population declines change ecosystems' trophic structures: the partitioning of energy and biomass between plant and animal guilds. Ecosystems with simplified trophic structures provide a reduced suite of functions and services[20]. Ultimately, they become less capable of recovering from external shocks and supporting human wellbeing and livelihoods[21].

To track species abundances (a prerequisite for measuring functional changes) conservationists have developed biodiversity intactness indices (BII)[3,22,23]. These indices estimate how human activity has changed the richness or abundance of species relative to remaining highly intact landscapes such as wilderness areas, which are assumed to be representative of historical animal abundances, nominally in the pre-colonial/pre-industrial period. Local intactness scores can be aggregated to determine BII across ecoregions, countries, and taxonomic groups. BII has been proposed as a metric for biodiversity in the planetary boundaries framework, which seeks to identify safe environmental conditions for human societies[24]; though BII was more recently abandoned because of the difficulty of relating it to ecosystem function[6]. Metrics such as BII, which aggregate changes to species abundances or richness, cannot estimate changes to ecosystem function, because they weight each species equally. In reality, some species disproportionately affect ecosystem function due to their population densities, body sizes, dietary preferences, rates of food consumption and behavioral features[13]. To quantify how the changing animal populations estimated by the BII alter ecosystem function, an approach is needed that accounts for species' variable ecosystem impacts using a common unit of measurement[25].

One option is to adopt an ecosystem energetics approach to compare how much energy species consume across land uses[2,25]. Such an approach quantifies energy flow through the trophic web, by calculating the annual food energy consumed by each species per unit area. Species within an ecosystem can be classified into functional groups. And changes to energy flows through these groups indicate changes to the provision of associated ecosystem functions[16,26]. This approach relies on the ubiquity of energy: in all terrestrial ecosystems, energy, captured as sunlight by plants, flows up the trophic web through guilds of herbivores, carnivores, scavengers, and detritivores. Compared to abundance and richness-based assessments of biodiversity loss, an energetics approach has three advantages: (i) it weights species impacts based on the ecologically meaningful metric of food consumption; (ii) the common currency of energy allows functions performed by different taxonomic or functional groups of species to be quantitatively compared across time and space; and (iii) energy flows can be quantitatively related to earth system processes like changing Net Primary Productivity (NPP) and carbon cycling.

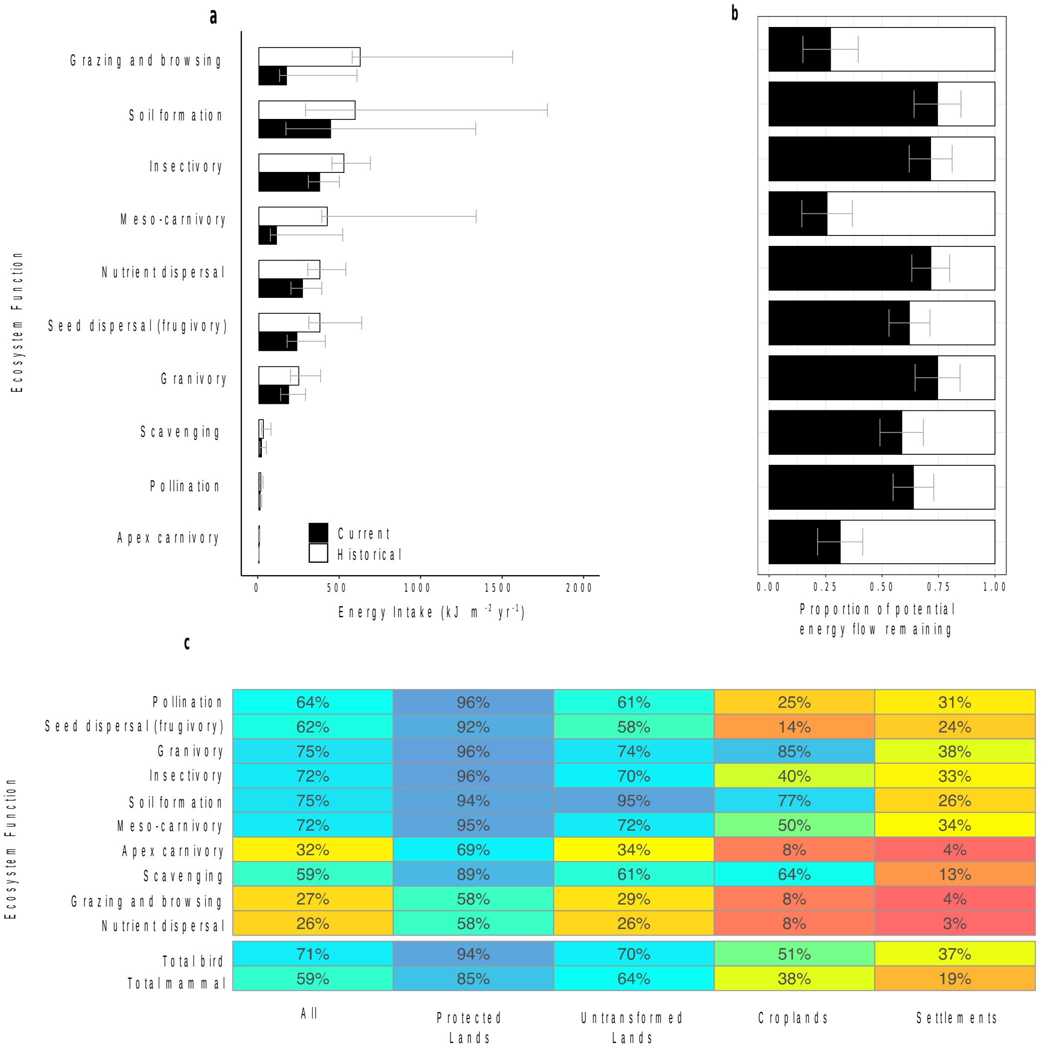
While energetics approaches have been previously used to measure how human modified landscapes alter ecosystem trophic structure[2,27], they have not been scaled beyond a few model ecosystems, as they require extensive data measuring species abundances across different land uses. Energetics approaches have never been applied at regional or continental scales. Here, we focus on Sub-Saharan Africa as a case study, due to the region's striking range of ecosystems, large gradients in ecological intactness, and (in some areas) relatively intact megafauna communities, which provide an opportunity to assess a wider range of animal-mediated ecosystem functions than elsewhere . We take advantage of new datasets that (i) model population densities of bird and mammal species[4,5] and (ii) estimate BII, or the impacts of land use changes on species abundances, across Sub-Saharan Africa[3,28]. The BII estimates are derived from a new dataset aggregating 30,000 expert estimates of how African species abundances respond to land use change. We use these datasets to quantify how biodiversity loss has degraded a suite of ecosystem functions across sub-Saharan Africa.

## 4.4 Approach

Our approach is to quantify how human modification of land uses has changed the distribution of energy among trophic guilds and functional groups. Energy flows are calculated for African bird and mammal species under contemporary versus pre-colonial/industrial (~1700 CE) conditions, which we henceforth refer to as historical conditions. Energy flows are aggregated across biomes (mapped before land use change) to compare how the dominant vegetation structures within Africa moderate the ecological impacts of land use change. To clarify the broad relationships between biodiversity loss and ecosystem functionality, we also assess how well biodiversity intactness predicts the intactness of energy flows through specific ecosystem functions and the entire community of birds and mammals, as well as whether energy flows can be predicted from species richness. We focus on birds and mammals because they are important components of animal biomass[29], as well as data-rich groups with well-understood ecological functions, while acknowledging that invertebrates play a major but data-challenged role in ecosystem energetics. While populations of some species, especially megafauna, declined substantially long before the colonial and industrial period, these declines appear to have been less severe in Africa than elsewhere, hence Africa's contemporary association with megafauna.[30,31] Africa therefore provides the unusual opportunity to examine how human activities have changed ecosystem function within historically near-intact ecosystems.

To estimate energy flows through African ecosystems, we calculated historical energy consumption by each species present in each 8 x 8 km cell across sub-Saharan Africa (317,000 cells in total). We used (i) modeled average species population densities[4,5] based on ~10,000 averaged empirical estimates of species population densities and (ii) habitat-adjusted IUCN range maps[32,33] to predict historical species abundances in each cell. To calculate the average absolute energy consumption of sub-Saharan Africa's ~3,000 bird and mammal species, we used published allometric equations[34] and datasets on species traits, diets, and food assimilation efficiencies (Supplementary Tables 1-3; Supplementary Data 2). We quantified current energy flows according to the remaining abundance of each species in each cell estimated by the BII[3,28]. To calculate the energy flows through animals performing ecosystem functions, we grouped species into trophic guilds and functional groups, based on their diets, lifestyles, body sizes, and, for mammals, social group sizes. Using these categories, we identified 23 unique ecosystem functions (11 for birds and 12 for mammals), which we aggregated across classes into ten major functions[14,31,35,36] (Extended Data Table 1).  These include both consumption functions directly correlated with energy intake including granivory, carnivory, browsing, grazing, and insectivory; and behavioral functions such as seed and nutrient dispersal, pollination, and soil disturbance, for which energy intake is a potentially less accurate proxy but can still usefully indicate changes in a function's strength. For each functional group, we calculated the absolute historical and current energy flows in kJ $m^{-2}$ $yr^{-1}$, as well as the proportional energetic intactness, defined as the percentage of historical energy flows through a group of species remaining in an ecosystem. In all cases, we estimate changes to energy flows through groups of birds or mammals performing a function (e.g. granivory, seed dispersal), rather than to the function itself, and we refer to changes in functions themselves only as a shorthand. Because uncertainty around energy flows decline as a greater number of species are analyzed (see Methods), we report and discuss guild-level rather than species-level results.

## 4.5 Changes to Ecosystem Trophic Structure and Function



| | All | Protected Lands | Untransformed Lands | Croplands | Settlements |
|---|---|---|---|---|---|
| Pollination | 64% | 96% | 61% | 25% | 31% |
| Seed dispersal (frugivory) | 62% | 92% | 58% | 14% | 24% |
| Granivory | 75% | 96% | 74% | 85% | 38% |
| Insectivory | 72% | 96% | 70% | 40% | 33% |
| Soil formation | 75% | 94% | 95% | 77% | 26% |
| Meso-carnivory | 72% | 95% | 72% | 50% | 34% |
| Apex carnivory | 32% | 69% | 34% | 8% | 4% |
| Scavenging | 59% | 89% | 61% | 64% | 13% |
| Grazing and browsing | 27% | 58% | 29% | 8% | 4% |
| Nutrient dispersal | 26% | 58% | 26% | 8% | 3% |
| Total bird | 71% | 94% | 70% | 51% | 37% |
| Total mammal | 59% | 85% | 64% | 38% | 19% |

**Fig 1 | Intactness of energy flows through birds and mammals performing key ecosystem functions.** Species were allocated into functional groups based on diet, lifestyle, body size, and group size. The intactness of each ecosystem function indicates the intactness of energy flows through the birds and mammals that perform the ecosystem functions. (a), Total absolute historical (white) and modern (black) mean energy flow through ten bird and mammal functional cohorts across sub-Saharan African. Error bars denote 95% confidence intervals derived from 10,000 Monte-Carlo simulation estimates incorporating uncertainty in body mass, population density, the daily energy expenditure equation, assimilation efficiency of different food types, composition of the diet of each species, and the biodiversity intactness of each species within each land use. (**b**), Average energy flow through modern sub-Saharan Africa (black) as a proportion of historical energy flow (white). Error bars are 95% confidence intervals derived from 10,000 Monte-Carlo simulation estimates of the biodiversity intactness of each species within each land use. **c**, Average remaining proportion of pre-industrial energy flows through birds, mammals, and each functional group, across sub-Saharan Africa and within its predominant land uses. Bluer cells indicate more intact functional groups, and redder cells indicate less intact groups.

Changes to the total flow of energy through animal populations, and to its distribution among guilds, can alter ecosystem functionality.[20] Energy flow through food consumption by wild African birds and mammals has decreased to 64% of historical values (54 – 74%; all ranges reported are 95% confidence intervals). Energy flow decreased most in high intensity land uses, falling to 27% (18 – 35%) of historical levels in settlements, 41% (30% – 53%) in croplands, 67% (56 – 76%) in unprotected untransformed lands (comprising rangelands and near-natural lands), and 88% (81 – 96%) in strict protected areas (Figure 1). Conversion to croplands and cities was responsible for 25% of the total decline in energy flows. In aggregate, birds were more resilient to land use change than mammals, with the fraction of energy flowing through birds (as opposed to mammals) rising from 37% to 41%. The greater reported decline of mammals was driven entirely by the collapse of large herbivores (including grazers, browsers, and frugivores), which historically accounted for over one-quarter of mammalian energy consumption. Energy flows through large herbivores decreased by 72% (61% – 85%), compared to a decrease of 29% (19% - 38%) for other mammals and 29% (20% – 38%) for birds. Large herbivorous mammals have undergone substantial population declines even in protected areas (Figure 1). Therefore estimated energy flows have fallen well below historical levels even in Africa’s relatively wilder regions.

Partitioning energy transfer by habitat and broad ecological niches, we find that energetic intactness has collapsed across all biomes, (which were mapped based on their historical occurrences before land use change). Total (bird and mammal) energy flows are estimated to be 63% (54 – 73%) intact in historical grassy systems, 65% (57 – 76%) intact in historical forests, and 69% (60 – 80%) intact in historical arid systems. Despite the similar magnitude of these declines, the trophic guilds most responsible for energy loss varied according to each biome’s dominant feeding pathways, suggesting that biome moderates changes to function (Figure 2). Arboreal species account for significantly more energy flow in historical forests, where they can take advantage of greater vertical space and habitat complexity (Figure 2)[37]. Of these arboreal species, birds make up nearly half of energy flow despite their much smaller body sizes than most primates and other arboreal mammals. Overall, reduced arboreal species populations accounted for 37% of energy decline in forests, compared to 10% and 5% of energy decline in grassy and arid systems. Fossorial species account for a large but highly uncertain proportion of energy flow in arid systems perhaps because burrowing helps animals regulate temperature and conserve moisture (Extended Data Fig. 5).[38] Fossorial mammals accounted for 26% of energy decline in historical arid systems, versus 10% and 3% of energy decline in grassy systems and forests; however, fossorial mammals' highly uncertain abundances means this should be analyzed cautiously. Large terrestrial herbivorous mammals were major contributors to energy decline (29–36%) in all historical biomes. However, the total fraction of loss attributable to terrestrial birds and mammals was notably lower in forests (50%) than in arid (61%) and grassy (68%) systems.

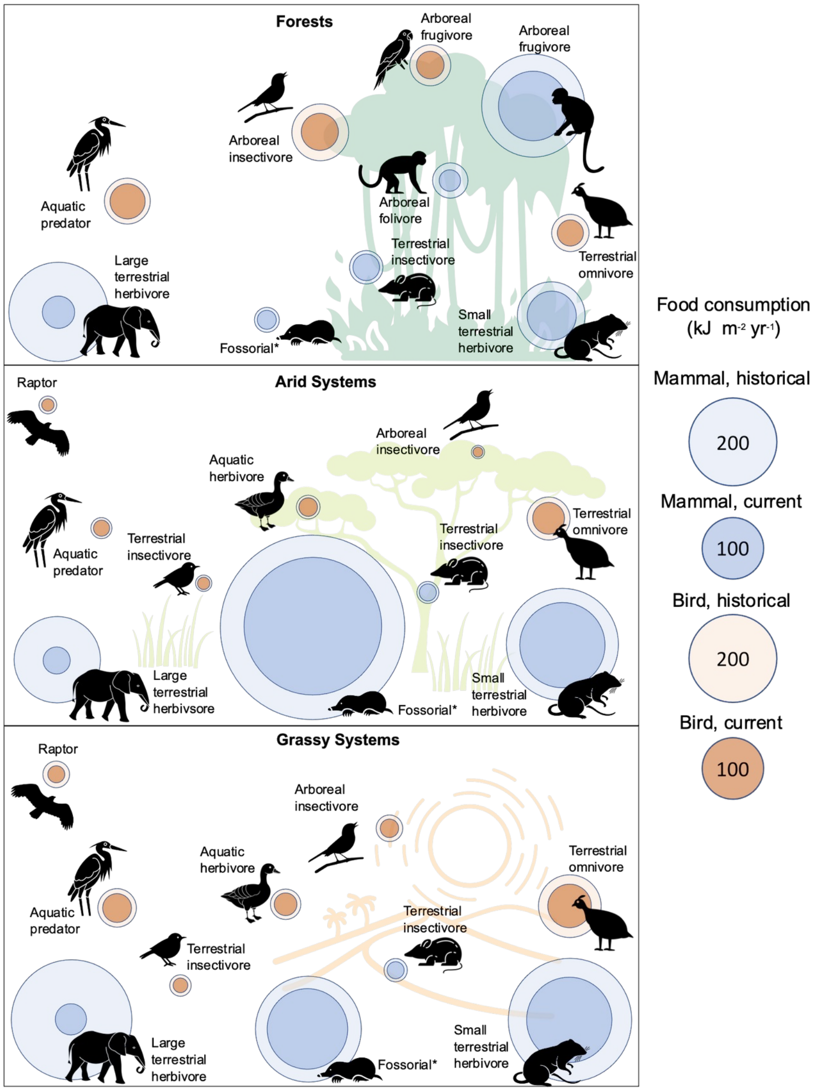


**Fig 2 | Mean magnitude of energy flows through bird and mammal trophic guilds across African biomes**. Values represent the mean energy flow through all cells given historical species abundances (light shading) and current species abundances accounting for human land use (dark shading). The size of the circle indicates the magnitude of food energy consumption (kJ m$^{-2}$ year$^{-1}$) by species in animal guilds. Flows through present day ecosystems were calculated using the mean intactness of bird and mammal groups according to the Biodiversity Intactness Index (BII). For clarity, guilds with small energetic flows are not shown, and complete results as well as uncertainty are available in Supplementary Data 1. The * associated with the fossorial mammals indicates the high uncertainty around energy flows through that trophic guild.

When we consider the proportion of total energy flow contributed by broad trophic guilds, we find that overall patterns have changed little over time, with flows through herbivorous birds and mammals  (including leaf-, grass-, seed-, fruit,- and nectar-eating animals) falling from 64% to 61% of total energy flow, flows through insectivores rising from 12% to 14%, and flows through carnivores remaining at 4%. However, the intactness of energy flows through functional groups varied widely, ranging from 26% (14% – 37%) intact for nutrient dispersal by large herbivores to 75% (64% – 85%) intact for granivory, when averaged across sub-Saharan Africa (Figure 1b).

Energy flows through megafauna-dominated functional groups, which include nutrient dispersers, grazers, browsers, and apex carnivores, were notably less intact (from 26-32%) than other ecosystem function groups (from 59-75% intact), and were twice as depleted in non-protected untransformed lands as in strict protected areas (Figure 1c). Megafauna play a key role in controlling vegetation structure, both directly through grazing, browsing, and nutrient deposition by large herbivores, and indirectly through the control of herbivore populations by apex carnivores[13,36].  Given that 80% of Africa is unprotected untransformed land, the collapse of large herbivores and carnivores is probably altering vegetation on a continental scale[36,39]. Megafauna extinctions on other continents have been estimated to have reduced mammal herbivory by 42%[26] and lateral nutrient flow by over 90%[16]. While some of this lost functionality is substituted by domestic herbivores, total (domestic and wild) herbivore biomass has decreased across most of Africa, as has the functional diversity of herbivore guilds[40].

Beyond megafauna decline, untransformed lands are relatively functional, with other ecosystem functions persisting above 55% intactness. However, the large absolute decreases in energy flows through arboreal guilds in historical forests, shared roughly equally between birds and mammals, translates to notable absolute declines in seed dispersal by frugivores outside of protected areas (Extended Data Fig. 2). Flows through seed dispersers are just 58% (50% – 66%) intact in untransformed lands and 14% (10% – 18%) intact in croplands. Flows through pollinators, dominated among vertebrates by birds and bats, also decline notably outside of protected areas, and are 63% (53% – 70%) intact in untransformed lands and 25% (17% – 32%) intact in croplands. Seed dispersal and pollination strongly influence plant community composition, vegetation structure and biomass. In tropical forests, primate and megafauna-dispersed tree species tend to have higher biomass than other species[41]. Reduced seed dispersal is likely to change the vegetation structure of defaunated forests and hinder ecosystem recovery.[42]

The most energetically intact functional groups are dominated by small and mid-sized herbivores, which account for a large proportion of energy in all biomes. These functional groups include granivores, soil disturbers, and avian grazers (mostly by water birds) (Extended Data Fig. 1). Energy flows through soil disturbers are potentially more intact in rangelands (95% intact, 82% – 107%) than in protected lands (94% intact, 85% – 103. The sole ecosystem function to become amplified after land use change was avian granivory, which reached  108% (84% – 135%) of historical levels in croplands, where birds can take advantage of seed-rich crops (Extended Data Fig. 5). These relatively stable functions can generate ecosystem disservices when they harm agricultural production.

The resilience of guilds and functions dominated by small birds and mammals (defined as < 3kg)[43] has created a striking pattern: African ecosystems are becoming dominated by smaller species. On average, the proportion of energy consumed by small birds and mammals rose from 69% of total energy to 78% of total energy, while the proportion consumed by megafauna (>65kg) fell from 16% to 7% (Extended Data Table 2). Moreover, even in intact systems, rodents and passerines account for a much larger proportion of energy flow than of biomass, due to their high energy consumption per unit mass[2]. Even as the absolute energy flows through small animals have marginally decreased, their proportion of total energy flow has risen: rodents accounted for 31% of total historical energy consumption but just 17% of biomass, rising to 36% of energy and 24% biomass today. Passerine birds accounted for 8% of historical energy consumption but just 2% of biomass, the same proportions as today. As large herbivores decline, these smaller animals are likely to exert greater relative control over the flows of nutrients, water, and material that structure ecosystems' vegetation, while not compensating for the attributes (such as large seed dispersal and greater daily transport ranges) that are particular to larger animals.

The species contributing most to total energy flow are elephants (family *Elephantidae*), which historically accounted for a striking 16% (9% – 26%) of total bird and mammal biomass across the region and 10% (6% – 26%) of total energy flow across sub-Saharan Africa. Savanna elephants (*Loxodonta africana)* historically consumed by far the most energy of any single species. Elephants perform the grazing and browsing and nutrient dispersal functions; however, the confidence intervals around functions performed by elephants are highly uncertain, due to elephants' disproportionate energy consumption: uncertainty around energy flow values are lower for guilds and functions that have more species and more even energy consumption among species (see methods). The high energy flows through elephants supports prior findings that they are the dominant large herbivore in Africa[44] and a keystone species with the potential to change ecosystem vegetation at the landscape scale and to affect continental-scale carbon sequestration[45]. Elephants and their close relatives were also widespread and abundant across Eurasia and the Americas until the Late Pleistocene megafaunal extinctions (REF)[1]; our finding indicates just how much of terrestrial vertebrate energy flow and associated functions once occurred through elephants. Our results also indicate that fossorial rodents, particularly mole rats, may consume an outsized proportion of energy, due to their high abundance and high food consumption per unit body mass (Extended Data Fig. 6). However, energy flows through fossorial rodents, and through their associated soil disturbance function, are highly uncertain as confidence intervals around modeled mole rat population densities span 2.5 orders of magnitude.[4] There is some evidence that fossorial rodents provide important belowground ecosystem functions[46], but in general their role in ecosystems is difficult to measure and poorly understood, (as indicated by their high uncertainty in this study) and is a ripe subject for further investigation.

## 4.6 Biodiversity and Ecosystem Energetics

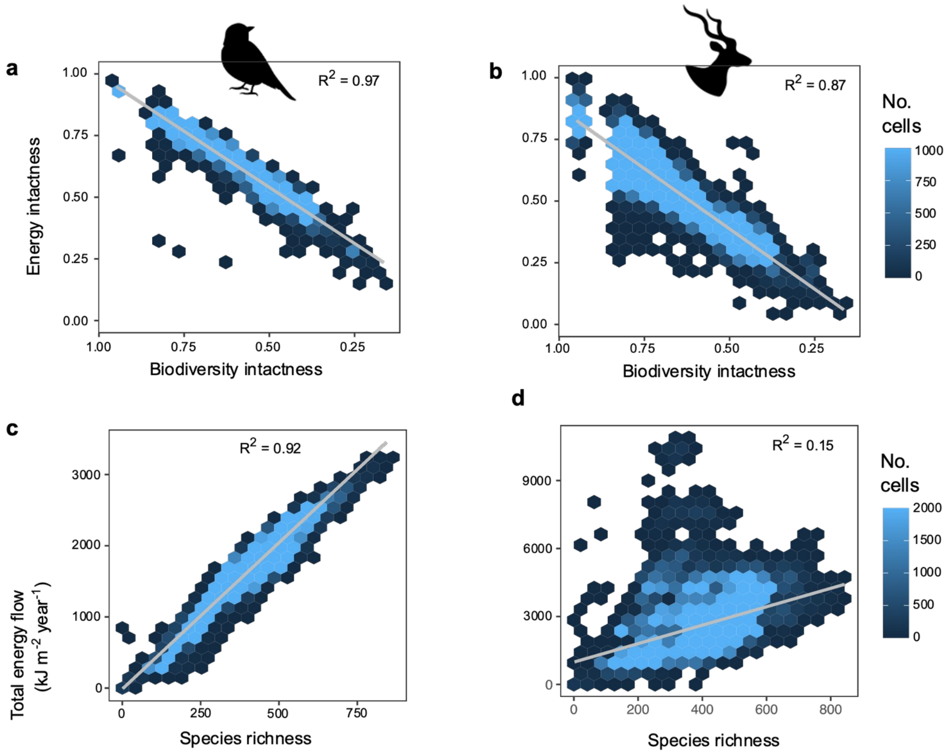


**Fig 3 | Relationships between biodiversity intactness, energetic intactness, total energy flow, and species richness. (a-d)** Relationships were calculated for each of the ~317,000 cells that compose sub-Saharan Africa, and color indicates the number of cells with a given relationship. $R^2$ values were calculated using linear regression. (**a-b**) Relationships between energetic intactness and biodiversity intactness were calculated over each cell for (**a)** birds and (**b**) mammals. Energetic intactness indicates the proportion of historical pre-modern energy flow remaining under modern landscapes, with species weighted based on their contribution to energy flow. Biodiversity intactness indicates the changes in species population abundances between pre-modern and modern land uses, with each species weighted equally (**c-d**) Relationships between species richness and total energy flow were calculated over each cell for (**d**) birds and (**d**) mammals. Species richness for each cell was calculated by summing species occurrences based on IUCN range maps.

Understanding how changes to biodiversity intactness alter an ecosystem’s suite of functions can help guide conservation and restoration. Biodiversity intactness equally weights changes to species abundances, whereas energetic intactness weights changes to ecosystem functions based on each associated species’ energy consumption. The ability of biodiversity intactness to predict changes to ecosystem functions varies widely among functions (Extended Data Figure 1). For some functions, BII is a strong proxy. These tend to be functions performed by a high number of species, and which are not dominated by a few keystone species. They include avian aquatic carnivory, avian terrestrial and perching insectivory, avian granivory, avian grazing, and mammalian insectivory. For other functions, BII is a noisy proxy, so that biodiversity intactness accurately predicts energetic intactness when averaged across Africa, but inaccurately predicts energetic intactness in any given cell. These functions include those dominated by arboreal species (avian and mammalian seed dispersal, canopy engineering, and ecosystem engineering/cavity creation), as well as mammalian granivory, mammalian scavenging, and pollination. Pollination in particularly unpredictable: in landscapes in which BII is 50% intact, energy flows through pollinators range from 22–75% intact. For still other functions BII poorly predicts even overall energetic intactness. BII substantially overestimates the intactness of the megafauna-performed functions: grazing, browsing, nutrient cycling, megaherbivore impacts, and apex carnivory. And BII underestimates the intactness of avian aerial insectivory, which is predominantly performed by swifts, martins, and swallows. At the ecosystem scale, biodiversity intactness is a strong predictor of total energetic intactness for birds ($R^2 = 0.97$), and a weaker predictor for mammals ($R^2 = 0.86$) (Figure 3a-b). The difference for mammals is driven by changes to large herbivore populations, which account for 16% of historical energy consumption, but just 3% of BII. Because large herbivores are 32% more intact within protected areas than outside them, protected areas conserve a higher proportion of energy flow (and therefore ecological functionality) than of biodiversity intactness. Thus, while BII can reasonably predict total energy flow, it cannot predict which ecosystem functions remain intact and which have been depleted. This is a key knowledge gap for practitioners working to conserve and restore ecosystem functionality that is uniquely addressed by our approach.

In addition to assessing intactness, an energetics approach can be used to estimate the absolute historical magnitude of energy flows through African landscapes. Large absolute energy flows supported by a rich diversity of species and guilds can indicate exceptionally vibrant ecosystems. One key question for clarifying the causes of functional resilience is whether species richness predicts absolute energy flows through animals, as it does other aspects of ecosystem function, including net primary productivity.[47] We found that the species richness–energy relationship differed between birds and mammals (Figure 3c-d). Richness predicts class-wide energy consumption strongly for birds ($r^2 = 0.92$), but weakly for mammals ($R^2 = 0.15$). This discrepancy is caused by the lower richness and less even apportionment of energy consumption among mammal species. Mammals account for 64% (57% – 75%) of total historical energy flows but just 36% of species, meaning that proportionally more energy is consumed by the average mammal than bird species. In addition, the 5% most energy-consuming mammals consumed 72% (64% – 84%) of energy flows through mammals, while the 5% most energy-consuming birds consumed just 48% (41% – 59%) of flows through birds. In contrast, the bottom 50% of mammals consumed just 0.7% (0.4% – 1%) of mammal-mediated flows, whereas the bottom 50% of birds consumed 7% (4% – 10%) of bird-mediated flows. These differences exists because species-level energy flows per unit area span a greater range of values for mammals (4.3 orders of magnitude) than for birds (2.1 orders of magnitude), due to mammal species' wider ranges of population densities, body masses, and assimilation efficiencies. Mammalian energy consumption thus appears more driven by the presence of keystone consumer species. These include large herbivores, especially elephants; highly abundant rodents; and primates, which dominate the arboreal guilds important in forests (Extended Data Fig. 3). The uneven allocation of energy among species has implications for the biodiversity-function relationship: bird-driven functions are likely to be far more resilient to biodiversity loss, as they are supplied more evenly by a wider range of species.

There are also clear biogeographical patterns in absolute historical energy flows. For birds, these tend to be highest in East Africa (Fig. 4a), where high energy landscapes broadly overlap with regions of volcanic soils and moderate to high rainfall along the Great Rift Valley. Birds and the insects many consume may benefit from nutrient-rich vegetation growing on fertile soils. Absolute historical energy flows through birds tend to be lowest in Africa's arid regions: the southwest, the Sahel, and the Horn of Africa. The map of historical absolute energy flow through mammals is more difficult to interpret, due to the high uncertainty associated with the energy consumption of dominant species (Fig. 4b). Still, mapping absolute energy flows across sub-Saharan Africa opens up a number of interesting questions about the biogeographical factors that control total energy abundance. For example, future research might ask why birds consume a greater fraction of total energy in forests than in arid systems, or whether climatic and soil variables predict how energy flows are distributed among trophic guilds, taxonomic groups, or ecosystem functions.

## 4.7 Applications to Restoration and Biodiversity Assessments

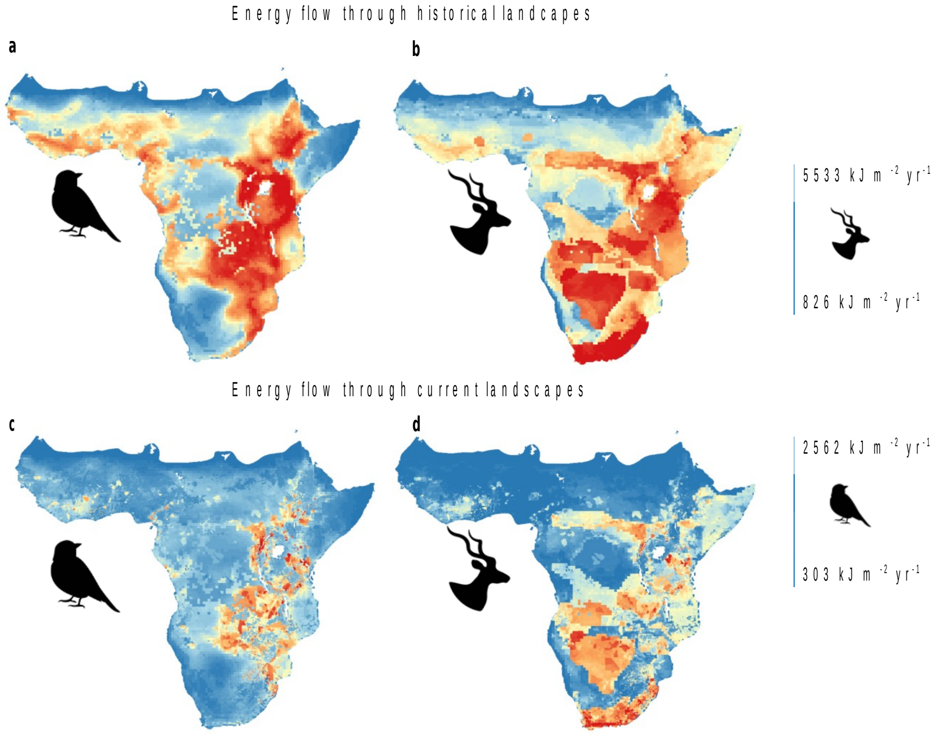


**Fig 4 | Aggregate energy flow through birds and mammals mapped across sub-Saharan Africa.** (**a-b**) To map historical energy flows, energy flows were summed for each (**a**) bird and (**b**) mammal species occurring in each 0.5˚ cell, assuming they existed in pre-industrial population densities. (**c-d**) To map energy flows through modern, transformed landscapes for (**a**) birds and (**b**) mammals, historical energy flows for each species were multiplied by the biodiversity intactness index (BII) value of each species, which is calculated independently for each species in each landscape based on the species response group and the cell's modern land use class and intensity. (**a-d**) The color gradients indicating aggregate energy flows were scaled independently for birds and for mammals.

As we advance through the United Nations Decade on Ecosystem Restoration (2021-2030), energy flows can contribute to ongoing efforts[48] to meet urgent demand from governmental and corporate sectors for metrics that can set and track progress towards nature restoration targets. In particular, energetics provides a novel and useful approach to quantitatively compare the restoration of ecosystem functions in recovering ecosystems in which species composition has changed substantially. When ecosystems recover in human-dominated landscapes, the allocation of biomass among remaining species can change dramatically[49]. In addition, extirpated or extinct species often become replaced with functionally similar substitutes, through migration, inadvertent introduction, and active rewilding[50]. Change in species abundances and composition can alter the strength of animal-performed ecosystem functions in an ecosystem, even after biomass and species richness recover to historical levels. Mapping ecosystem energy flows allows organizations to quantify the intactness of an ecosystem's trophic guilds and functions, independent of species composition. This information can complement richness or abundance based metrics, such as the various BIIs, which struggle to translate species composition into function. Once functional changes are mapped, practitioners can then focus on restoring the most energetically depleted guilds across land uses and biomes, to restore ecosystem function and trophic complexity. For example, amplifying energy flows through depleted arboreal birds and primate guilds might be prioritized in forests, where seed dispersers consume a large proportion of energy and are important for ecosystem resilience[42]. By comparing energy flows between these guilds in intact and recovering landscapes, practitioners can set quantitative benchmarks for restoring functions, independent of species composition.

Another application of energetics approaches to studying biodiversity loss is to advance global biodiversity assessments. In particular, ecosystem energetics can provide metrics tracking how animal-mediated ecosystem function are changing. The novel scale of this study, which expands previous plot-based energetics analyses to an area of over 20 million km$^2$, allows these metrics to be integrated into global assessments of biodiversity loss. For example, energy-based metrics of ecosystem change can complement the richness and abundance-based metrics that currently underpin assessments by the Intergovernmental Science Policy Platform on Biodiversity and Ecosystem Services (IPBES).[21] Ecosystem function metrics are additionally valuable because they can serve as an intermediate step linking changing biodiversity intactness to changing ecosystems services.[21] Energetics can also improve efforts to integrate biodiversity loss into the planetary boundaries framework.[6] It is contested whether a planetary boundary for biodiversity is meaningful because of the heterogeneous, local and spatially disconnected nature of ecological functions[12]; boundaries and thresholds may be more meaningful at local scales. Biodiversity intactness was proposed as a metric for such a planetary boundary[24], although recent planetary boundaries literature abandoned BII as a metric because of the difficulty of relating it to ecological functions, favoring Human Appropriation of Net Primary Productivity (HANPP) instead[6] (Figure S1)  However, it is challenging to see how HANPP can be mechanistically related to actual declines in ecological function, beyond a broadly positive relationship between two indicators of human impact. The energetics approach we have outlined here shows a way forward that enables biodiversity and its intactness to be related to a suite of ecosystem functions, whether at local, regional or planetary scales.

## 4.8 Caveats

Like any other biodiversity metric produced by modeling, energy flows have a number of caveats in addition to their advantages. Relying on energy consumption alone as a metric does not capture the intrinsic value of rare and/or native species, or the ecological impacts of species that translate energy into function exceptionally efficiently, or that perform unusual functions not easily captured by their traits. High energy flows through a guild or function do not necessarily indicate that ecosystems are functional, stable, or resilient. The diversity of species contributing to an ecosystem function also matters. When energy flows through a function are dominated by a single species the increase in function is likely to be accompanied by a substantial increase in instability, as individuals species are more subject to sudden shifts in abundance or extirpation than are groups of species. This caveat is crucial for restoration: when assessing the recovery of a function, practitioners should evaluate not only the strength of an energy flow but the diversity of contributing species.

There is also evidence that some forms of anthropogenic disturbance can amplify animal energy consumption[2] at local scales, even as land use change has degraded biodiversity intactness and ecosystem function at the sub-continental scale. It is not sufficient to assume that land use change degrades overall ecosystem functionality or individual ecosystem functions. Here, we find that some species and functions do better in rangelands and croplands than in protected areas. Logging has previously been found to amplify vertebrate energy consumption in some tropical forests by increasing vegetation palatability and accessibility to herbivores[2]. Positive relationships between some functions and forms of human modification also seem likely in disturbance-dependent grassy ecosystems. The broad patterns revealed in regional and continental scale analyses should be tested and refined through empirical plot-based studies. Researchers can use energetics approaches to quantitatively test which types of disturbance maintain (or even enhance) biodiversity intactness, trophic complexity, or ecosystem function.

