How is biodiversity in savanna landscapes structured and effectively conserved?

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General summary

Globally, we are experiencing a crisis of biodiversity loss. Increasing human dominance of the Earth has led to widespread land-use change, overexploitation of species and natural resources, and climatic change all of which have caused precipitous declines in the abundance and richness of species. Understanding how biodiversity is structured across regions is vital to maintain ecosystem resilience and to identify effective conservation action. Savannas are widespread covering around 20% of the Earth's surface, playing a vital role in global carbon cycles, and harbouring some of the most endangered and charismatic megafauna. Despite their global importance, patterns of biodiversity and effective conservation actions in savanna landscapes remain understudied in comparison to analyses in moist tropical forests. This thesis investigates broad biodiversity patterns and effective conservation actions in savanna landscapes of Africa. In Chapter two, I use plot-level data from across the savannas of eastern and southern Africa to assess how the alpha, beta, and phylogenetic diversity of savanna tree communities respond to environmental and disturbance gradients. I find that wetter savannas contain more species rich and phylogenetically diverse communities than drier savannas, whilst high taxonomic turnover across the region is largely driven by precipitation regimes. Chapter three built on this by assessing how these same gradients affect the functional composition of tree communities in the region. I collated a functional trait matrix for tree species from a range of sources and used clustering analyses to group species into functional groups. Comparing mean trait values between clusters, I identified three distinct functional syndromes adopted by savanna species to cope with water-limitation and disturbance by fire and herbivory. The relative abundance of these clusters changes in response to environmental and disturbance gradients suggesting that turnover in functional composition of communities is what drives previously identified taxonomic turnover. In combination, chapters two and three demonstrate the importance of climate and disturbance regimes in dictating tree community composition in

savanna systems, highlighting the importance of regional studies and plot-level data to identify these patterns. In Chapter four, I assessed the potential for carbon-based payments for ecosystem services to protect habitats on low-intensity farmland in Ghana. I used farm economic data in combination with tree inventory data to show that protection of farmland trees can be achieved at very low carbon breakeven prices (BEP), ranging from US$2.49 - US$6.45 t^{-1} CO_2. Reintroduction and extension of fallowing periods can also be achieved at competitive BEP, US$4.67—US$15.45 t^{-1} CO_2, when combined with tree protection. This chapter proposes a novel approach to conservation within savanna landscapes that moves beyond traditional conservation attempts that aim to conserve pristine habitats or return farmland to woodland.

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Chapter 1:

General introduction

1.1 The global climate and biodiversity crises

We face two extreme crises without precedent in human history, both of which will have profound effects on the planet and its inhabitants. These two major events have led Earth into a novel, human-dominated geological epoch termed the Anthropocene (Lewis & Maslin, 2015). Since the industrial revolution, we have transferred vast quantities of carbon from secure terrestrial pools into the atmosphere, the oceans, and the biosphere (Ciais et al., 2013). Subsequent rises in global temperature from this interruption of the carbon cycle will have, and are already having, severe effects on climate systems. Extreme weather events, like droughts, wildfires, and extreme heat, will become more frequent and severe, seriously affecting global food production and biodiversity, and reducing the habitability of large areas of the Earth (IPCC, 2023).

Meanwhile, humans have caused an extirpation of species on a scale not seen since the last mass extinction event 65 million years ago, leading to a sixth mass extinction event (Barnosky et al., 2011). The mass extinction of species has created a global biodiversity crisis, primarily driven by land-use change, climate change, overexploitation, invasive species, and pollution (Maxwell et al., 2016; IPBES, 2019). Of particular concern is the recent and rapid expansion of these activities in the most biodiverse areas of the globe – the tropics (Groombridge & Jenkins, 2003). From 2001 to 2022, 459 Mha (12%) of tree cover was lost globally, releasing 195 Gt of CO_2 into the atmosphere (Global Forest watch report, 2023), and causing wholesale replacement of important habitats leading to mass species loss (Gibson et al., 2011). Additionally, overexploitation of timber and animal products degrades forest structure, further threatening millions of species (Lewis et al., 2015; Maxwell et al., 2016). The loss of these habitats and species undermines ecosystem functioning which is responsible for the delivery of vital ecosystem services (Fisher et al., 2009).

Whilst there has been growing acknowledgment of the issues that the global climate and biodiversity crises pose, targets to limit their impacts on biodiversity are repeatedly missed (Butchart et al., 2010). Global carbon emissions are still to peak (IPCC, 2023), deforestation and land-use change continues (Global Forest watch report, 2023) whilst global funding for conservation lags behind necessary expenditure (Waldron et al., 2013). We have already crossed several planetary boundaries and continue our charge towards disastrous tipping points (Steffen et al., 2015). The consequences of inaction on climate change and the global biodiversity crisis are unconscionable.

1.2 Global patterns of tree biodiversity

Trees are a fundamental part of the majority of Earth's ecosystems. They play a pivotal role in the carbon cycle, with global forest carbon stock estimated at 861 ± 66 Pg C (Pan et al., 2011), as well as in water and nutrient cycles (Ellison et al., 2017). Trees provide habitat and food to a diverse array of taxa, with forests harbouring 68%, 80%, and 75% of mammal, amphibian, and bird species, respectively (FAO, 2020). Trees also deliver food, fuel, and timber to billions of people (Fisher et al., 2009; Gamfeldt et al., 2013), with the timber market alone worth $USD 1.5 trillion in 2015 (FAO, 2022). Tree communities are highly variable, ranging from highly diverse, closed-canopy tropical rainforests to open savannas to low diversity boreal forests. Understanding the processes that cause this wide variety in tree community composition and diversity has been a major focus of ecology.

Globally, tree species richness shows strong geographical patterns, with richness being highest across the tropics and reducing with latitude (Currie *et al*., 2004), a pattern repeated across several other taxa and scales (Hillebrand, 2004). These patterns of richness show very strong covariation with temperature and water availability (Hawkins et al., 2003; Esquivel-Muelbert *et al*., 2017). Climate-richness relationships are also repeated at sub-global scales,

with species richness increasing across the Amazon with precipitation (ter Steege et al., 2003). Other facets of biodiversity, such as functional and phylogenetic diversity, also show strong relationships to rainfall and temperature. However, these relationships differ from climate-richness relationships, for example, tree phylogenetic diversity in lowland South American forests peaks at intermediate rainfall levels (Neves *et al*., 2020).