In addition, the large-scale approach used here is built by combining a number of datasets, each of which relies on assumptions and simplifications. There are therefore caveats associated with each dataset used, namely the species population density estimates, the range maps, the biodiversity intactness index, the data on species traits and allometric equations, and the process used to sort species into functional groups. These methodological caveats are systematically stated in the caveats section of the Methods section and should guide application. In broad terms, the large-scale approach used here does not capture many kinds of local and regional variation in historical species population densities and intactness values, limiting its application at local scales. In addition, the estimates are highly uncertain for individual species, but decline as more species are analyzed in a guild, allowing us to report reasonable uncertainties around guild-level energy consumption.

## 4.9 Conclusion

This analysis has demonstrated how an energetics approach can quantify the decline and recovery of ecological functions mediated by birds and mammals. It fills an important gap: while it is increasingly clear that animals shape landscapes, biomes and the Earth system in important ways, their functions have been inadequately quantified over large spatial scales and have not been integrated into Earth system models. As a tool to estimate changes to animal-mediated ecosystem function, the energetics approach presented here provides at least three advantages over approaches that consider species richness or abundances alone. These advantages clarify ecosystem function at the scale of the species, the ecosystem, and the Earth system. Together, they provide a framework to relate changes to animal-mediated ecosystem functions across these scales.

First, instead of weighting species equally, an energetics approach weights species based on food consumption, an ecologically meaningful indicator of a species' ecological importance within a landscape. Identifying each species' trophic importance can help reveal where keystone species disproportionately contribute to various ecosystem functions, and how the importance of key species varies across biomes, land uses, and functions. The energetics lens used here also reveals the importance of smaller species, including birds and rodents, which have higher metabolic rates and are important contributors to energy flows and many ecosystem functions, but which other mass-based metrics often underrepresent due to their minor contribution to biomass.

Second, as a common currency, energy can be used to quantitatively compare how changes in species composition alter the strength of ecosystem function across land uses and biomes. For example, the distribution of energy among species differs between arid, grassy, and forested biomes, causing these biomes to have very different suites of functions even where overall species richness or animal biomass are similar. In contrast, metrics that aggregate changes in species richness or abundances are unable to compare the variable pathways through which biodiversity loss alters functionality, pathways moderated by the species composition of an ecosystem and the vulnerability of those species to various kinds of land use change.

Third, energetics provides a mechanism for bringing animal activity into the quantitative, mechanistic framework of biosphere modeling and Earth System Science, which to date has been dominated by the ecological functions provided by vegetation and is largely blind to the functions provided or modified by animals. Using energetics, changes in animal populations can be related to Earth system processes by estimating how animals affect vegetation structure, both directly through grazing and browsing, and indirectly through seed and nutrient dispersal, insectivory (of herbivorous insects), and soil disturbance. Changes in herbivory, insectivory, or nutrient dispersal by birds and mammal can be related to changes in NPP, and from there to the effects of changing vegetation on albedo, fire regimes, or carbon cycling. These analyses rely on translating biodiversity intactness into energy flows, as energetics can be physically related to Earth system processes, while species richness, abundance, and biomass alone cannot.

Like any metric (for example, carbon stock), energy flows should be considered as only one lens on the multifaceted nature and value of biodiversity and ecological function. In particular, energy flow needs to remain coupled with consideration of the number of species contributing to energy flow to avoid wrongly labeling the persistence of a few generalist species as ecological intactness. Some future steps could include integrating energy flows into global biodiversity assessments, expanding this energetic analysis to a planetary scale, incorporating domesticated animals within the same framework, extending to the much more data-challenged question of invertebrate energetics, and relating animal energy flows to vegetation structure captured through vegetation plots and through dynamic global vegetation models (DGVMs). We believe the subcontinental-scale analysis presented here presents a significant step forward in the challenge of relating animal biological richness and intactness to large-scale ecological and planetary function.

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## 4.11 Methods

### Study Scope

The geographical scope of the study was sub-Saharan Africa, defined as comprising ecoregions[51] in the Afrotropic realm within continental Africa. We calculated energy flows for the 1088 mammal and 1955 bird species for which data was available, composing 98% of total African species excluding seabirds. Energy flows were calculated independently for each 8x8 km grid cell, the scale at which biodiversity intactness data is available. The study area comprises ~317,000 cells. To assess change over time, energy flows were calculated twice for each cell: once based on estimated historical species abundances in the pre-industrial/pre-colonial Holocene (~1700 CE), and once based on contemporary abundances, given human land use, according to the population changes estimated by the biodiversity intactness index (BII)[28]. A visual overview of the methods is presented in Extended Data Figure 5.

### Historical Species Abundances

To determine which bird and mammal species were historically present in each 8x8 km grid cell, we used historical IUCN/Birdlife range maps, adjusted for species habitat requirements following ref.[52]. For each species, the initial IUCN/Birdlife range maps were divided into 1/12˚ grid cells, and grid cells were excluded from the species range when the cell's historic, natural biome did not match the species' habitat requirements, as documented by the IUCN. The 1/12˚ grid cells were then aggregated into 1/2˚ cells, and cells were included if they contained any available habitat. For a few small-range species, 1/2˚ habitat-adjusted maps eliminated all available range due to their exclusion from 1/12˚ cells , so unadjusted IUCN/Birdlife ranges were used. For the 11 large mammal species for which historical range maps are not available within the IUCN database, we adapted vector maps from other sources, following ref.[44], and then applied the gridded habitat filter detailed in ref.[52] (see Supplementary Information).

To calculate historical species abundances, we used published median population density estimates for bird[5] and mammal[4] species. These were modeled as a function of trait, environmental, and phylogenetic predictors, using additive mixed-effect models and Bayesian inference, based on ~36,000 empirical records of bird and mammal population densities across 737 mammal and 1853 bird species. Population density estimates for species lacking empirical data were extrapolated using the model. To estimate species abundances across sub-Saharan Africa, we used mean species population densities[2]. Mean densities were calculated using log-normal distributions based on published median densities and uncertainty intervals. Because population density distributions for most species are left-skewed, mean species population densities are higher than median values for species with wide confidence intervals. Given that ~75% of the global terrestrial surface is modified by humans to some extent[53] the exclusion of non-natural population densities is not realistically possible, and is not necessarily desirable given that hominids have modified African species population densities for millions of years.

## Contemporary Species Abundances from the Biodiversity Intactness Index

To estimate contemporary species abundances we multiplied historical abundances by the proportional intactness of each species in each 8x8 km cell under modern land use. We used the intactness values for species under various land uses that are published in the Biodiversity Intactness Index for Africa dataset (BII)[3]. The BII employs a structured expert elicitation process to estimate and validate the proportional changes to species abundances under nine land uses: strict protected areas, near-natural lands, rangelands, intensive croplands, smallholder croplands, tree croplands, timber plantations, dense settlements, and urban areas. The BII allocates each species into one of 17 bird and 76 mammal "response groups" containing species that respond similarly to land use change. The average impact of each land use class on the abundance of species in each response group was calculated from ~30,000 individual estimates produced by 200 experts on African biodiversity. To map changes in abundance, each cell was assigned a land use class and intensity according to the land use classification outlined in ref[28]. Cells within protected areas and timber plantations were classified categorically, and cells within croplands, rangelands, and settlements were classified and then scaled along a land use intensity gradient. In cases where land use change benefited a species, the intactness of that species was greater than 1, and its abundance increased compared to the historical baseline.

### Daily energy expenditure and food uptake

To calculate ecosystem energy flows, we first calculated the short-term equilibrium rate of food consumption for each species following ref[2]. For each species, daily energy expenditure was calculated from body mass using multi-species allometric equations (See Supplementary Table 1 for equations).[34] Food consumption was calculated from energy expenditure based on published assimilation efficiency values for each food type and taxonomic group of birds and mammals (See Supplementary Table 2). Where available, assimilation efficiency values were assigned at the family level; otherwise they were assigned at the order or class level. Values for the body mass of each species, and for the composition of food types within each species' diet, were derived from the Eltontraits database for mammals[54] and from the Avonet database for birds[55]. Energetic food intake was calculated in units of kJ $m^{-2}$ $year^{-1}$ and then averaged across cells.

### Allocation of species into trophic guilds and functional groups

To understand how human land use has altered ecosystem trophic structure, we allocated species into trophic (i.e. feeding) guilds. Each species was allocated into a single trophic guild, to shed light on how an ecosystem's trophic structure, defined as the distribution of energy among guilds, varies between biomes and land uses. Species were allocated into guilds based on their taxonomic class, their diet (e.g. omnivore, carnivore, nectarivore, folivore, frugivore), and their lifestyle (e.g. arboreal, terrestrial). Data on diet and lifestyle was extracted from the Eltontraits database for mammals[54] and from the Avonet database for birds[55]. Throughout the text, herbivore is used as an umbrella term to capture species eating any kind of plant matter, including foliage, seeds and nuts, nectar, and fruit. The terms folivore, granivore, nectarivore, and frugivore are used to refer to these groups independently. In addition, large and small terrestrial herbivores were split according to a published list of African large herbivores[44] to better isolate how the distinctive vulnerability of large herbivores to human activity alters ecosystem trophic structure.

To understand how human land use has altered ecosystem function, we allocated species into 23 functional groups: 11 for birds and 12 for mammals. Species that perform multiple functions were allocated into multiple groups, so that the sum of energy flows through functional groups is greater than the total flow through the ecosystem's birds and mammals. By contrast, the energy flows through guilds sum to the total energy flow through birds and mammals. We adapted a list of 11 bird functions from a published list of major avian ecosystem functions[14]. We added a function for aquatic carnivory and subdivided the invertivory function based on species lifestyle (e.g. insessorial, aerial, terrestrial), as invertivory is performed by over half of all bird species. We sorted birds into functional groups based on their lifestyles and diets (see Extended Data Table. 1 for sorting criteria for both birds and mammals). Unlike for birds, there is no single authoritative source on functions performed by mammals. After reviewing the literature we designated twelve mammal functions performed by large herbivores[13,31], carnivores[36,56], primates[35], bats[57], fossorial mammals[46], and other small mammals[58]. We sorted mammals into functional groups based on their diet, body mass, and lifestyle. For the grazing and browsing functions performed by large terrestrial herbivores we used published data on the leaf versus grass component of large herbivore diets[44], and included large, terrestrial, herbivorous primates (*Gorilla* spp. and *Theropithecus gelada*) based on the expert knowledge of the authors. We additionally used published data on herd size[44] to select herbivores that perform a nutrient dispersal function, as herd forming species have a distinctive effect on nutrient distribution within ecosystems[13]. We included in the megafauna impacts function those species that have unique ecological impacts because their large body size frees them from predation[31]. We determined the diet thresholds for each function iteratively, running the species allocation process multiple times and refining thresholds based on the authors' expert knowledge. To clarify our results in the main text, we further aggregated our 23 preliminary functions into 10 aggregate functions, some of which are performed by both birds and mammals (See Extended Data Table 1).

## Comparison of energy flows across functions, biomes, and land uses

To calculate energy flows through functions, we summed the energy flows through all species that contribute to each function. This approach weights the contributions of species to associated functions based on species' average daily energy consumption. The proportionate contribution of each species to its functions therefore changes depending on whether energy flows are calculated based on historical species abundances or based on present day, human impacted species abundances. Beyond energy flow, we did not scale species-level contributions to functions based on other metrics of functional efficiency: for example, based on pollen deposition rates, seed dispersal distance, or diet proportion. These causes of efficiency vary widely between functions and species[14] and are difficult to measure consistently. To avoid biases, we therefore assumed that all species use energy equally efficiently to perform their associated ecosystem functions. For the analysis, we compared energy flow within specific functions across space and time. It is not meaningful to compare energy flows across ecosystem functions (e.g. predation vs soil disturbance) as how each function uses energy is very different.

We also calculated the average energy flows through functional groups and trophic guilds across biomes and land uses. The biome is commonly proposed as the appropriate unit of analysis for assessing biodiversity trends, because biomes are biologically coherent subunits of the biosphere with structures and functions that respond to land use change in relatively consistent ways[12]. We allocated cells into biomes based on the biome map of the RESOLVE Ecoregions dataset[51]. To allow for broad comparisons between vegetation types, we further aggregated biomes into forests, grassy systems comprising savannas and grasslands, and arid systems comprising deserts and shrublands. For the biomes analysis, we excluded cells falling into the fynbos and thicket biomes, which are not easily classifiable and make up less than 2% of sub-Saharan Africa. We also excluded cells falling into mosaic biomes, as the low accuracy of available continent-scale vegetation maps makes it infeasible to subdivide mosaics into component biomes within the study scope. We calculated average energy flows through each guild and functional group across each of these three aggregated biomes under historical conditions and under modern land use conditions.

We allocated cells into land uses using an adapted version of the 8x8 km resolution African land use map created for the biodiversity intactness index for Africa[28]. Following source[28], cells were allocated into four land uses: strict protected areas (IUCN categories I:III); settlements (>20% urban cover or a population density over 1000 per km$^2$); croplands (>20% crop cover); and unprotected untransformed land (remaining cells). We calculated average energy flows through each guild and functional group across each of these four land uses.

## Comparison of energy flows to biodiversity intactness, and species richness values

To understand how well biodiversity intactness values predict functional intactness, we related the BII of each cell to the intactness of energy flows through each cell. We related the BII of birds and mammal species to the intactness of total energy flows through bird and mammal species (Fig 4a-b) and to the intactness of energy flows through species in each functional group (Extended data Fig 1). We identified functional groups for which biodiversity intactness is a good proxy (slope approximately 1 and high $r^2$ value), a noisy proxy (slope approximately 1 and low $r^2$ value), and a poor proxy (a non-linear slope or a slope that is not near 1). Functional groups with shallower slopes maintain high levels of energy consumption as biodiversity intactness declines, and were deemed more resilient to human impacts. We also related total energy flows to native bird and mammal species richness, to understand the extent to which high-energy keystone species versus rich communities of species drive ecosystem function (Fig 4c-d). We analyzed these relationships across all cells using linear regression.

## Uncertainty Calculation

Following ref.[2], we quantified uncertainty in our estimates of energetic intake by running 10,000 Monte Carlo simulations of energy flow through animal species and groups. For each simulation, we replaced the values in our original calculations with values drawn from random distributions. We assumed there was uncertainty in the following variables: species body mass, population density, daily energy expenditure equation (DEE), assimilation efficiency, and fractional diet composition of each species. Following ref.[3], we also assumed there was uncertainty in the estimated intactness of each species in each land use.

For body mass, we drew values from a truncated normal distribution (lower bound = 1g) in which the mean was published mean body mass[54,55] and standard deviation was 15% as described in ref.[2] For population densities, we drew from a log normal distribution, using mean and uncertainty values for each species published in refs.[4,5]. For DEE, we estimated the 95% confidence intervals following the methods described in ref.[34]. For assimilation efficiency, we drew from a random beta distribution using the mean and standard deviation by taxonomic group and food type in the literature (Supplementary Table 1). For diet composition, we drew from a symmetrical beta distribution with uncertainty parameters assigned following ref.[2]. For the proportional intactness of species abundances in each land use, we drew from a random beta distribution using the mean intactness values and standard deviations published in ref.[3]. Intactness values were previously validated in ref.[3] through a structured expert elicitation process.

The uncertainty in each of these variables captures the natural variability occurring within species among individuals and groups, as well as ecologists' uncertainty about mean values. For example, the population density of a given species will naturally vary geographically based on habitat suitability, resource availability, and competition. But there is also absolute uncertainty about the mean species population density of each species based on limitations on empirical data and model accuracy. This division of uncertainty into geographic and absolute components is true of the other variables as well. The uncertainty derived from natural variability decreases as there is an increasing number of analyzed landscapes in which the species occurs. We assumed that half the uncertainty in species energy flow in a given landscape is from natural variability and that half is from absolute uncertainty about mean values, which does not decline as geographic area increases.

To account for the effects of area in our uncertainty estimates, we grouped species-level energy flows into 1° grid squares (~12,000 km$^2$ at the equator) following ref.[44]. We treated uncertainty about natural variability as independent in each 1° square in which a given species occurs and drew from independent distributions in each square. For each species, we calculated range-wide spatial means of energy flow for each of the 10,000 Monte Carlo simulations, and then propagated this area-scaled uncertainty into the absolute uncertainty about mean energy flow values generated from the area-independent Monte Carlo simulation estimates. We estimated total uncertainty by assuming uncertainty in all variables simultaneously, and calculated the 2.5th and 97.5th confidence intervals to derive 95th confidence intervals for our estimates.

## Caveats

There are a number of caveats to our analysis, which we present here systematically in the order of their associated dataset or analysis. To estimate historical species abundances, we use range-wide average population densities for each species. For the vast majority of 3000 bird and mammal species we analyzed, there is insufficient data to predict how population densities vary along environmental gradients. We assumed that using flat densities would not substantially alter our results, hypothesizing that the intra-species variation in population densities would even out when summing energy flows across tens, hundreds, or thousands of species. To test these assumptions we calculated the declines in energy flows through the 92 large herbivore species for which spatially variable population densities are available over the whole of sub-Saharan Africa[44]. Using flat instead of variable densities changed the total energy flow through all 92 species by less than 1%, justifying our assumption (See Supplementary Discussion). Another issue with our flat densities is that they do not account for intra-specific competition. It is expected that species reach higher densities when competitors are missing. The approach may therefore overestimate energy flows through species-rich guilds in species-rich cells, although this was not supported in our sensitivity test.

A second set of caveats regards our use of range maps. Because these range maps are coarse (0.5˚ grid cells), they can overestimate abundances of species restricted to specialist habitats. Energy flows through colonial species including some fossorial rodents and water birds may be overstated. Another challenge is that the accuracy of the range map polygons varies between species groups and subregions, with maps of well-known species and well-known regions better accounting for fine-scale habitat heterogeneity. As a result, both historical energy flows and declines may be overestimated in poorly known areas, where maps are likelier to include inappropriate habitat not occupied by species. In contrast, where maps for poorly known species do not include historical ranges, declines in energy flows may be underestimated.

A third set of caveats regards our data on species traits and allometric equations. Our analysis also assumes that species' diets, body masses and assimilation efficiencies do not vary consistently across land uses and biomes. However, a prior analysis of bird and mammal energetics across a land use gradient showed that shifts in diet had negligible effects on total energy flows. In addition, we accounted for substantial uncertainties around all three of these variables in our uncertainty analysis. A similar caveat is that the allometric equations, which we used to predict energy requirements based on species body sizes, do not account for environmental variables, for example the impact of temperature on energy needs. Consequently, the analysis may underestimate energy flows through cold regions, particularly afro-alpine and afro-temperate ecoregions. However, these regions make up a very small part of Sub-Saharan Africa, which is overwhelmingly tropical or subtropical.

A fourth set of caveats regards the Biodiversity Intactness Index, used to estimate species responses to land use change. Because the BII averages responses from experts in different countries and regions, it does not account for how national political factors impact species abundances. These factors include war, protected area management, wildlife legislation, and cultural differences about hunting. The analysis may therefore overestimate energy flows in regions where unique national factors cause anomalously high overexploitation of wildlife, independent of land use transformation (and the converse where regions have anomalously low exploitation of wildlife such as taboos against bushmeat). In addition, only protected areas within IUCN categories I-III were designated as protected areas on the BII map. The analysis may therefore overestimated energy intactness across the region's *de jure* protected areas and underestimated intactness in some *de facto* strictly protected areas, for example private reserves. This study analyzes continent-wide average energy flows through guilds in different land use classes and biomes, which are less likely to be affected by national factors. However, an effort to use this approach to analyze energy flows over smaller areas (e.g. within a country or protected area) would need to account for regional and national variables affecting species abundances.

Finally, a fifth set of caveats regards species' allocation into functional groups and the estimation of functional intactness. The study assumed that species contribute evenly to an ecosystem function, accounting for population density and allometry. For many functions, species were allocated based on their diets, after reaching a certain diet threshold (e.g. 25% or 50%). The analysis may therefore overestimate absolute energy flows through functions performed by species that have a broader array of diets. However, this should not substantially affect comparisons of energy intactness within functions across time and space, the core aim of the study. In addition, for the vast majority of species and functions, there was insufficient data to estimate how variations in behavior moderates the efficiency with which species use energy when performing functions. This caveat is less important for diet-based functions such as grazing, browsing, insectivory, granivore, and carnivory, where energy consumption by definition correlates closely with functionality. However the lack of data about behavior may create more uncertainty for functions dependent on movement, such as seed dispersal, nutrient dispersal, and soil disturbance. The analysis may underestimate declines in these movement-dependent functions where species movements are highly constrained by habitat fragmentation (i.e. in forests), even when landscapes and abundances remain relatively intact.

## 4.12 Methods References

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## 4.13 Additional Information

### Author Contributions

T.L. led the analysis, drafted the paper, and conceptualized the visualizations, with input and supervision from Y.M., N.S., and I.O.M., as well as input from H.S.C., L.S., S.T., and J.A.T. Y.M. conceived the analysis, developed the energetics approach, and provided feedback on the analysis, visualization, and structure of the paper. R.B. produced the habitat-adjusted species range maps. H.S.C. collected and supplied the data on biodiversity intactness and provided input on the designation of land uses. N.S. provided input on the designation of biomes, land uses, and ecosystem functions. I.O.M. guided and provided input on the uncertainty analysis. L.S. collected, modeled, and supplied the data on species population densities. S.T. aggregated data on bird and mammal ecosystem functions and worked on the ecosystem function classification. J.A.T. provided input on the ecosystem function classification as well as on the discussion of bird trophic guilds and bird-performed ecosystem functions. All authors commented on the draft.

### Competing Interest Declaration

The authors declare no competing interests.

### Additional Information

*Supplementary Information Line*

This file contains the Supplementary Discussion, Supplementary figures 1-2, Supplementary Tables 1-4, and a description of the data and code.

*Corresponding Author Line*

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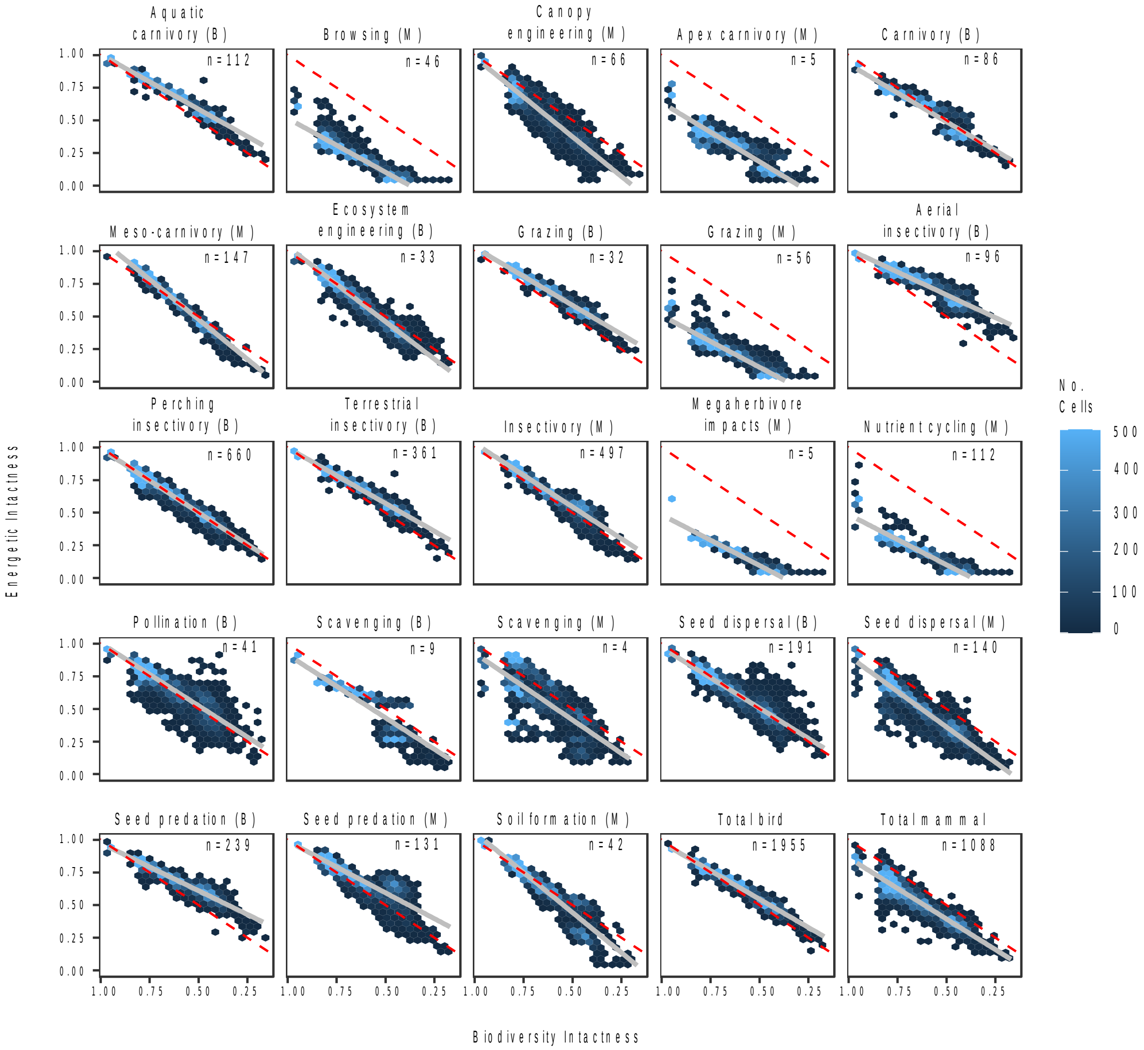
### Data Availability Statement

The data on energy flows through each species, trophic guild, and functional group are available in Supplementary Data 1 and 2. Input data on species population densities are available through the TetraDENSITY dataset (https://ecaslab.com/tetradensity-database/). Input data from the biodiversity intactness index are available through the BII4Africa project (https://bii4africa.org/). Input data on species ranges are available in the associated data with Beyer and Manica (2020, https://doi.org/10.1038/s41467-020-19455-9). Input data on species traits (i.e. diet, body mass, lifestyle) are available through the EltonTraits database (mammals) and through the Avonet database (birds).

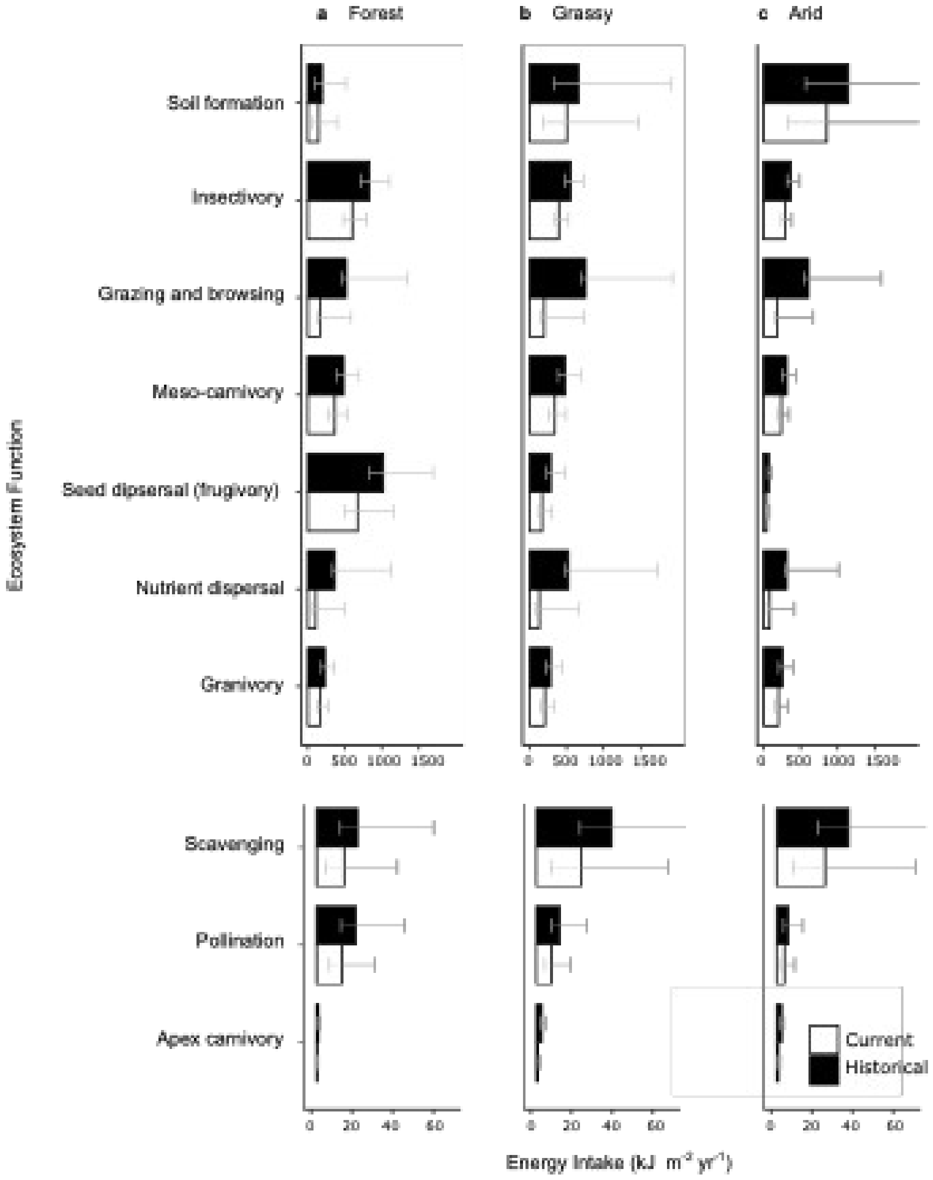
### Code Availability Statement

R Scripts as well as adapted data are available online at the project's Mendeley Data site: https://data.mendeley.com/preview/8j4j85f82c?a=8a584c71-23c8-48ad-b025-c93e27f36de0, or from the corresponding author upon reasonable request (ty.loft@chch.ox.ac.uk)

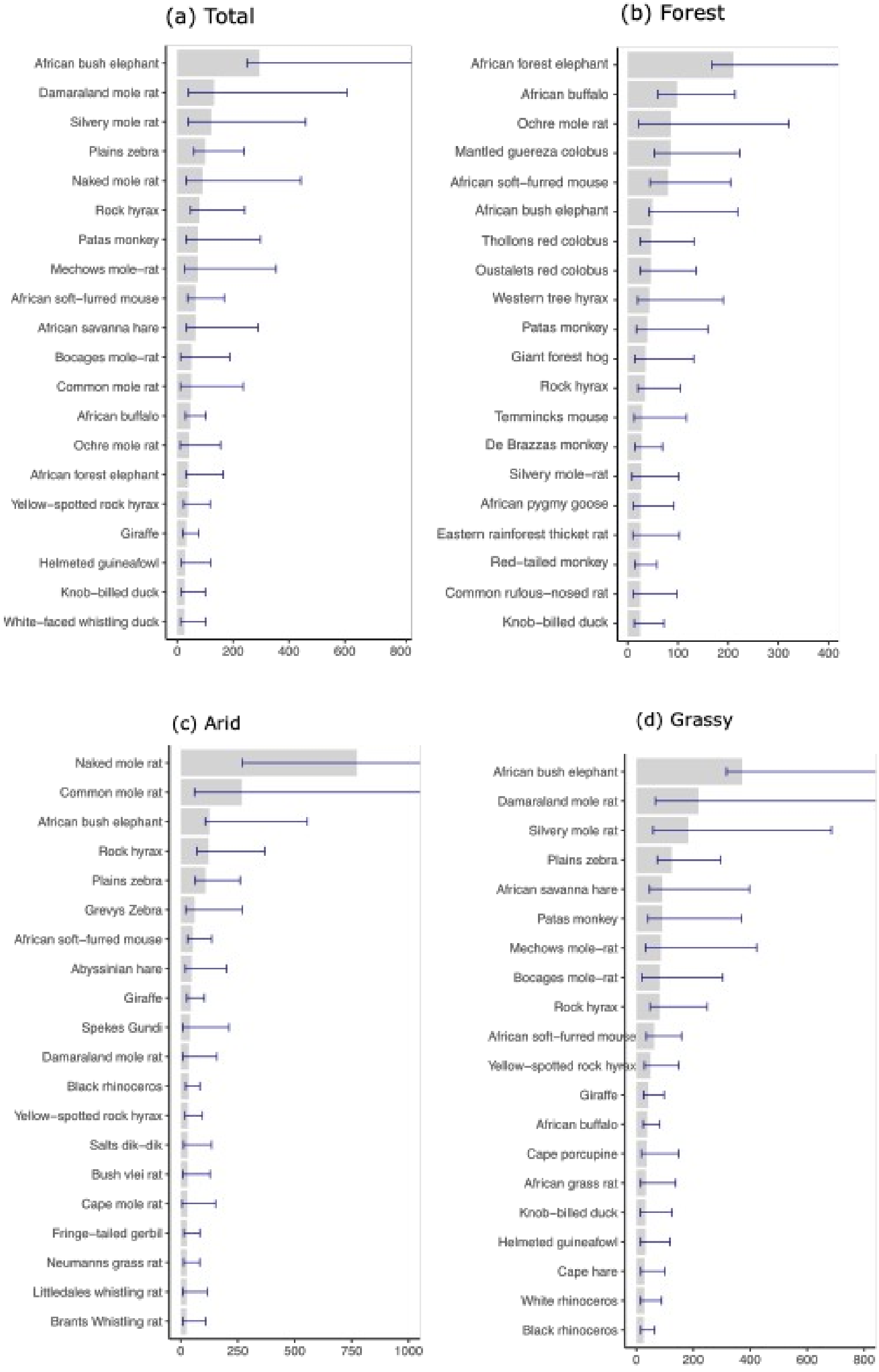
## 4.14 Extended Data Figures



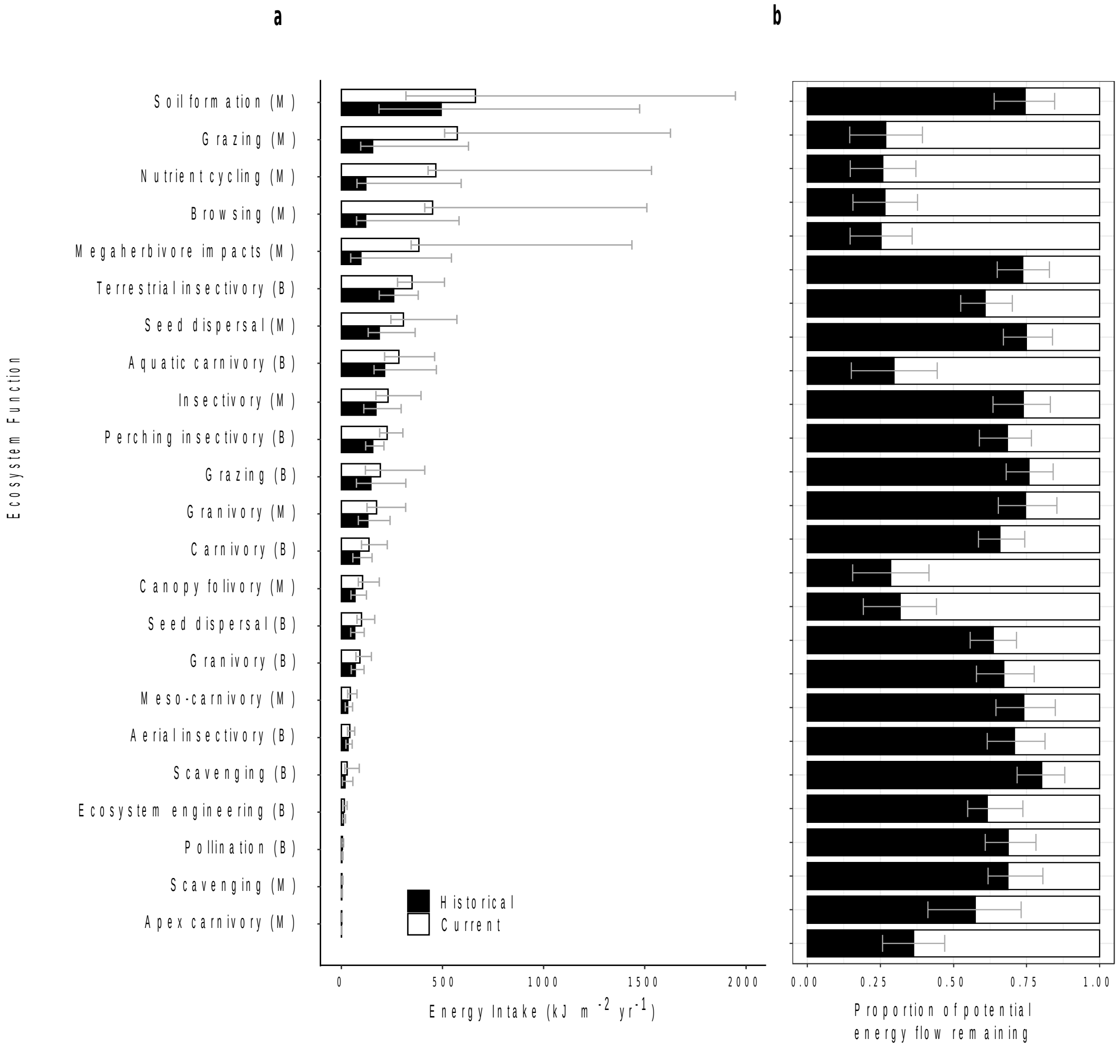
**Extended Data Fig. 1 | Relationships between declining biodiversity intactness (BII) and the intactness of energy flows through functional groups**. Relationships between total (bird and mammal) BII and energy flow intactness were calculated for each functional group in each 8x8 km$^2$ cell. The color of the hexagon indicates the number of cells with a given relationship between biodiversity intactness and energy flow intactness. Functions performed by birds are marked (B) and functions performed by mammals are marked (M). N refers to the number of species in each functional group. Gray lines signify the linear regression relationship between BII and energetic intactness, and the red dashed line indicates a reference slope of 1. BII refers to the changes in species abundances, with each bird and mammal species weighted equally.



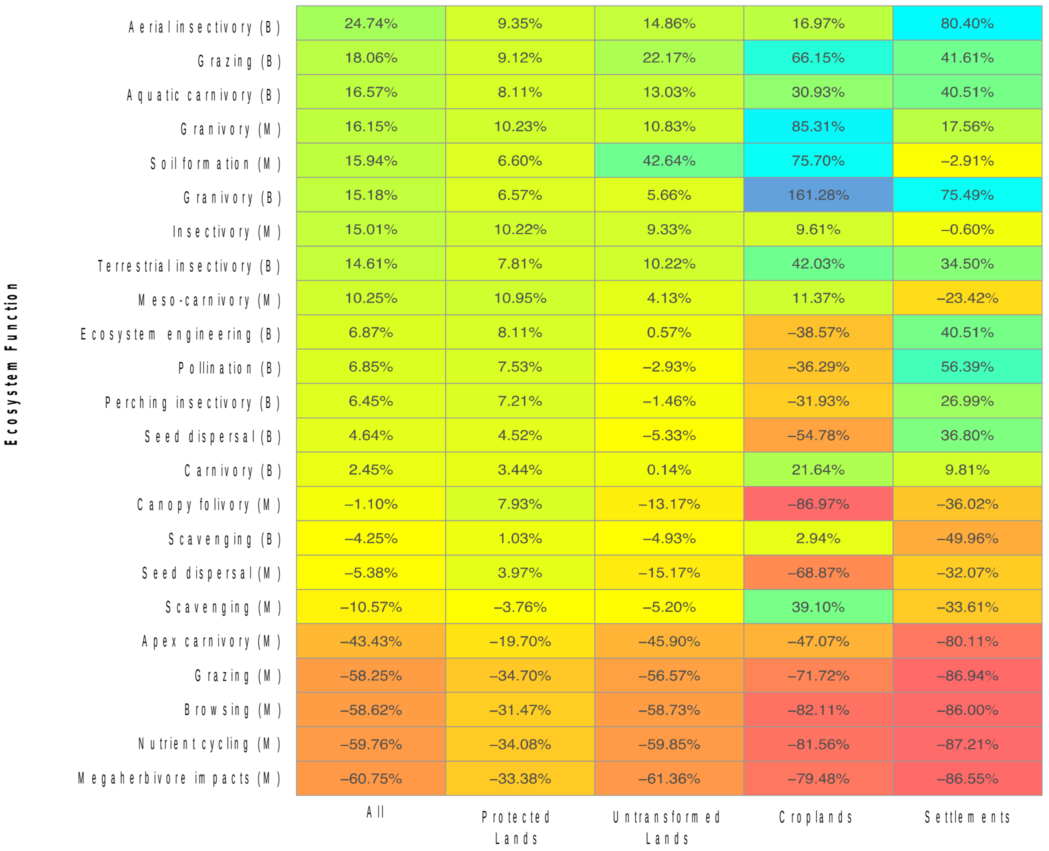
**Extended Data Fig. 2 | Intactness of energy flows through animal-mediated ecosystem functions across biomes.** Bars represent mean energy flows through functional groups for historical (black) and current (white) land uses within three groups of African biomes: forests (**a**), grassy systems including savannas and grasslands (**b**), and arid systems including deserts and shrublands (**c**). A separate scale is used for the scavenging, pollination, and apex carnivory functions. Error bars denote 95% confidence intervals derived from 10,000 monte-carlo simulations incorporating various sources of uncertainty.



**Extended Data Fig. 3 | The historically dominant bird and mammal species in terms of food energy consumption in sub-Saharan Africa and across biomes.** Species-level energy consumption by the top 20 energy consumers in sub-Saharan Africa (a) and across major biomes (b-d). Error bars denote 95% confidence intervals derived from 10,000 monte-carlo simulations incorporating various sources of uncertainty.

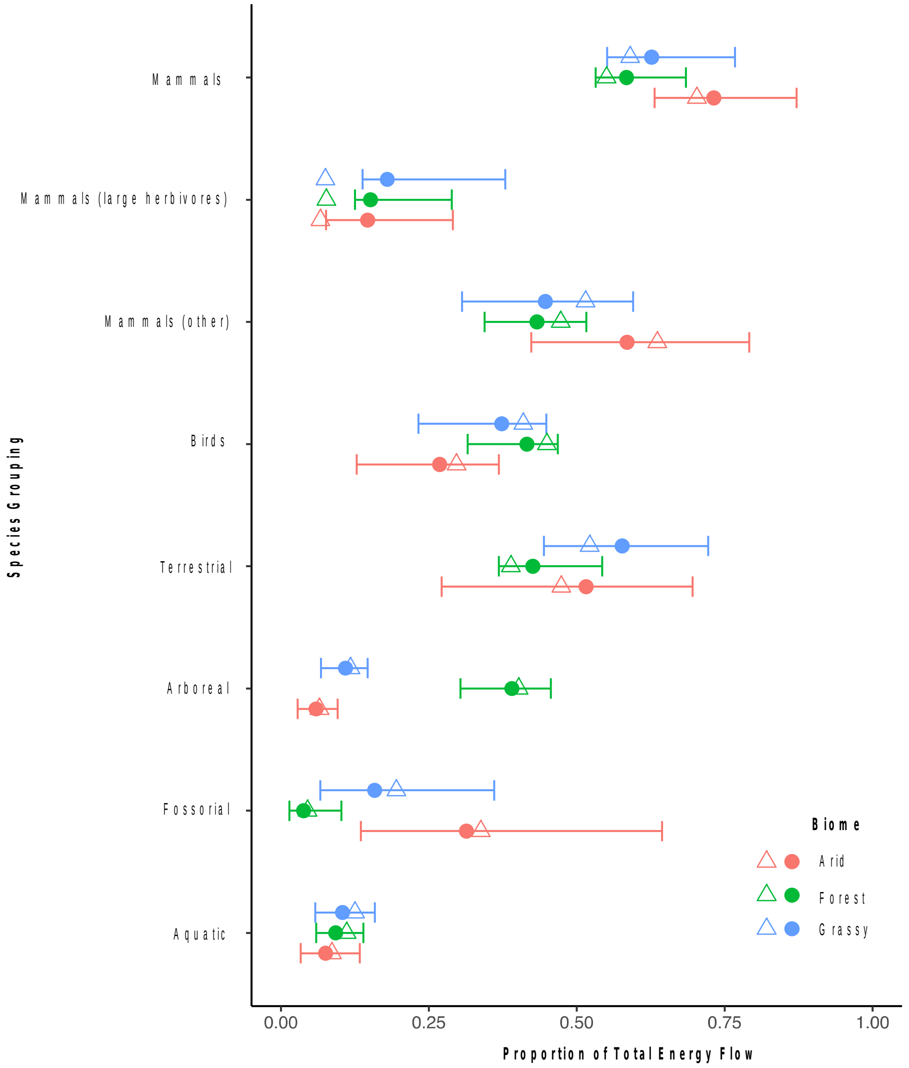


**Extended Data Fig. 4 | Energy flows through groups of species performing 23 fine-scale ecosystem functions, separated by birds and mammals**. Functions performed by birds are marked (B) and functions performed by mammals are marked (M). **a,** Total historical (white) and modern (black) mean energy flow through ten bird and mammal functional cohorts across sub-Saharan African. **b**, Average energy flow through modern sub-Saharan Africa (black) as a proportion of historical energy flow (white). Error bars denote 95% confidence intervals derived from 10,000 monte-carlo simulations incorporating various sources of uncertainty.

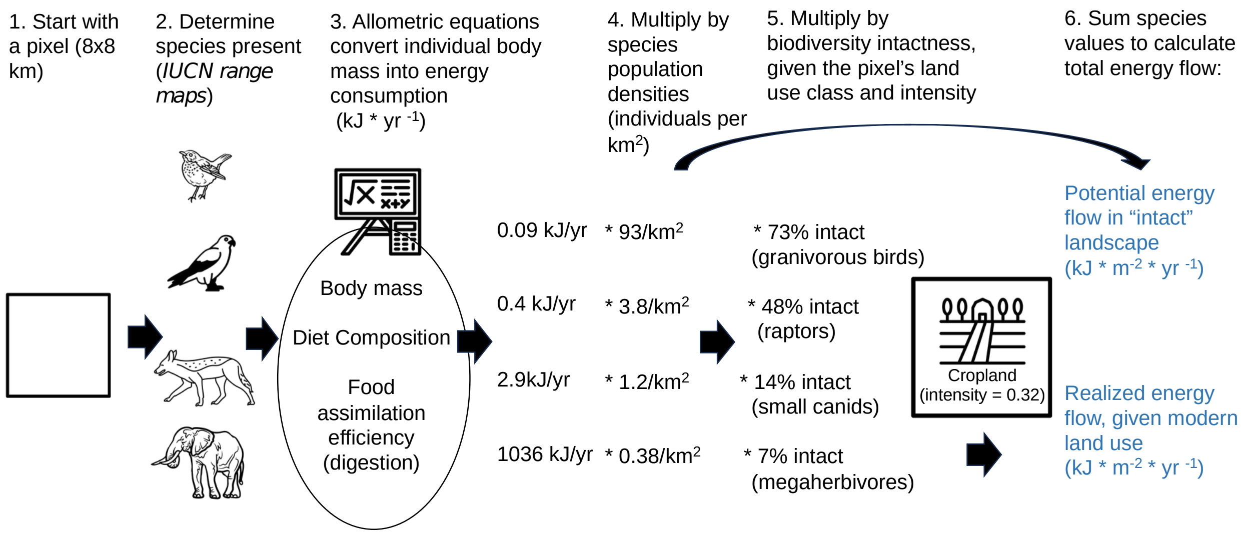


| Ecosystem Function | All | Protected Lands | Untransformed Lands | Croplands | Settlements |
|---|---|---|---|---|---|
| Aerial insectivory (B) | 24.74% | 9.35% | 14.86% | 16.97% | 80.40% |
| Grazing (B) | 18.06% | 9.12% | 22.17% | 66.15% | 41.61% |
| Aquatic carnivory (B) | 16.57% | 8.11% | 13.03% | 30.93% | 40.51% |
| Granivory (M) | 16.15% | 10.23% | 10.83% | 85.31% | 17.56% |
| Soil formation (M) | 15.94% | 6.60% | 42.64% | 75.70% | –2.91% |
| Granivory (B) | 15.18% | 6.57% | 5.66% | 161.28% | 75.49% |
| Insectivory (M) | 15.01% | 10.22% | 9.33% | 9.61% | –0.60% |
| Terrestrial insectivory (B) | 14.61% | 7.81% | 10.22% | 42.03% | 34.50% |
| Meso-carnivory (M) | 10.25% | 10.95% | 4.13% | 11.37% | –23.42% |
| Ecosystem engineering (B) | 6.87% | 8.11% | 0.57% | –38.57% | 40.51% |
| Pollination (B) | 6.85% | 7.53% | –2.93% | –36.29% | 56.39% |
| Perching insectivory (B) | 6.45% | 7.21% | –1.46% | –31.93% | 26.99% |
| Seed dispersal (B) | 4.64% | 4.52% | –5.33% | –54.78% | 36.80% |
| Carnivory (B) | 2.45% | 3.44% | 0.14% | 21.64% | 9.81% |
| Canopy folivory (M) | –1.10% | 7.93% | –13.17% | –86.97% | –36.02% |
| Scavenging (B) | –4.25% | 1.03% | –4.93% | 2.94% | –49.96% |
| Seed dispersal (M) | –5.38% | 3.97% | –15.17% | –68.87% | –32.07% |
| Scavenging (M) | –10.57% | –3.76% | –5.20% | 39.10% | –33.61% |
| Apex carnivory (M) | –43.43% | –19.70% | –45.90% | –47.07% | –80.11% |
| Grazing (M) | –58.25% | –34.70% | –56.57% | –71.72% | –86.94% |
| Browsing (M) | –58.62% | –31.47% | –58.73% | –82.11% | –86.00% |
| Nutrient cycling (M) | –59.76% | –34.08% | –59.85% | –81.56% | –87.21% |
| Megaherbivore impacts (M) | –60.75% | –33.38% | –61.36% | –79.48% | –86.55% |

**Extended Data Fig. 5 | Winning and losing ecosystem functions after human impacts**. Values represent the change in the proportion of energy flowing through each ecosystem function after accounting for human land use. Values were calculated proportionally, as the percentage change to the historical proportion of energy that flowed through each ecosystem function. Only one function, avian granivory in croplands, experienced an absolute increase in energy flow compared to historical values. But many functions experienced a relative increase in importance, even as absolute energy flows through those ecosystem functions declined. Bluer cells indicate “winning” functions, which experienced increasing relative importance, while redder cells indicate “losing” which experienced decreasing relative importance.



**Extended Data Fig. 6 | Proportional energy flow through species groups.** Circles indicate the historical fraction of total bird and mammal energy flow accounted for by a given of group of species. Triangles indicate the current fraction of total bird and mammal energy flow accounted for by a given of group of species. Species were grouped based on taxonomic class, lifestyle. Large herbivores were designated based on Hempson et al., 2015. Error bars denote 95% confidence intervals for historical values, derived from 10,000 Monte-Carlo simulation estimates incorporating uncertainty in body mass, population density, the daily energy expenditure equation, assimilation efficiency of different food types, composition of the diet of each species, and the biodiversity intactness of each species within each land use.



**Extended Data Fig. 7 | Diagram of methods.** The diagram demonstrates the steps that were used to calculate the current and historical energy flows of trophic and functional guilds of species within each cell, as explained in the methods portion of the main text.

## Extended Data Table 1 | Criteria for allocating bird and mammal species into ecosystem function groups.

| Broad scale ecosystem functions | Fine scale ecosystem function | Species number | Designation Criteria |
|---|---|---|---|
| Pollination | Pollination (B) | 41 | Trophic niche = nectarivore. |
| Seed dispersal (frugivory) | Seed dispersal (B) | 140 | Trophic niche = frugivore. |
| | Seed dispersal (M) | 191 | Diet > 25% fruit. |
| Granivory | Granivory (B) | 239 | Trophic niche = granivore. |
| | Granivory (M) | 131 | Diet > 25% seeds, and body mass < 500g. |
| Insectivory | Aerial insectivory (B) | 96 | Trophic niche = insectivore, and lifestyle = aerial. |
| | Terrestrial insectivory (B) | 361 | Trophic niche = insectivore, and lifestyle = terrestrial. |
| | Perching insectivory (B) | 660 | Trophic niche = insectivore, and lifestyle = insessorial. |
| | Insectivory (M) | 497 | Diet > 25% insects. |
| Soil disturbance | Soil disturbance (M) | 42 | Locomotion = fossorial, or aardvark. |
| Meso-carnivory | Carnivory (B) | 86 | Trophic niche = vertivore. |
| | Aquatic carnivory (B) | 112 | Trophic niche = aquatic predator. |
| | Meso-carnivory (M) | 147 | Diet > 50% vertebrates, and body mass < 15kg, and not fossorial. |
| Apex carnivory | Apex carnivory (M) | 5 | Diet > 50% vertebrates, and body mass > 15kg. |
| Scavenging | Scavenging (B) | 9 | Trophic niche = scavenger (i.e. vultures), or marabou stork. |
| | Scavenging (M) | 4 | Diet > 25% scavenging. Body mass > 500g. These include brown hyena, striped hyena, black backed jackal, and side striped jackal. |
| Grazing and browsing by large herbivores | Grazing (M) | 56 | Large terrestrial herbivores (Hemspon et al., 2015) with diets > 25% monocots, and *Gorilla* spp. |
| | Browsing (M) | 46 | Large terrestrial herbivores (Hemspon et al., 2015) with diets > 25% dicots, and gelada. |
| Nutrient dispersal by large herbivores | Nutrient dispersal (M) | 29 | Large terrestrial herbivores with average herd size ≥ 30. |
| Other | Grazing (B) | 32 | Trophic niche = aquatic herbivore or terrestrial herbivore. |
| | Ecosystem engineering (B) | 33 | Family = *Picidae* (woodpeckers). |
| | Canopy folivory | 66 | Diet >25% leaves and arboreal locomotion. |
| | Megaherbivore impacts | 5 | Mammals with body mass > 1000kg (i.e. invulnerable to predators). These include black and white rhinoceros, savanna and forest elephant, and hippopotamus. |

Species were initially allocated into fine scale ecosystem functions, and these were then aggregated into the broad scale ecosystem functions visualized in the main text figures.

## Extended Data Table 2 | Changes in energy flow through species groups based on body mass and land use.

| **Land Use** | **Size Class** | **Energy - Historical (KJ * m-2 * yr-1)** | **Energy - Current (KJ * m-2 * yr-1)** | **Proportion of Energy-Historical** | **Proportion of Energy-Current** |
|---|---|---|---|---|---|
| all | large | 685 | 186 | 16% | 7% |
| all | medium | 636 | 398 | 15% | 15% |
| all | small | 1818 | 1314 | 43% | 49% |
| all | smallest | 1061 | 776 | 25% | 29% |
| **all** | **all** | **4200** | **2675** | 100% | 100% |
| Croplands | large | 728 | 45 | 16% | 2% |
| Croplands | medium | 722 | 248 | 16% | 13% |
| Croplands | small | 1978 | 979 | 44% | 53% |
| Croplands | smallest | 1086 | 581 | 24% | 31% |
| **Croplands** | **all** | **4514** | **1853** | 100% | 100% |
| Protected Lands | large | 858 | 499 | 17% | 11% |
| Protected Lands | medium | 657 | 613 | 13% | 14% |
| Protected Lands | small | 2269 | 2151 | 46% | 49% |
| Protected Lands | smallest | 1143 | 1095 | 23% | 25% |
| **Protected Lands** | **all** | **4928** | **4358** | 100% | 100% |
| Settlements | large | 672 | 24 | 15% | 2% |
| Settlements | medium | 671 | 129 | 15% | 11% |
| Settlements | small | 1993 | 644 | 44% | 53% |
| Settlements | smallest | 1220 | 414 | 27% | 34% |
| **Settlements** | **all** | **4557** | **1211** | 100% | 100% |
| Untransformed Lands | large | 665 | 188 | 16% | 7% |
| Untransformed Lands | medium | 619 | 410 | 15% | 15% |
| Untransformed Lands | small | 1756 | 1315 | 43% | 49% |
| Untransformed Lands | smallest | 1050 | 789 | 26% | 29% |
| **Untransformed Lands** | **all** | **4090** | **2702** | 100% | 100% |

Species were allocated into body mass classes according to the following thresholds: smallest (<0.5 kg), small (< 3kg), medium (<65 kg), large (> 65 kg). The thresholds between the small, medium, and large groups follow Pringle et al., 2023. The threshold between the small and smallest groups was added to provide additional detail.

## 4.15 Supplementary Materials

### Supplementary Discussion

*Flat versus variable population densities*

To calculate the energy flows through African birds and mammals, we used a single, range-wide or "flat" estimate of each species' population density. In reality, intra-species population densities vary across species' ranges, according to environmental variables: they are not "flat" but "variable". We used flat densities, because variable densities are only available for a few species. We assumed that our simplifying assumption would not substantially alter our results, hypothesizing that intra-species variation in population densities would even out when summing energy flows across tens, hundreds, or thousands of species.

To test this assumption, we calculated the declines in energy flows through the 92 large herbivore species for which spatially variable population densities are available over the whole of sub-Saharan Africa[1]. We did these calculations using both the spatially explicit variable densities provided by Hempson et al., and using flat densities calculated by averaging the spatially-explicit densities, and then applying average values across the whole of each species' range. We calculated the difference between (i) the total range-wide energy flows through the guild; (ii) the range-wide energy flows through each individual species, and (iii) the guild-wide energy flows through our four major land uses and three major biomes. The 92 analyzed large herbivore species account for over one quarter the total energy flow through mammals, and are therefore a meaningful proxy for the larger set of species assessed in the main analysis.

We found that assuming flat densities did not meaningfully change the decline in energy flow across any of these categories, except for a few individual species (**Table S1**). The total, range-wide energy flow through large herbivores was 0.8% more intact when calculated using flat densities than using variable densities (25.75% versus 24.96%). In no land use or biome was the difference in energy flows greater than 1%. In addition, the difference in intactness was less than 1% for 72 of the 92 assessed species, with the largest differences apparent for sable antelope (*Hippotragus equinus*, 4.9%), impala (*Aepyceros melampus*, 4.8%) and steenbok (*Raphicerus campestris*, 4.3%). These results indicate that assuming flat densities does not meaningfully change the results of the study, at least for the important large herbivore guild. The results further suggest that although many landscapes have been highly transformed by humans, these transformed landscapes do not correlate with regions that feature exceptionally high or low population densities across a wide suite of species. In other words, intra-species population densities do not vary consistently across species in a way that correlates with highly transformed or protected landscapes. We therefore conclude that using flat densities does not substantially change the key results of our studies.

**Table S1**. Differences in energy flows through 92 large herbivore species calculated using flat range-wide average population densities versus variable, spatially explicit population densities. For the calculations using flat density, each species was assumed to occur in it range-wide mean population density across its entire range. For the variable population densities, we used the spatially explicit estimates in Hempson et al. (*Science,* 2014); these densities varied across the range of each species according to environmental variables (e.g. climate, soil, biome).

| **Group** | Intactness –flat densities | Intactness – variable densities | Difference in intactness |
|---|---|---|---|
| Total energy flow (large herbivores) | 25.75% | 24.96% | 0.78% |
| Median difference in energy flow for 92 large herbivores species | 32.94% | 32.88% | 0.07% |
| **Land Use** | | | |
| Settlements | 3.68% | 3.68% | 0.00% |
| Croplands | 5.87% | 5.87% | 0.00% |
| Untransformed lands | 26.90% | 26.20% | 0.70% |
| Protected lands | 58.90% | 58.90% | 0.00% |
| **Biome** | | | |
| Forest | 29.99% | 29.15% | 0.84% |
| Grassy | 24.60% | 24.25% | 0.35% |
| Arid | 27.78% | 28.39% | -0.60% |

## *Relationship between HANPP and the energetic intactness of animal-mediated functions*

Human-appropriated net primary productivity (HANPP) has recently been proposed as suitable metric to use for determining a planetary boundary for biosphere integrity[2], replacing the previous metric, biodiversity intactness (BII). We suggest that using HANPP as a solitary metric for biosphere integrity poorly captures changes to the animal component of the biosphere. HANPP estimates the amount of potential plant energy appropriated by humans through agricultural harvests and land use change[3]. A proportionate HANPP value (between 0% and 100%) can be calculated by dividing the absolute HANPP in a cell by the absolute potential NPP of a cell. HANPP is a reasonable proxy for how much humans have impacted the plant component of the biosphere, given that HANPP measure the proportion of plant energy that humans have appropriated. In contrast, HANPP is unlikely to accurately capture change to the integrity of the animal component of the biosphere, for three reasons. First, populations of different animal species and their associated ecosystem functions decline asynchronously in response to different kinds of land use change[4]. For example, rising HANPP in rangelands, where vegetation is consumed by livestock, may simultaneously benefit species adapted to open grassy vegetation, and harm species adapted to closed, woody vegetation[5]. Second, a key driver of change to animal populations—overharvesting—is uncorrelated or very weakly correlated with changes to NPP. Ecosystems with intact vegetation, and thus low HANPP, can be "empty" or largely devoid of birds and mammals, where hunting pressure is high but land clearance and logging is low. Third, there is no established mechanistic basis through which changes to animal abundances and functions can be inferred based on changes to HANPP; at best, efforts to use HANPP as a proxy for the animal component of a biosphere integrity planetary boundary would rely on correlations. For all these reasons, we suggest that an energetics-based measure of animal-mediated ecosystem function would complement HANPP by revealing a different aspect of biosphere change.

To test our assumption that HANPP is *not* an accurate proxy for changes to animal-mediated ecosystem functions, we used a linear regression to test the strength of the relationship between proportional HANPP and the proportional intactness of energy flows through birds and mammals. We expected to find a weak correlation between the two metrics, indicating their correlation with aggregate human impacts on a land use, but expected the relationship to be noisy, given the different ways plants and animals respond to human activity. As expected, we found a weak, noisy relationship between increasing HANPP and declining energetic intactness of birds and mammals (slope = -0.24, $p < 0.01$, $r^2 = 0.15$).

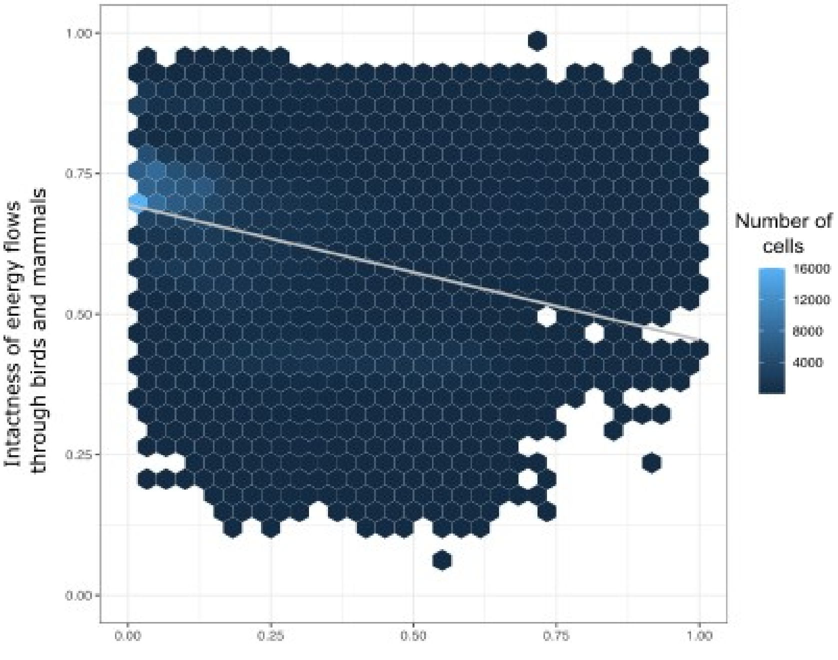


**Figure S1. Relationship between HANPP and the intactness of energy flows through birds and mammals.** Across all 8x8 km cells in sub-Saharan Africa, proportional human appropriated net primary productivity (HANPP) was related to the proportional intactness of energy flows through birds and mammals.

We suggest the weakness of the relationships is not only a consequence of the different methodologies used to map HANPP and biodiversity intactness, but also reflects the divergent ways animal versus plant energetics respond to human land use. Factors such as overharvesting, protected area management, and competition with livestock are likely to affect animals and the functions they perform in ways that diverge from their impacts on plant primary productivity. We therefore conclude that mapping changes to energy flows through animal functional groups is likely to provide useful information about changes to the earth system not captured by changes to HANPP.  Integrating HANPP and animal energetics provides a way forward for setting a planetary boundary for biosphere integrity that captures changes to both the plant and animal components of the biosphere.

*Energetic Intactness of Birds and Mammals*

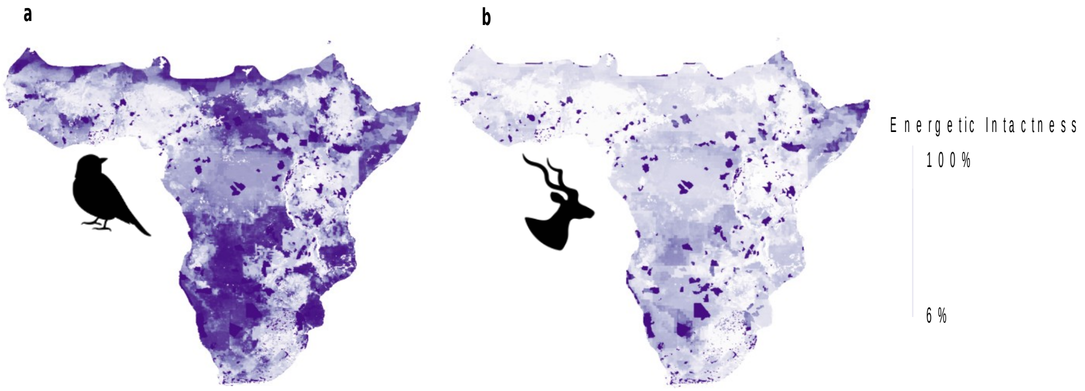


**Figure S2. | Intactness of energy flows through birds and mammals after human impacts.** Maps indicate the proportional intactness of (a) birds and (b) mammals. Fractional energetic intactness was calculated by dividing the current absolute energy flow through each 8x8 km grid cell by the historic absolute energy flow through each 8x8 km grid cell. Current absolute energy flows were calculated by multiplying the energy flows through each species present in a grid cell by the species' change in abundance, as estimated by the biodiversity intactness index for Africa.

## Supplementary data for the allometric equations used to calculate energy flows

**Table S2**: Parameter values for the allometric equations for field metabolic rates (FMR) of mammals and birds, derived from ref.[6].

| Animal Group | a | b | Mean log x | c | d | e | Equation number in ref.[1] |
|---|---|---|---|---|---|---|---|
| Birds | 10.5 | 0.681 | 1.95 | 0.328 | 1.011 | 0.012 | 17: all birds |
| Mammals | 4.21 | 0.772 | 2.364 | 0.423 | 1.017 | 0.01 | 2: Eutherian mammals |

FMR = a* body mass ^ b, where the units are kJ day-1 for field metabolic rate and g for body mass.

Equation for calculating 95% confidence intervals of the prediction: 95%CIlog(FMR)= log(predicted FMR) ± c{d + e[log(body mass) – (mean log x)]^2}^0.5

**Table S3.** : Assimilation efficiencies (%) used for each feeding group. Uncertainties indicated are standard deviations across studies. Assimilation estimates for birds are by taxonomic order; the category 'All birds' is used for those orders for which data is not available. Derived from ref.[7].

| **Diet** | **Vertebrates** | **Invertebrates** | **Fruit** | **Leaves** | **Seeds and Nuts** | **Nectar** |
|---|---|---|---|---|---|---|
| **Struthioniformes** | 0.78±0.093 | 0.78±0.093 | 0.75±0.17 | 0.36±0.075 | 0.63±0.15 | 0.94±0.11 |
| **Gruiformes** | 0.34±0.093 | 0.34±0.093 | 0.45±0.17 | 0.59±0.016 | 0.63±0.14 | 0.94±0.11 |
| **Charadriiformes** | 0.69±0.058 | 0.69±0.058 | 0.75±0.17 | 0.44±0.15 | 0.63±0.14 | 0.94±0.11 |
| **Pelecaniformes** | 0.8±0.027 | 0.8±0.027 | 0.76±0.17 | 0.44±0.15 | 0.63±0.14 | 0.94±0.11 |
| **Strigiformes** | 0.77±0.09 | 0.77±0.09 | 0.75±0.17 | 0.44±0.15 | 0.63±0.14 | 0.94±0.11 |
| **Falconiformes** | 0.84±0.022 | 0.84±0.022 | 0.75±0.17 | 0.44±0.15 | 0.63±0.14 | 0.94±0.11 |
| **Accipitriformes** | 0.82±0.017 | 0.82±0.017 | 0.75±0.17 | 0.44±0.15 | 0.63±0.14 | 0.94±0.11 |
| **Ciconiiformes** | 0.8±0.032 | 0.8±0.032 | 0.75±0.17 | 0.44±0.15 | 0.63±0.14 | 0.94±0.11 |
| **Anseriformes** | 0.87±0.093 | 0.87±0.093 | 0.75±0.17 | 0.41±0.019 | 0.83±0.011 | 0.94±0.11 |
| **Galliformes** | 0.7±0.098 | 0.7±0.098 | 0.57±0.035 | 0.42±0.017 | 0.65±0.026 | 0.94±0.11 |
| **Coliiformes** | 0.78±0.093 | 0.78±0.093 | 0.56±0.025 | 0.44±0.15 | 0.63±0.14 | 0.94±0.11 |
| **Piciformes** | 0.64±0.093 | 0.64±0.093 | 0.75±0.17 | 0.61±0.024 | 0.63±0.14 | 0.94±0.11 |
| **Passeriformes** | 0.76±0.011 | 0.76±0.011 | 0.67±0.015 | 0.76±0.066 | 0.8±0.01 | 0.9±0.039 |
| **All birds** | 0.78±0.093 | 0.78±0.093 | 0.75±0.17 | 0.44±0.15 | 0.63±0.14 | 0.94±0.11 |

**Table S4.** : Assimilation efficiencies (%) used for each feeding group. Uncertainties indicated are standard deviations across studies. Assimilation estimates for mammals are by taxonomic group (for ruminants) and body size. Values for other are derived from ref.[8]. Values for large insectivores (> 0.5kg) come from refs.[9,10]. Values for *Proboscidea* come from ref.[11]. Values for *Perissodactyla* come from refs.[12,13]. Values for other ruminants come from ref.[14]. Values for *Hippopotamidae* come from ref.[15] Values for *Suidae* come from ref.[16].

| **Diet** | **Vertebrates** | **Invertebrates** | **Fruit** | **Leaves** | **Seeds and Nuts** | **Nectar** |
|---|---|---|---|---|---|---|
| Other >0.5kg | 85±5.8 | 65±5.9 | 83±8.5 | 32±8.4 | 83±8.5 | 94±11 |
| Other <0.5kg | 85±5.8 | 88±5.9 | 83±8.5 | 46±10.7 | 83±8.5 | 94±11 |
| Perissodactyla | | | | 43±8.4 | | |
| Suidae | | | | 64±8.4 | | |
| Hippopotamidae | | | | 54±8.4 | | |
| Proboscidea | | | | 19±8.4 | | |
| Other ruminants | | | | 50±8.4 | | |

## Reconstruction of historical large mammal ranges.

Historical range maps are not available on the IUCN red list database for 11 large mammal species. We reconstructed range maps by adapting range maps from other sources, following ref.[1]. These range maps were than adjusted for area of habitat, following ref.[17]. We used the following sources for the relevant species: *Loxodonta africana*[1]. *Loxodonta cyclotis*[1], *Ceratotherium simum*[1], *Diceros bicornis*[1], *Equus zebra*[1], *Giraffa camelopardalis*[1], *Equus quagga*[18], *Equus grevyi*[18], *Taurotragus derbianus*[18], *Panthera leo*[19], and *Lycaon pictus*[20].

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# 5. Extensive Woody Encroachment Altering Angolan Miombo Woodlands Despite Cropland Expansion and Frequent Fires

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## 5.1 Chapter Statement

This chapter adopts a remote sensing approach to investigate changes to vegetation structure in the Angolan miombo woodlands. It assesses the extent of the woody encroachment in the ecoregion as well as potential drivers of changes to vegetation structure, including fire, cropland expansion, rising $CO_2$, changes in temperature, and changes in precipitation. It contributes to the broader goal of assessing changes to consumer-mediated ecosystem functions by assessing how vegetation structure in a consumer controlled ecosystem is responding to global change, acknowledging that changes to vegetation structure is the key pathway through which both consumers and resource constraints control ecosystem function in African savannas.

This paper is published in *Global Change Biology* (published February 5, 2024, available at https://onlinelibrary.wiley.com/doi/10.1111/gcb.17171). The ideas and research questions, study design, methods, data collection, data analysis, and writing presented in this chapter are the work of the first author, Ty Loft. All these activities benefited greatly from the contributions of Imma Oliveras Menor and Nicola Stevens. Francisco Maiato Gonçalves provided expertise on Angolan ecosystems and provided constructive comments during the writing of the manuscript.

## 5.2 Abstract

Woody encroachment (WE) and agricultural expansion are widespread in tropical savannas, where they threaten biodiversity and ecosystem function. In Africa’s largest savanna, the miombo woodlands, cropland expansion is expected to cause extensive habitat loss over the next thirty years. Meanwhile, widespread WE is altering remaining untransformed vegetation. Quantifying the extent of both processes in the Angolan miombo woodlands (~570,000km$^2$) has been challenging due to limited infrastructure, a history of conflict, and widespread landmines. Here, we analyze spectral satellite imagery to investigate the extent of WE and cropland expansion in the Angolan miombo woodlands since 1990. We asses WE using two complementary metrics: multi-decade canopy greenness trends and conversion from grassland to woodland. We also examine whether woody encroachment trends are driven by landscape fragmentation and decreasing fire frequency. We found that from 1990 to 2020, 34.1% of the Angolan miombo woodlands experienced significant woody encroachment or was converted to cropland, while open grassy vegetation declined by 62%. WE advanced rapidly even in areas experiencing extraordinarily high burn frequencies, and was not adequately explained by changing temperature or precipitation. WE was concentrated far from the agricultural frontier, in remote areas with low population densities. These results challenge the hypothesis that human-altered fire regimes are the primary driver of WE in mesic savannas. The results will help decisionmakers conserve the miombo woodlands’ biodiversity and ecosystem services, by highlighting that strategies to slow habitat loss must address WE and cropland expansion together.

## 5.3 Introduction

Tropical savannas cover 20% of the world’s land and supply ecosystem services to hundreds of millions of people (Bond, 2019). They provide habitat for thousands of endemic species composing a rich, ancient, and disturbance-dependent biodiversity (Bond and Parr, 2010; Veldman et al., 2015). These benefits are threatened by two global change processes: woody encroachment and land conversion for agriculture (Potapov et al., 2022; Stevens et al., 2022). Savannas include grassy ecosystems that span a tree cover gradient from nearly treeless grasslands to dense woodlands (Staver et al., 2011). In virtually all savannas, interactions between fire, herbivory, and climate maintain a balance between C4 grasses and open-canopy trees (Lehmann et al., 2011; Scholes and Archer, 1997). Interpreting how savannas are changing therefore requires understanding how disturbance regimes such as fire interact with anthropogenic changes (Strömberg and Staver, 2022). Although long acknowledged, the interactions between woody encroachment, cropland expansion, and fire are seldom viewed together and remain poorly understood in mesic savannas (Archibald et al., 2009; to Bühne et al., 2023). Clarifying these interactions can guide efforts to conserve biodiverse, resilient savannas under changing conditions (SEOSAW, 2020).

Tropical savannas are experiencing the world’s highest rates of agricultural conversion, and have experienced greater historical conversion than tropical rainforests (Ellis, 2021; Potapov et al., 2022). In Africa, 430 million hectares of natural vegetation is expected to be cleared for agriculture by 2060 (Tilman et al., 2017). Cropland expansion poses the leading threat to global biodiversity (Maxwell et al., 2016). It also degrades ecosystem services such as soil maintenance and water provision, which sustain long-term food production (Brondizio et al., 2019). In savannas, agriculture irrevocably destroys belowground root structures, permanently decreasing the capacity of savannas to conserve biodiversity and store soil carbon (Buisson et al., 2019; Nerlekar and Veldman, 2020).

Unconverted savannas, meanwhile, are experiencing long term increases in woody cover (Rosan et al., 2019; Stevens et al., 2017; Venter et al., 2018). This phenomenon, termed woody encroachment (WE), is driven by varying combinations of global and local factors. Global factors include rising atmospheric $CO_2$, increasing temperatures, and changing precipitation regimes (Bond and Midgley, 2012; Buitenwerf et al., 2012; Franco et al., 2014; Moncrieff et al., 2014). Local factors include altered fire, herbivory, and land use regimes (Devine et al., 2017; Rosan et al., 2019; Stevens et al., 2016). WE threatens livelihoods by inhibiting livestock grazing and reducing available water for crops (Luvuno et al., 2018; White et al., 2022). WE also threatens biodiversity, particularly specialist species, including birds, mammals, and plants, that are adapted to open, grassy ecosystems (Abreu et al., 2017; Sirami and Monadjem, 2012; Smit and Prins, 2015).