The processes that determine tree community assembly are complex and unresolved. Several proposed hypotheses largely attribute observed climate-richness relationships to climatic, evolutionary, and geological factors (Currie et al., 2004; Mittelbach et al., 2007). For example, the energy-richness hypothesis posits that greater energy availability leads to more individuals and consequently more species, but evidence for this is conflicting (Keil & Chase, 2019). The long evolutionary history and stability of tropical regions may be the driving force behind their hyperdiversity (Mittelbach et al., 2007). Alternatively, the physiological tolerance hypothesis suggests that diversity is greater in wetter and warmer environments as these conditions allow a greater range of functional strategies to persist (Currie et al., 2004; Spasojevic et al., 2014). Climate change, deforestation, and forest degradation all pose significant threats to trees and consequently all the functions and services reliant on them. Any effort to mitigate the biodiversity crisis requires proper understanding of the processes that lead to the formation and maintenance of diverse, fully functioning ecosystems.

Increasingly functional traits are used to understand community assembly mechanisms since the ability of a tree to survive in any given environment is likely to be dictated by its morphological and physiological traits (McGill et al., 2006; Westoby & Wright, 2006). Global syntheses of functional traits in woody plants show that trees primarily orientate themselves along a continuum of leaf traits termed the leaf economics spectrum (LES; Wright *et al*., 2004, Maynard *et al*., 2022). Along this continuum, trees trade-off between acquisitive leaf traits, like high specific leaf area (SLA) and leaf nitrogen, that efficiently attain resources and allow rapid

growth, and conservative traits, such as leaf longevity, which reduce growth rates (Wright *et al*., 2004). These strategies also pose risks in terms of water loss, with faster growth being riskier than slow growth (Oliveira et al., 2021). Maintaining functionally diverse communities of trees are required for the resilient delivery of ecosystem services in the face of widespread global change (Cadotte et al., 2011).

Environmental conditions filter communities to consist of species that are able to persist and successfully reproduce under those conditions - a process known as environmental filtering (Cadotte & Tucker, 2017). This process of filtering is mediated by species' functional traits given they dictate species' responses to external stimuli (McGill et al., 2006). Environmental filtering interacts with trait trade-offs to dictate mechanisms of tree community assembly. For example, species with acquisitive leaf traits, including high SLA and leaf nitrogen, for rapid growth are selected for in high resource environments (Ordoñez *et al*., 2009). In systems with lower nutrient availability and water availability, conservative species, those that invest in long-term tissues (e.g. thick leaves, dense wood), are more common (Wright *et al*., 2004, Maynard *et al*., 2022). Disturbance regimes, such as fire and herbivory, also filter species. For example, thick bark protects the cambium and reduces tree mortality during fire events (Hoffman & Solbrig, 2003), with more fire-prone environments filtering for trees with thicker bark (Hoffman et al., 2003).

Filtering of species based on their ability to survive under differing environmental conditions could lead to two alternative outcomes when assessing patterns of beta-diversity. Species in less-diverse communities are subsets of communities in the most-diverse areas – nestedness – or species are replaced by those better able to survive and compete as environmental conditions change – turnover (Socolar et al., 2016). Observations of both outcomes have been made in tropical moist forests, with trees in Panama exhibiting

compositional and functional turnover across rainfall gradients (Umaña et al., 2021), whilst trees in South America show nestedness (Esquivel-Muelbert et al., 2017).

1.3 Savanna ecosystems

Savannas are the dominant land cover across the tropics and sub-tropics, covering over 20% of the Earth's surface (Pennington *et al*., 2018), dominating the land cover of the African continent (Chidumayo & Gumbo, 2010). They are characterised by the coexistence of trees and a continuous grass layer, differentiating them from shrublands, thickets, and dry forests (Scholes & Archer, 1997). Savannas provide a multitude of important ecosystem services. They harbour a diverse array of flora and fauna, including many endemics and critically endangered, charismatic megafauna (Linder et al., 2012). Savannas are highly peopled biomes, consequently they provide an array of goods and services to the people that live there, including water and food, timber, fuelwood and charcoal, and medicinal products (Ryan et al., 2016). The savanna woodlands of eastern and southern Africa alone support the livelihoods of around 150 million people, with the estimated annual value of the goods and services savannas provide globally exceeding $9 billion (Ryan et al., 2016). Savannas are globally important carbon stores, with the southern African woodlands alone containing ~5.5PgC in aboveground woody carbon (McNicol et al., 2018), a function underpinned by their tree diversity (Godlee et al., 2021).

The global distribution and the structure of savannas is determined by a combination of fire, herbivore, and precipitation regimes, and the interaction of these (Lehmann et al., 2011). In drier savannas, low tree cover and open canopies are maintained by water limitation (Sankaran et al., 2005), but in savannas with intermediate rainfall, between 1000 and 2000 mm mean annual precipitation (MAP), canopy cover is kept below its rainfall-determined upper limit by disturbances from fire and herbivory. These "top-down" processes prevent

canopy closure, allowing the maintenance of a continuous grass layer, and means savannas and forests exist as two alternative stable states differentiated by disturbance regimes (Staver et al., 2011).

Precipitation regimes have also been shown to influence the diversity of savanna tree communities. The floristic richness of dry miombo woodlands (< 1000 mm MAP) is reduced compared to that of wet miombo woodlands (> 1000 mm MAP; Frost, 1996). Similarly, the species richness of southern African woody flora increases in areas with greater rainfall (O'Brien et al., 1998), a pattern repeated in the savannas of northern Australia (Williams et al., 1996). Although evidence of this relationship in southern African savannas is based on coarse herbarium data, and whether these patterns are maintained at a broader scale using plot data is not known. The tree communities of southern and eastern Africa show great variation spatially, splitting into six floristic clusters with high turnover in species composition between these (Fayolle et al., 2018).

Top-down disturbance regimes also influence both the woody structure and community composition of savannas. Experimental burn plots in Kruger National Park, South Africa, show that the frequency, timing, and intensity of fires all influence woody vegetation structure, with increasing frequency and dry-season fires reducing woody cover (Smit et al., 2010). Experimentally, fire has less of an effect on tree diversity (Makumbe et al., 2020) and grass composition (Andersen et al., 2005), but whether this is the case in plots, at large scales, remains unknown. Herbivory by browsers influences woody plant composition in South Africa, with plants with favourable forage (high leaf nitrogen content) showing decreased abundance outside of exclosure experiments (Wigley et al., 2014). In East African savannas, browsing works in conjunction with edaphic factors to filter tree species out of habitats, promoting beta-diversity across the region (Pringle et al., 2016). In combination, herbivory and fire act to

repress sapling growth, imposing a demographic bottleneck and limiting canopy cover (Staver et al., 2009).