While land use change can interact with woody encroachment and fire in multiple ways, one prominent hypothesis suggests that cropland expansion drives WE by suppressing fire (Andela et al., 2017). Cropland expansion prevents fires from spreading, as it fragments flammable natural vegetation (Andela et al., 2017). As burned area decreases across African savannas, woody plants are released from disturbance, and woody cover increases (Sagang et al., 2022; Venter et al., 2018). Following this hypothesis, we would expect to see increasing woody cover concentrated around areas with expanding cropland and declining fire frequencies. Contrasting models of fire behavior, however, suggests that cropland expansion has little impact on fire spread in mesic savannas. In ecosystems such as the miombo woodlands, high fuel accumulations would combine with long dry seasons to make fire inevitable (Archibald et al., 2009). Such models are supported by empirical evidence that suggests WE is advancing rapidly in some frequently burning landscapes (see e.g. Stevens et al., 2016; Veenendaal et al., 2018).

To test theses hypotheses, we conducted a spatially explicit analysis of cropland expansion, woody encroachment, and fire regimes in the Angolan miombo woodlands. The miombo woodlands are Africa's largest savanna, covering 1,969,000 $km^2$ (Huntley and Walker, 2012). They are defined by the floristic uniformity of their dominant tree genera—*Brachystegia, Julbernardia, and Isoberlinia*—and occur over areas characterized by infertile soil, mesic rainfall conditions (650–1400mm) and a long dry season (Campbell et al., 1996). Despite their size, the miombo woodlands are chronically understudied (SEOSAW, 2020). Their Angolan portion ranks among the world's least studied ecosystems due to war (1961-2002), landmines, and travel restrictions (Huntley and Ferrand, 2019). Yet a lack of research understates the miombo woodlands' importance: in addition to containing Africa's richest savanna plant biodiversity, the miombo woodlands store globally significant carbon stocks and supply ecosystem services to 75 million people (Dewees et al., 2010; Kier et al., 2005; Ryan et al., 2016).

The miombo woodlands are an ideal ecosystem in which to investigate interactions between global change and disturbance, because they feature both rapid ecosystem change and frequent fires. Angola is currently experiencing the world's highest annual rate of cropland expansion and constitutes part of a broader agricultural frontier spanning the miombo woodlands (Estes et al., 2016; Potapov et al., 2022). In addition, continent-scale remote sensing analyses have found that the miombo woodlands are experiencing exceptionally high rates of woody encroachment among African savannas (McNicol et al., 2018; Mitchard and Flintrop, 2013; Venter et al., 2018). These changes are occurring within a fire-dependent landscape: though miombo covers just 17% of Southern Africa's area, it accounts for 37% of the region's fires (Archibald et al., 2009). Frequent burning maintains the ecosystem's vegetation structure, biodiversity, and ecosystem function (Campbell, 1996; Ryan et al., 2016; Saito et al., 2014; Staver et al., 2011).

This paper contributes novel evidence to the literature on global change in mesic African savannas by investigating WE, cropland expansion, and fire jointly; at the ecoregion scale; and using updated remote sensing methods. WE, cropland expansion, and fire have rarely been considered together in mesic savannas, despite projections that their combined impacts pose a widespread threat to savanna biodiversity and function (Newbold, 2018; Stevens et al., 2022). Adopting the scale of the ecoregion instead of the continent capitalizes on the ecoregion's floristic and structural uniformity, to ensure ecological differences among savannas will not confound results (Olson et al., 2001). Ecoregion-scale remote sensing studies also complement plot-based studies by examining fewer metrics of ecosystem change across a greater area (Nagendra et al., 2013). Finally, we employ two complementary but unrelated remote sensing metrics to report woody encroachment in order to increase confidence in the results. The first metric, a landcover classification, showcases areas where tree cover has crossed the 10% threshold used by UNESCO to differentiate grassland from savanna woodland. This approach highlights threats to Angola's vanishing and ecologically unique grasslands. But it fails to capture shifts in woody cover that do not cross the 10% tree cover threshold. The second metric, a vegetation index analysis of canopy greenness trends, uses a single tailored measure of woody encroachment: median May EVI. This metric accurately captures minor changes in canopy greenness that accrue over decades. But it has higher sensitivity than landcover classifications to annual phenological variation.

The aim of this study is to examine how two of the principal threats to African savannas—cropland expansion and woody encroachment—are progressing and interacting with fire in the Angolan Miombo woodlands. Our first objective was to determine the rate and extent of cropland expansion and woody encroachment in the Angolan miombo woodlands since 2000. Our second objective was to clarify the relationships between woody encroachment, cropland expansion, and fire frequency. To do so, we assessed woody encroachment trends within land use classes and burn frequency classes. We also related woody encroachment to precipitation and temperature. The results provide novel evidence that the miombo woodland's grasslands are giving way to woodlands and croplands despite the ecoregion's frequent fires. This evidence can help decisionmakers attune conservation and fire management plans to the changes transforming Africa's largest savanna.

## 5.4 Methods and Materials

### Study Area

The study analyzed the Angolan miombo woodlands (Figure 1), a mesic savanna ecosystem defined by the floristic uniformity of its tree genera, and featuring a May–September dry season and a unimodal October–April wet season (650-1400mm rainfall) (Huntley, 2023). The Angolan miombo woodlands cover 570,000km$^2$. Boundaries were defined using, using the Resolve Ecoregion dataset (Dinerstein et al., 2017). The study area included all portions of the Angolan Miombo Woodlands ecoregion (>90% of the ecoregion) falling within Angola's borders (Figure 1).

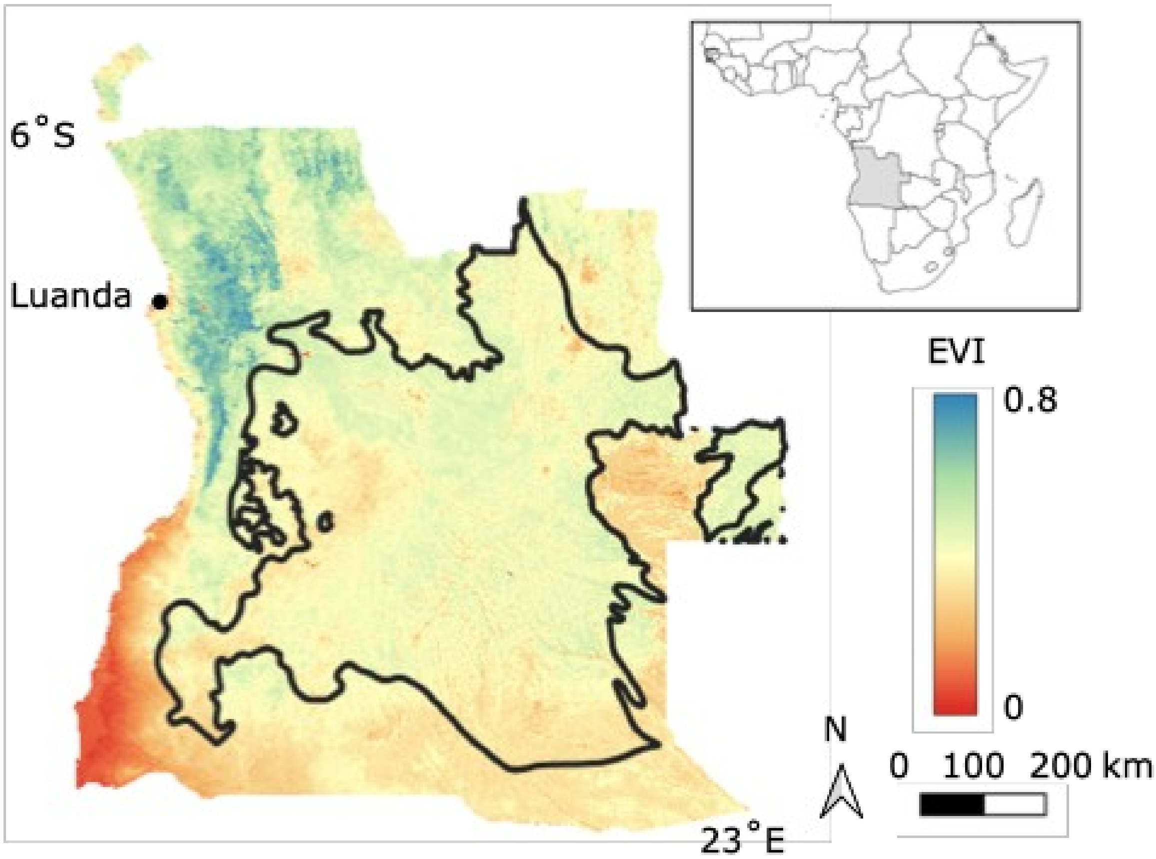


FIGURE 1. Location of the Angolan miombo woodlands ecoregion (black outline), the study area, within the country of Angola. Colors designate average values of the median May enhanced vegetation index (EVI), a proxy for canopy greenness, over the 2000-2020 period. The value of EVI for healthy vegetation ranges from 0.2 to 0.8. Inset shows Angola's location within Africa. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

## Landcover Classification

All analyses were carried out within Google Earth Engine (Gorelick et al., 2017). We built a land use classification to classify Landsat surface reflectance imagery into four landcover classes: grassland, savanna woodland, cropland, and urban. Landsat provides a near-complete set of 30m satellite imagery for the Angolan miombo woodlands from 1986 until 2022 (Woodcock et al., 2008). First, we processed 4 epochs of Landsat imagery to create multi-temporal composite, multi-band images of the Angolan miombo woodlands for the years 1990, 2000, 2014 and 2020. Landsat 5 Thematic Mapper (LS5 TM) imagery was used for the 1990 composite, Landsat 7 Enhance Thematic Mapper Plus (LS7 ETM+) was used in combination with LS5 TM imagery for the 2000 composite, and Landsat 8 Operational Land Imager (LS8 OLI) was used for the 2014 and 2020 images. We used published cross-calibration coefficients to harmonize spectral values across the Landsat datasets (Roy et al., 2016). We analyzed imagery from 2014 rather than 2010 due to the Landsat 7 satellite's scan line corrector failure, which left systemic gaps in 2004–2013 Landsat imagery.

For each year of analysis, we extracted a time series of Landsat images spanning Angola's May-September dry season to prevent wet season cloud cover from distorting the imagery, and applied a cloud mask to create cloud-free image collections. Reflectance data for each image in the series was derived from visible, near-infrared, and short-wave infrared bands, as well as from four vegetation indices: the normalized difference vegetation index or NDVI (Tucker, 1979), the enhanced vegetation index or EVI (Liu and Huete, 1995), the normalized difference built-up index (Zha et al., 2003) and the bare soil index (Li and Chen, 2014). While cropland and natural vegetation can sometimes appear spectrally similar in the late dry season, in the early dry season (i.e. May) unharvested crops provide a distinctive phenological signal (Domptail et al., 2013). Because crops and miombo vegetation display different phenological patterns (Frost, 1996), we created multi-temporal composite images for each year of analysis by extracting multiband, median-value images for three seasons: early dry season (April 29–May 30), mid dry season (June 1–July 31), and late dry season (August 1–September 15). These periods align with different phenological stages of deciduous miombo trees, respectively leaf flush, leaf fall, and pre wet-season green-up (Frost, 1996). To avoid temporal inconsistency, these seasonal images were retained as separate bands within the composite images. Because the 1990 and 2000 Landsat collections feature data gaps for Angola, we mosaicked multitemporal composite images spanning the surrounding years (1989–1991 and 1999–2001) where necessary.

We mapped landcover change between 1990 and 2020 by performing supervised classification using a 100-tree random forest classifier. We trained the classifier on the 2020 LS8 multi-temporal composite image, consisting of separate bands for each wavelength and vegetation index in each of the three seasons. We then applied the classifier to the 2014, 2000, and 1990 composite images. To create training data, we manually classified 5,000 30x30m pixels of Landsat 8 imagery. These pixels were selected using a stratified random sampling approach and were evenly divided between each of four classes: urban areas, cropland, savanna woodland, and grassland, with the cutoff for closed savanna placed at 10% tree cover, following the UNESCO vegetation structure classification (UNESCO, 1973). A drawback of this approach is that fallow cropland may be misclassified as grassland or woodland. Since 2000, however, Angolan smallholders have switched to a system of semi-permanent farming with scarce fallow periods, mitigating the problem (Schneibel et al., 2017). Pixel class was determined by comparing Landsat 8 imagery to very high spatial resolution images derived from Google Earth, following Venter et al. (2018). Where Google Earth imagery was not available for 2020, we compared 2019 Google Earth imagery to lower resolution 2020 PlanetLabs imagery to determine whether land use had changed. In addition, training pixels within each class were distributed evenly into 10 sampling quadrats encompassing the Angolan miombo woodlands. This ensured that training data for each class was distributed across the entire gradient of the ecoregion, so that urban pixels, for example, were not dominated by a few major cities. We trained the classifier using 70% of the training data, reserving 30% of pixels for out-of-bag validation, following standard practice (Breiman, 1999).

The classifier was highly accurate when tested on the validation dataset, with an overall accuracy of 86.6% when assessed following Olofsson et al (2014). User’s accuracies ranged from 79–90% (Table S2). Across all years classified, producer’s accuracies range from 90-97% for woodland, 70-91% for grassland, 61-88% (75-88% from 2000) for cropland, and 24-52% for urban and bare ground. The low value for bare urban and bare ground does not undermine the analysis, as bare ground and urban areas made up less than 2% of the study area and are not hypothesized to be experiencing woody encroachment. To reconstruct land cover in 1990, 2000, 2014, and 2020, we applied the classifier to each of the four multi-temporal composite Landsat images. We calculated the areas of each landcover class in the 1990, 2000, 2014, and 2020 classified images. We analyzed shifts from grassland to woodland as a proxy for woody encroachment, alongside the results of our EVI trend analysis. Although in some years, some areas of bare ground were unintentionally classified as urban areas, these represented 0–2% of the study area.

## **Burn Frequency Classes**

To create burn frequency classes, we used the monthly MODIS Burned Area pixel product (FireCCI51 v 5.1) at 250m resolution (Giglio et al 2009) We composited burned area into annual images of the study area. We then counted the number of years each pixel burned from 2002 to 2021 (inclusive) and divided the ecoregion into five classes based on burn frequency: areas that burned 0, 1–5, 6–10, 11–15, and 16–20 years of the 20-year study period.

## **EVI from MODIS**

We used median May values of the enhanced vegetation index (May $\mathrm{EVI}_{\mathrm{med}}$) as a proxy for woody encroachment. Spectral vegetation indices are designed to measure canopy “greenness,” a metric that captures chlorophyll and photosynthetic activity as well as canopy and leaf structure. Vegetation indices isolate this greenness signal from spatiotemporal variability (Huete et al., 2002). The EVI was developed to optimize vegetation signals in high biomass tropical regions. It reduces interference from atmospheric aerosols and from background soil signals (Huete et al., 2006). These features are advantageous in the miombo woodlands, where frequent fires raise aerosol concentrations, and an open canopy reveals soil (Frost, 1996). Prior studies show that MODIS EVI accurately captures seasonal cycles of canopy phenology and leaf area in miombo (Ryan et al., 2014). In more arid savannas, however, the contribution of grass greenness to EVI can overwhelm that of trees greenness, so results should be interpreted with caution (Archibald and Scholes, 2007).

The miombo woodland's climate and phenology make May $EVI_{med,}$ a better measure of woody encroachment than annual $EVI_{max}$, the metric employed by Rosan *et al.*, (2019). May is the optimal month for measuring EVI to ensure (i) cloud cover does not create unmanageable imagery gaps; (ii) trees retain full, green leaf cover and (iii) the grass signal is minimized. In the April to October wet season, cloud cover can mask the period of annual maximum greenness (Frost, 1996). Between June and October, deciduous miombo trees lose their leaves, confounding canopy greenness metrics (Chidumayo and Frost, 1996). In September and October, some species flush with red foliage (Chidumayo and Frost, 1996). While grass phenology varies within the Angolan miombo woodlands, many areas features green-up after dry season fires in June, making the winter a poor time to measure canopy greenness (Estes, 1974). We used median rather than maximum May EVI to reduce covariation between greenness and cloudiness, which are both highest in early May.

To measure the change in May $EVI_{med}$, we extracted 250m resolution, 16-day composite images, from the MODIS Terra Vegetation Indices product (MOD13Q1 V6) and masked clouds. These images spanned 2000 to 2022. We used a pixel-by-pixel reducer to create 23 annual images of pixelwise May $EVI_{med}$. To locate areas where woody encroachment is occurring, we ran a pixel-wise linear regression of May $EVI_{med}$ against time following Rosan et al, (2019). We considered pixels significant when they presented a best fit line using an $F$ test with a 90% confidence level. Following Rosan et al. (2019) and Mitchard and Flintrop (2013), we only designated pixels as encroached when their EVI increased by at least .03 EVI units over the 20 year study period ($p<0.1$).

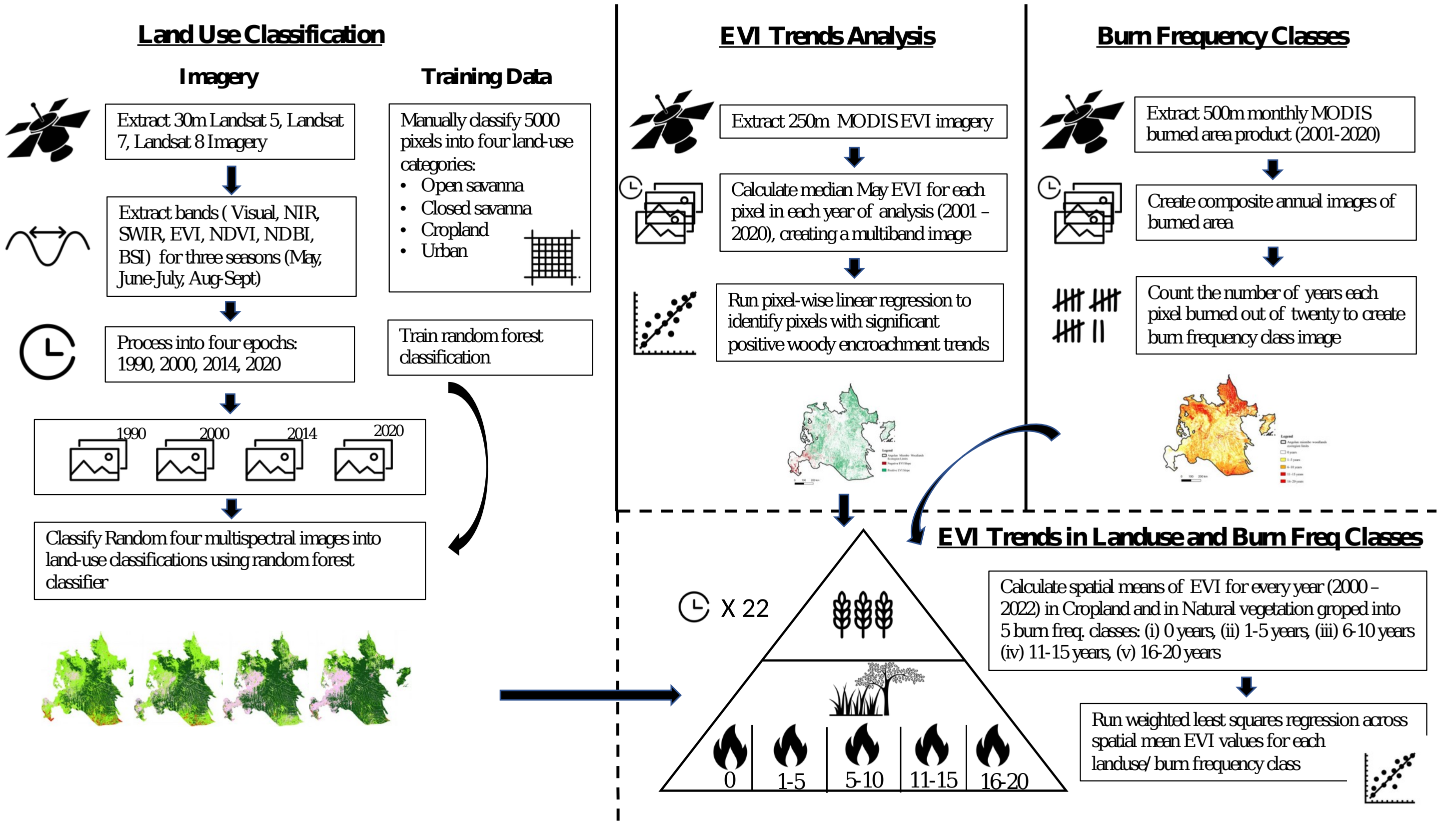
## **EVI Trends in Land Use and Burn Frequency Classes**

To compare EVI trends across landcover classes, we first upscaled 30m Landsat pixels into 250m MODIS pixels. We classified 250m pixels as either mixed or pure, with pure pixels comprising over 90% of either 30m cropland pixels or 30m natural vegetation pixels (Figure S6). Pure pixels were treated separately from mixed pixels. Pure pixels were upscaled using nearest neighbor resampling.

We calculated average EVI trends for mixed pixels as well as for each class of pure pixels: urban, cropland, grassland, and woodland. Pixel class was assigned according to the 2020 land use classification. We also calculated average EVI trends for pixels that had transitioned between and remained within land use classes from 2000 to 2020. Assessing trends based on class changes allowed us to avoid conflating natural vegetation with fallows, as well as to assess EVI trends in pixels that had transitioned from grassland to cropland. Finally, we calculated average EVI trends within each burn frequency class. As we sought to assess whether fire hinders woody encroachment in natural vegetation, we masked urban, cropland and mixed pixels. To compare EVI trends, we calculated the spatial means of May $EVI_{med}$ for each class across each year of the study. We extracted the annual spatial means and variances of pixel values for the EVI of each class in each year. We then analyzed EVI trends using weighted least squares regressions, a common technique for analyzing vegetation change across large landscapes (Zhang et al., 2020).

## **EVI Trends and Climatic Variables**

Finally, we assessed the relationship between EVI trends and two climatic variables previously found to be associated with woody encroachment: mean annual precipitation and mean annual temperature. We extracted temperature and precipitation data from the Era 5 Monthly climate dataset (ECMWF/ERA5_LAND/MONTHLY_AGGR) and calculated each variable’s average annual values across natural vegetation pixels within the study area. We used linear regressions to relate temperature and precipitation to EVI trends within natural vegetation pixels.



Extract 30m Landsat 5, Landsat 7, Landsat 8 Imagery

Extract bands ( Visual, NIR, SWIR, EVI, NDVI, NDBI, BSI) for three seasons (May, June-July, Aug-Sept)

Process into four epochs: 1990, 2000, 2014, 2020

Classify Random four multispectral images into land-use classifications using random forest classifier

Manually classify 5000 pixels into four land-use categories:

- Open savanna
- Closed savanna
- Cropland
- Urban

Train random forest classification

Extract 250m MODIS EVI imagery

Calculate median May EVI for each pixel in each year of analysis (2001 – 2020), creating a multiband image

Run pixel-wise linear regression to identify pixels with significant positive woody encroachment trends

Extract 500m monthly MODIS burned area product (2001-2020)

Create composite annual images of burned area

Count the number of years each pixel burned out of twenty to create burn frequency class image

Calculate spatial means of EVI for every year (2000 – 2022) in Cropland and in Natural vegetation groped into 5 burn freq. classes: (i) 0 years, (ii) 1-5 years, (iii) 6-10 years (iv) 11-15 years, (v) 16-20 years

Run weighted least squares regression across spatial mean EVI values for each landuse/ burn frequency class

**Supplementary Figure 1**
Specification of methods for remote sensing analysis of land use classes, burn frequencies, and May EVI (i.e. canopy greening) trends. Analyses were conducted in Google Earth Engine and R.

## 5.5 Results

### Savanna Woodland and Cropland Expanded at the Expense of Grassland

The study area experienced widespread conversion of grassland to woodland. The area of savanna woodland (>10% tree cover) increased by 54% between 1990 and 2020, expanding from 38.2% ± 3.87 to 58.8% ± 10.73 (335,309 km$^2$) of the study area (Figure 2). Grassland contracted by nearly two thirds over the same period, from 50.6%. ± 7.6 to 19.2% ± 2.9% of the study area (Figure 2e). Grassland area decreased by 13% between 2014 and 2020, declining proportionally faster than woodland or cropland expanded. Landcover change was distributed unevenly across the ecoregion (Figure 2). Shifts from grassland to woodland were concentrated in the ecoregion’s northeast and southeast, areas with low human population densities, few roads, and high landmine densities (Mendelsohn, 2019). Closed woodland persisted in the ecoregion's center. Urban areas and bare ground made up less than 2% of the ecoregion over the study period.

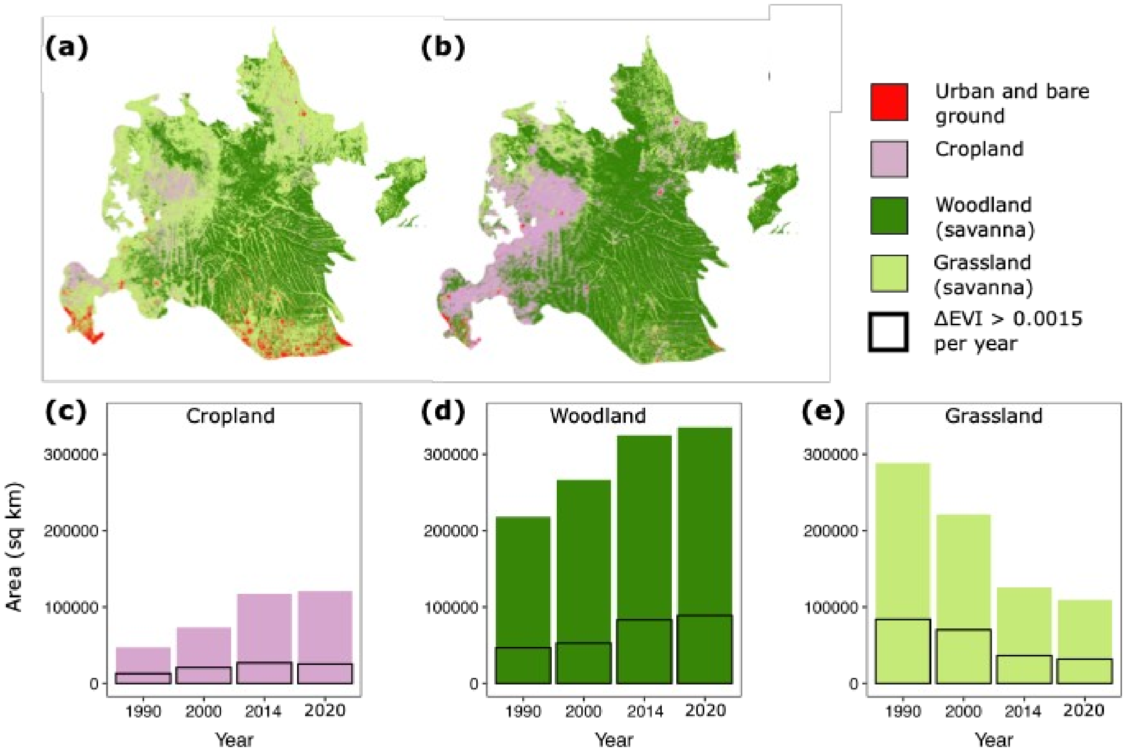


FIGURE 2. Mapping and quantifying land use change in the Angolan miombo woodlands. Panels (a-b) show landcover of open savanna, closed savanna, cropland, and urban areas/bare ground in (a) 1990 and (b) 2020. Open savanna is defined as having less than 10% woody cover. Classifications were generated from Landsat imagery using a random forest classification trained on 5000 manually classified pixels. Panels (d-f) quantify the change in area since 1990 of the dominant landcover classes within the Angolan miombo woodlands, displayed in the maps above. The panels display changes in (c) cropland (d) open savanna (e) closed savanna. The bars outlined in black indicate areas of each land use class experiencing canopy greening according to the EVI trend analysis. Data were extracted from a supervised classification of landcover in the ecoregion.

To test whether woodland was expanding more quickly in areas experiencing canopy greening, we analyzed landcover change within pixels showing positive May $EVI_{med}$ trends, a proxy for increasing canopy greenness. As expected, closed savanna expanded more quickly in areas showing positive greening trends than in the study area at large (89% versus 54% increase;

Figure 2). Woodland expanded within greening pixels more rapidly after 2000, suggesting that woody encroachment accelerated.

Cropland area increased by 155% between 1990 and 2020, expanding from 8.3% ± 1.0 to 21.2% ± 2.7 of the ecoregion, with 94.7% of that increase occurring before 2014 (Figure 2c). Agricultural areas expanded only 3% between 2014 and 2020. Cropland expanded disproportionately outside of greening pixels, and expansion within greening pixels largely occurred before 2000 (Figure 2c). Most cropland expansion took place in the ecoregion's west, a densely populated highland region (Mendelsohn, 2019).

## Woody Encroachment as Measured Through Canopy Greenness was Widespread in Natural Vegetation

To test for woody encroachment trends, we analyzed May $EVI_{med}$ trends, a proxy metric for canopy greenness. Nearly ten times more land exhibited positive greenness trends than negative trends (Figure 3). EVI increased significantly in 25.9% of the study area (147,788km$^2$) over the study period ($p < 0.1$; increase of at least 0.03 EVI units). By contrast, just 2.8% (15,923km$^2$) of the study area showed decreasing EVI trends ($p < 0.1$; decrease of at least 0.03 EVI units; Figure 3).

Canopy greenness increased by 8.3% when averaged across pixels of pure natural vegetation in 2020, an annual increase of 0.36% ($p < 0.01$; Figure 4a). The average increase was 7.8% in woodland ($p < 0.01$) and 10.1% in grassland ($p < 0.01$). In contrast, average canopy greenness did not increase significantly in pixels designated as cropland or urban areas in 2020 ($p > 0.05$). Greenness also did not significantly increase in mixed pixels, defined as having 10%–90% cover of both natural vegetation and cropland ($p > 0.05$). The increasing trend through time explained 47.6% of variation in mean EVI values within natural vegetation, with greater explanatory power in woodland (49.5%) than in grassland (40.4%; Table 1).

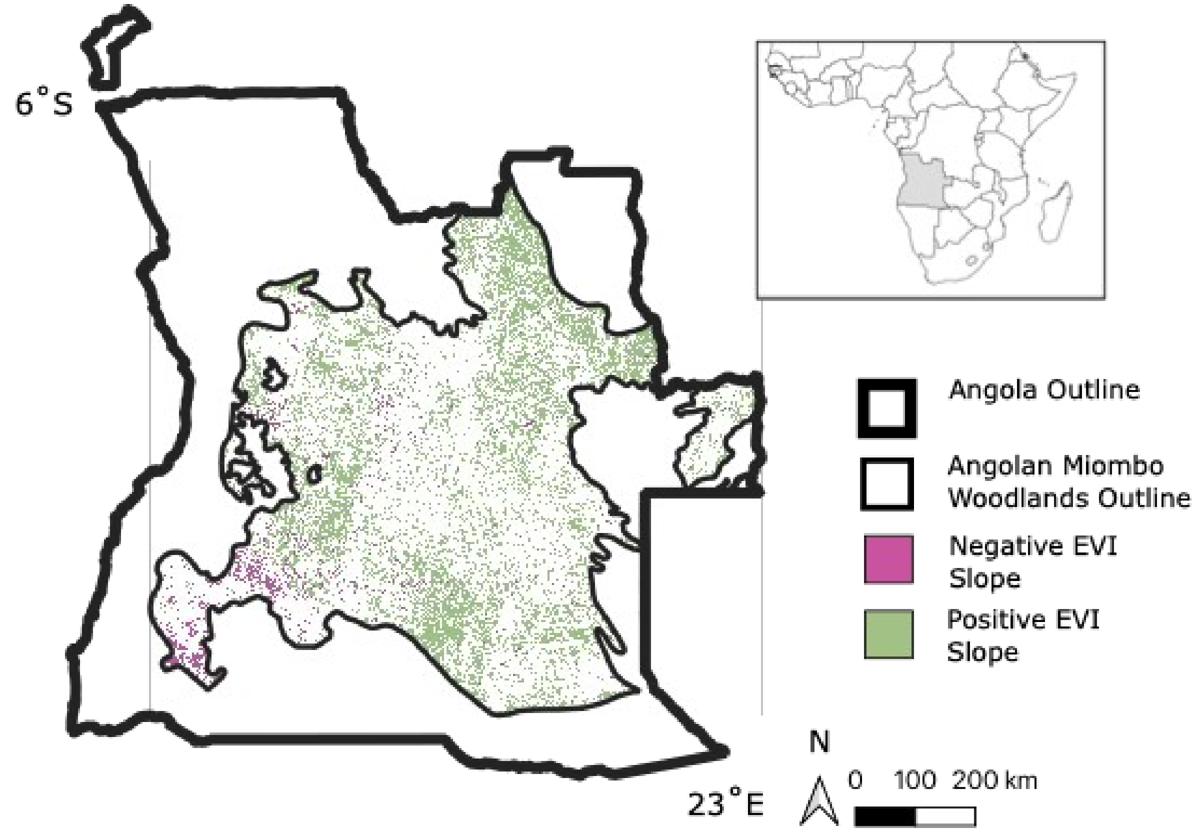


FIGURE 3. Trends of median May EVI, a proxy for canopy greenness, calculated within the Angolan miombo woodlands vegetation over the 2000 to 2022 study period. Trend values were calculated at 250m resolution. All the pixels presented on the map were masked at a level of confidence $p < 0.1$ and exhibited changes of at least 0.03 (positive trends) or -0.03 (negative trends) over the 20-year study period. 25.9% of pixels exhibited positive trends of least 0.03 ($p<0.1$) and 2.8% of pixels exhibited negative trends of at least 0.03 ($p<0.1$). The inset indicates Angola's location within sub-Saharan Africa. Map lines delineate study areas and do not necessarily depict accepted national boundaries

We also examined EVI trends in pixels that transitioned land use classes between 2000 and 2020 (Figure 4c-e). As expected, the greatest increase in canopy greenness occurred in pixels that transitioned from grassland to woodland (10.8%; $p < 0.001$, $r^2 = 0.50$). In this vegetation class, the positive trend through time explained 50.3% of variation, the highest explanatory power of any land use class. Average canopy greenness also increased significantly in pixels that persisted as grassland between 2000 and 2020 (10.6% increase; $p < 0.01$; $r^2 = 0.41$); in pixels that persisted as woodland (7.0% increase; $p < 0.01$; $r^2 = 0.49$); and in pixels that experienced succession from cropland into woodland (9.4% increase; $p < 0.01$; $r^2 = 0.37$). In this last category, less variation

(37%) was explained by the positive trend through time than in other land use transition classes. Canopy greenness did not increase significantly in pixels that remained cropland between 2000 and 2020, or in pixels that transitioned from cropland and woodland to grassland ($p > 0.05$; Table 1).

Areas with positive EVI trends were concentrated along the ecoregion's periphery, in the northeast, southeast, and northwest (Figure 3). These positive trend areas border the higher rainfall Congolian savanna-forest mosaic to the north, and the lower rainfall *Baikiaea* savanna woodlands to the south. Areas with decreasing EVI were concentrated in the ecoregion's southwest and along the central agricultural frontier. Pixels showing no change were concentrated in ecoregion's center and east.

**TABLE 1**. May $EVI_{med}$ trends, a proxy for canopy greenness, were averaged across 2020 landcover classes, 2000–2022 landcover transition classes, and burn frequency classes. Values for burn frequency classes were calculated within pixels of pure natural vegetation. Trends were calculated using weighted linear regressions.

| 2020 Landcover | 2000 Landcover | Burn Freq. | $R^2$ | F Stat | P Value | Slope | Change in EVI (annual) | Change in EVI (total, 2000-2022) |
|---|---|---|---|---|---|---|---|---|
| **By 2020 landcover** | | | | | | | | |
| Urban | | | 0.04 | 0.80 | 0.3822 | -0.0004 | -0.18% | -4.03% |
| Cropland | | | 0.01 | 0.13 | 0.7225 | 0.0002 | 0.06% | 1.43% |
| Mixed | | | 0.13 | 3.21 | 0.0876 | 0.0007 | 0.24% | 5.61% |
| Grassland | | | 0.40 | 14.24 | 0.0011 | 0.0012 | 0.44% | 10.09% |
| Woodland | | | 0.50 | 20.59 | 0.0002 | 0.0011 | 0.34% | 7.85% |
| Natural | | | 0.48 | 19.12 | 0.0003 | 0.0011 | 0.36% | 8.27% |

|  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
| **By landcover transition** |  |  |  |  |  |  |  |  |
| Grassland | Grassland |  | 0.42 | 14.96 | 0.0009 | 0.0013 | 0.46% | 10.62% |
| Woodland | Grassland |  | 0.50 | 21.22 | 0.0002 | 0.0014 | 0.47% | 10.82% |
| Cropland | Grassland |  | 0.20 | 5.20 | 0.0332 | 0.0009 | 0.35% | 7.96% |
| Woodland | Woodland |  | 0.49 | 20.54 | 0.0002 | 0.0010 | 0.30% | 6.97% |
| Cropland | Woodland |  | 0.03 | 0.62 | 0.4406 | -0.0003 | -0.09% | -2.12% |
| Grassland | Woodland |  | 0.12 | 2.87 | 0.1053 | 0.0006 | 0.20% | 4.64% |
| Cropland | Cropland |  | 0.05 | 1.07 | 0.3132 | 0.0005 | 0.18% | 4.12% |
| Woodland | Cropland |  | 0.37 | 12.41 | 0.0020 | 0.0012 | 0.41% | 9.38% |
| Grassland | Cropland |  | 0.24 | 6.64 | 0.0176 | 0.0010 | 0.35% | 8.04% |
| **By burn frequency class** |  |  |  |  |  |  |  |  |
| Natural |  | 0 | 0.47 | 18.82 | 0.0003 | 0.0010 | 0.30% | 6.94% |
| Natural |  | 1–5 | 0.49 | 20.33 | 0.0002 | 0.0011 | 0.34% | 7.80% |
| Natural |  | 6–10 | 0.40 | 14.29 | 0.0011 | 0.0011 | 0.35% | 7.99% |
| Natural |  | 11–15 | 0.44 | 16.2 | 0.0006 | 0.0012 | 0.40% | 9.30% |
| Natural |  | 16–20 | 0.38 | 13.07 | 0.0016 | 0.0014 | 0.46% | 10.65% |

## EVI Trends Were Not Impacted By Frequent Fires

To understand how woody encroachment trends related to fire frequency, we assessed average EVI trends within burn frequency classes (Figure 4b). These were designated based on how many years each pixel burned over the study period. To isolate fire's impact on natural vegetation, we masked cropland, urban, and mixed pixels. Canopy greenness increased significantly across pixels in every burn frequency class, when values were averaged across natural vegetation pixels (Figure 4b; Table 1). Canopy greenness as measured by mean May $\text{EVI}_{\text{med}}$ increased most quickly in areas that burned 15–20 of 20 years (10.7% increase; $r^2 = 0.38$; $p < 0.01$). May $\text{EVI}_{\text{med}}$ increased least quickly in unburned pixels, although the positive trend was still significant (6.9% increase; $r^2 = 0.47$; $p < 0.001$ ). That there was no significant relationship between burn frequency and May $\text{EVI}_{\text{med}}$ trends suggests that even near-annual burning is not suppressing canopy greening in the Angolan miombo woodlands.

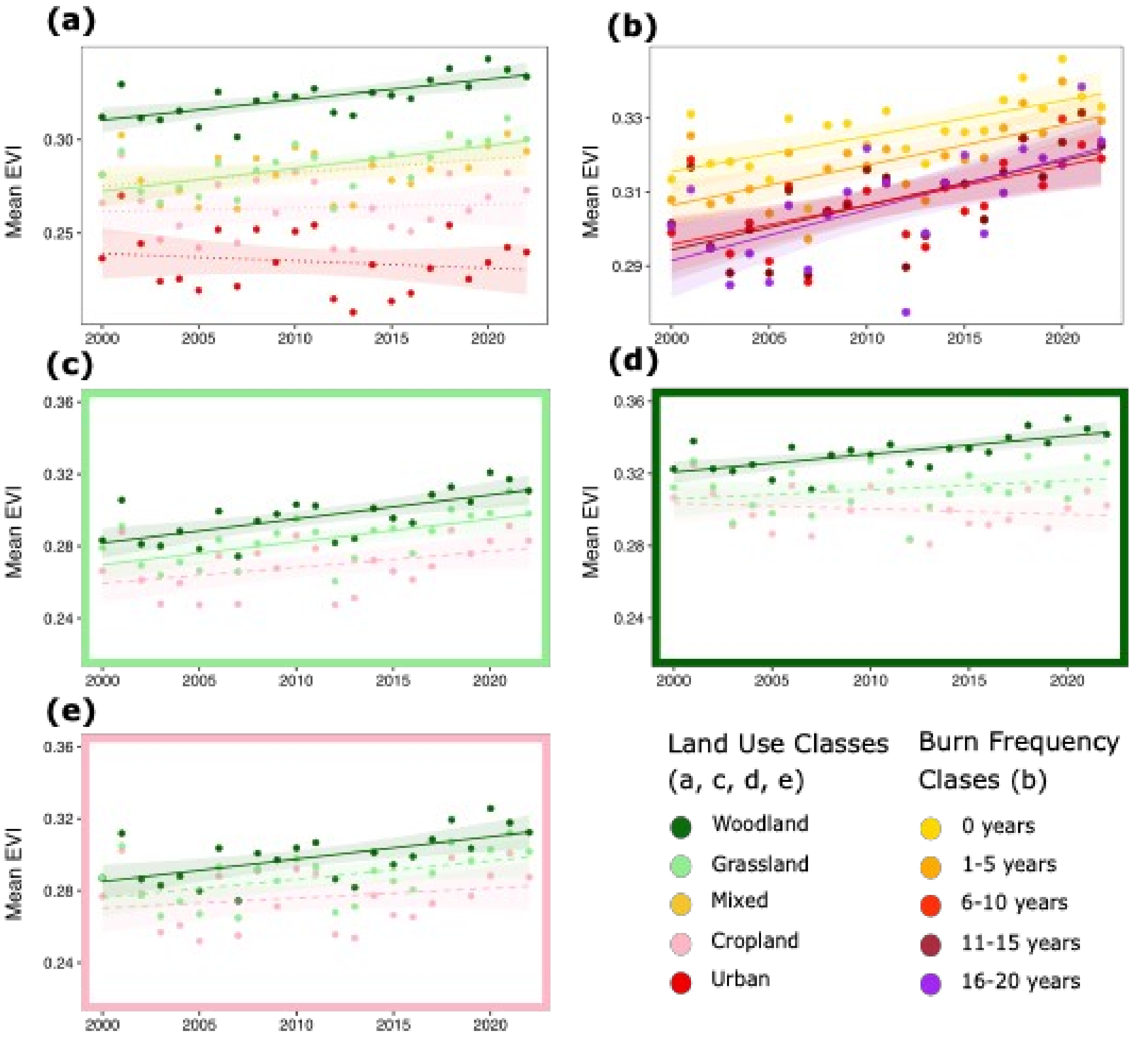


FIGURE 4. Time-series data for mean May EVI, a proxy for canopy greenness, averaged over pixels of different land use classes (a, c, d, e) and burn frequency classes (b). Points represent average annual values, solid lines represent significant linear trends ($p < 0.01$) and dashed lines represent insignificant linear trends. Shading represents 95% confidence intervals. Colored lines in a, c, d, and e represent the 2020 land use classes of analyzed pixels. The panel outlines in c, d, and e represent the 2000 land use classes of analyzed pixels. Mixed pixels in (a) include upscaled 250m pixels comprising ≥10% 30m pixels of both natural vegetation and cropland. For the burn frequency class analysis in (b), only pixels of pure natural vegetation were analyzed.

Pixels were distributed relatively evenly within burn frequency classes: 22.39% of the study area had no fire occurrence over the study period, and 32%, 18%, 13%, and 12% had fire occurrences of up to 5, 10, 15, and 20 years respectively (Figure S3). When assessed spatially, the most extensive area of high fire frequencies was in the ecoregion's northeast, a subregion exhibiting extensive woody encroachment, as measured both through canopy greenness trends and through conversion from grassland to woodland (Figure S3). The ecoregion's northwest, and southeast also exhibited high fire frequencies, while the central and southwest burned less frequently.

### **Precipitation and Temperature Trends Do Not Explain Canopy Greening**

Finally, we assessed the relationship between canopy greenness and two relevant climatic variables: precipitation and temperature. There was no relationship between mean annual precipitation and mean annual canopy greenness, as measured through May $EVI_{med}$ ($r^2 = 0.03$; $p = 0.43$; Figure S5). There was a significant positive relationship between mean annual temperature and canopy greenness within natural vegetation ($r^2 = 0.28$; $p = 0.01$). However, variation in canopy greenness was explained less well by rising temperature ($r^2 = 0.28$) than by a linear trend over time ($r^2 = 0.48$; Figure S5).

## 5.6 Discussion

The results reported here add to previous evidence that woody encroachment is combining with cropland expansion to alter a significant proportion of Africa's mesic savannas. We provide novel evidence that fire is not slowing woody encroachment in the Angolan miombo woodlands, one of Africa's least understood ecosystems. The analysis also highlights the unique threat to Angola's grasslands: between 1990 and 2020, 62% of the Angolan miombo woodlands' grasslands vanished, even as woody encroachment and cropland expansion altered just 34% of the ecoregion overall. Grassy ecosystems have a rich, unique, and threatened biodiversity unsuited to woodlands or forests (Murphy et al., 2016). The following discussion of the drivers of global change in the miombo woodlands can help policymakers conserve grassland biodiversity in Angola.

## Extent of Woody Encroachment

Woody encroachment was found to be widespread in Angola, a result in line with previous continental and subcontinental-scale analyses. Two previous studies assessed woody encroachment across Africa by manually classifying canopy cover and by quantifying plant biomass using radar (McNicol et al., 2018; Venter et al., 2018). Both found widespread woody encroachment in the Angolan miombo woodlands. A third study found decreasing woody cover in Angola from 1982–2006, but analyzed imagery from seasons inappropriate for capturing miombo canopy foliage (Mitchard and Flintrop, 2013). The results reported here provide further evidence of widespread woody encroachment using two additional independent methods: vegetation index analysis and landcover classification. We found that canopy greenness increased by 0.36% per year between 2000 and 2022, broadly in line with findings by Venter et al. (2018) that tree cover increased by 0.7% per year between 1986 and 2016 across Angola. We have further confidence that woody encroachment is occurring due to the concurrence between our independent landcover change and canopy greenness analyses: we found that canopy greenness increased most rapidly and consistently in pixels that transitioned from grassland to woodland. This agreement suggests that the satellite-derived proxies for woody encroachment are recording real ecological change.

The joint analysis of woody encroachment, landcover change, and fire frequency reveals three key features of woody encroachment's distribution in Angola. First, woody encroachment has overwhelmingly occurred within remaining natural vegetation. Canopy greenness increased rapidly in grassland and woodland, increased moderately in recovering fallows, and did not increase in mixed-used pixels and cropland. Second, woody encroachment occurred across the gradient of tree cover and fire frequency. Canopy greenness increased significantly across pixels of both grassland and woodland and across all burn frequencies. Third, woody encroachment was distributed widely but unevenly within the ecoregion. The ecoregion-sized scale of the analysis allowed us to analyze the spatial distribution of woody encroachment in greater detail than in previous studies (e.g. Cabral et al., 2011; Palacios et al., 2015). Both the classification and EVI trend analysis suggest that greening was concentrated near the ecoregion's northern and southern borders, and rarer in the ecoregion's center. The only region experiencing negative greenness trends was the southwest. This region's reliance on cattle ranching is unique within the Angolan miombo woodland (Huntley, 2022). Our results support evidence that cattle overstocking, charcoal gathering, and drought are transforming this region's woodland into shrubland (Huntley, 2022).

The ability to ground truth this study's results is constrained by the absence of long-term plot data and the limited accessibility of rural Angola. Few roads and numerous landmines make a rigorous ground-truthing protocol difficult to carry out. We validated our classification results against high resolution satellite imagery available. However, high resolution time series imagery is inconsistently available on Google Earth, so we were unable to verify EVI trends using it. This gap raises the possibility that long-term changes in tree or grass phenology over the study period could affect the results reported here. Such changes have not to our knowledge been reported in the miombo woodlands but the ecosystem is understudied (SEOSAW, 2020).

## Drivers of Woody Encroachment

While a consensus has emerged that woody encroachment is widespread across the miombo woodlands, its causes remain contested, with previous studies proposing both global, climatic factors and local, disturbance factors (Luvuno et al., 2018; Sagang et al., 2022; Venter et al., 2018). Hypothesized drivers of woody encroachment include changes to fire, landscape fragmentation, temperature, precipitation, herbivory, and atmospheric $CO_2$ concentrations.

The results here suggest that fire is unlikely to be controlling woody encroachment in the Angolan miombo woodlands. This finding contrasts with the outcomes of fire experiments in the miombo woodlands, which have suggested that frequent fires inhibit woody vegetation cover. (Furley et al., 2008; Ryan and Williams, 2011). It also contrasts with findings that fire suppressed woody encroachment in Cameroonian mesic savannas (Sagang et al., 2022). What explains these discrepancies? One explanation is that fire experiment results have been distorted by pre-clearing treatments. Without such treatments, fire effects alone are unlikely to maintain open ecosystems under elevated $CO_2$ conditions (Veenendaal et al., 2018). Future work should systematically analyze the long-term impacts of fire regimes on woody encroachment across mesic African savannas. If, as these results suggest, other drivers are constraining fire's capacity to maintain the miombo's grasslands, global change would threaten fire-dependent biodiversity and ecosystem services.

A second set of hypotheses suggests that landscape fragmentation is driving woody encroachment. Expanding cropland suppresses fire and herbivory in remaining patches of natural vegetation, releasing woody vegetation from disturbance. If landscape fragmentation were driving woody encroachment, we would expect to see canopy greening in mixed pixels, where natural vegetation and cropland are interspersed. Instead, canopy greenness advanced most quickly in pixels of pure natural vegetation. Moreover, greening areas were concentrated in the ecoregion's northeast and southeast, regions with little agriculture, low population densities, and unfragmented vegetation cover. Woody encroachment appears to be advancing in areas of natural vegetation relatively unimpacted by human land use change, suggesting that a global rather than local driver may be responsible.

An exception is the western highlands, a densely populated region showing positive greenness trends but little conversion of grassland to woodland. What explains this discrepancy? One possibility is that positive greenness trends in this region are explained by recovering fallows. This zone has experienced rapid agricultural expansion since 1990, and perhaps some abandoned fields have not been adequately captured by the land use classification (Safarik, 2020). Alternatively, the positive trend pixels may be capturing regional changes in crop phenology or in crop greenness. Investigating the factors driving positive EVI trends within this cropland-savanna mosaic is a rich area for future study.

This study did not directly assess the impact of herbivory on woody encroachment in the study area, as little accurate data on herbivory in Angola exists. However, we can infer from other analyses that changes to herbivory are unlikely to be driving the observed woody encroachment. Biomass in the Angolan miombo woodlands is overwhelmingly consumed by fire, not by herbivores (Archibald and Hempson, 2016). Previous work has found that historical herbivore biomass in the Angolan miombo woodlands was low and that contemporary biomass has not changed much in the ecoregion (Archibald and Hempson, 2016). Moreover, in the Mozambican miombo woodlands, where wartime hunting did significantly decrease herbivore populations, suppressed herbivory was not associated with increasing woody cover (Daskin et al., 2016).

If disturbance is not driving woody encroachment in the study area, climatic factors may be. This study found that changing precipitation was not associated with canopy greenness in the ecoregion. Rising temperature was weakly associated with canopy greenness. Time, a proxy for rising $CO_2$ concentrations, was strongly associated with increasing canopy greenness within areas of natural vegetation. There is some evidence that trees in the miombo woodlands will benefit disproportionately from rising $CO_2$ due to their root suckering propagation strategy. By enhancing root suckering, miombo trees directly benefit from increasing belowground $CO_2$ reserves (Kgope et al., 2010; Wakeling and Bond, 2007). Climatic factors are less easily manipulated than disturbance factors at plot scales, so it is difficult to experimentally validate relationships between rising temperature, rising $CO_2$ and woody encroachment. If fire and herbivory cannot arrest woody encroachment, conservation management strategies would need to manipulate anthropogenic disturbances such as charcoal gathering and to focus on adaptation.

Like woody encroachment's causes, its ecological character remains contested and understudied in the miombo woodlands (SEOSAW, 2020). It is unclear whether the canopy greening trends observed through satellite imagery indicate (a) increases in the canopy cover of savanna tree species; (b) increases in the cover of shrubby vegetation or thicket; or (c) the transition of savanna woodland into a closed canopy forest formation comprising Congolian rainforest or Zambezian *Cryptosepalum* dry forest species. The analyses found that woody encroachment is concentrated discontinuously on the ecoregion's peripheries. This raises the possibility that different forms may be occurring in different subregions. For example, the wetter northern portion might be experiencing transformation into closed canopy forest and the drier southern portion encroachment by shrubs or thicket, a common process in arid savannas (Stevens et al., 2016). Fieldwork-based studies are needed to assess how different forms of woody encroachment impact the miombo woodland's biodiversity and ecosystem services.

## Drivers of Cropland Expansion and Deceleration

In addition to woody cover, land cover changed dynamically over the last thirty years. Cropland expanded rapidly in Angola's miombo woodlands until 2014 and decelerated afterward. In all, cropland was found to have expanded by 155% in thirty years, just below the 160% expansion reported by Potapov et al., (2022). Cropland expansion was distributed unevenly in the ecoregion. Until 2000, expansion was concentrated in the western highlands, which historically supported intensive agriculture but saw output collapse by 70%-95% during the 1975–2002 civil war (Safarik, 2020). Since 2000, an agricultural frontier has developed, with cropland expanding northeastward out of the highlands (Figure 2). The development of a post-conflict agricultural frontier has been reported by previous field-based and remote sensing studies of Angolan agriculture (Mendelsohn, 2019; Schneibel et al., 2017).

The deceleration in cropland after 2014 has not been reported before, and contrasts with warnings that cropland expansion will accelerate in Angola, the miombo woodlands, and savannas globally (e.g. Tilman et al., 2017; World Bank, 2019). We provide three hypotheses to explain the slowdown. First, the collapse of oil prices in 2014, which account for 89% of Angola's export revenues, decreased the fertilizer and seed subsidies paid to subsistence farmers. (OPEC, 2021; Safarik, 2020). Costlier inputs may have slowed expansion. Second, Angola's well-documented and rapid rural-to-urban migration may be slowing expansion, as a stagnant rural population needs less new cropland (Safarik, 2020). Third, the agricultural frontier may be physically limited by the Kalahari Sands soil formation. The Kalahari sands' low nutrient concentration likely hinder agriculture to the east of the present agricultural frontier (Huntley, 2022).

## Conservation and Governance Implications

Both cropland expansion and woodland expansion occurred at the expense of grasslands. The unique biodiversity within Angola's grassy ecosystems are likely to be especially threatened by global change (Huntley and Ferrand, 2019). This threat may be moderated by the low commercialization of Angola’s agricultural system, with  just 2-3% of Angolan cropland farmed industrially (Safarik, 2020). In addition, some cropland expansion over the study period may be recultivation of colonial-era plots, given the collapse in agricultural production during the 1974–2002 Angolan civil war (Safarik, 2020). Nevertheless, conservation strategies should highlight the biodiversity within Angola’s rapidly vanishing grassy ecosystems. Because Angola is experiencing both food insecurity and biodiversity loss, decisionmakers will need to balance conservation with food production (Becker-Reshef et al., 2020; Huntley, 2022) There is an urgent need to understand the causes of Angola’s agricultural expansion and deceleration, in order to attain that balance. Decisionmakers will also need to actively manage woody cover in protected areas spared from agriculture, if they are to successfully conserve grassland species. Combining remote sensing with sociological study of Angola’s agricultural systems and protected areas is an important area of future research (Vijay and Armsworth, 2021).

Finally, the comprehensive scope of ecoregion-wide remote sensing results can usefully challenge assumptions about ecosystem change based on individual perceptions. Across the miombo woodlands, there exists a widespread perception that logging and charcoal production are converting the miombo woodlands to grassland and shrubland (Huntley, 2017; Mendelsohn, 2019; World Bank, 2019). In Angola, deforestation and charcoal are consistently mentioned as threats to the miombo woodlands in policy reports (e.g. National Biodiversity Strategy And Action Plan,  2019–2022; 5th National Report on Biodiversity in Angola, 2007 – 2012). Yet to the best of our knowledge, no government reports, laws, or policies discuss woody encroachment. We suggest that the spatial distribution of woody encroachment may be obscuring its extent from practitioners, as research on Angolan ecology is concentrated in southwest Angola, the sole subregion exhibiting widespread negative EVI trends (Figueira and Lages, 2019). Additionally, casual and scientific observations of the miombo woodlands are concentrated around roads and towns, the areas most affected by logging and charcoal gathering (Mendelsohn, 2019). In contrast, woody encroachment is concentrated in remote areas difficult for research teams to access (Figueira and Lages, 2019). Ecoregion-scale remote sensing analyses can complement empirical fieldwork by providing data on these inaccessible, under-researched landscapes.

## 5.7 Conclusions

Our results indicate that widespread woody encroachment and cropland expansion are simultaneously transforming the Angolan miombo woodlands. Global change has significantly altered over one third of the ecoregion in the last 30 years, while an additional 8% of the ecoregion was converted to cropland before the study's timeframe. The results corroborate previous studies finding widespread greening in African savannas (García Criado et al., 2020; Venter et al., 2018), while extending results into one of the world's least studied and understood ecoregions (Russo et al., 2019).

In addition, woody encroachment is occurring in areas that burn extremely frequently (>15 of the last 20 years), suggesting that global drivers such as rising temperature and $CO_2$ concentrations may be outweighing local drivers such as fire and land use change. While increasing woody cover can enhance savanna carbon sequestration, it degrades ecosystem functions such as grazing capacity and water provision (Luvuno et al., 2018; White et al., 2022). The uncertainty around woody encroachment's impacts in the miombo woodlands highlights the need for fieldwork. We affirm calls to dramatically expand research on global change in neglected, misunderstood, and threatened grassy ecosystems (Bond and Parr, 2010; Parr et al., 2014).

These results have implications for ecosystem management and biodiversity conservation in the miombo woodlands. First, the results complicate calls to manage woody encroachment by manipulating disturbance, as they suggest that neither fire nor herbivory are likely to arrest woody encroachment in the Angolan miombo woodlands. Second, the results highlight the need to address cropland expansion and woody encroachment jointly, as dual threats to savanna biodiversity (Abreu et al., 2017; Tilman et al., 2017). Analyses premised solely on habitat loss driven by land use conversion will underestimate risk to endemic savanna species. Instead, biodiversity risk assessments must account for the ways disturbance, rising $CO_2$, and climate change interact to shift species composition within savannas. These findings will be useful as Angola rebuilds its conservation system post-conflict and coordinates with neighboring countries to conserve Africa's largest savanna.

Finally, we emphasize the value of focused, ecosystem-level and national-level analyses as a complement to global and local studies, including to the continental scale analyses prominent in global change ecology (Xiong *et al.*, 2017). By focusing on a single ecoregion, we were able improve the accuracy of long-term cropland mapping in the miombo woodlands from ~60% to 86% (Xiong et al., 2017). The creation of land cover classifications with highly accurate cropland classes is essential for mapping habitat loss and woody encroachment, key drivers of biodiversity loss and carbon emissions. We suggest future researchers coordinate creating ecoregion-scale maps of African savannas. Another advantage of national level analyses is that they expose the ways a country's unique history and geography can moderate how global change affects its ecosystems. For example, we hypothesize that in Angola, low oil prices and post-conflict, urban-to-rural migration dynamics contributed to the deceleration of cropland expansion since 2014. Angola's oil-dependence and post-conflict politics are unique in the miombo region and likely shape its global change ecology in distinctive ways. However, the nature of these relationships between politics and ecology in Angola is poorly understood and is a rich area for future study.

## 5.8 Author Contributions

T.L. and I.O.M. conceived the initial study design and developed methodology. T.L. led data analysis and wrote the first draft of the manuscript, with supervision by I.O.M. and N.S. F.M.G. provided export knowledge on woody encroachment trends and cropland expansion in the study landscape. All co-authors provided critical feedback at different stages of the analyses and contributed to manuscript writing

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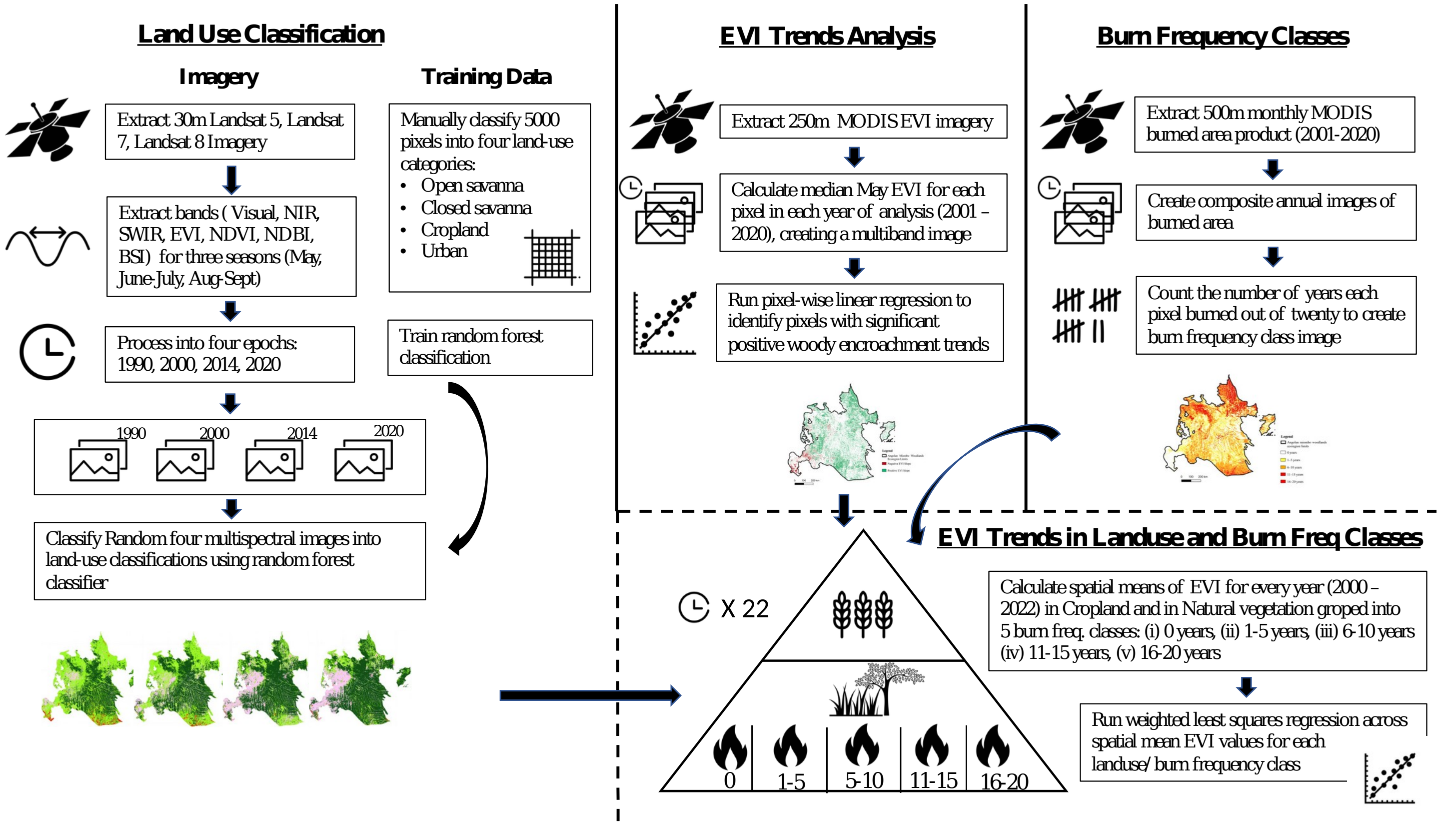
## 5.10 Supplementary Figures



Extract 30m Landsat 5, Landsat 7, Landsat 8 Imagery

Extract bands ( Visual, NIR, SWIR, EVI, NDVI, NDBI, BSI) for three seasons (May, June-July, Aug-Sept)

Process into four epochs: 1990, 2000, 2014, 2020

Classify Random four multispectral images into land-use classifications using random forest classifier

Manually classify 5000 pixels into four land-use categories:
- Open savanna
- Closed savanna
- Cropland
- Urban

Train random forest classification

Extract 250m MODIS EVI imagery

Calculate median May EVI for each pixel in each year of analysis (2001 – 2020), creating a multiband image

Run pixel-wise linear regression to identify pixels with significant positive woody encroachment trends

Extract 500m monthly MODIS burned area product (2001-2020)

Create composite annual images of burned area

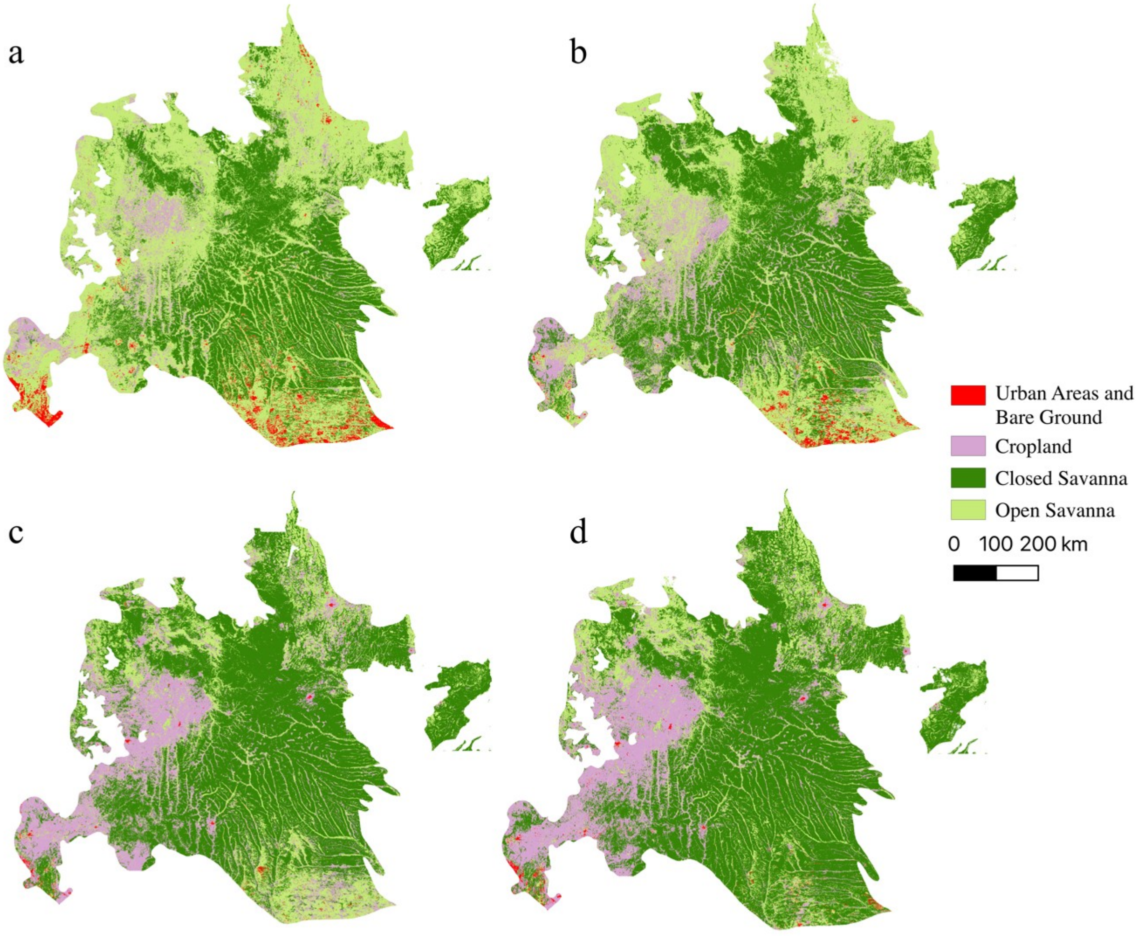
Count the number of years each pixel burned out of twenty to create burn frequency class image

Calculate spatial means of EVI for every year (2000 – 2022) in Cropland and in Natural vegetation groped into 5 burn freq. classes: (i) 0 years, (ii) 1-5 years, (iii) 6-10 years (iv) 11-15 years, (v) 16-20 years

Run weighted least squares regression across spatial mean EVI values for each landuse/ burn frequency class

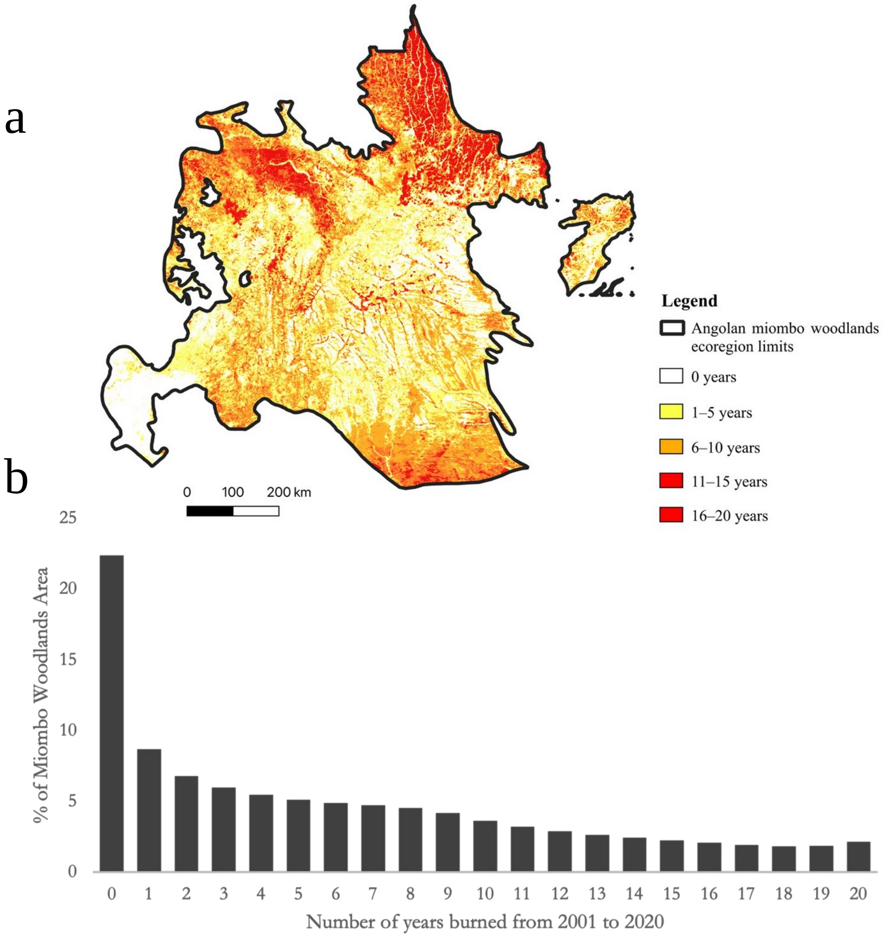
**Supplementary Figure 1**

Specification of methods for remote sensing analysis of land use classes, burn frequencies, and May EVI (i.e. canopy greening) trends. Analyses were conducted in Google Earth Engine and R.



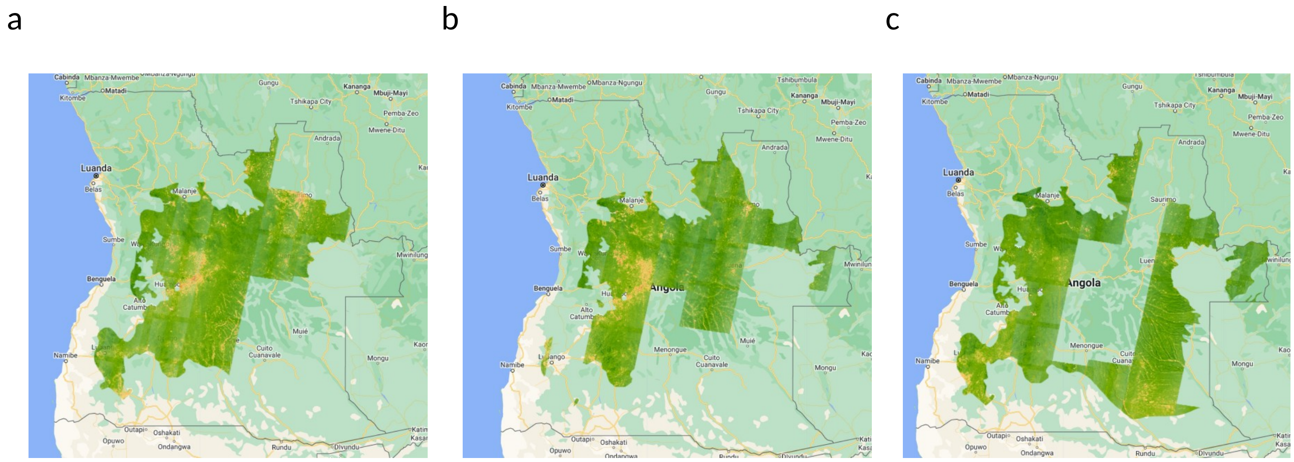
**Supplementary Figure 2**

Classification of land cover in the miombo woodlands in (**a**) 1990, (**b**) 2000, (**c**) 2014 and (**d**) 2020. Open savanna (i.e. grassland) is defined as possessing less than 10% woody cover and closed savanna (i.e. woodland) is defined as possessing greater than 10% woody cover, following the UNESCO vegetation classification (UNESCO, 1973). Land use classifications were generated from Landsat imagery using a random forest classification trained on 5000 manually classified 30m Landsat pixels. A 2014 rather than 2010 land use classification was created due to the failure of the Landsat 7 satellite's scan line corrector, which has left 2003-2013 imagery incomplete.



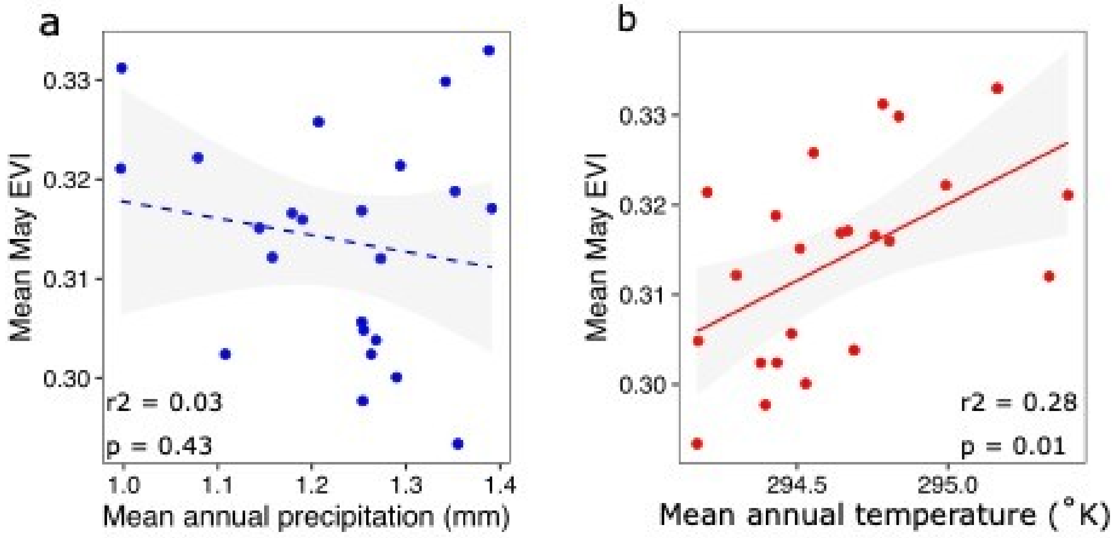
**Supplementary Figure 3**

(**a**) Burn frequency classes mapped in the Angolan miombo woodlands, indicating the number of years burned between 2000 and 2020, from 0 to 20. (**b**) Proportion of the Angolan miombo woodland's area falling into each annual burn frequency class. Burn frequency classes were mapped in Google Earth Engine using 250m MODIS imagery.



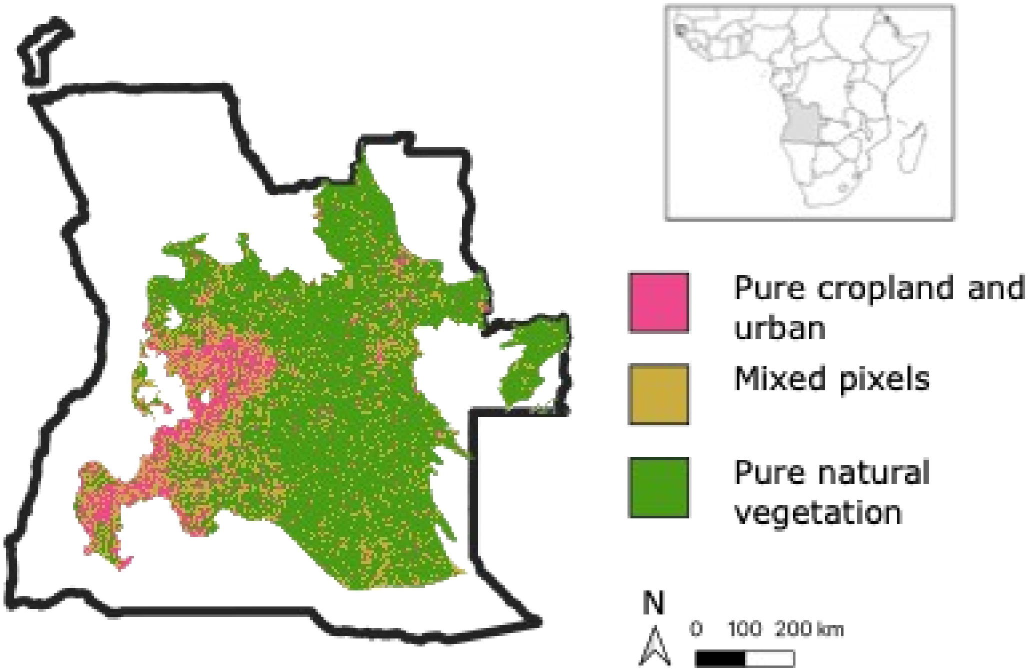
**Supplementary Figure 4**

Landsat imagery of May EVI values for the Angolan Miombo Woodlands has major gaps from 2003 to 2013. Panels (**a-c**) show available imagery for 2007, 2009, and 2010 respectively. Because of these gaps, woody encroachment cannot be reliably assessed using temporal trend analyses of 30m Landsat imagery. We therefore used 250m MODIS EVI imagery instead, despite the lower spatial resolution. We addressed MODIS's lower resolution by following an upscaling protocol that differentiated pure MODIS pixels from mixed MODIS pixels. Pure pixels comprise >90% Landsat pixels of natural vegetation or cropland, while mixed pixels comprise a mix of land use types.