In response to frequent and intense disturbance regimes savannas species have evolved a variety of functional traits that allow them to survive. Many savannas species readily resprout following top-kill disturbances (Bond & Midgley, 2001), have thick bark to protect their stems from fire (Hoffman & Solbrig, 2003), and have spines and branching architecture to limit herbivory (Charles-Dominique et al., 2016). These traits allow savanna species to occupy a unique persistence niche (Bond & Midgley, 2001), which enables them to survive in areas where forest trees cannot, governing savanna-forest boundaries (Hoffman et al., 2012). The processes that structure the biodiversity of savanna woodlands remain understudied. The bulk of research focusing on patterns of plant species composition in the tropics is based on tropical moist forests (Parr et al., 2014), but whether these same patterns are replicated in disturbance-driven savannas is unresolved.

1.4 Threats and conservation of savanna landscapes

The consequences of increasing human dominance of Earth through the Anthropocene are increasingly evident in savannas. Woody savannas are experiencing high rates of both deforestation and degradation (Hansen et al., 2013; McNicol et al., 2018), largely driven by expansion of smallholder agriculture (Ryan et al., 2012) and timber and charcoal extraction (Ahrends et al., 2010), although there is evidence that this is offset by woody gains at the regional level (McNicol et al., 2018). Additionally, increasing atmospheric CO_2 concentrations can have a fertilization effect leaving savannas vulnerable to woody encroachment (Stevens et al., 2017). This interferes with usual ecosystem processes, having negative consequences for soil carbon storage (Berthrong *et al*., 2012), grazing regimes (Angassa & Baars, 2000), and biodiversity (Ratajczak *et al*., 2012).

These pressures on savanna systems are only likely to increase as we move through the 21st century, particularly in the savannas of Africa which are expected to experience the highest global rises in population (United Nations, 2017) and pressures to expand large-scale commercial agriculture (World Bank, 2009). However, expansion of commercial agriculture in tropical moist forests has precipitated major declines in biodiversity and carbon storage (Gibson et al., 2011; Archard et al., 2014), with the same effects to be expected from agricultural expansion into savannas (Searchinger et al., 2015). Likewise, suggestions that savannas could be suitable areas for mass tree planting to mitigate carbon emissions (Bastin et al., 2019) have been met with valid concerns on the outcomes this would have on the integrity of savannas (Veldman et al., 2019) and exemplify the undervalued nature of these diverse systems (Parr et al., 2014; Murphy et al., 2016).

Proper protection of savannas requires a comprehensive understanding of their ecology. Climate change is expected to alter rainfall and fire regimes across savannas (Niang et al., 2014; Andela & van der Werf, 2014) so understanding how these factors influence vegetation composition patterns and community assembly is important for conservation planning. Likewise, effective restoration of degraded savannas requires that the right trees are planted in the right places at the right densities, necessitating knowledge of the processes of savanna tree assembly and diversity patterns. Functional traits dictate how species will respond to climate change, so understanding patterns of functional trait compositions will also be important to ensure resilient woodlands that continue to provide multiple services to local people (McGill et al., 2006; Cadotte et al., 2011). Increasingly, anthropogenic pressures shape savanna communities. Ecological insights can help to mitigate these pressures, for example, assessing the resilience of miombo woodlands, an important source of fuel in southern Africa, to charcoal production is useful to inform sustainable harvesting rates (Kalaba et al., 2013).

Agriculture is now the dominant global land use (Ellis and Ramankutty, 2008). In savanna landscapes, smallholder agriculture is likely to expand to feed a growing population, therefore retaining and creating porous landscapes that also produce food is vital. Wildlife-friendly farmland features increase on-farm biodiversity (Pywell et al., 2014). Lone trees in agricultural landscapes have a disproportionately positive effect on biodiversity (Fischer *et al*., 2010), whilst fallowed land provides habitat for migratory bird species (Deikumah *et* al., 2017). However, these features are under threat from agricultural intensification, with farmland tree cover declining (Gonzalez *et al.,* 2014) and fallow cycles being shortened or abandoned entirely to increase productivity (Evenson and Gollin 2003). In increasingly human-dominated landscapes, having permeable matrices that allow mixing of populations and tracking of climatic changes by animals is vital to maintaining biodiversity and resilient ecosystems.

Finding cost-effective methods of retaining and increasing biodiversity is vital given the already underfunded nature of conservation (Maxwell et al., 2015). Carbon-based payments for ecosystem services could offer one option to fund both biodiversity protection and carbon sequestration, paying landowners and farmers for practices that protect the carbon stored in landscapes (Santilli et al., 2005). Abandonment of cattle pasture in the Colombian Andes can allow forest regeneration for around US$2 t^{-1} CO_2 (Gilroy *et al*., 2014), whilst sustainable intensification of charcoal production in Tanzania can prevent forest conversion for US$6.50 t^{-1} CO_2 (Fisher *et al*., 2011). These actions often focus on protecting extant natural habitats or returning farmland to forest, what is overlooked is whether carbon-based PES could effectively encourage farmers to protect biodiversity and carbon within farmland.

1.5 Thesis overview

Proper understanding of patterns of biodiversity and community composition is of great importance to effectively mitigate the biodiversity crisis and assess how tree communities will

respond to global change. Understanding of patterns and drivers of biodiversity and community composition in savannas is a particular key knowledge gap given the global importance of these ecosystems. Additionally, identifying effective conservation actions in these highly peopled landscapes that are beneficial for both people and biodiversity and allow porous and resilient landscapes is also key to halt species loss and maintain ecosystem functioning. The overall aim of this thesis was to further the understanding of patterns and drivers of tree community composition on savannas and to identify effective conservation action to protect extant wildlife-friendly features in these landscapes.

Chapter 1: Precipitation gradients drive high tree species turnover in the woodlands of eastern and southern Africa

Taxonomic diversity shows strong positive relationships with rainfall and temperature, globally and across taxa. Tree community composition in tropical moist forests varies with climate, but whether these same patterns of diversity are repeated in disturbance-driven savannas remains a key knowledge gap. Are typical climate-richness relationships interrupted in savannas that undergo long periods with zero rainfall, and experience regular fires and chronic herbivory? The objective of this study was to investigate how tree biodiversity is structured over large environmental and disturbance gradients across the savannas of eastern and southern Africa. Specifically, I investigated how three facets of biodiversity: (i) species richness, (ii) beta diversity, (ii) phylogenetic diversity, respond to environmental and disturbance gradients.