**Supplementary Figure 5**

Linear regressions suggest that mean May EVI (i.e. canopy greening) trends are not related to precipitation ($p = 0.43$, $r^2 = 0.03$) and only weakly related to temperature ($p = 0.01$, $r^2 – 0.28$). Climate data was extracted from the ERA5 Monthly Aggregate dataset (ECMWF/ERA5/ MONTHLY), and averaged over the year (temperature) and rainy season (precipitation).



**Supplementary Figure 6**

“Mixed” pixels of natural vegetation and cropland were created when upscaling the 30m Landsat data used for landcover mapping to the 250m resolution of the MODIS EVI data. We reclassified 250m pixels as mixed when they included ≥10% natural vegetation and ≥ 10% cropland or urban area. We ran separate EVI trend analyses in pure pixels of natural vegetation (i.e. woodland and grassland), in mixed pixels, and in pure pixels of cropland. When averaged across pixels within a land use class, EVI trends were significant for woodland and grassland and were insignificant for mixed pixels and cropland.

**Supplementary Table 1**

Confusion Matrix for the land use classification of the Angolan miombo woodlands. Accuracy was tested against 1602 points withheld as an out of bag sample from training the land use classifier.

| | **urban** | **agriculture** | **woodland** | **grassland** | **Total** | **Accuracy** |
|---|---|---|---|---|---|---|
| **urban** | **347** | **25** | **3** | **22** | 397 | 0.87 |
| **agriculture** | **32** | **350** | **16** | **43** | 441 | 1.26 |
| **woodland** | **1** | **6** | **327** | **30** | 364 | 1.11 |
| **grassland** | **13** | **27** | **20** | **340** | 400 | 1.18 |
| **Total** | 393 | 408 | 366 | 435 | 1602 | |
| **Accuracy** | 0.88 | 0.86 | 0.89 | 0.78 | | |

**Supplementary Table 2**

Accuracy statistics for the land use classification of the Angolan miombo woodlands, calculated for each year (1990, 2010, 2014, 2020) following the Olofsson et al., (2014). Overall accuracy for the land use classification was 86.6%. Calculations were done in R, using the “mapaccuracy” package.

| Year | Statistic | Urban/ Bare | Agriculture | Woodland | Grassland |
|---|---|---|---|---|---|
| 2020 | User's Accuracy | 87.41% | 79.37% | 89.84% | 85.00% |
| 2020 | Producer's Accuracy | 24.32% | 87.92% | 96.82% | 70.06% |
| 2020 | SE of User's Accuracy | 1.67% | 1.93% | 1.59% | 1.79% |
| 2020 | SE of Producer's Accuracy | 2.81% | 2.13% | 0.50% | 2.75% |
| 2014 | User's Accuracy | 87.41% | 79.37% | 89.84% | 85.00% |
| 2014 | Producer's Accuracy | 18.81% | 86.87% | 96.50% | 73.56% |
| 2014 | SE of User's Accuracy | 1.67% | 1.93% | 1.59% | 1.79% |
| 2014 | SE of Producer's Accuracy | 2.32% | 2.19% | 0.55% | 2.55% |
| 2000 | User's Accuracy | 87.41% | 79.37% | 89.84% | 85.00% |
| 2000 | Producer's Accuracy | 36.80% | 74.53% | 94.55% | 86.40% |
| 2000 | SE of User's Accuracy | 1.67% | 1.93% | 1.59% | 1.79% |
| 2000 | SE of Producer's Accuracy | 4.04% | 3.19% | 0.94% | 1.60% |
| 1990 | User's Accuracy | 87.41% | 79.37% | 89.84% | 85.00% |
| 1990 | Producer's Accuracy | 52.42% | 60.97% | 92.33% | 91.24% |
| 1990 | SE of User's Accuracy | 1.67% | 1.93% | 1.59% | 1.79% |
| 1990 | SE of Producer's Accuracy | 5.03% | 3.90% | 1.39% | 1.11% |

# 6. Woody Plant Encroachment Alters Bird Community Composition but not Ecological Function in a Zimbabwean Savanna

**Authors**: Ty Loft[1,2], Karen Chiro[3], Peter Makumbe[4,5], Yadvinder Malhi[6], Imma Oliveras-Menor[2,1], Chevonne Reynolds[7] , Nicola Stevens[1,6]

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## 6.1 Chapter Statement

This chapter uses field data and a Bayesian modeling approach to investigate how fire suppression and resulting changes to savanna vegetation structure have altered bird-mediated ecosystem functions in a Zimbabwean savanna. It estimates changes to energy flows through 70 common bird species along a woody encroachment gradient, and then breaks down energy flows by food source to link flows to trophic ecosystem functions. It contributes to the broader goal of assessing changes to consumer-mediated ecosystem functions by directly relating woody encroachment, a consumer-mediated change in vegetation structure, to animal-mediated ecosystem functions.

This paper has been submitted to the journal *Conservation Biology*. The ideas and research questions, study design, methods, data collection, data analysis, and writing presented in this chapter are the work of the first author, Ty Loft. All these activities benefited greatly from the contributions of Nicola Stevens, Imma Oliveras Menor, Chevonne Reynolds, and Yadvinder Malhi. Karen Chiro and Peter Makumbe contributed to the field data collection, to the study design and methods. They also provided constructive comments during the writing of the manuscript.

## 6.2 Abstract

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Woody plant encroachment (WPE) is a widespread symptom of global change in African savannas, where it is altering animal community composition. However, it remains unclear (1) which animal species are most affected by increasing woody cover; (2) whether certain functional traits increase species vulnerability to it and (3) how changes in species composition alter the animal-mediated ecosystem functions that support productivity and resilience. We investigated these questions using bird abundance point-count data along a woody encroachment gradient in a central Zimbabwean savanna. We used a hierarchical Bayesian multispecies n-mixture model to estimate how WPE changes species abundances, and assessed whether functional traits predicted species responses. We then adopted an ecosystem energetics framework to predict changes to bird-mediated ecosystem function. We found that among 70 common savanna bird species, increasing woody cover decreased the abundances of 27% of species (losers), and increased the abundances of 34% of species (winners). Losing species were distributed evenly across functional lifestyle, diet, and nesting categories, while winning species were strongly predicted by nesting strategy. We also found that dramatic shifts in species composition along the WPE gradient did not translate into significant changes in bird-mediated ecosystem functions. Our results suggest that WPE is homogenizing bird communities across African savannas, impacting the conservation of nearly a quarter of savanna birds. While the high diversity and functional redundancy of savanna bird communities may make their functions resistant to WPE, their overall trophic efficiency, and thus ability to shape savanna function, is likely declining. We urge that efforts to conserve savanna bird diversity focus on manipulating disturbance to maintain open ecosystems, in addition to the traditional emphases on land use and climate change.

## 6.3. Introduction

The human transformation of the biosphere has depleted global biodiversity, endangering species and their associated ecosystem functions (Díaz et al. 2019; Cardinale et al. 2012). Tropical savannas and grasslands are particularly vulnerable: while they host extensive biodiversity, they have historically been more impacted by humans than other tropical biomes, and are experiencing the world’s highest rates of land use change (Ellis 2021; Potapov et al. 2022; Bond 2019). Traditionally, conservation in tropical savannas has focused on preventing habitat loss and hunting via setting aside extensive protected areas (Dinerstein et al. 2020). However, in Africa, the continent with the largest extent of savanna, most savannas remain in unprotected rangelands jointly used by wildlife, livestock, and people (Clements, In review). Although these unprotected savannas are spared from intensive agricultural conversion, they are threatened by other global change drivers, including climate change, overhunting, and alterations to fire and herbivory-driven disturbance regimes (Stevens et al. 2022; D’Antonio and Vitousek 1992).

One process affecting untransformed African savannas is woody plant encroachment (WPE), defined as a unidirectional increase in woody plant cover (Archer et al. 2017; Stevens et al. 2017). WPE is caused both by local changes to disturbance regimes, such as fire suppression and overgrazing, and by global factors such as rising atmospheric $CO_2$ and changes to precipitation and temperature (Bond and Midgley 2000; Archer et al. 2017). In Africa, there is consistent evidence that most untransformed savannas are experiencing long-term increases in plant woody cover, with a continental analysis reporting that woody cover increased by 8% between 1986 and 2016 (Venter, Cramer, and Hawkins 2018; García Criado et al. 2020). Woody encroachment in savannas causes more than a simple increase in tree and shrub cover. It represents a regime shift, changing the structure, functional composition, and system properties (e.g. flammability) of savannas (Parr, Gray, and Bond 2012; Luvuno et al. 2018). While the extent of woody encroachment is increasingly recognized (García Criado et al. 2020; Venter, Cramer, and Hawkins 2018), its impacts on plant and animal communities remain underemphasized and poorly understood (Stevens et al. 2022).

A particularly under-researched aspect of WPE is its impact on animal-mediated ecosystem functions, despite increasing evidence that animals shape ecosystems in important ways (Sekercioglu 2006; Pringle et al. 2023; Bello et al. 2015). There is empirical evidence that WPE changes  animal assemblage composition (Smit and Prins 2015; Sirami and Monadjem 2012) through altering patterns of ecosystem structure and function, including vegetation structure and habitat availability, food and nutrient availability, and predation risk (Tews et al. 2004). Changes in animal communities may alter ecosystem functions: birds provide functions such as invertivory and carnivory, which mediate insect and rodent populations; nectarivory, which mediates pollination; and granivory and frugivory, which mediate seed dispersal and thus an ecosystem's capacity to recover from shocks (Sekercioglu 2006; Loft, Oliveras Menor, et al. 2024). In turn, these ecosystem functions shape patterns and flows of carbon, water, nutrients, and genetic material, which ultimately affect ecosystem resilience and productivity (Bello et al. 2015; Doughty, Wolf, and Malhi 2013). Yet studies investigating how WPE shapes ecosystem function have consistently emphasized plant-moderated functions, so that researchers have a limited understanding of whether changes in animal communities threaten savannas' stability, resilience, and functionality (McCleery et al. 2018). A major limitation to this research agenda has been finding a quantifiable metric that can translate changes in animal communities into changes in ecosystem function strength (Richardson et al. 2023).

Recently, scientists have adopted energetics approaches to address the problem of linking biodiversity loss to ecosystem function (Loft et al. in review; Antunes et al. 2024). Energetics approaches account for a key principle of functional ecology: that animal species unevenly impact ecosystem function, based on their population densities, body sizes, dietary preferences, and behaviors (Pringle et al. 2023; Malhi et al. 2016). Rather than assigning species equal weighting, these approaches quantify energy flows through the trophic web by calculating the annual food energy consumed by each species per unit area (Malhi et al. 2022). To estimate changes to functions, animals in an ecosystem can be classified into functional groups, based on their diets and behaviors. Ecologists can then aggregate energy flows within each species group, and assess how these functional flows change along environmental gradients such as woody cover (Loft et al. in review). Traditionally, energetics approaches have been limited by a lack of high quality data on species abundance. To address this problem, we take advantage of new

Bayesian species abundance models that use bird point count data to estimate relatively accurate species population densities (Doser et al. 2024; Graser et al. 2025).

Here, we apply an energetics framework to changes in bird abundances in a fire-suppressed acacia savanna in Central Zimbabwe. Zimbabwe represents an excellent study system due to the country's high faunal species richness (Burgess et al. 2004), and high rate of WPE averaging 0.7% per year (Venter, Cramer, and Hawkins 2018). We focus on birds, because they are an indicator clade: they are diverse, well understood, easily observable, and can indicate broader changes to biodiversity and function in an ecosystem (Canterbury et al. 2000; Virkkala et al. 2022). Previous studies suggest many savanna bird species are vulnerable to woody encroachment, with studies in South Africa, Swaziland, and Lesotho finding that 27% - 34% of savanna and grassland birds decreased in occupancy in response to increasing woody cover, and that 28% of threatened savanna birds species are threatened by changing fire regimes (Sirami and Monadjem 2012; White et al. 2024; Kelly et al. 2020). There is still conflicting evidence, however, as to which species are most at affected, and whether affected species can be reliably predicted based on their functional traits (White et al. 2024). We are also not aware of any previous studies investigating how WPE changes animal-mediated ecosystem functions.

The aim of this study was to reveal how woody encroachment is altering the avian biodiversity and associated ecosystem functions of a Zimbabwean acacia savanna. Our first objective was to identify how woody cover changes the abundance of 70 common savanna bird species. Our second objective was to assess whether species functional traits are reliable predictors of responses to those changes. Our third objective was to investigate whether WE also changes the energetic structure of savanna bird communities, examining whether the proportional distribution of energy among species shifts from open-ecosystem to closed-ecosystem specialists. Our fourth objective was to use ecosystem energetics to estimate how WE affects the strength of key bird-mediated ecosystem functions. Our analysis will provide novel evidence of how changes in species composition affect key ecosystem functions. This evidence can help decision-makers prioritize conservation interventions around encroachment-vulnerable species, as well as guide further investigations into the functional resilience of savannas.

## 6.4 Methods

### Study Area

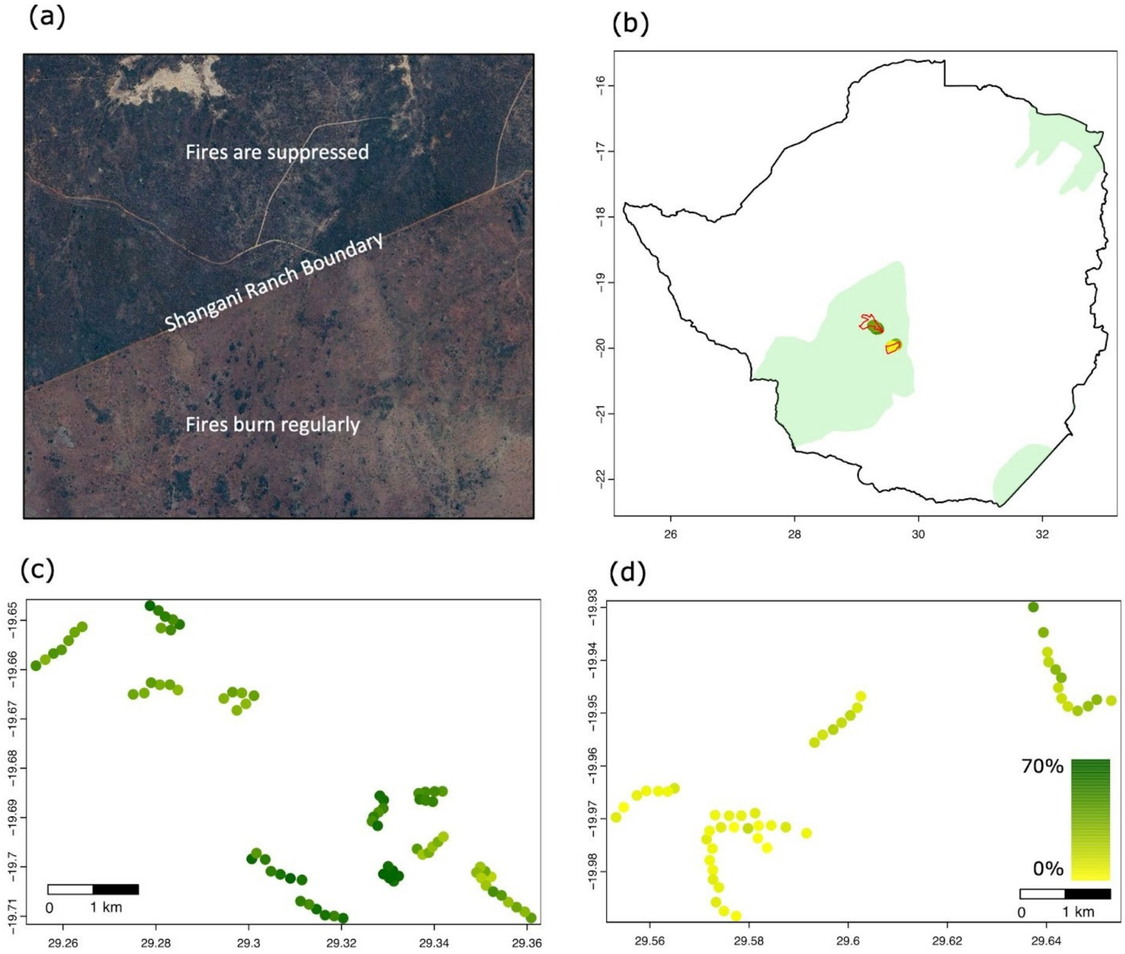

**Figure 1. Overview of study sites.** (a) Satellite imagery of the boundary of Shangani Ranch clearly shows the higher woody cover in a section of acacia savanna within the ranch where fire is suppressed compared to outside the ranch where fires burn regularly. (b) The location of Shangani Ranch, outlined in red; and the sampling plots, as green and yellow points; within the Zambezian Mixed Savanna ecoregion, shaded in light green; and within the bounds of Zimbabwe, in black. (c-d) The location of the plots on the northern section of the ranch, where fire is suppressed, and in the southern section of the ranch, where fires burn regularly. Woody cover within the plots ranges from 0% (yellow) to 70% (green).

Shangani Holistic Ranch is an 800 $km^2$ mixed-use cattle and wildlife ranch in central Zimbabwe, characterised as an acacia savanna ecosystem. Rainfall in Shangani averages 612 mm $y^{-1}$ (average of twenty years) and falls mostly between October and April, and temperatures range between 8.5°C and 31.4°C (Dunham, Robertson, and Swanepoel 2003). The ranch is in the Zambezian-Limpopo mixed woodlands ecoregion within the Afrotropical savanna biome, and contains a mix of acacia, terminalia, mopane, miombo, and combretum-dominated savannas, often occurring in a catenal pattern (Burgess et al. 2004). Much of Shangani Holistic Ranch has been fire-suppressed since the late 1960s and woody cover has increased dramatically in many areas over the same period, with encroachment primarily driven by *Acacia karoo* and *Dichrostachys cinerea* (Frost 1999). However, some areas of the ranch have burned more regularly, and in others fire has been reintroduced in the last five years. This variability in fire frequency, alongside variability in herbivory intensity and potentially other factors, has created a gradient of woody cover in the ranch's acacia savannas, ranging from <1% to ~ 70% woody cover.

### Sampling Design

To select ecologically consistent sites we first identified areas of acacia-dominated savanna using visual observation as well as a vegetation map of Shangani developed using remote sensing and ground truthing. We selected acacia savanna areas because they span the largest gradient of woody cover within any one savanna type, from <5% woody cover to ~70% woody cover. To select sites along this gradient, we classified Shangani's acacia savanna into low, medium, and high woody cover areas using google earth imagery and visual surveys. Most medium woody cover sites were formerly high woody cover sites that had burned between 6 and 24 months previously, causing the vegetation to open. Within each category, we selected 6-7 sampling sites of 1 $km^2$. We selected areas that were (a) dominated by acacia savanna, (b) not adjacent to large water features or rocky areas, and (c) contained a relatively uniform woody cover with a range of less than 20%. In each site, we selected at least six 50 m radius plots, following the Sentinel (Social and Environmental Trade-Offs in African Agriculture) Protocol for bird sampling (see

Supplementary Information). Plots were located at least 200 m away from each other to limit counting the same individuals and to minimize spatial autocorrelation, while facilitating access to at least six plots during the morning period when birds are most active. Because we undertook additional surveys when conditions remained favorable, sites contain up to 11 plots. We acknowledge as a limitation in the study that the proximity of the plots means that some spatial autocorrelation likely persists in the dataset, as the need to walk to and survey at least six plots each morning required locating the plots reasonably near to one another.

### 2.3 Surveys

Bird communities were sampled across 127 plots via 10-minute point counts, following standard bird point count methodology, following Reynolds and Howes (2023). Each count involved two experienced observers (T.L. and K.C.) recording the number and species of all individual birds seen and heard within a 50-meter radius over a ten-minute period. Birds flushed while walking from the edge to the center of the plot were included in the count. Birds flying overhead without interacting with the landscape were excluded from the surveys, while overhead birds interacting with the landscape, for example via hunting insects, were included (Reynolds and Howes 2023). Censuses were not conducted in rainy or high-wind conditions. All censuses took place between 5:30am and 8:30am in the morning, or between 15 minutes before sunrise and 140 minutes after sunrise. In each plot, we also conducted a rapid vegetation survey of key structural variables after the bird count, recording the number of trees; mean canopy height; mean grass height; minimum, mean, and maximum visibility in meters; as well as estimated wind speed, temperature, and cloud cover. Sampling was carried out in the wet season (February 22 – March 14) and in the dry season (September 10 – October 3) of 2024, and most plots were surveyed at least once during each season. In total, we recorded 1724 individual birds across 120 surveys during the dry season, and 1659 birds across 103 surveys during the wet season. We surveyed each plot between 1 and 4 times, depending on accessibility and weather conditions. In total, we recorded 156 bird species, and we modeled abundances for the 70 species recorded in at least 8 surveys. We modeled species accumulation curves for wet and dry season surveys and found that even after >100 surveys in each season, species richness had not yet reached an asymptote

(Figure S1). The analysis therefore excludes many rarer birds, which may be more or less vulnerable to woody plant encroachment than the common birds assessed.

### Woody Encroachment Estimation

We estimated the woody cover of each plot using 2023-2024 very high resolution satellite imagery (0.5m per pixel) freely available in Google Earth pro. These images were accessed at maximum zoom in Google Earth Pro at each plot coordinate on November 15, 2024. To estimate woody cover we randomly generated fifty points within each 50 m-radius plot, and manually counted the proportion of points that overlapped with woody vegetation, including shrubs, bushes, and trees (Figure S2). Woody cover across plots ranged from 0% to 70% (Figure S3), consistent with similar previous studies (Sirami et al., 2009). There was no linear correlation ($r^2 = 0.01$, $p = 0.24$) between the percentage of woody cover and number of trees within plots, indicating that the woody cover gradient captures a harmful increase in bush and shrub cover, rather than a natural variation in savanna tree cover (Figure S3). Across the 127 plots, the mean woody cover was 33.5% , with a standard deviation of 21%.

### Species Abundance Model

We evaluated how the abundances of 70 bird species varied with WE using the *spAbundance* package in R (Doser et al. 2024). For our abundance model, we used a Bayesian formulation of a hierarchical, multispecies n-mixture model with a negative binomial distribution. All code for the model and analysis is available on figshare, via the link in the supplementary materials. To isolate how woody cover affected bird species abundances, and account for variation in weather, time, and plot visibility, the model accounted for the effects of environmental and survey covariates on species abundance and on species detection probability. As covariates for abundance, we included both linear and quadratic terms for woody cover within the single bayesian model. Because woody cover above ~40% has been shown to change savanna system properties in non-linear ways, a quadratic term is needed to account for potential nonlinear effects of woody cover on bird communities (Staver, Archibald, and Levin 2011). As covariates for detection, we included linear and quadratic terms for minutes-past-sunrise, mean visibility, wind speed, cloud cover, and season (either dry or wet).

We standardized all covariates as Z-scores (mean = 0, SD = 1) to improve model convergence, and we specified diffuse prior distributions for all parameters, using the default parameter and tuning values specified in the *spAbundance* package (Doser et al. 2024). We set the hypermeans to 0 and the hypervariances to 100 for the abundance coefficients, and to 2.72 for the detection coefficients. The variance of 2.72 corresponds to a relatively flat prior on the probability scale along which the detection covariates are estimated (Doser et al. 2024). We sampled the posterior distribution with four independent Markov chains, each set to 360,000 samples with a burn-in of 40,000 samples, and thinned chains by 40. In comparison to similar studies (Andersen and Steidl 2019), we used a higher number of samples to achieve acceptable r-hat values for all species, given that including more species required a more complex model. We assessed convergence by visual inspection of chains and Brooks-Gelman-Rubin statistics, assuming convergence when r-hat <1.1. All r-hat values were < 1.05 for the woody encroachment covariate parameters, with higher r-hat values reserved for detection and abundance intercepts. We considered species abundance to be affected by WE when the 90% credible interval excluded zero for the linear woody cover term, following Andersen and Steidl (Andersen and Steidl 2019).

### Functional Traits and Ecosystem Functions

We assessed whether the modeled species responses to WE were correlated with three avian functional traits: dietary preference, lifestyle, and nesting strategy. Trait data were extracted from the AVONET database (Tobias et al. 2022). To assess the relationship with diet, we grouped species into seven categories: frugivore, granivore, herbivore, invertivore, nectarivore, omnivore, and vertivore. To assess the relationship with lifestyle, we grouped species into four categories: aerial, generalist, insessorial, and terrestrial. To assess the relationship with nesting strategy, we grouped species into seven categories: birds that nest in cavities, in grass, on the ground, in shrubs or bushes, in trees, and birds that breed out of the region. To determine whether different functional groups disproportionately contained winning and losing species, we used chi-square tests and post-hoc tests where appropriate, following White et al. (White et al. 2024).

## Energetic Analysis and Uncertainty Calculation

Another way to understand a species' role in an ecosystem is to quantify its food energy consumption. More energy consuming species generally do more work in an ecosystem and contribute more to ecosystem functions (Nagy, Girard, and Brown 1999; Antunes et al. 2024). To calculate the food energy consumption of the ecosystem's bird populations, we first calculated the daily energetic expenditure for individuals of each species from body mass, using published multi-species allometric equations for field metabolic rates for birds (Malhi et al. 2022; Nagy, Girard, and Brown 1999). We then estimated the fraction of energy for each species derived from each food type using data on bird species traits available in the Avonet database (Tobias et al. 2022). Next we estimated food energy consumption rates for an individual of each species on the basis of each species' daily energy expenditure and the food assimilation efficiency for each feeding guild and food types (Crocker et al. 2002; Malhi et al. 2022). Finally, we estimated the food energy consumption of each species in kilojoules per unit area, by multiplying the annual food energy consumption of each species by the population densities produced from the Bayesian species abundance model.

We quantified uncertainty in our estimates of energetic intake by running 10,000 Monte Carlo simulation estimates of energy intake, incorporating the presumed sources of uncertainty. Following Malhi et al., (2022), we assumed that there was uncertainty in the following variables: species body mass, population density, daily energy expenditure (DEE) allometric equations, assimilation efficiency of the different food types, and composition of diet for each species. For body mass, we drew values from a truncated normal distribution (lower bound = 1g), in which the mean was the observed body mass and standard deviation was 15%, based on a study of tropical birds (Read et al. 2018). For population densities at each level of WPE, we used 10,000 predictive estimates of species population density produced by the Bayesian multi-species abundance model. For DEE, we estimated the 95% confidence intervals for the prediction of species-level energy expenditure based on variability in the allometric equation coefficients used to estimate energy consumption, as described in Nagy et al. (1999). For assimilation efficiency, we drew from a random beta distribution, using the mean and standard deviation by food type and guild from the literature, following Malhi et al., (2022). For fractional diet composition, we drew from a symmetrical beta distribution, with the peak uncertainty of 20% when the food group made up 50% of a species' diet, and no uncertainty when the food group made up 0% or 100% of the diet. To quantify uncertainty from these sources, we ran 10,000 simulations, replacing the values in our original calculations with values drawn from random distributions. We then calculated the 2.5% and 97.5% percentiles of the simulations to derive the 95% confidence intervals for our estimates.

## 6.5 Results

### Change in Abundance

We found a relatively even split between species whose abundances increased (winners), decreased (losers), or were indifferent to woody plant encroachment (neutral). Among the 70 species, there were 19 "losers", exhibiting a significant negative linear response to WPE, 24 "winners" with significant positive linear responses, and 27 indifferent species with abundances that were not significantly related to woody cover (Figure 2). The mean response to a 10% increase in WPE for "loser" species was a 39% decrease in abundance (26% - 51%; all reported ranges are 95% credible intervals), and the mean response for "winner" species was a 35% increase (14% - 64%) in abundance. Linear responses ranged from a 113% (60% - 200%) increase for violet-eared waxbill (*Granatina granatina*) to a 61% (53% - 70%) decrease for rufous-naped lark (*Mirafra africana)*. Based on the historical (1986–2018) rate of WPE in Zimbabwe, a 10% increase in woody cover would occur over 15 (Venter, Cramer, and Hawkins 2018).

In addition to the linear responses, 34 species had significantly negative quadratic responses to WPE, and 4 species had significantly positive responses to woody cover (Supp. Table). These relationships suggest that as woody cover approaches 70%, more species decline in abundance than would be expected based on linear responses alone. This pattern is visible in the high frequency of species with abundances that show a humped response to woody cover (Figure S4).

In contrast, u-shaped responses to woody cover were rare. Excluding a quadratic term for WPE did not alter these proportions of winning, losing, and indifferent species, suggesting that linear responses alone serve as a reasonable proxy for classifying species responses.

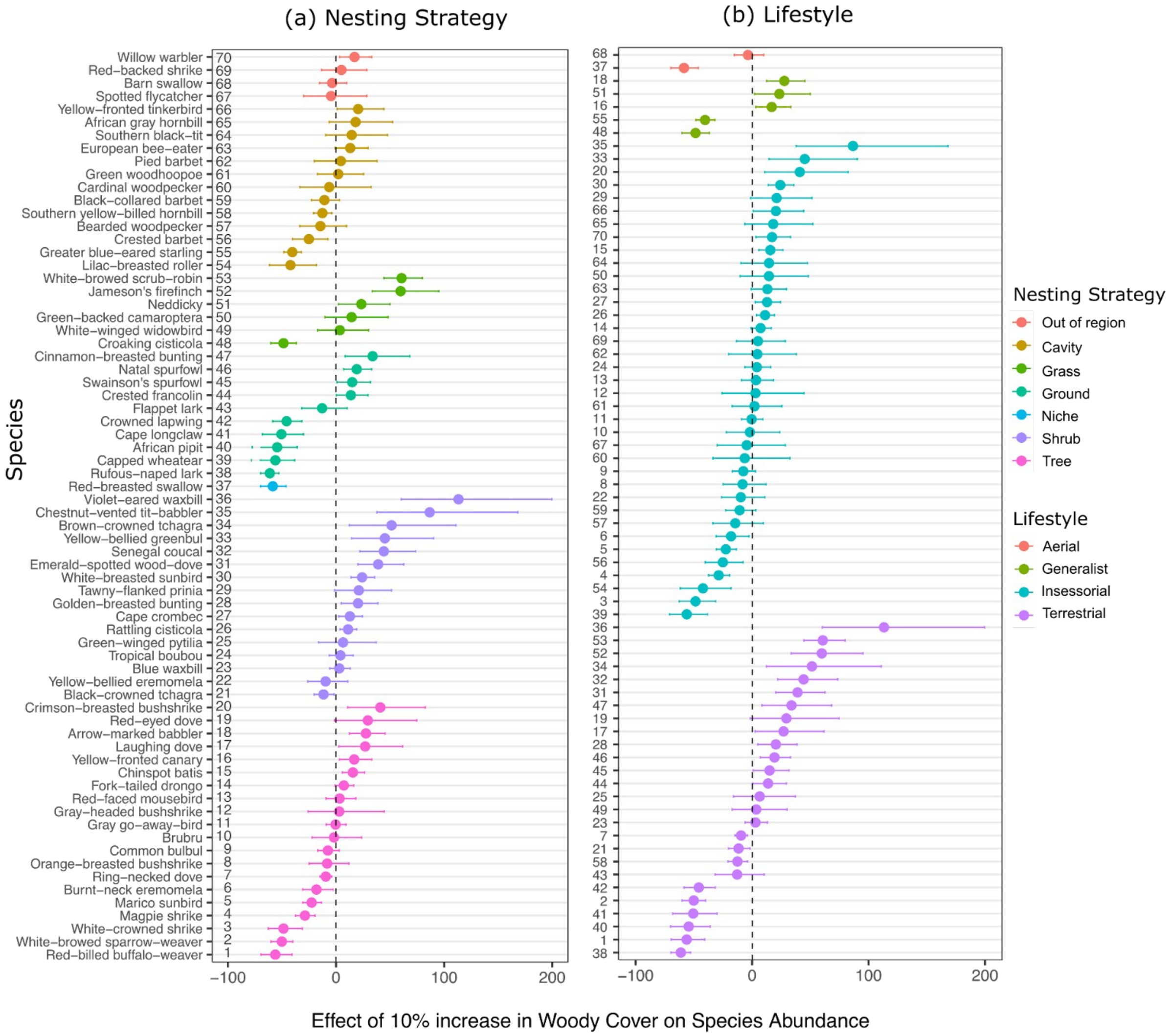

**Figure 2. Responses of common savanna bird species to woody cover, sorted by nesting strategy and lifestyle.** Values represent the percentage change in abundance for savanna bird species resulting from a 10% increase in woody cover. Bars represent 90% credibility intervals. Both the mean parameter values and 90% credibility intervals were derived from a Bayesian formulation of a hierarchical, multispecies n-mixture model with a negative binomial distribution. Species were sorted by their functional traits, including (a) nesting strategy guilds and (b) lifestyle guilds, based on trait data from the AVONET database. Data on bird abundances is from point counts.

None of the three functional traits we tested—diet, lifestyle, and nesting strategy—predicted which species responded negatively to woody encroachment (Figure 2, Table S1). However, nesting strategy predicted which species responded positively to woody encroachment ($\chi^2$ = 11.10, p = 0.025, df = 4. Shrub-nesting birds were overrepresented among winners, and cavity nesters were underrepresented among winners (Tables S3). In addition, a species' primary lifestyle, meaning whether it is aerial, terrestrial or insessorial (i.e. perching), strongly predicted whether a species was responsive or indifferent to woody cover (p = 0.002, $\chi^2$ = 12.45, df = 2), although it did not predict the direction of the species' response. Insessorial species were overrepresented among species indifferent to WPE, while terrestrial species were overrepresented among responsive species (Tables S4). These results provide evidence that some aspects of a species' functional role in an ecosystem predict whether it will benefit from woody encroachment.

### Energetics and Ecosystem Functions

Increasing woody cover dramatically changed the composition of the species that consume the most energy. In open savannas at 5% woody cover, most energy was consumed by species negatively affected by WPE, with losing species consuming 56% of energy, winning species consuming 21% of energy, and indifferent species consuming 23% of energy (Figure 3). In closed savannas at 65% woody cover, most energy was consumed by species benefiting from WPE, with winning species consuming 60% of energy, losing species consuming 17% of energy, and indifferent species consuming 23% of energy. In moderately encroached savannas the mix of winners and losers was more balanced, with winning species consuming 47% of energy, losing species consuming 28% of energy, and indifferent species consuming 26% of energy. Although a 37% plurality of species were indifferent to woody encroachment, they never consumed more than 26% of the total energy flow through birds (Figure 3). The distribution of energy consumption among species was also highly uneven between rare and common species at all points along the woody cover gradient. At every level from 0% to 70% woody cover, the most energy consuming decile of species accounted for 57–65% of energy flows, and the least energy consuming half of species accounted for 3% to 10% of energy flows  (Figure 3).

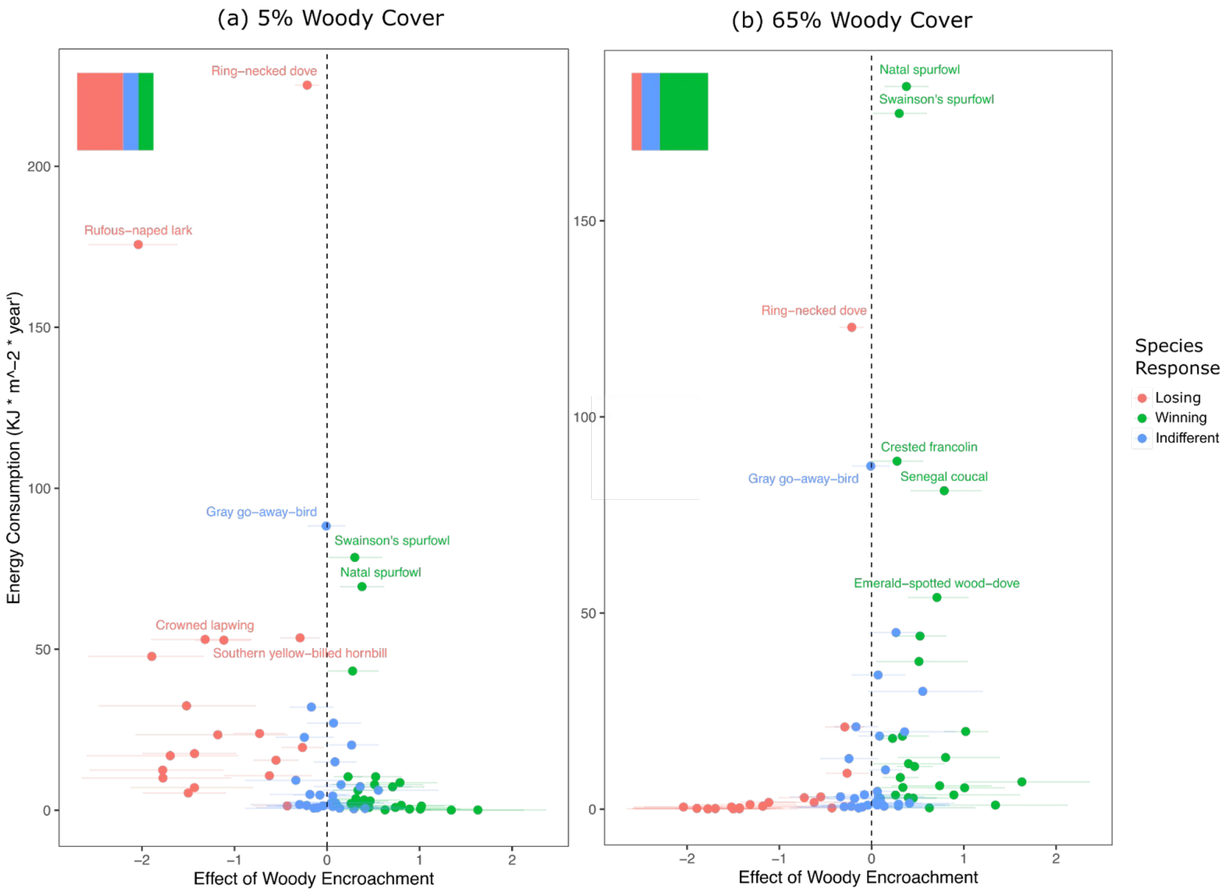

**Figure 3. The mean energy consumption and effects of woody encroachment on abundance for 70 species of common savanna bird under (a) 5% woody cover and (b) 65% woody cover.** In each scenario, the seven most energy-consuming bird species are labeled. The color of the points indicate the significance and direction of the species' response to increasing woody cover. The square charts in the top left of each panel represent the proportion of energy flowing through losing, winning, and indifferent species. Bars represent 90% credibility intervals for species responses to increasing woody cover, derived from a Bayesian formulation of a hierarchical, multispecies n-mixture model.