Chapter 2: Determinants of trait variation among African savanna trees

Functional traits determine species' ability to withstand environmental conditions and disturbance regimes and are therefore increasingly used to understand patterns of composition and processes of community assembly. Environmental constraints lead to trait trade-offs in

species as limited resources are assigned to one purpose or another, potentially leading to shared functional syndromes across species that have adapted to similar environmental conditions. We collated functional trait data for tree species from across the savannas of eastern and southern Africa to better understand how the functional composition of these tree communities changes over environmental and disturbance gradients. We asked three questions: (i) How do the traits of savanna tree species cluster and trade-off against one another? (ii) How does the relative basal area of functional clusters change over climate, soil, fire, and herbivory gradients? (iii) How does community-level functional trait composition vary over climate, soil, fire, and herbivory gradients?

Chapter 3: Protecting habitats in low-intensity tropical farmland using carbon-based payments for ecosystem services

Conservation efforts in the tropics and sub-tropics mostly seek to protect existing habitats or to return deforested farmland to forest. These approaches overlook the important role played by farmland habitats in low-intensity agriculture in storing carbon, providing habitats, and maintaining porous landscapes. Carbon-based payments for ecosystem services (PES) offer a potential funding mechanism to jointly limit carbon emissions and protect biodiversity. Combining farm-level economic and tree inventory data from across Ghana, we assess if carbon-based PES can protect farmland trees and fallowing in Ghana. We simulate the opportunity costs and carbon breakeven prices associated with (i) protecting existing trees in agricultural land and (ii) extending and reintroducing fallows to farmland, under several different management scenarios.

Chapter 2:

Precipitation gradients drive high tree species turnover in the woodlands of eastern and southern Africa

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2.1 Abstract

Savannas cover one-fifth of the Earth's surface, harbour substantial biodiversity, and provide a broad range of ecosystem services to hundreds of millions of people. The community composition of trees in tropical moist forests varies with climate, but whether the same processes structure communities in disturbance-driven savannas remains relatively unknown. We investigate how biodiversity is structured over large environmental and disturbance gradients in woodlands of eastern and southern Africa. We use tree inventory data from the Socio-Ecological Observatory for Studying African Woodlands (SEOSAW) network, covering 755 ha in a total of 6780 plots across nine countries of eastern and southern Africa, to investigate how alpha, beta, and phylogenetic diversity varies across environmental and disturbance gradients. We find strong climate-richness patterns, with precipitation playing a primary role in determining patterns of tree richness and high turnover across these savannas. Savannas with greater rainfall contain more tree species, suggesting that low water availability places distributional limits on species, creating the observed climate-richness patterns. Both fire and herbivory have minimal effects on tree diversity, despite their role in determining savanna distribution and structure. High turnover of tree species, genera, and families is similar to turnover in seasonally dry tropical forests of the Americas, suggesting this is a feature of semiarid tree floras. The greater richness and phylogenetic diversity of wetter plots shows that broad-scale ecological patterns apply to disturbance-driven savanna systems. High taxonomic turnover suggests that savannas from across the regional rainfall gradient should be protected if we are to maximise the conservation of unique tree communities.

2.2 Introduction

Savannas cover one-fifth of the Earth's surface and are responsible for up to 30% of terrestrial primary productivity (Scholes & Archer, 1997). The distribution of savannas is limited by fire and precipitation regimes globally (Lehmann et al., 2011), and more locally by soil properties and herbivory (Oliveras & Malhi, 2016). Savannas are characterised by the co-existence of trees and grasses that supports substantial biodiversity (Scholes & Archer, 1997), and the livelihoods of 150 million people alone in the savanna woodlands of eastern and southern Africa (Ryan et al., 2016). Despite harbouring high biodiversity (Byers, 2001) and being globally important carbon sinks (McNicol et al., 2018) – a function underpinned by their tree diversity (Godlee et al., 2021) - the processes that structure the biodiversity of savanna woodlands remain understudied. The bulk of research focusing on patterns of plant species composition in the tropics is based on tropical moist forests (Parr et al., 2014), but whether these same patterns are replicated in disturbance-driven savannas is unresolved.

Tropical tree community composition is strongly structured over environmental gradients, with the co-variation of climate and taxonomic diversity being one of the most widely observed, broad-scale patterns in ecology (Currie et al., 2004). Within the well-studied moist lowland tropical forests, species richness increases with precipitation at large scales (ter Steege et al., 2003). Rainfall seasonality and water deficit during the dry season are also important in determining community structure in moist forests (Engelbrecht et al., 2007) with tree species richness in western South America increasing with declining water deficit (Esquivel-Muelbert et al., 2017), and dry season length predicting Amazonian tree alpha diversity (ter Steege et al., 2003) and the beta diversity of trees in the Western Ghats (Davidar et al., 2007). Additionally, tolerance to freezing (Segovia et al., 2020) and gradients of soil nutrient availability (Aleman et al., 2020) are important determinants of diversity at both broad

and fine spatial scales. However, there are fundamental differences between the ecology of moist tropical forests and that of savannas (Frost, 1996), and there is a lack of regional- to continental-scale studies that use plot-level data to investigate these patterns in disturbance-driven savannas.

Precipitation and disturbance, such as fire and herbivory, are important determinants of the physiognomy and distribution of savannas (Sankaran et al., 2005; Lehmann et al., 2011). Rainfall determines tree cover globally, but at intermediate rainfall tree cover is bimodal with fire differentiating between forest and savanna (Staver et al., 2011). The species richness of southern African woody flora increases linearly with precipitation (O'Brien et al., 1998), whilst wet miombo woodland (> 1000 mm mean annual precipitation) contains greater floristic richness than dry miombo (< 1000 mm; Frost, 1996). In northern Australian savannas, woody plant species richness increases with increasing rainfall and decreasing soil clay content (Williams et al., 1996).

Fire regimes strongly influence woody vegetation structure (Smit et al., 2010), but in savanna fire experiments, show little effect on both tree richness (Makumbe et al., 2020) and grass composition (Andersen et al., 2005). Browsing herbivores change woody plant composition in Kruger national park, South Africa, by preferentially eating species with high leaf nitrogen, decreasing their abundance outside of exclosures (Wigley et al., 2014), whilst also promoting tree beta-diversity in East African savannas (Pringle et al., 2016). Additionally, the number of woody stems per ha – a possible indication of disturbance by fire and herbivory (Sankaran et al., 2008) - is positively correlated with tree species diversity in southern African woodlands (Godlee et al., 2021). However, the impacts of fire and herbivory on savanna woody plant composition are largely observed in experimental settings. Assessing how these factors influence diversity at broad scales is important for understanding biogeography and to inform effective conservation and restoration action (DRYFLOR, 2016).