Although the species-level energy flows responded strongly to woody cover, aggregate energy flows through the total community and through trophic ecosystem functions remained overwhelmingly stable. Woody cover did not significantly influence the size of the aggregate energy flow through all 70 bird species (Figure 4). Woody cover also did not significantly influence energy flows through seven of the eight measured ecosystem functions: total invertivory, terrestrial invertivory, insessorial invertivory, granivory, frugivory, and nectarivory

(Figure 4). Increasing woody cover marginally decreased the strength of the aerial invertivory function (at 90% confidence), but this function was performed by just two species of swallow, and so may not be a robust result. Apart from aerial invertivory, the median ecosystem function was performed by 15 species, ranging from 2 species for aerial invertivory and nectarivory to 54 species for total invertivory (Figure S5). Finally, the trophic structure of the bird community remained stable: at all levels of woody cover, the greatest proportion of energy was consumed by invertivores, followed by granivores. Frugivores, carnivores, and nectarivores consumed much less energy (Figure S5).

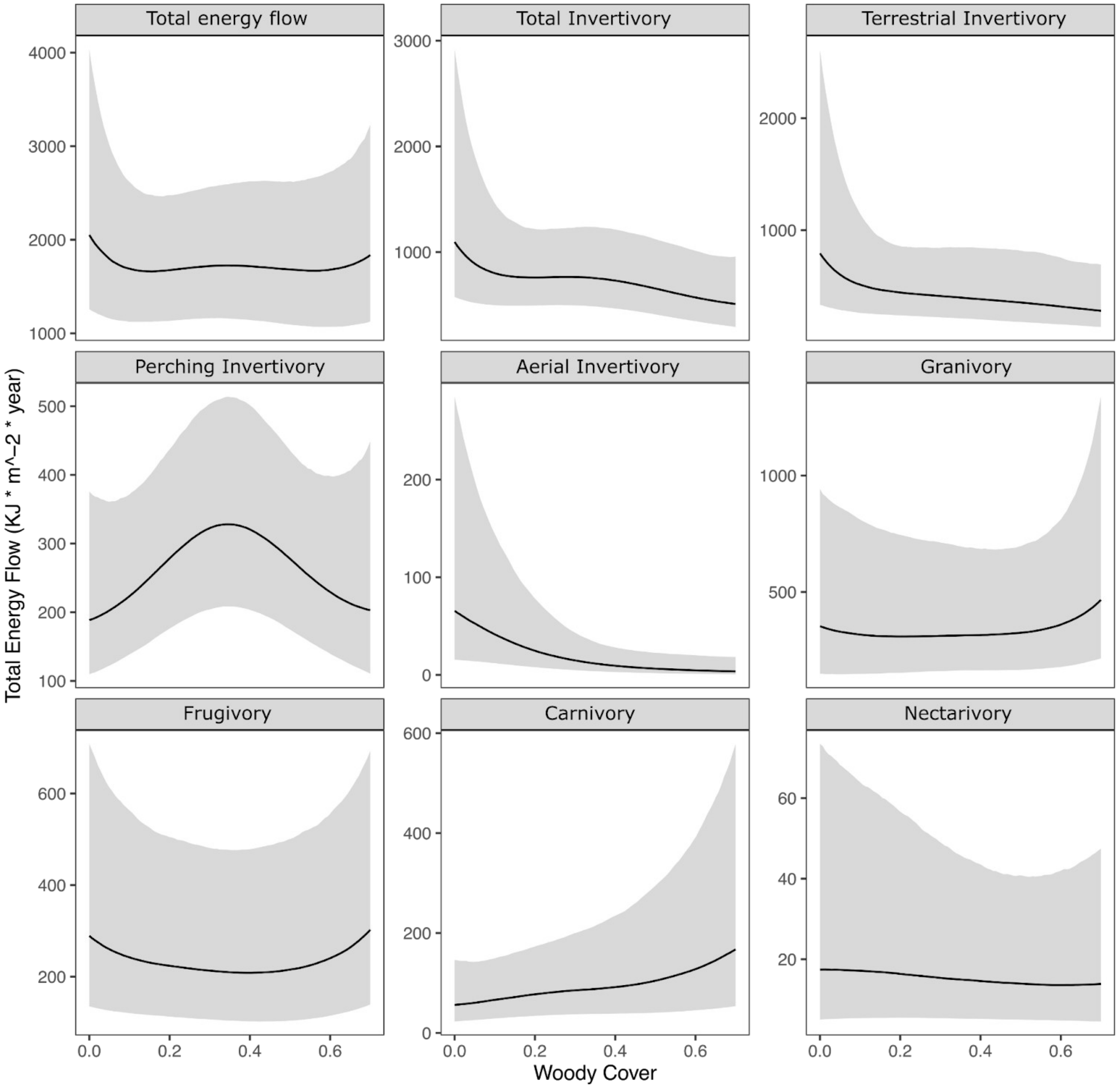

**Figure 4. Changes in energy flows through key ecosystem functions performed by common savanna bird species, across a gradient of woody cover in a Zimbabwean acacia savanna.** Birds were grouped into functional groups based on their diet preferences and lifestyles. Function strengths were estimated as the summed food energy consumption of each dietary component by all bird species. The light gray error bars denote 95% confidence intervals derived from 10,000 Monte Carlo simulation estimates, incorporating uncertainty in body mass, population density, the daily energy expenditure equation, assimilation efficiency of the different food types, and composition of the diet of each species. Bird abundances were modeled using a Bayesian hierarchical species abundance model.

## 6.6 Discussion

The results reported here support previous findings that increasing woody cover is dramatically changing the composition of animal communities in savannas, potentially putting over a quarter of savanna bird species at risk. We reported that increasing woody cover increases the abundance of 36% of species and decreases the abundance of 28% of common savanna bird species, indicating substantial community turnover. However, the energetics analysis suggests that even these large shifts in abundance and species composition do not necessarily translate into changes in ecosystem function. Here, we draw on our results and the literature to discuss the possible mechanisms that relate changes in species composition to species traits and to avian ecosystem functions. We also discuss implications for conservation and future research.

Throughout, we also demonstrate how applying an energetics approach to biodiversity change can provide new insights that complement traditional, species-focused analyses. In particular, an energetics framework provides ecologists with a unified, ecologically meaningful metric to solve the problem of translating changes in species composition into ecosystem function. In this case, energetics reveals that ecosystem functions and species populations respond differently to global change, a finding that would have been absent from a study using only traditional metrics of biodiversity. Finally, we suggest that the energetics approach used here could be applied to a much wider range of ecosystems and processes to clarify how global change is transforming the biosphere's capacity to support biodiversity and livelihoods.

### Species-Level Responses

The proportion of increasing and decreasing species reported here is in line with previous studies that show woody encroachment drives substantial changes in savanna bird communities. Two previous studies found that across all common South African bird species, WPE caused the occupancy of 39% species to increase and 34% to decrease (White et al. 2024), while in Swazi savannas, WPE caused the occupancy of 30% of species to increase and 27% to decrease (Sirami and Monadjem 2012). Although this is only the third study investigating WPE-bird relationships in African savannas, the combined evidence suggests that WPE significantly affects the abundance of over half of all common savanna bird species, causing declines in between 25% and 35% of common species.

The relatively even distribution of winners and losers suggest that the richness of savanna bird communities may remain constant at the plot or landscape scale. In contrast, woody encroachment is likely to homogenize bird communities at the regional or biome scale, because increases in woody cover are vastly more common than decreases (García Criado et al. 2020; Stevens et al. 2017). Since 1986, woody cover has increased across 37% of Zimbabwe's land and decreased across just 1%, with much of the remaining unaffected land agricultural (Venter, Cramer, and Hawkins 2018). This imbalance suggests that species benefiting from woody encroachment are able to do so in many savanna systems, while species benefiting from increasing openness have few opportunities to expand. Losing species are thus likely to be experiencing consistent rangewide declines, potentially threatening their long term conservation (White et al. 2024). Moreover, WPE is just one threat to bird populations among many, such as land conversion, overhunting, and climate change.  These additional threats may exacerbate declines among losing species, and offset increases among winning species (Shaw et al. 2024, 202). In South Africa, for example, even many species that respond positively or indifferently to WPE are declining at a regional level due to other drivers of global change. (White et al. 2024).

Given that losing species are likely declining over wide areas, it is important to understand the possible mechanisms determining how species respond to WPE. Losing species were dispersed among a variety of diets, lifestyles, and nesting strategies, in line with previous evidence from a South African study (White et al. 2024). One potential explanation is that adaptation to open environments may be a key niche encompassing birds with a wide variety of traits related to diets, lifestyles, and nesting strategies. In contrast, winning species were significantly predicted by their nesting strategy: unsurprisingly, shrub nesting species were more likely to benefit from encroached landscapes, which generally feature higher shrub coverage. Cavity-nesters, which comprise species such as hornbills, woodpeckers, and barbets, were much less likely to benefit. Because cavity-nesting birds rely on large old trees (>6m in height) with deadwood, they are unlikely to benefit from the increases in shrub cover that often characterize WPE (Joseph et al. 2011). This finding highlights that WPE does not provide the same conservation value as old-growth savanna trees (Parr, Gray, and Bond 2012), a distinction important when evaluating the benefits of carbon projects that seek to increase woody cover through tree planting or fire suppression (Loft et al. 2024).

Species indifferent to woody cover were also strongly predicted by lifestyle, with insessorial (i.e. perching) species more likely to be indifferent, and terrestrial species more likely to be responsive both as winners and losers. One possible explanation for this result may be interactions between terrestrial species and predators. High woody cover may help one subset of heavily predated terrestrial species, including spurfowl and francolins, avoid aerial predation by raptors. Meanwhile it may harm another subset of open habitat-adapted terrestrial species, including larks, pipits, and wheatears, that are already adapted to avoiding predators in open savannas through camouflage (Troscianko et al. 2016). Future research might investigate the mechanisms causing terrestrial birds to react strongly to woody cover, for example exploring whether other aspects of life history interact with lifestyle to determine winners and losers. New research might also investigate what makes perching species more adaptable to changes in woody cover, and assess whether their indifference extends to other datasets and regions.

## Changes to Community Structure and Function

It is surprising that energy flows through ecosystem functions were not affected by the dramatic shifts in species abundances and species-level energy flows. Here, we present three hypotheses to explain why WPE does not affect bird-mediated ecosystem functions. First, functions may be resistant because they are highly redundant: that is, they are performed by many species that respond differently to changing woody cover. Previous research has shown that the amount of savanna woody cover strongly determines species composition among savanna bird communities (Péron and Altwegg 2015). In evolutionary terms, woody cover may drive niche creation and speciation in savannas, so that functionally similar sister species perform the same functions at different levels of woody cover (Smith et al. 2014). Savanna bird communities are also highly diverse, with several hundred species inhabiting a given savanna landscape (Harrison et al. 1997). This high diversity and functional redundancy may allow species to fill a similar level of functional niches at each level of woody cover, allowing ecosystem functions to remain resistant to large shifts in species composition, even including the widespread decline of 25-30% of savanna birds. Were this hypothesis supported, it would highlight the importance of conserving biodiversity as an end in itself rather than as a means to function, a point we discuss in detail below.

A second hypothesis is that the relatively high uncertainty associated with the energy flows analysis masks subtle changes to the strength of ecosystem functions. While an energetics approach can effectively translate species composition into function, doing so requires propagating five sources of uncertainty. The results therefore contain substantial uncertainty around the quantity of energy consumed by species performing each function, particularly around functions performed by fewer species. Researchers can decrease this uncertainty by improving the precision of the underlying datasets on population density, and by refining the allometric equations used to calculate energy expenditure (Malhi et al. 2022). In addition, we used fairly coarse functional groups, and a more detailed functional group breakdown might alos reveal responses to WPE. We suggest that with more data, it would be worth reexamining the marginally significant decline in aerial invertivory, which was performed in our analysis by only two swallow species. Most aerial invertivores, which include swifts and swallows, are open-habitat specialists, so it would not be surprising for their functional contributions to decrease in encroached landscapes (Sinclair et al. 2020). Because aerial invertivores are important for controlling mosquito populations (Sekercioglu 2006), a decrease in this function might have significant consequences for global health outcomes. We would also further investigate the trendlines for terrestrial invertivory and for arboreal invertivory. In both cases, the trends were non-significant, but their directionality matched expectations: energy flows through perching invertivores increased with woody cover, which would create more perches, while energy flows through terrestrial invertivores decreased with shrub cover, which would suppress grass forage for terrestrial invertebrates (Little 2012). A more precise analysis might reveal that woody cover subtly changes the strength of these two invertivory functions.

A third hypothesis is that changes in ecosystem function strength were confounded by selectively including only common bird species observable at point counts. We analyzed only species that were observed at eight point counts. Given the methodology's limitation, we exclude rare species secretive species, and species that forage at a larger scale than the plot. These species included all raptors and waterbirds, and many swifts, swallows, and grass-hiding birds such as quails buttonquails, and flufftails. If these rare, excluded species are especially vulnerable to woody encroachment, then change to the functions they perform may have been understated. For example, populations of raptors, which dominate the carnivory function, are collapsing across African savannas, in part because high woody cover limits their ability to spot and pursue prey (Shaw et al. 2024). In most functional groups, however, abundant species account for most of an ecosystem's food energy consumption (Loft et al. In review). Thus most energy is probably accounted for in the estimates of invertivory, granivory, and frugivory, even though many contributing species are excluded.

In terms of community structure, the results indicate that just a few keystone species account for most of the energy consumed by acacia savanna birds. These include dove (*Columbidae spp.)* and spurfowl (*Phasianidae spp.*), particularly in closed savanna, the grey go-away bird (*Crinifer concolor*) across the woody cover gradient, and greater blue-eared starling (*Lamprotornis chalybaeus),* rufous-naped lark (*Corypha africana*), and wattled lapwing (*Vanellus senegallus*) in open savanna. All but one of these energetically dominant species are significantly affected by increasing woody cover. Identifying dominant species can guide future research into bird-mediated ecosystem function by indicating which species should be subject to in depth ecological analysis. For example, further research might investigate whether the shifts in composition among these possible keystone species change the composition of the dispersed seed or of predated insect communities within a savanna, potentially leading to cascading effects on vegetation and nutrient flows.

It is also notable that as species composition shifted in response to woody cover, the energetic structure of the bird community did not converge with that of tropical forests. Previous studies suggest that compared to savanna communities, tropical forest bird communities consume proportionately more energy through frugivory and nectarivory, and less through granivory (Malhi et al. 2022; Loft, Menor, et al. 2024). Were WPE to resemble afforestation in ecological terms, we would expect to see a shift toward a forest-like energetic structure, but we observed no such shift. Tropical forests are also more dominated by arboreal or insessorial species (Loft, Menor, et al. 2024). Yet we found that increases in woody cover caused some of the energetically dominant terrestrial francolin species to consume an even greater proportion of the community's energy. These results suggest that tropical forests have fundamentally different energetic community structures than savannas, and that these differences are unrelated to simple metrics of woody cover. These divergent community structures are likely to cause encroached savannas and forests to provide different suites of ecosystem functions and services. Conflating increases in woody cover with afforestation may therefore lead to unanticipated and potentially harmful conservation outcomes.

Finally, although the absolute energy flow through the bird community remained constant, the community's trophic efficiency probably fell along the woody cover gradient. Trophic efficiency refers to the proportion of energy fixed by plants in an ecosystem (i.e. of NPP) that is consumed by animals instead of by fire or by microbes (Hairston and Hairston 1993). In encroached, fire-suppressed savannas, plants fix ~70% more carbon and energy than plants do in open savannas (Zhou et al. 2023). If, as this study suggests, energy consumption by birds remains constant in encroached savannas, then the trophic efficiency of the bird community would decline. Plants would be locking up a greater proportion of the ecosystem's energy, potentially through increased defenses such as thorns or decreased nutrient concentrations and palatability, preventing that energy from supporting animals (Polis 1999). High trophic efficiency is a distinctive feature of acacia savannas, where plant structure and ecosystem function is shaped by consumption by fire and animals rather than by resource constraints such as climate and nutrients (Bond 2005). A decrease in trophic efficiency could therefore have substantial effects on overarching ecosystem function, even if measures of animal-mediated ecosystem function remain constant.

### Caveats and Complexity of Space-for-time Substitutions

To assess how WPE impacts bird abundance, we used space-for-time substitutions, because there has not been long-term sampling of birds in encroached Zimbabwean savannas. This methodological choice raises a number of caveats. First, space-for-time substitutions do not account for other factors that change bird abundance over time, such as changes in climate, pollution, hunting and other anthropogenic activity. These factors may exacerbate, mitigate, or otherwise interact with the changes caused by WPE over decades. Consequently, researchers should not interpret the rates of change presented here as the actual rates at which woody encroachment changes bird abundances and functions. Rather, these rates can help conservationists understand which species and functions may be vulnerable to WPE, and how WPE changes community structure. Nevertheless, the results here are in line with those presented by long-term studies of birds and woody encroachment in South Africa, suggesting that this study broadly captures the proportion of birds decreasing in response to WPE, as well as the complexity around how bird functions mediate those changes (White et al. 2024; Sirami and Monadjem 2012).

Another caveat is that the data was affected by the environmental conditions particular to the study year, including a low rainfall wet season. Environmental conditions beyond Zimbabwe would also have affected migrant bird abundances. Annual changes in rainfall and temperature may mediate species responses to woody encroachment by changing habitat structure and resource availability. These responses are difficult to predict: in wet years, losing species may be more resistant to woody encroachment due to food abundance, or alternatively more vulnerable due to increased competition. Changes in annual conditions are also likely to benefit some bird species more than others, independent of their responses to WPE. These responses will have altered the modeled population density estimates we used to estimate ecosystem function strength, contributing to the high uncertainty around these functions.

A third set of caveats concerns the environmental factors that fuel and constrain woody encroachment in the study area. In Shangani, fire suppression has primarily driven woody encroachment, but changes to herbivory regimes and climate may also be driving it (Frost 1999). Endogenous factors such as nutrient distributions and microclimates likely determine how susceptible different plots are to encroachment. All of these factors may affect species abundances in ways not related to woody cover and not captured by the model. Fire frequency in particular is correlated with WPE, but may also be influencing species abundances independently. Some of these factors may therefore alter bird communities in ways that are correlated with increasing woody cover but mechanistically unrelated. We controlled for some of this complexity by selecting plots with similar vegetation composition, including dominant *Acacia* species as well as the encroaching species, sicklebush (*Dichrostachys cinerea*) and sweet thorn (*Acacia karoo*). However, much of this complexity is inherent to an ecological study in a spatially variable savanna and cannot be controlled for via methodological design or modeling choices. The uncertainty associated with these choices is presented in the results' credibility intervals. We urge researchers to consider these caveats and complexity when interpreting the results, and particularly to recall that rates of change in species abundances in response to spatial woody cover gradients should not be extrapolated over time. To address these caveats, there is an urgent need for long-term studies of how woody encroachment impacts savanna bird communities, ideally through a series of multi-year point counts on cleared and uncleared plots experiencing WPE.

## Conservation Implications

Although we recorded dramatic changes in species composition along the woody cover gradient, we did not record changes to associated ecosystem functions. These findings raise implications for conservation, in particular highlighting the split between functionalist versus compositionalist conservation paradigms. Our findings may reassure function-focused conservationists, concerned primarily with how biodiversity change affects ecosystem productivity and services. We provide the first evidence that bird-mediated ecosystem functions may be resistant to woody encroachment despite dramatic changes in species composition. However, the results may worry composition-focused conservationists, concerned with the conservation of species and biodiversity as an end in itself. We add to evidence that 20% – 30% of African savanna bird species are declining due to widespread woody encroachment. This finding raises the possibility that in the long-term, WE will cause biome-level species diversity to decline substantially, even if the familiar threats of habitat loss and climate change are mitigated.

This study also expands the geographical scope of this threat to savanna birds north of South Africa and Eswatini, beyond the region where analogous studies have taken place. Our findings suggest that WE may be homogenizing and decreasing avian biodiversity at a regional, biome, or even continental level. Acacia savannas structurally similar to the study site occur in East Africa, the Sahel, and the southwest arid zone, and we hypothesize that similar patterns of species change may be progressing throughout these regions. We also urge researchers to investigate changes in mesic savanna woodlands, including the miombo woodlands and the Sudano-Guinean savannas, which are experiencing Africa's highest rates of woody encroachment. Changes to structure and animal diversity within these savannas are even less understood than changes in arid, acacia savannas. To coordinate these efforts, we call for a systematic investigation into the impacts of WE on African biodiversity, an effort similar to the assessment around biodiversity and land use undertaken by the Biodiversity Index for Africa (Clements et al. 2024).

Finally, the results suggest that in an era of widespread WPE, species conservation efforts will need to manage savanna ecosystems beyond the establishment of development-free protected areas. While protected areas suppress traditional threats to biodiversity such as habitat loss and overharvesting, they have a mixed record of mitigating woody encroachment (Stevens et al. 2017). Conservationists can take a number of actions to increase bird community diversity both in protected areas and in the rangelands and near-natural lands that contain most of Africa's remaining biodiversity (Clements In preparation). One option is to focus on creating heterogenous levels of woody cover within a landscape, by manipulating disturbance through fire, herbivory and targeted mechanical clearing (Venter, Hawkins, and Cramer 2017; Stafford et al. 2017; Estell et al. 2012). Previous research suggests that efforts to diversify habitat in savannas by varying fire regimes can increase species richness and improve ecosystem functionality (Docherty et al. 2020). Another approach is to investigate which factors maintain grassland refugia, which we observed in the study system despite generally high woody encroachment and fire suppression. Conservationists can also push back on afforestation programs in savannas, which are popular strategies for mitigating carbon, but which can lead to the loss of remaining open habitats and associated biodiversity. The results here add to mounting evidence that conservationists will need to use all these strategies to combat woody encroachment if they are to ultimately reverse species loss in Africa's savannas.

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## 6.8 Supplementary Materials

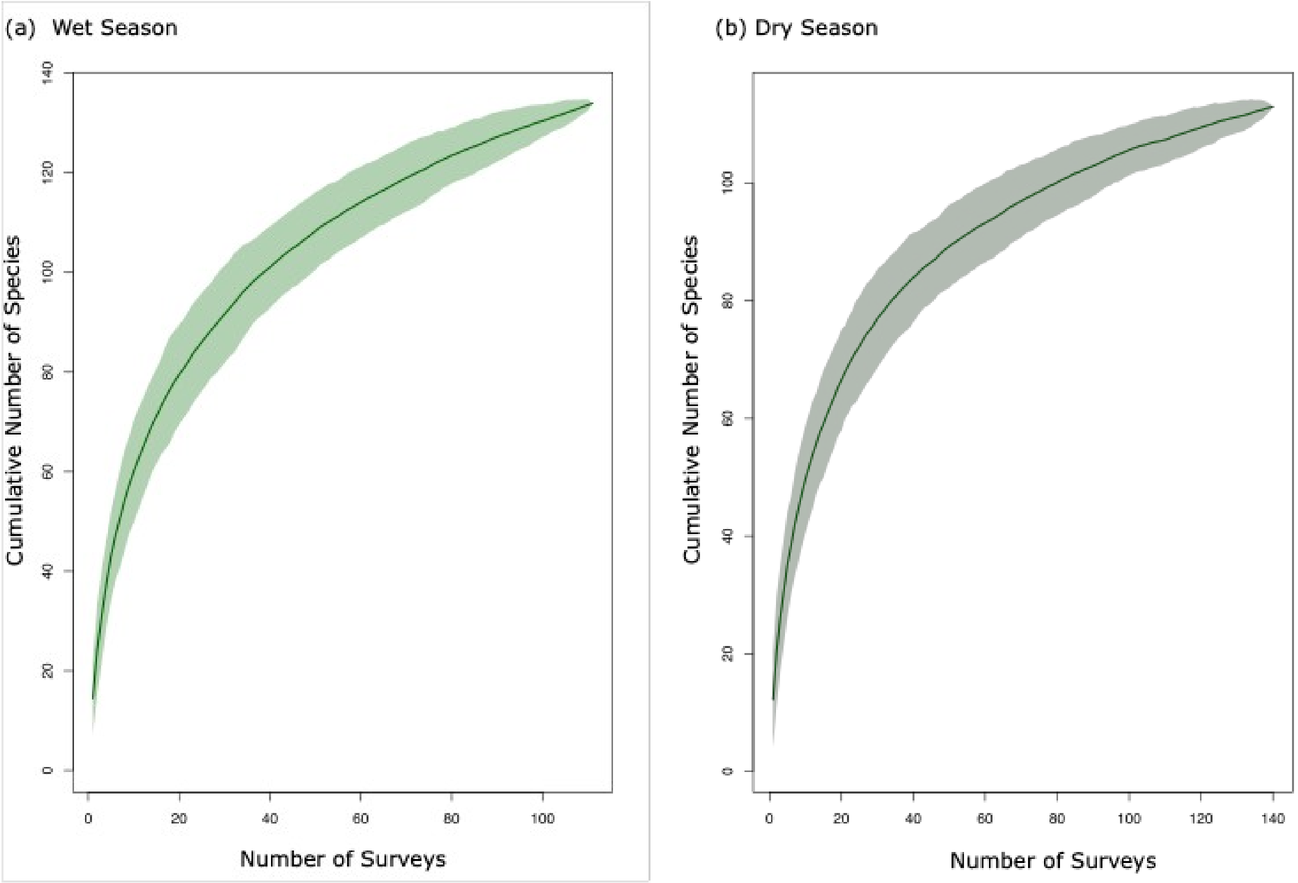


**Figure S1.** Species accumulation curves for (a) 103 bird surveys conducted in the wet season and (b) 123 bird surveys conducted in the dry season, modeled in R using the Vegan package.

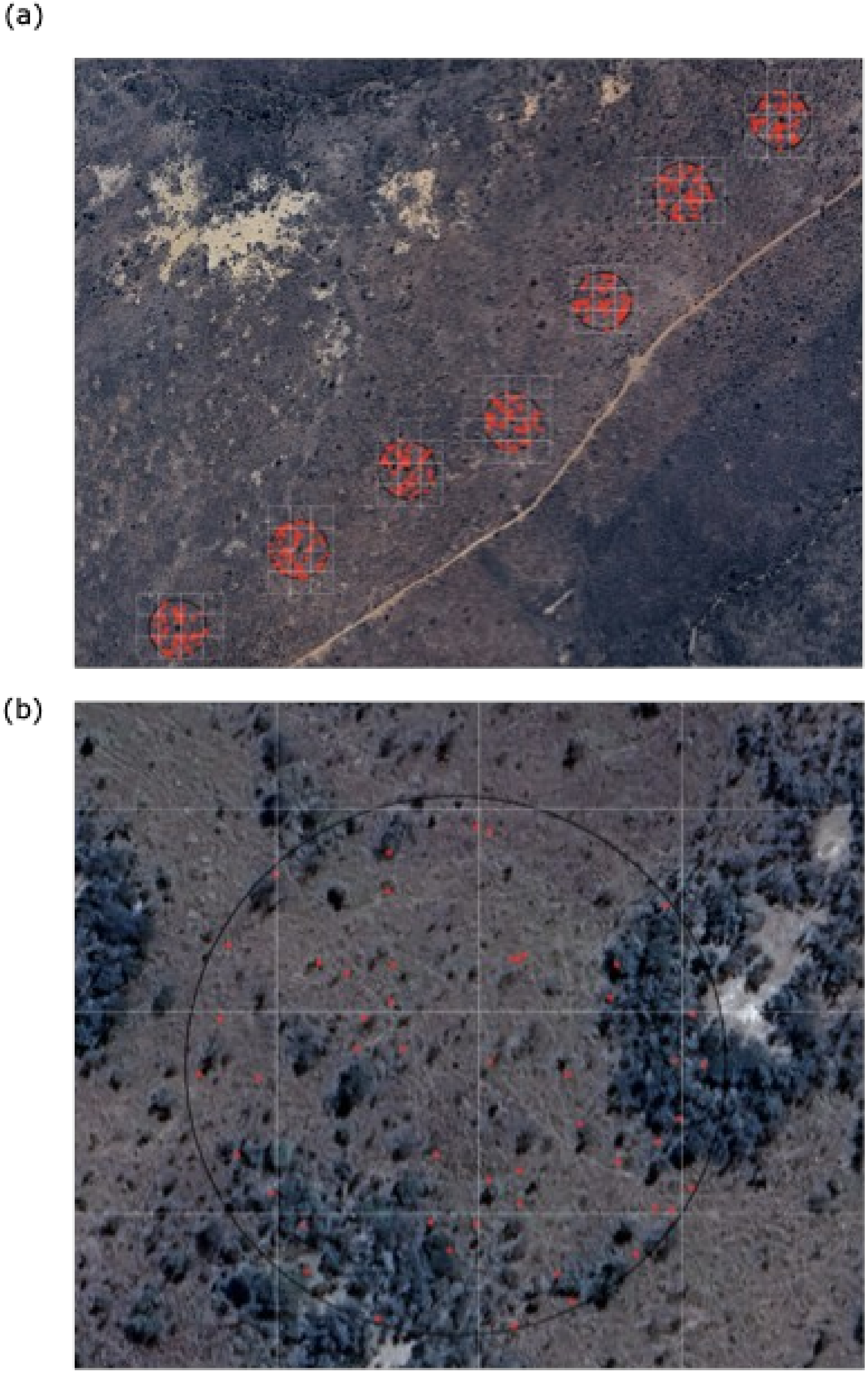


**Figure S2.** (a) Seven 50m radius plots in a partially encroached savanna with random points in red. (b) To estimate woody cover we randomly generated fifty points within each 50 m-radius plot, and manually counted the proportion of points that overlapped with woody vegetation, including shrubs, bushes, and trees. The grid was used to facilitate counting the points.

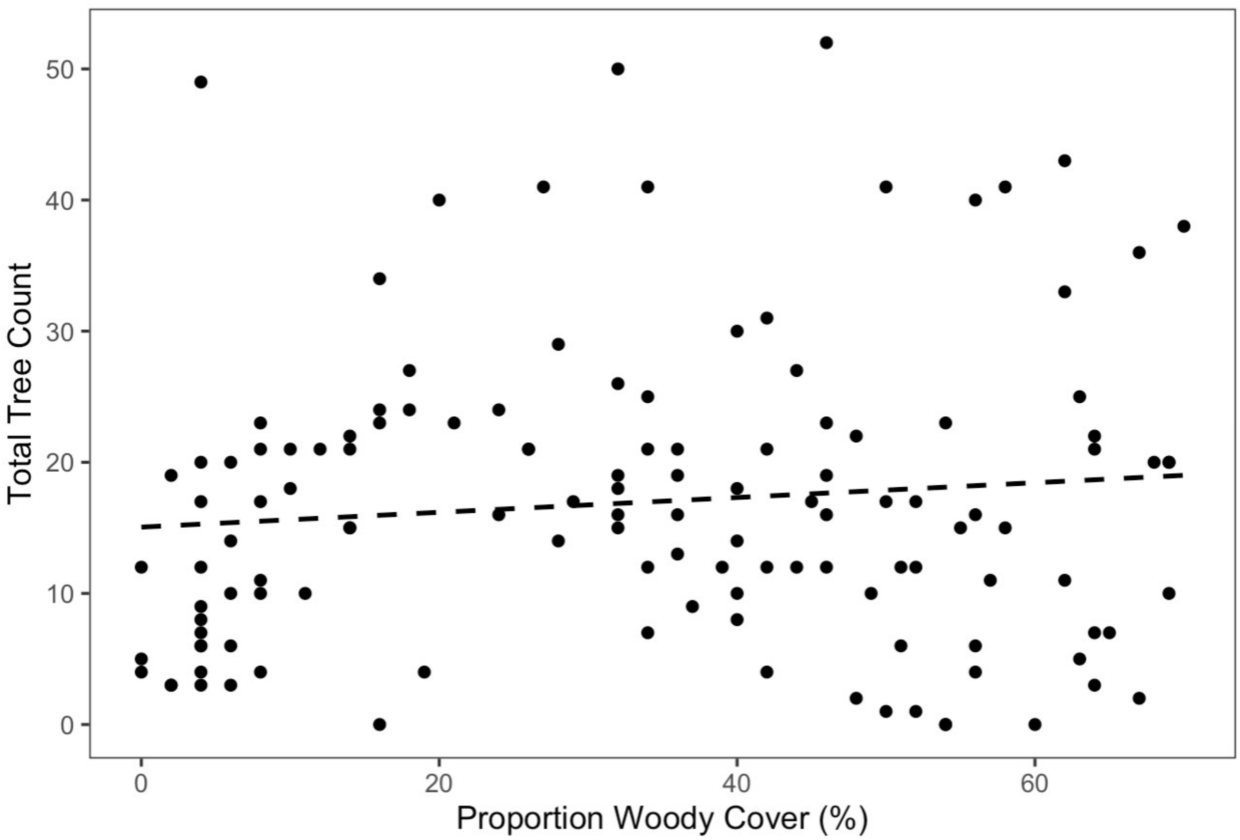


**Figure S3.** Across the 127 plots, there was no significant relationship between a plot's woody cover and its number of trees (p = 0.22). The lack of a significant relationship indicates that woody plant encroachment is driven by shrubs and bushes, rather than by the recovery of woodland or forests trees.

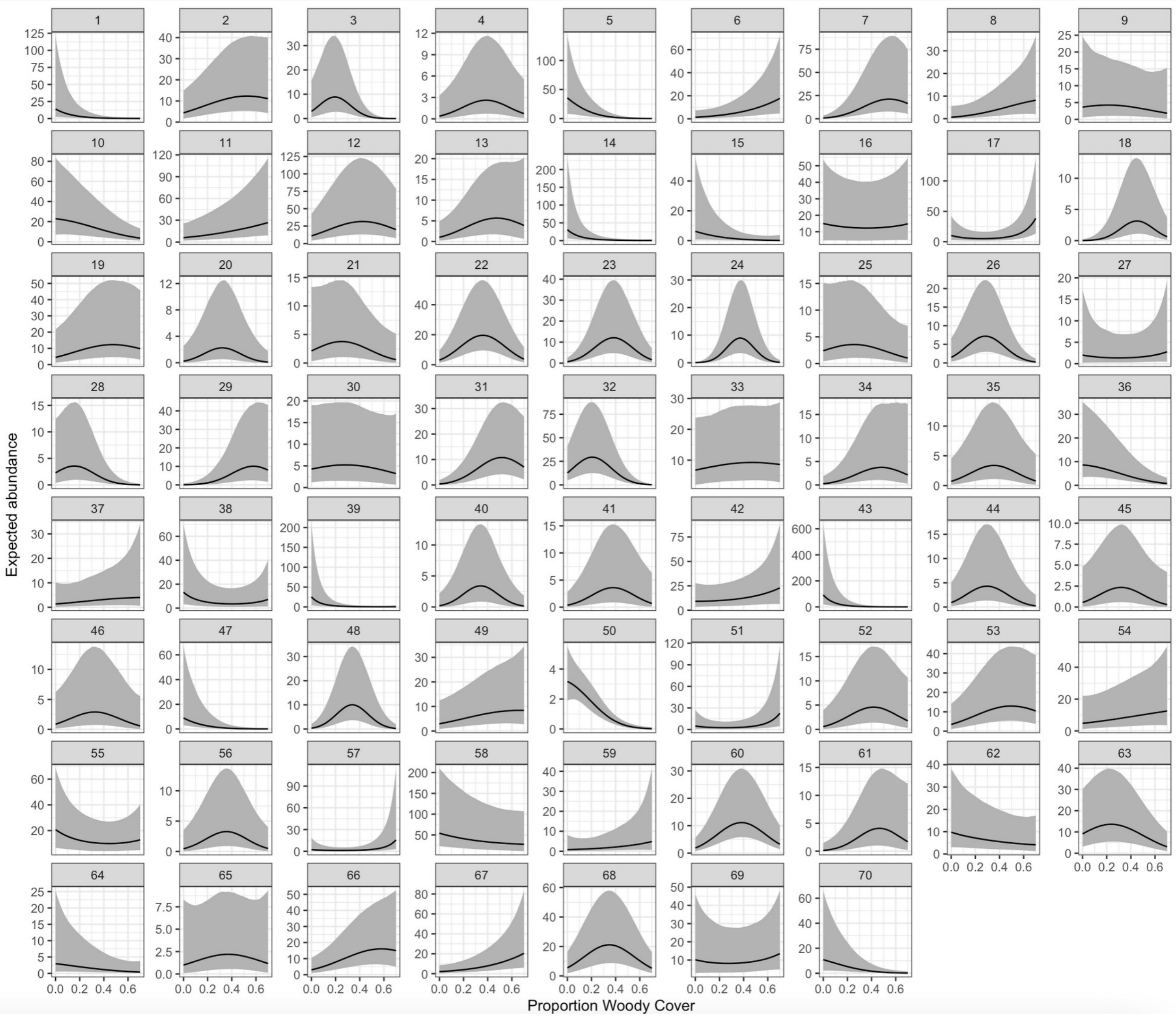


**Figure S4.** Changes in abundance of 70 common savanna birds, across a gradient from 0% to 70% woody cover (x-axis). Bird abundances were modeled as a function of both linear and quadratic terms for the percent woody cover covariate, as well as of detection covariates. Many species exhibit humped responses to woody cover, with abundances highest at moderate levels of cover.