It is expected that species resilient to climate extremes will be widely distributed, whilst those with narrow tolerances will have restricted distributions (Esquivel-Muelbert et al., 2017). This could produce two outcomes for the structure of β-diversity: communities in less-diverse areas are subsets of the species found in the most-diverse areas (nestedness), or species are replaced by better-adapted species as environmental conditions change (turnover; Socolar et al., 2016). Contrasting evidence for these two outcomes has been observed in tropical forests. Trees in Panama exhibit compositional and functional turnover across rainfall and phosphorous gradients (Umaña et al., 2021), whereas trees of western South America exhibit compositional nestedness over water availability gradients (Esquivel-Muelbert et al., 2017) albeit over a much greater geographical area and with very little coverage of dry tropical forests. Patterns of turnover could provide further evidence of discontinuous floristic boundaries previously identified across southern African woodlands (Fayolle et al., 2019).

The phylogenetic composition of communities is also structured over environmental gradients due to the different survival and life history trade-offs that have evolved in lineages in response to environmental filters (Neves et al., 2020). Phylogenetic diversity peaks at intermediate precipitation in lowland South American forests and savannas (Neves et al., 2020), with semideciduous forests containing specialised lineages from both extremes, whilst the phylogenetic beta-diversity of Colombian plant assemblages increases with temperature but remains unaffected by differences in precipitation (González-Caro et al., 2014). Climate is a strong predictor of both taxonomic and phylogenetic turnover of tree species in Amazonia, but overall phylogenetic turnover is low (Andino et al., 2021). Patterns of phylogenetic alpha- and beta-diversity over environmental gradients remain largely unstudied in savannas. Given the positive effects of maintaining phylogenetic diversity on ecosystem function and service provision (Cadotte, 2013), deciphering the effect of environmental gradients on evolutionary diversity is of great importance to conservation efforts and management.

Here, we assess how species richness and community composition of savanna trees are structured over environmental gradients. We do this by focussing on the world's largest savanna - the woodlands of eastern and southern Africa (White, 1983). We use an extensive network of 6780 plots (SEOSAW, 2021), covering a wide range of climatic conditions from across the region, to investigate whether patterns of savanna tree diversity follow those found in the moist tropics. We do this by asking three key questions:

1) What are the effects of environmental and disturbance gradients on tree species richness?

2) How is tree β-diversity structured across environmental and disturbance gradients, and in turn, is there a difference between the tree species composition of wet and dry miombo woodlands?

3) What are the effects of environmental and disturbance gradients on tree phylogenetic α- and β-diversity?

2.3 Methods

Study area

Our study covers several savanna types from across eastern and southern Africa - a conservation priority area that supports high levels of diversity and endemism (Byers, 2001). We focus on savannas with a substantial woody component, sampling from mopane woodlands, mixed woodlands, Acacia (sensu lato) savannas, and miombo woodlands (sensu White, 1983). The latter is the most extensive tropical woodland type of Africa - covering an area of 1.9 million km^2 (Ribeiro et al., 2020) which are dominated by trees from the genera Brachystegia, Julbernardia, and Isoberlina (Frost, 1996). We used tree inventory data from 6780 plots from the Socio-Ecological Observatory for Studying African Woodlands (SEOSAW) database (SEOSAW, 2021), spanning nine countries across eastern and southern Africa (See Figure S1 in Supporting Information). Plots were sampled between 2002 and 2019, with the vast majority of plots (97%; 6583/6780 plots) sampled from 2012. We sample over a mean annual precipitation (MAP) gradient of 367 mm to 1968 mm (Figure S2) and mean annual temperature (MAT) of 17.2°C to 26.3°C (Fick & Hijmans, 2017).

Data collection

We selected plots from the SEOSAW database that were designated as woodland under White's vegetation map of Africa (White, 1983). We used plots between 0.1 and 1 ha, representing a trade-off between coverage within our target region and sampling homogeneity. While larger plots are likely to have more species (as per the species-area relationship; Dengler, 2009), the inclusion of plots of differing size was appropriate because we: (1) included plot size as a model predictor, enabling us to analyse how species richness responds to other environmental and disturbance variables whilst controlling for plot area (conditional effect plots in Figure 2 show the effect of individual predictors on species richness whilst all other model variables, including

plot area, are held at their mean value); (2) checked for correlations between the predictor variables included in our models prior to modelling (see Table S1), this showed that plot area was not correlated with any of the other variables included in our model so it is unlikely to be masking or confounding the effects we see from the other model variables; and (3) ran individual univariate models for each predictor, and found similar effects to when all variables were tested in the same model (Figure S4).

We included only living stems >10 cm diameter at breast height (DBH, 1.3 m) in our counts of species richness. Where possible we used tree-level species richness as many trees were comprised of multiple stems at breast height. Trees were then identified to the species-level where possible (91% of trees were identified to species-level, 95% identified to genus), individuals not identified to the species-level were included in analyses as morpho species and counted as unique species.

We extracted climatic data from the WorldClim version 2.1 database (Fick & Hijmans, 2017). Mean annual precipitation (MAP; BIO12) and mean annual temperature (MAT; BIO1) were taken as the mean value between 1970 and 2000 at 30 arc seconds resolution, with precipitation seasonality (BIO15) calculated as the mean of the coefficient of variation of monthly mean precipitation. Soil nitrogen and phosphorous content (g kg-1), and soil sand proportion data were extracted from the ISRIC SoilGrids data product at 250 m resolution (Hengl et al., 2017). Fire count data was extracted from the MODIS burned area product (Giglio et al., 2015) and taken as the number of times a pixel was recorded as burned between 2001 – 2018 at a resolution of 1 km. Fire intensity data was extracted from the MODIS active fire product (MODIS Collection 6 NRT Hotspot / Active Fire Detections MCD14ML) measured as the mean fire intensity, again at a 1 km resolution. Present day herbivore biomass was taken from maps created by Hempson et al. (2017) at 0.5° resolution. The number of frost days was taken as the mean annual number of frost days from 1990-2019 at 0.5° resolution from the

Climate Research Unit gridded Time Series climate dataset (Harris et al., 2020). We assessed human pressure on our plots using maps of human footprint at a resolution of 1 km (Venter et al., 2018). We initially included more variables in our models but collinearity between variables prevented their inclusion (see table S1).

Phylogenetic tree and diversity

We used the 'V.PhyloMaker' package to create a phylogenetic tree for all of our species based off a backbone provided by Open Tree of Life (Jin & Qian, 2019), with names standardised according to The Plant List (2010). Species that were not present in the backbone, or that were not identified to the species level, were placed into the phylogeny at the lowest-level taxonomic clade possible using the default scenario 3 method (see Jin & Qian, 2019 for details). A very small number of species were not present in the phylogenetic tree (7/799 of species; 8,121/160,970 trees) and were dropped from this analysis. Using this phylogeny, we calculated phylogenetic diversity (PD; Faith, 1992) and the standardised effect size of phylogenetic diversity (sesPD), as phylogenetic diversity is positively correlated with species richness and we aimed to test for phylogenetic patterns independent of species richness (Swenson, 2014). Standardised effect sizes for each plot were calculated by comparing the observed phylogenetic indices of communities to those of 999 null communities using the "taxa.labels" algorithm. Positive values of sesPD indicate that a plot has higher PD than expected by chance, with negative values suggesting the opposite. These analyses were performed in the 'picante' R package (Kembel et al., 2010).

Statistical analysis

Species richness and phylogenetic diversity

To assess the effect of environmental gradients on species richness and phylogenetic diversity, we used Bayesian linear models fit using the 'brms' package (Bürkner 2017). We fit the

following models for species richness, PD, and sesPD to assess the effects of environmental gradients on biodiversity:

$$\text{Species richness} \sim \text{Negative binomial}(\alpha,\beta)$$

$$\text{PD} \sim \text{Gamma hurdle}(\alpha,\beta)$$

$$\text{sesPD} \sim \text{Gaussian}(\mu,\sigma)$$

For the species richness model, we applied a negative binomial likelihood with a log link as we used over-dispersed count data. The PD model was fit using a gamma-hurdle likelihood with an exponential link as this allowed us to first model the probability of a plot containing any PD (i.e., plots with >0 species) using a Bernoulli distribution before passing those results with a positive outcome to a truncated gamma distribution. sesPD was modelled using a gaussian likelihood as the model residuals followed a normal distribution. For each of the three models we included the following predictors:

$$= \alpha + \text{plot area} + \text{MAP} + \text{MAT} + \text{precipitation seasonality} + \text{frost days} + \text{soil nitrogen} + \text{soil phosphorous} + \text{soil sand proportion} + \text{fire count} + \text{fire intensity} + \text{herbivore biomass} + \text{MAP*precipitation seasonality} + \text{human footprint index}$$

We included plot area as a predictor to account for sampling effort differences between different sized plots as larger plots often contain more species (Dengler, 2009). We included the interaction term to assess whether seasonality had a differential effect on woodland diversity along the precipitation gradient. Herbivore biomass included both browsers and grazers as both are likely to influence tree composition - browsers through direct herbivory on trees and grazers through grazer-grass-fire interactions which may reduce fire intensity and grass competition with trees (Staver & Bond, 2014). All predictors were standardized to zero mean and one standard deviation, prior to model fitting. We were unable to compute sesPD values for plots with one species as it is not possible to create null communities with only one

species in the pool, therefore these plots were dropped from the sesPD analysis (598/6780; 8.8%). We repeated these analyses at the genus-level because if the results between species and genus richness differed this could provide evidence for effects of recent diversification.

Models were fit using weakly informative, non-flat priors (see supplementary methods), with four chains run for 1000 warmup and 3000 post-warmup samples. Checks of chain convergence and posterior predictive ability were performed on all models. Spatial autocorrelation between plot residuals was tested using Moran's I through the 'spdep' package (Bivand et al., 2013). All statistical analyses were carried out in R (R Core Team 2017).

β-diversity and phylogenetic β-diversity analysis

We assessed whether compositional changes between plots were a result of patterns of turnover or nestedness using multi-site Sørensen dissimilarity at the species, genus, and family level. Sørensen dissimilarity (βsor) gives total β-diversity and is comprised of two components: species turnover (βsim) and nestedness (βnes) (Baselga et al., 2010). Beta-diversity metrics were calculated using the 'betapart' R package (Baselga & Orme, 2012). This process was also performed for phylogenetic β-diversity.

We used Generalized Dissimilarity Modelling (GDM; Ferrier et al., 2007) to identify which environmental predictors best explain observed β-diversity and phylogenetic β-diversity patterns. GDM is an extension of matrix regression, allowing non-linear relationships between compositional turnover and environmental gradients, whilst also depicting the rate of turnover at different points along an environmental gradient. This is achieved through I-spline functions that are fit for each predictor, with the maximum height of an individual I-spline representing the size of a predictor's effect on β-diversity (Ferrier et al., 2007).

Using the 'gdm' R package (Fitzpatrick et al., 2020), we first fitted full GDMs that contained all the predictors from our species richness and PD models, excluding plot area, in

addition to the pairwise geographical distance between plots. We did this for both taxonomic (Sørensen dissimilarity) and phylogenetic β-diversity. After fitting full models, we removed predictors that had no effect on dissimilarity to maximise explained variance and minimise the number of predictors included in the model (Ferrier et al., 2007). Maps of predicted taxonomic turnover were created by projecting our final GDMs back onto rasters of the most influential predictor variables (Ferrier et al., 2007).

Comparing community composition of wet and dry miombo

To test previous assertions that wet and dry miombo are floristically different (Frost, 1996), we compared species composition between wet (>1000 mm MAP; White, 1983) and dry (<1000 mm MAP) miombo plots using Permutational Multivariate Analysis of Variance (PERMANOVA). We first filtered plots to only include those from the miombo (White, 1983), giving 1663 plots in dry miombo and 3049 plots in wet miombo. We then computed the community composition distances between all pairs of communities using Sørensen dissimilarity, before testing for differences in composition between plots designated as wet or dry miombo using the adonis2 function from the 'vegan' package (Oksanen et al., 2011).

2.4 Results

The effect of environmental gradients on savanna woodland tree species richness

Mean annual precipitation (MAP) had by far the greatest effect on species richness, with richness increasing with rainfall (β_{MAP} = 0.24; 95% Credible Interval (CI) = 0.20-0.27; model R^2 = 0.12 ± 0.01; Figure 1 & 2a). Species richness also increased with plot area, mean annual temperature, the number of frost days, herbivore biomass, precipitation seasonality, and soil nitrogen content (Figure 1, 2b & c), although the size of these effects were much smaller than for MAP. Conversely, species richness decreased slightly with increasing human footprint index, soil phosphorous content, and fire intensity (Figure 1 & 2d). The model was highly confident of the direction of these effects, with 0 lying outside of the 95% CI of the posterior for all predictors (Figure 1). There was no effect of the remaining variables on species richness (Figure 1), with the 95% credible interval of the posterior overlapping 0 in each case. Our results were similar when we analysed at genus level (Figure S3) and the model residuals showed no evidence of spatial autocorrelation (Moran's I = 0.006; $p < 0.001$).