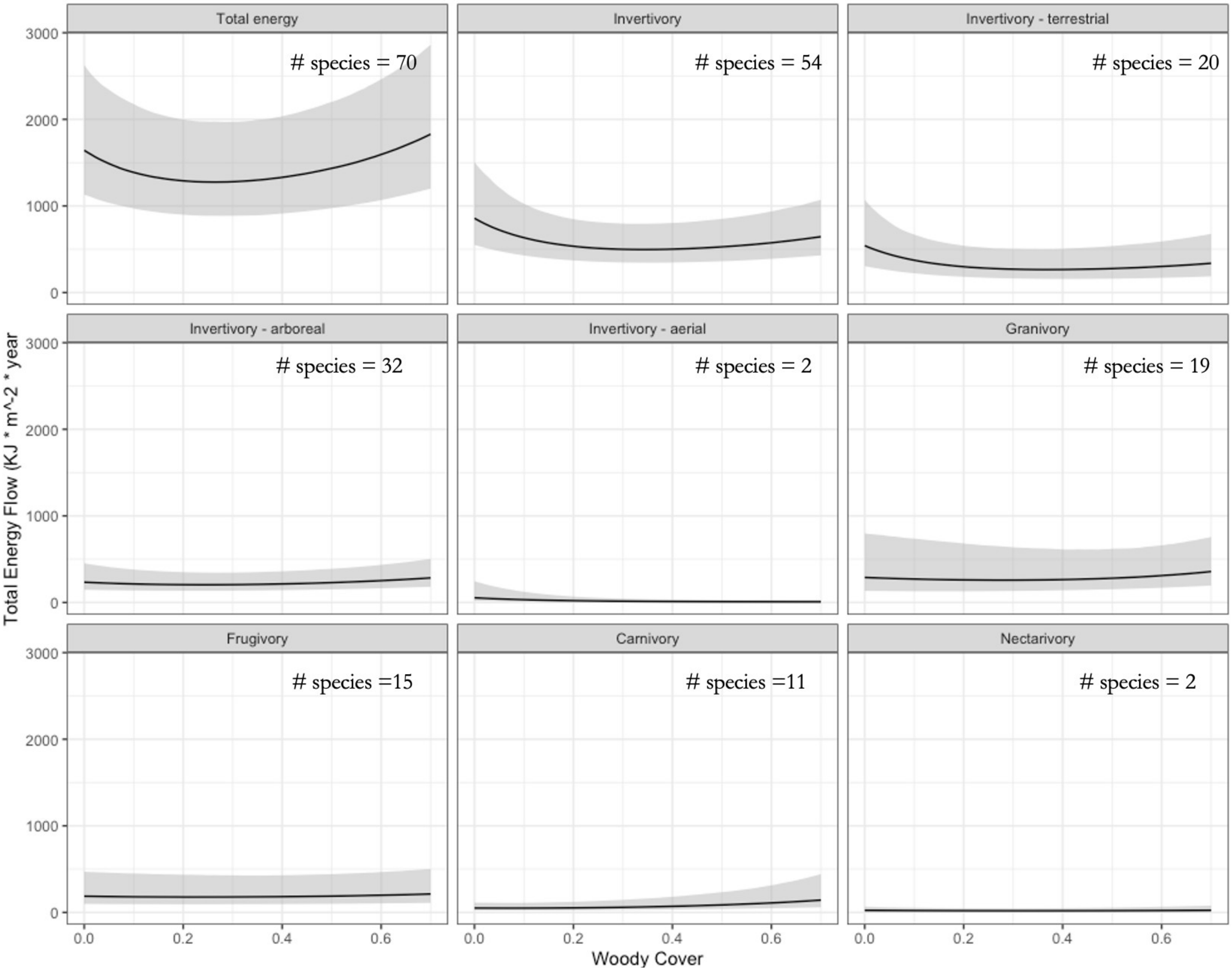


**Figure S5.** Changes in energy flows through key ecosystem functions performed by common savanna bird species, across a gradient of woody cover in a Zimbabwean acacia savanna. The fixed axis allows for comparison of the absolute size of energy flows between bird-mediated trophic functions.

**Table S1.** Results of chi-square tests that related species responses to woody plant encroachment to functional traits.

| **Nesting Strategy - Losers** | |
|---|---|
| p-value | 0.1298 |
| df | 4 |
| X-squared | 7.1182 |
| **Nesting Strategy - Winners** | |
| p-value | *0.02544 |
| df | 4 |
| X-squared | 11.102 |
| **Lifestyle - Indifferent** | |
| p-value | 0.001983 |
| df | 2 |
| X-squared | 12.446 |
| **Nesting Strategy - Indifferent** | |
| p-value | 0.1451 |
| df | 4 |
| X-squared | 6.83 |
| **Diet - Losers** | |
| p-value | 0.4712 |
| df | 6 |
| X-squared | 5.5853 |
| **Diet - Winners** | |
| p-value | 0.3451 |
| df | 6 |
| X-squared | 6.7443 |
| **Diet - Indifferent** | |
| p-value | 0.06505 |
| df | 3 |
| X-squared | 7.2253 |
| **Lifestyle - Winners** | |
| p-value | 0.09883 |
| df | 2 |
| X-squared | 4.6287 |
| **Lifestyle - Losers** | |
| p-value | 0.2952 |
| df | 2 |
| X-squared | 2.4405 |

**Table S2-S4.** Post-hoc tests of significant or near-significant relationships between functional traits and species responses to woody plant encroachment.

| **Nesting Strategy - Losers** | | | | | |
|---|---|---|---|---|---|
| | cavity | grass | ground | shrub | tree |
| Loser | 0.2771861 | -0.6334879 | 1.7137922 | -2.2075895 | 0.8777561 |
| Non-Loser | -0.2771861 | 0.6334879 | -1.7137922 | 2.2075895 | -0.8777561 |

| **Nesting Strategy - Winners** | | | | | |
|---|---|---|---|---|---|
| | cavity | grass | ground | shrub | tree |
| Non-winner | 2.33459 | -0.785853 | -0.3318242 | -2.6125174 | 1.167295 |
| Winner | -2.33459 | 0.785853 | 0.3318242 | 2.6125174 | -1.167295 |

| **Lifestyle - Indifferent** | | | |
|---|---|---|---|
| | Generalist | Insessorial | Terrestrial |
| Indifferent | -1.827811 | 3.433581 | -2.537296 |
| Responsive | 1.827811 | -3.433581 | 2.537296 |

## Sentinel Protocol – Bird Diversity Guidelines

*N.B. The methods used to sample birds for this article were adapted from the Sentinel protocol for bird sampling, below. Instead of a sampling strategy that compared birds in forest land and agricultural land, we used a strategy that compared birds along a gradient of woody cover.*

For a comparison of forest land and agricultural land bird species diversity, six plots will be sampled per study site. Sampling of these locations will be done between dawn (e.g., 5:30 am in Ghana) and about 0900 hours (last approx. 3hours), so as to coincide with the maximum activity of forest birds. Fieldwork can continue later if conditions are ideal, but there needs to be enough time off to rest if bat surveys occur in the evenings.

After reaching a sampling location, the observers should wait quietly for around 1 minute to allow any birds disturbed by their arrival to resume their normal activity. A count should then be undertaken for 10 mins.

- Each individual bird either seen or heard should be identified to species level, up to a distance of 50m from the observer, with an estimate of the number of individuals in the group (where possible). With efforts to avoid ‘double counting’ individuals or groups already recorded.
- Additional species observed beyond the 50m point or flying overhead can be recorded in the appropriate detection categories on the datasheet (See Appendix 1).
- Simultaneously, a recording of this 10 min period should be done using the provided Tascam audio recorder and shotgun microphone (in order to help with later species identification).

After the 10 min count period is over, the observers should move to the next sampling point and repeat the process. Additional rapid vegetation structure measurements (See Appendix 2) will be required at each point count sampling location (once per season). This is probably best accomplished either just before or just after the point count surveys.

# 7. Synthesis and Conclusion

## 7.1 Review of Results

The aim and objectives of this thesis were investigated through three research articles, which together examined how human activity is affecting consumer-mediated ecosystem function in African savannas. Below, I briefly review the main results of each chapter. I then present a synthesis of the findings, which focuses on the work's implications for trophic ecology, global change ecology, and future research.

**Objective 1: To quantitatively estimate how changes to land use and biodiversity intactness have altered key bird and mammal-mediated ecosystem functions across sub-Saharan Africa.**

This objective was addressed in chapter 4, which employed an energetics framework to examine historical changes to animal-mediated ecosystem functions across sub-Saharan Africa. In total, I found that trophic energy flows through birds and mammals had decreased by over one-third since the 1700s. That decline included a ~75% decrease in functions performed by megafauna, including by large herbivores and apex carnivores, which experienced population collapse outside protected areas. The pattern of decreasing function varied by biome, driven by arboreal birds and primates in forests, terrestrial herbivores in grassy systems, and fossorial mammals in arid systems. On a taxonomic level, elephants were historically the continent's dominant energy consumers in Africa. Fossorial mammals, such as mole rats, also may be major energy consumers, although their contribution is highly uncertain. In general, the article's energetics approach highlighted the functional importance of keystone species such as elephants and mole rats, and of smaller animals, which are often underrepresented by other metrics. Birds in particular consumed 37% – 41% of total energy flows, a much greater proportion than would be inferred from their biomass alone. I concluded that by relating biodiversity intactness to energy and material flows, ecosystem energetics approaches can advance efforts to integrate animal-driven functions into biosphere and earth system models, helping to identify possible regional or planetary boundaries for biodiversity.

**Objective 2: To assess how changing land use and fire regimes have altered the vegetation structure of the Angolan miombo woodlands by driving and/or inhibiting woody encroachment.**

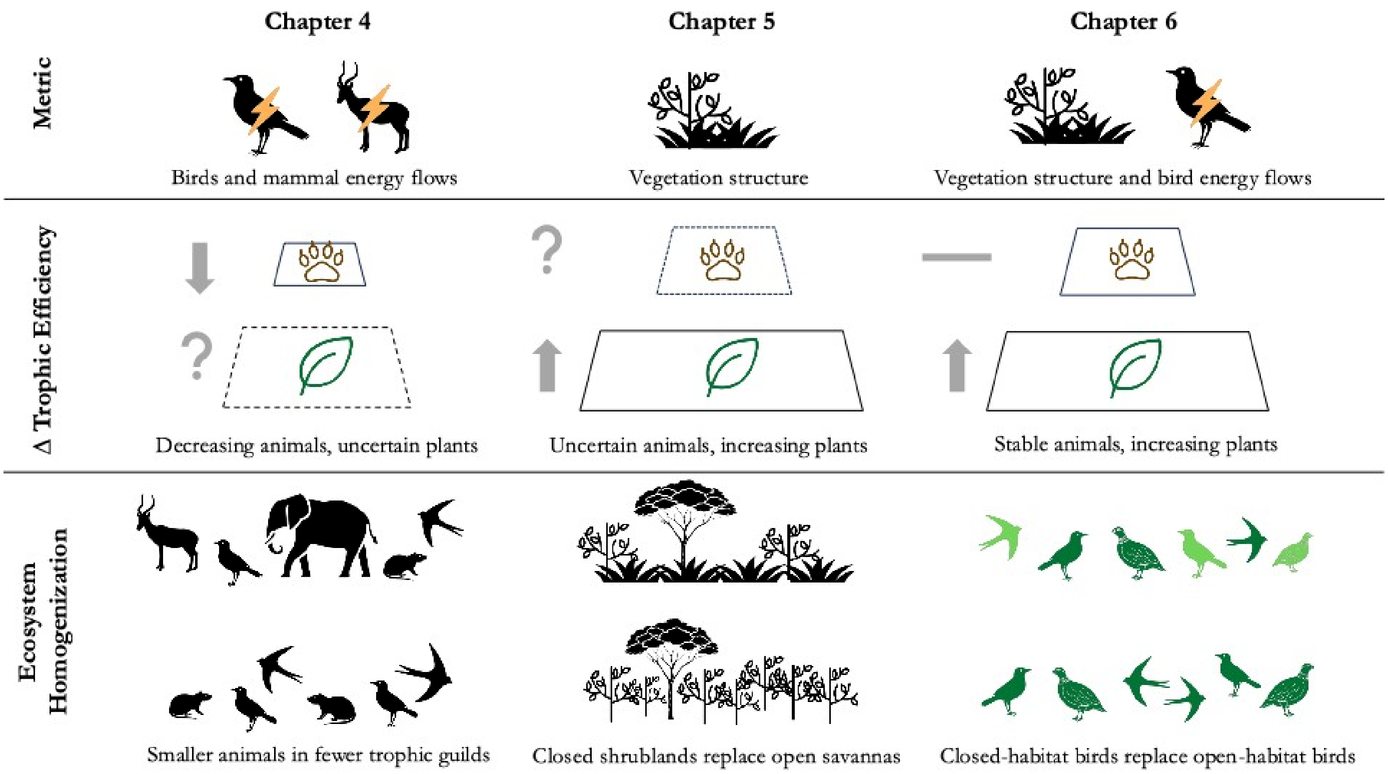
This objective was addressed by chapter 5, which examined the causes and extent of woody encroachment in the Angolan miombo woodlands. It specifically investigated how fire, cropland expansion, and atmospheric change determined the ecoregion's vegetation structure. I found that from 1990 to 2020, 34.1% of the Angolan miombo woodlands experienced significant woody encroachment, while the canopy greenness of natural vegetation—a proxy for woody cover—increased by 8.3% over the 2000 to 2020 period. Meanwhile, open grassy vegetation declined by 62%, indicating that habitat for open-ecosystem specialists is disappearing astonishingly quickly. Woody encroachment advanced rapidly even in areas experiencing extraordinarily high burn frequencies, and was not adequately explained by changing temperature or precipitation. In addition, woody encroachment was concentrated far from the agricultural frontier, in remote areas with low population densities. These results challenge the hypothesis that human-altered fire regimes are the primary driver of woody encroachment in mesic savannas, and instead point to increased $CO_2$ concentrations. The large scale of changes to vegetation structure suggests that woody encroachment is likely transforming savannas' species composition and ecosystem function, a hypothesis I investigated in my third paper.

**Objective 3: To quantify how fire suppression and resulting changes to savanna woody cover have altered bird-mediated ecosystem functions in a Zimbabwean savanna.**

This objective was addressed by chapter 6, which built on chapters 4 and 5, by examining how woody encroachment in a Zimbabwean acacia savanna is changing bird species abundances and ecosystem functions. I found that among 70 common savanna bird species, increasing woody cover decreased the abundances of 27% of species and increased those of 34%. Losing species were distributed evenly across functional lifestyle, diet, and nesting categories. In contrast, winning species were strongly predicted by nesting strategy, and indifferent species were predicted by lifestyle. Although increasing woody cover dramatically shifted the bird community’s structure, it did not change the absolute strength of bird-mediated ecosystem functions. Even so, the trophic efficiency of the bird community likely declined, because the bird community’s stable energy consumption would have been outpaced by the higher plant energy fixation caused by woody encroachment. These results highlight the risk that woody encroachment homogenizes bird communities across African savannas, threatening the diversity and conservation of open-habitat specialists. However, the results also suggest that the high functional redundancy of savanna birds may make their functions resilient to woody encroachment, even as overall consumer control of the ecosystem decreases.

## 7.2 Synthesis

Together, these results reveal two major consequences of human impacts on African savannas. First, African savannas are becoming less trophically efficient. As woody plants become more abundant in savannas, they lock up a greater proportion of the ecosystem’s energy, leaving consumers—fire and animals—less able to alter vegetation structure. And it is by altering vegetation structure that consumers influence the flows of carbon, nutrients, and water that make up ecosystem function. Second, savannas are becoming more homogenous. They are experiencing structural homogenization as woody vegetation encroaches into open areas (chapter 5); functional homogenization as human activity depletes megafauna (chapter 4); and taxonomic homogenization as communities of open-ecosystem animals are replaced by closed-ecosystem specialists (chapter 6). Combined, these processes are making African savannas more like ecosystems elsewhere: more closed, more dominated by plants, and more devoid of the big animals that trample and devour vegetation and in doing so transform landscapes. Those animals, alongside fire, have kept African savannas open and dynamic for millions of years, endowing them with a unique biodiversity adapted to disturbance (William J. Bond and Parr 2010). As African savannas close, a transformed suite of ecosystem functions is likely to threaten that biodiversity and to leave savannas less functionally distinct and more ordinary.



## Savannas are becoming less trophically efficient

One major contribution of this thesis is to clarify how consumer control is changing in African savannas. Consumers, meaning fire and herbivores, consume a greater proportion of plant energy in African savannas than in other biomes (Bond, Woodward, and Midgley 2005). This higher consumption amplifies consumers' control over vegetation structure and over vegetation-moderated flows of nutrients, water, and energy. To assess the strength of animal-mediated consumer control, ecologists can measure trophic efficiency: the proportion of energy fixed by plants each year (i.e. of NPP) that is consumed by animals. Previous work has found that trophic efficiency is substantially higher in some African savannas than in other terrestrial biomes (Hairston and Hairston 1993). Additional work had proposed that this discrepancy exists because vegetation in savannas is limited by fire and animals, while vegetation in most other biomes is limited by climate and nutrients (Archibald and Hempson 2016; Bond 2005). But to my knowledge, no previous work has used the lens of trophic efficiency to clarify how human activity is changing consumer control of vegetation across Africa.

This results of this thesis support previous evidence that closed, woody ecosystems have lower trophic efficacy than open grassy ones. Studies of NPP by biome show that on average, forest plants fix two to three times more energy per unit area than savanna plants (Grace et al. 2006). By contrast, I found that bird and mammal communities in African forests consumed on average the same amount of energy per unit area as those in African savannas (chapter 4). Savanna birds and mammals would therefore consume a greater proportion of NPP, giving savannas a higher trophic efficiency. While I did not quantify energy flows through invertebrate herbivores, energy flows through the birds and mammals that eat invertebrates were about equal in forests and savannas. We can therefore tentatively hypothesize that forests do not have larger invertebrate populations offsetting forest vertebrates' lower trophic efficiency. I found a similar relationship between high woody cover and low trophic efficiency along a woody cover gradient *within* savannas (chapter 6). Previous work has shown that severe woody encroachment in savannas increases NPP by about 35% (Zhou et al. 2023). However, I found that the absolute size of energy flows through birds remained constant across savannas ranging from 0% - 70% woody cover. These results provide further evidence that open ecosystems have a higher trophic efficiency than closed ones: as woody cover increases, the trophic efficiency of at least one major guild, birds, declines.

As African savannas lose megafauna and gain woody cover, it is reasonable to hypothesize that their trophic efficiency would shift toward the lower efficiency of other woody ecosystems. Each chapter of this thesis depicts a different mechanism through which global change is driving that shift. Chapter four shows that human activity across sub-Saharan Africa has decreased the amount of energy consumed by birds and mammals by 36%. That figure includes a 72% decrease in energy consumption by the large herbivores that most effectively control savanna vegetation (Owen-Smith 1987; William J. Bond 2005). Assuming ecosystem NPP stays constant, a decline in herbivory would reduce trophic efficiency, locking up a greater proportion of energy in plants. That herbivory-driven increase in plant energy stocks could be offset by a concurrent increase in fire or livestock populations. But other studies show that burned area is broadly decreasing across Africa, and that in most savannas, livestock populations have not offset disappearing wild herbivores (Andela et al. 2017; Hempson, Archibald, and Bond 2017). The loss of wild animal populations is likely therefore leading to a more plant-dominated trophic structure in savannas.

Increasing savanna woody cover (chapter five) should also reduce trophic efficiency, assuming that two conditions are met. The first is that greater plant energy fixation is not accompanied by proportionally greater herbivory. That assumption likely holds, since declining herbivores populations are unlikely to be consuming excess vegetation (chapter 4, see also Hempson, Archibald, and Bond 2017). The second condition is that increases in aboveground carbon are not offset by decreases in belowground carbon. This assumption also likely holds, as previous work has found that higher atmospheric $CO_2$ fertilizes savanna plants, causing belowground savanna carbon stocks to increase (Bond and Midgley 2000) or at least stay stable (Zhou et al., 2023). The trophic efficiency of African savannas is therefore very likely to be decreasing, and to be doing so over a wide geographical area: regional studies suggest that the woody encroachment I documented in Angola is in line with continent-scale woody encroachment across Africa (Venter, Cramer, and Hawkins 2018; Stevens et al. 2017). While that increase in woody cover is now widely reported, this thesis is among the first studies to show an ecoregion-scale encroachment of grasslands despite continued frequent fires. This result suggests that even near-annual burning will not prevent global change from restructuring African savannas into more plant-dominated ecosystems.

Finally, chapter six indicates that animal energy consumption is being outpaced by plant energy fixation even in ecosystems with stable animal guilds. Among Shangani (Zimbabwe) birds, energy consumption has remained constant across a woody encroachment gradient. But woody encroachment has increased plant energy fixation, meaning that even the ecosystem's energetically stable bird community is becoming less trophically efficient. Why are Shangani's bird populations unable to take advantage of greater plant energy? One explanation is that bird populations are limited by nutrients rather than calories. Increasing plant biomass would dilute nutrient stoichiometry, leaving the key resources limiting bird populations unchanged (Polis 1999). Another possibility is that birds are limited by plant defenses. Increasing $CO_2$ would let plants allocate more resources toward physical and chemical defenses, slowing down seed predation and suppressing invertebrate populations, birds' prey (Wigley, Fritz, and Coetsee 2018; Coley and Barone 1996). In any case, nonlinear scaling relationships between trophic guilds are widely documented in ecology. For example, relationships between the biomass of higher and lower trophic levels adhere to a generalized exponential scaling law (with exponents consistently near ¾) that leaves biomass pyramids increasingly bottom-heavy in ecosystems with higher biomass (Hatton et al. 2015). This thesis suggests that similarly nonlinear scaling may define the relationship between large increases in plant energy flows and smaller or non-existent increases in animal energy flows. Why these trophic scaling relationships are nonlinear is not yet well understood, and is a rich area for future research (Hatton et al. 2015).

I hypothesize that the consequence of decreasing trophic efficiency in savannas will be their transition from consumer-controlled to resource-controlled ecosystems. Consumers' declining influence will allow plants to hijack a greater share of ecosystem energy, hindering energy flows into animals. Plants' enhanced control of energy should buffer plant-mediated ecosystem functions from changes caused by herbivores. Reduced influence by herbivores should also suppress predators' ability to launch trophic cascades that shape patterns of carbon, nutrients, and water. Researchers might test these hypothesis by comparing the strength of trophic cascades in consumer versus resource-controlled ecosystems.

Another consequence of decreasing trophic efficiency will be a decline in savannas' ratio of energy flows to energy stocks. In forests, stocks of energy are deep and annual inflows and outflows of energy are proportionately small. In savannas, by contrast, stocks of energy have historically been shallower and inflows and outflows of energy proportionately large (Prentice et al. 2001). The average joule of energy therefore spends more time in closed ecosystems than in open ones. As consumers become less able to control savanna vegetation, however, the energy stored in woody plants will grow, causing energy to flow through savannas more slowly. Ecologists have very little understanding of how an ecosystem's function is shaped by its energetic architecture, meaning the division of energy among key stocks (e.g. plants, animals, soils) and the relationships between energy stocks and flows. A research agenda to address this gap might begin by describing the energetic architecture of each biome, and then proceed to examine whether there are consistent relationships between an ecosystem's energetic architecture, its patterns of material flows (i.e. its function), and its patterns of plant and animal populations. Such an approach might even help ecologists develop a unified theory of biome formation.

Finally, it is important to clarify that even as the trophic efficiency of savannas comes to resemble that of forests, the structure of trophic guilds in savannas has remained distinctive, leaving encroached savannas unlikely to support forest-like ecosystem functions or biodiversity. Chapter 4 of this thesis shows that forests and savannas have fundamentally different arrangements of trophic guilds. In forests, a higher proportion of energy flows through arboreal species and through frugivores and nectarivores, while less energy flows through fossorial species and granivores. An analogous study of energetics in Bornean bird communities also found that forests have higher relative energy flows through frugivorous and nectarivorous birds (Malhi et al. 2022). In Chapter 6, I show that woody encroachment does not cause savanna bird communities to become more like those of forests, even as woody cover approaches 70%. These different trophic structure should be reinforced by the by the fundamentally different functional traits of forest and savanna plant species: forest plants are adapted to shade and stability, while savanna plants are adapted to sun and disturbance (Oliveras and Malhi 2016; Charles-Dominique et al. 2018). Together, this evidence cautions against efforts to “reforest” savannas (Parr, Te Beest, and Stevens 2024). It shows that suppressing fire in savannas will not actually create an ecosystem with forest-like functions, but rather a novel, degraded form of savanna, a point I emphasized in a letter published in Global Change Biology that I led during this thesis (See Appendix). The benefits of afforesting savannas for biodiversity and carbon sequestration are likely to be underwhelming compared to restoring actual forest ecosystems.

## Savannas are becoming more homogenous

Taken together, the results of this thesis suggest that African savannas are becoming more homogenous along three axes: physical structure, animal-mediated function and taxonomic diversity.

First, savannas are undergoing functional homogenization (chapter 4), with complex trophic webs made of many functional guilds replaced by simpler trophic structures weighted more heavily toward smaller animal guilds. In particular, there has been a collapse of megafauna-performed ecosystem functions, which include large-scale herbivory, long-distance nutrient dispersal, and apex carnivory. Meanwhile, the functions performed by birds and small mammals are proving resistant to land use change. Both birds and small mammals remain relatively abundant outside of croplands and urban areas, especially in the lightly used rangelands losing megafauna. These results build on previous evidence from case studies by measuring and mapping trophic downgrading at a near-continental scale (Estes et al. 2011).

Second, savannas are experiencing structural homogenization (chapter 5). Savannas that have historically been co-dominated by grassy and woody vegetation are being replaced by closed, encroached systems and by cropland. While this pattern has been documented by many studies (e.g. Venter, Cramer, and Hawkins 2018; García Criado et al. 2020; Stevens et al. 2017), this thesis is among the first to report that frequent fire may no longer be able to maintain the open portions of mesic savannas under current, high-$CO_2$ conditions.

Third, I demonstrate that savannas experiencing woody encroachment are also undergoing taxonomic homogenization (chapter 6). Given the continental scale of woody encroachment, it is likely that changes in savanna vegetation structure are causing the same shrub-favoring species to succeed across Africa, at the expense of their open habitat-favoring competitors (Venter, Cramer, and Hawkins 2018; White et al. 2024). While previous studies have also documented widespread declines of African open ecosystem-specialist birds (White et al. 2024; Sirami and Monadjem 2012), this study is the first to link changes in species composition to quantified changes in trophic ecosystem functions. Despite the widespread homogenization of bird communities, the results suggest that bird-mediated functions may remain intact even in encroached savannas. When viewed in aggregate the chapters of this thesis reveal an African savanna that is becoming more uniform across multiple dimensions, a portrait of change obscured by a focus on each chapter as a standalone journal article.

African savannas are among the last and largest remnants of the megafaunal landscapes that once covered the Earth (Svenning et al. 2024). Global change in savannas is therefore homogenizing the world in a broader sense by making African savannas more like those of other continents. Since the Pleistocene extinctions, Africa’s savannas have been exceptional in three related ways. First, African savannas have had far more disturbance than other savannas due to their near-intact suite of megafauna, a difference dating back tens of thousands of years (Owen-Smith 1987; Malhi et al. 2016; Svenning et al. 2024). Second, African savannas have not been subject to widespread fire suppression, which has shaped other savannas over the last century or so (Archibald 2016). Finally, African savannas have been far more open than savannas elsewhere, with more grass and less woody vegetation (Lehmann et al. 2011; Bond 2019). Most evidence suggests that that openness is maintained by fire and animals (Strömberg and Staver 2022). The current decreases in megafauna and fire, alongside advancing woody encroachment, is therefore likely to cause African savannas to converge structurally and functionally with savannas elsewhere. To understand where African savannas are going, ecologists might look to other savannas that have been under intense human pressure for centuries, for example those of Texas (Schmidly 2002). In subtropical Texan savannas, which occupy the same climatic envelope as South Africa’s Kruger National Park, fire has been heavily suppressed since the 19th century. Most megafauna collapsed ~10,000 years ago, and the remaining herds of bison were extirpated by the 1870s (Schmidly 2002). Texan savannas still contain a rich and abundant fauna of small and medium-sized mammals and birds. But they have experienced heavy encroachment and the transformation of open grasslands into thicket and shrubland (Ansley, Wu, and Kramp 2001). Both the structure of Texan savannas and their consumer-mediated functions have fundamentally changed.

How might some of these functional changes unfold in more detail? What kinds of changes should be investigated? Here, I hypothesize about four possible directions of change, which, while informed by the results of this thesis, are speculative and should be investigated further. First, the decline of large herbivores, particularly browsers such as elephants, might exacerbate woody encroachment, creating a positive feedback loop (Stevens et al. 2016). If woody vegetation increases as soil nutrient levels remain constant, nutrient concentrations in plants would probably decline, making plants a less rich fodder for herbivores (Archer et al. 2017).

Less nutritious vegetation may cause large herbivore populations to decline further, particularly where the megaherbivores best adapted to low quality forage are now absent. Fewer large herbivores would amplify woody encroachment, initiating a positive feedback loop.

A second set of changes concerns animal-dispersed nutrients. As large herbivore herds and migrations disappear, fewer animals will transport nutrients long distances, from nutrient hotspots like Africa’s volcanic landscapes, to nutrient poor regions like the Kalahari sands (Hempson, Archibald, and Bond 2017). Without this transport, many savannas will have less nutrients available for plants and animals. Whether changes in plant nutrient stoichiometry will impact insect abundances, and thus populations of avian and mammalian insectivores, is highly uncertain (Abraham et al. 2023). There is very little research on how invertebrate abundances respond to nutrient concentrations in wild savanna plants. As such, future research might employ plant stoichiometry and allometric equations to relate food availability to nutrient and energetic requirements in animals, ranging from insects through birds to megaherbivores. There is also a need for more studies on nutrient dispersal dynamics in savannas, particularly research into how stocks and flows of nutrients are affected by long-term changes to disturbance regimes.

A third set of changes concerns the further homogenization of local-scale savanna landscapes, due to the loss of large herbivore functions such as grazing, browsing, wallowing, and trampling. This homogenization may be exacerbated by extirpations of apex predators, which allow remaining herbivores and livestock to graze landscapes continuously, instead of avoiding high predation areas. By decreasing the number of niches in the savanna landscape, local-scale homogenization would decrease local-scale biodiversity (Tews et al. 2004; August 1983). To investigate these changes, researchers might analyze the niche partitioning of small African vertebrates, which is very little understood. They might also investigate whether changes in megafauna populations impact the functions performed by small vertebrates, perhaps by using an energetics framework. In particular, researchers could assess how changing animal functions affect savannas’ structural and functional homogeneity, as well as how changes to small vertebrate populations interact with large herbivore extirpations.

Finally, research might investigate the ecosystem functions performed by fossorial mammals in savannas. Chapter 4 makes the startling observation that fossorial mammals, particularly mole rats, may be major energy consumers in arid savannas and shrublands. Although data on fossorial mammals is highly uncertain, they may consume substantial belowground biomass, shaping belowground vegetation in parallel with aboveground herbivores such as elephants. In doing so, mole rats may impact soil nutrients, soil structure, and the ability of soils to support vegetation and sequester carbon (Eldridge and Soliveres 2023). Essentially no research has investigated the effects of global change on fossorial mammals in Africa. There is no data on how processes such as fire suppression, woody encroachment, and aboveground defaunation affect belowground animals, although woody encroachment in particular would change the root systems that mole rats eat. Feedback loops linking aboveground change to belowground processes are especially intriguing. Could woody encroachment decrease soil carbon sequestration by changing fossorial communities? Would such a change further advantage shrubs over grasses and thus exacerbate woody encroachment? Research into these belowground ecological processes in savannas is a rich area for future study.

## 7.3 Conclusion

Together, the findings of this thesis call on decisionmakers to rethink how savannas are modeled, managed, and valued. As savannas shift from consumer-controlled to resource-controlled systems, with declining trophic efficiency and rising structural, functional, and taxonomic homogenization, they are losing the dynamics that have made them globally distinctive. These changes are likely to threaten savannas’ unique biodiversity and to reshuffle the ecosystem functions that have supported people living in savannas for millennia.

Scientifically, this work highlights the need to better integrate animal-mediated functions into Earth system models to avoid underestimating the ecological consequences of defaunation and woody encroachment. The energetics approach trialed in this thesis provides a pathway to do just that. This thesis also identifies new research frontiers. These include investigation into the energetic architecture of ecosystems; the relationships between woody encroachment, animal-mediated nutrient flows, and trophic cascades; and the potential impact of belowground consumers, such as fossorial mammals, on ecosystem function.

As for policy outcomes, the results of this thesis warn against simplistic climate mitigation strategies such as efforts to increase woody cover in African grassy ecosystems and to suppress fire. These strategies are likely to threaten savannas' unique disturbance-adapted biodiversity by further degrading consumer control, while providing only limited and uncertain contributions to long-term carbon sequestration (see Annex 1). This thesis also highlights the importance of conserving megafauna populations and other forms of natural disturbance for African savanna biodiversity. Efforts to restore megafauna in rangelands and near-natural lands may help maintain consumer-mediated ecosystem function in landscapes otherwise being transformed by global change. These efforts will require work to improve human-wildlife coexistence, enhance wildlife economies, and better value animal-mediated ecosystem services. Decisionmakers will need to better integrate fire and megafauna into management plans if they are to conserve savannas' consumer controlled functions—the functions that sustain African savannas as a unique bastion of the dynamic Pleistocene ecosystems that once covered the Earth.

As for policy outcomes, the results of this thesis warn against simplistic climate mitigation strategies such as efforts to suppress fire and increase woody cover in African grassy ecosystems. These strategies are likely to threaten savannas' unique disturbance-adapted biodiversity by further degrading consumer control, while providing only limited and uncertain contributions to long-term carbon sequestration (see Appendix). This thesis also highlights the importance of conserving megafauna populations and other forms of natural disturbance for African savanna biodiversity. Efforts to restore megafauna in rangelands and near-natural lands may help maintain consumer-mediated ecosystem function in landscapes otherwise being transformed by global change. These efforts will require work to improve human-wildlife coexistence, enhance wildlife economies, and better manage and value disturbance regimes. Only by doing so will societies conserve savannas' consumer controlled functions. It is these fire- and animal-shaped functions that have made African savannas a unique bastion of the dynamic Pleistocene ecosystems that once covered much of the Earth.

## 7.4 References

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*The following letter to the editor, which I led, was published in Global Change Biology on June 5, 2024, and can be accessed here: [https://onlinelibrary.wiley.com/doi/10.1111/gcb.17369](https://onlinelibrary.wiley.com/doi/10.1111/gcb.17369)*

# Appendix: Central Africa's mesic savannas should be conserved, not afforested

**Authors**: Ty Loft, Anabelle Cardoso, William J. Bond, Francisco M.P. Gonçalves, Manoela Machado, Imma Oliveras Menor, Carla Staver, and Nicola Stevens

Djiofack *et al*. estimated how eliminating fire would impact biodiversity and carbon stocks across 1.2 million km$^2$ of Central African savanna. Extrapolating from 109 vegetation plots, they find that eliminating fire would increase tree species richness while allowing reforested savannas to sequester 12 additional Gt of carbon by 2100. Unfortunately, their proposal to reforest 1.2 million km$^2$ of "artificial savanna" is based on a fundamental misunderstanding of savanna ecology, exacerbated by mis-citations and incorrect data. Here, we show that the savannas allocated for "reforestation" are (i) not artificial savannas but ancient natural ecosystems shaped by fire over millions of years; (ii) home to a rich endemic biodiversity, which fire suppression would imperil; and (iii) likely to sequester far less carbon than the authors predict.

The authors target two ecosystems for afforestation: the miombo woodland savanna and the Congolian savanna-forest mosaic. Both are ancient, fire-dependent ecosystems, not charred former forests, so we define efforts to increase tree cover within them as afforestation. Pollen records show that African savannas have been shaped by fire for 5-10 million years, long predating human mastery of fire (Strömberg 2011). In addition, mesic savannas contain distinct communities of specialist tree species, which could not have evolved over a few thousand years of human-induced burning (Aleman et al. 2020). Remote sensing provides further evidence that fire is intrinsic to the core miombo woodlands even in the absence of humans, due to a combination of frequent lightning strikes, long dry seasons and abundant grassy fuel (Archibald et al. 2009). In fact, human activity has suppressed fire, so that less of Africa burns now than since savannas first spread across the continent (Andela et al. 2017).

Rather than acknowledging these ancient ecosystems, however, the authors propose to afforest all “artificial unstable” savannas, which they define as any mesic savanna receiving more than 783mm of mean annual precipitation. This definition incorrectly conflates unstable savannas with artificial ones. To support their “unstable” description, they miscite Staver et al. (2011), who show that even where mesic savannas exist in conditions that could support forest, they are not unstable, but rather one of two alternative *stable* states maintained by natural disturbance over millennia. To support their “artificial” description, they miscite Sankaran et al. (2005), who argue that mesic savannas are a *natural* outcome of burning and herbivory. In contrast, truly artificial savannas are created through degrading old growth forests. By confusing all bistable savannas as artificial, the authors deny the existence of natural mesic savannas, a major biome.

Djiofack et al. also find that afforesting Central African savannas will increase biodiversity, incorrectly claiming that “recent evidence [shows] that savannas are floristically impoverished.” The savannas allotted for afforestation are overwhelmingly part of the Zambezian center of endemism, a distinct biogeographic region encompassing savannas containing ~8,500 plant species of which 53% are endemic (White 1983). The similarly sized Guinea-Congolian rainforests contain about 8,000 plant species, of which 80% are endemic (White 1983). Because most plant diversity in savannas is in the herbaceous layer, plant richness in these savannas cannot be assessed via tree diversity, as Djiofack et al do. The authors acknowledge that mesic savanna specialists species are threatened by encroachment, noting that “savanna specialists have been dying rapidly since the start of the experiment.” And yet they would erase such species from the flora of Central Africa by afforesting their only habitat. The authors further diminish the value of savannas through misleading analytical choices. They exclude all savanna specialist species from their figures tracking tree species diversity over time and from their long-term carbon and biodiversity projections. These decisions, which the authors do not justify, inflate the benefits of fire suppression for carbon sequestration, while understating its costs for species diversity. When we re-ran the analysis with all savanna species included, we found that species diversity increased by 26% after the first five years, rather than by an astonishing 1188% (Table 1).

Finally, the study’s estimate that 12 GT of carbon will be sequestered through fire suppression is probably unrealistic. Central African savannas have hot dry summers and abundant lightning, which could spark fires even if anthropogenic ignitions were suppressed. Forest specialist trees are not adapted to disturbance, leaving the carbon they store highly vulnerable to fire (Buisson et al. 2019). Moreover, most carbon in savannas is stored underground, and belowground carbon responses to afforestation are highly uncertain (Grace et al., 2006). A commentary by Veldman et al. (2019), applying savanna ecology principles to a study of the global forest potential found a fivefold decrease in the carbon sequestration capacity of reforestation. Given that the proposed intervention would transform the ecology of an area greater than France and Germany combined, such small increases in carbon must be carefully weighed against the dramatic consequences of afforestation for biodiversity, ecosystem services, and livelihoods.

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