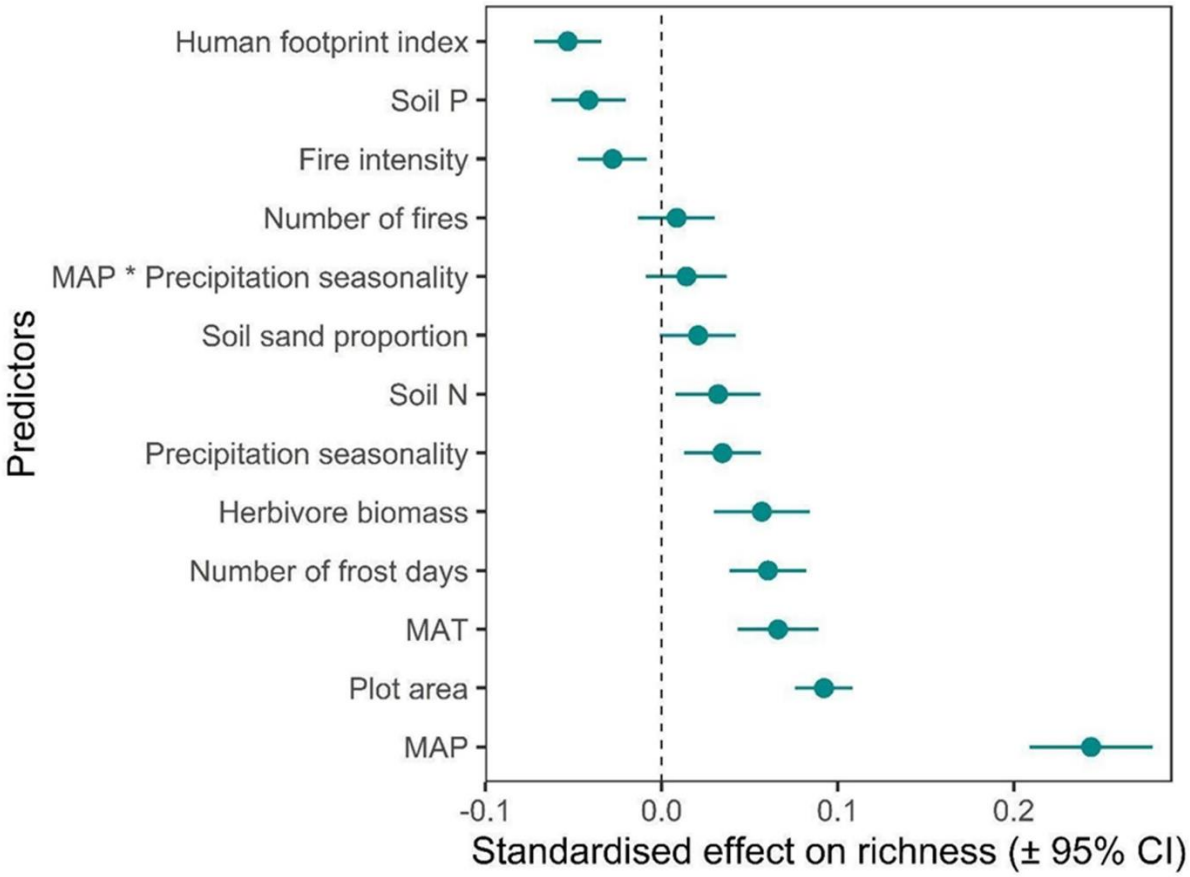

Figure 1. Determinants of tree species richness in the woodlands of eastern and southern Africa. Standardised effect sizes are shown for each variable included in the negative binomial regression model. Points and lines show the mean and 95% credible intervals (CI) respectively. Points to the left of the dashed line had a negative effect on species richness, whilst those to the right had a positive effect.

β-diversity of savanna woodland tree communities over environmental gradients

Changes in community composition across our sampled plots overwhelmingly showed patterns of turnover ($\beta_{SIM} \sim 1$) as opposed to nestedness ($\beta_{NEST} < 0.01$) at the species, genus, and family levels. Turnover between communities increased as the difference in the environmental conditions between communities increased (Figure 3a). The GDM predicted a clear turnover in species composition over rainfall gradients (Figure 3a).

Precipitation seasonality (Figure 3b) and MAP (Figure 3c) are the most important predictors of community dissimilarity, as judged by the I-spline heights. Their influence was

most evident in communities with low seasonality of precipitation and in communities with up to ~ 800 mm MAP (Figure 3b & c). Geographic distance has the third highest I-spline, with its influence increasing with pairwise distance (Figure 3d). MAT (Figure 3e) and herbivore biomass had a greater influence on predicting community dissimilarity as temperatures and herbivore biomass increased, although the overall amplitude of their effects was smaller than that of precipitation seasonality, MAP, and geographic distance. Human footprint index, and fire count and intensity had a small but consistent effect on dissimilarity. Soil P and soil sand proportion had a small effect on dissimilarity at the extreme of their ranges. Soil nitrogen content and number of frost days were not included in the final GDM as they had no influence on community dissimilarity.

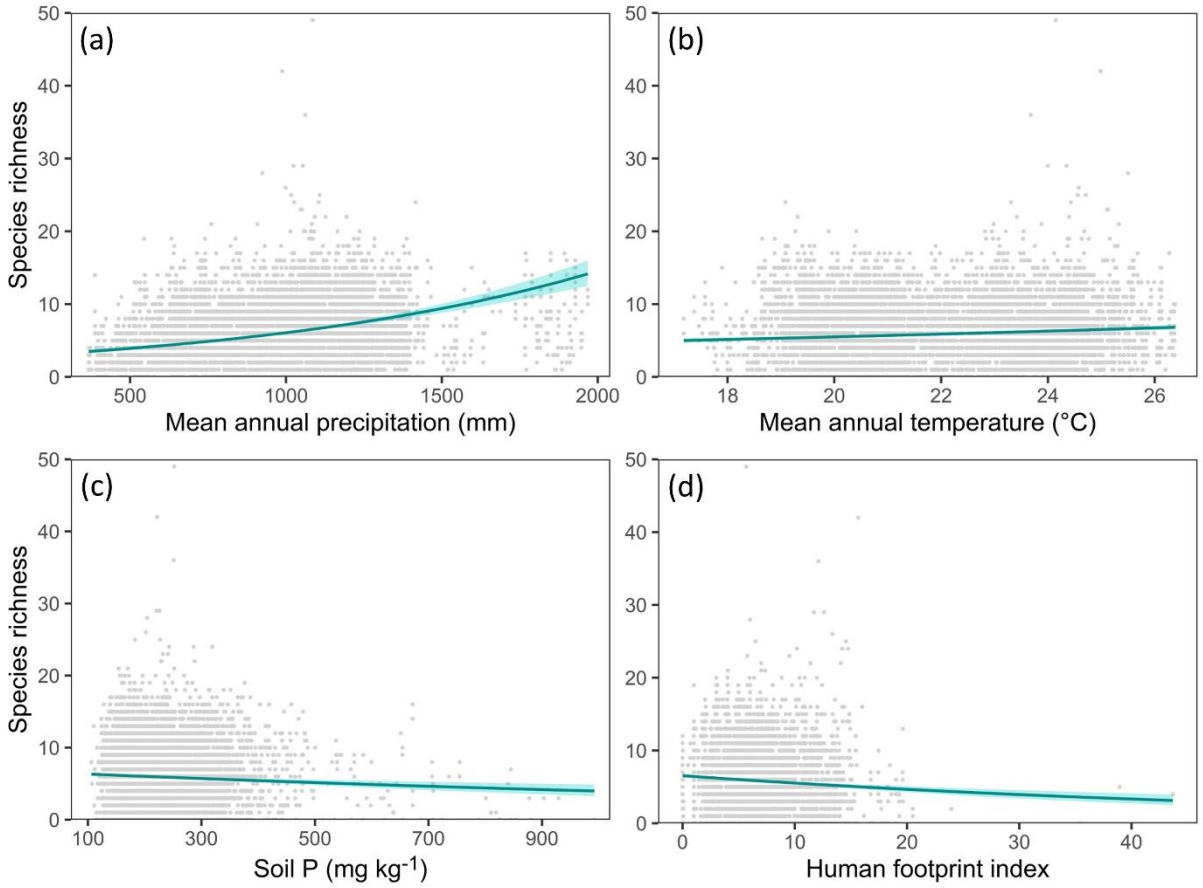

Figure 2. Conditional effect plots of tree species richness as a function of (a) mean annual precipitation, (b) mean annual temperature, (c) soil phosphorous content and (d) human footprint index.

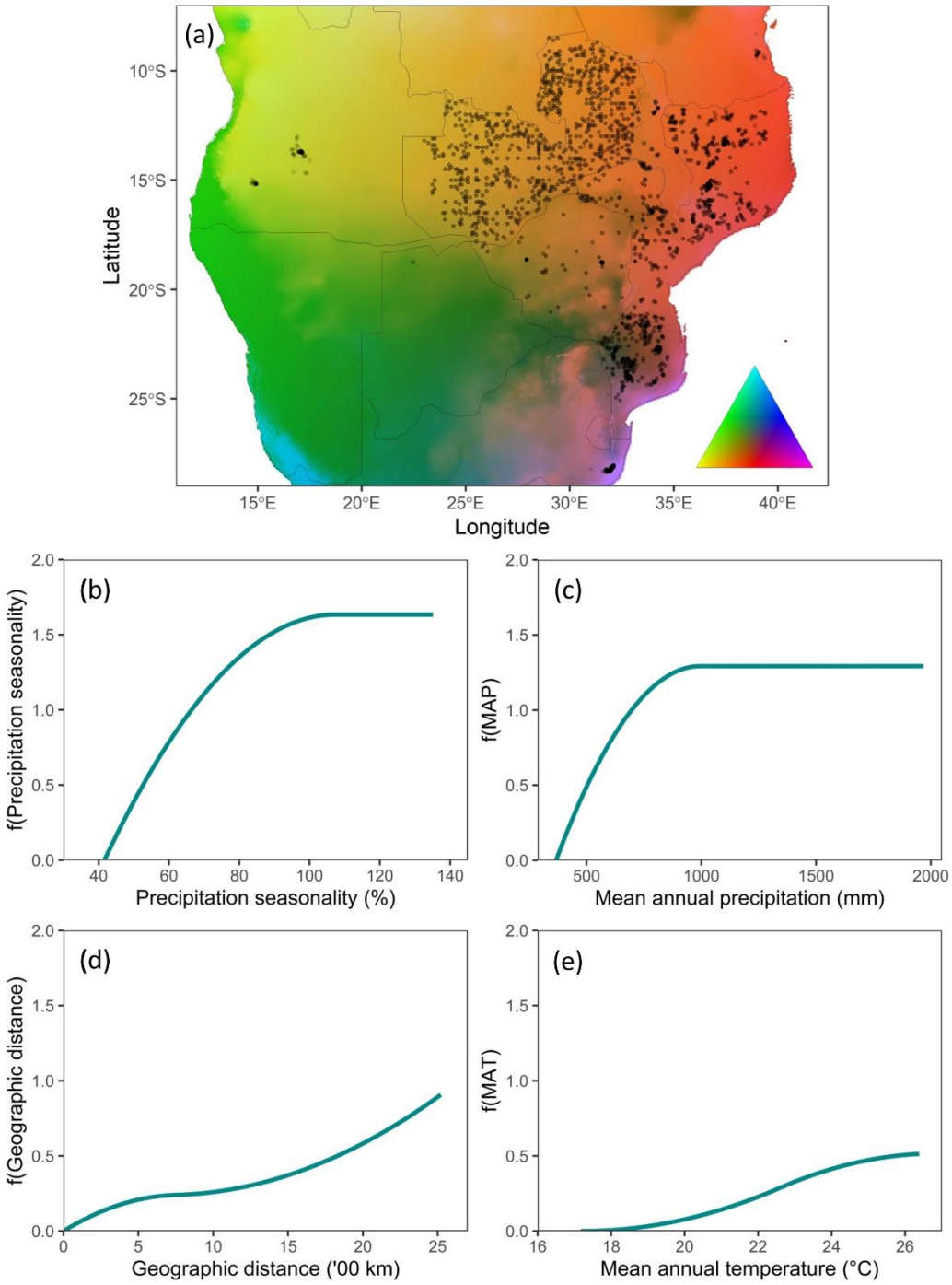

Figure 3. (a) Differences in predicted community composition based on principal component analysis (PCA) of the most important generalized dissimilarity modelling (GDM)-transformed environmental predictors, where more similar colours indicate more similar expected composition (Mokany et al. 2022), black dots indicate plot locations, and inlaid is a triangular colour key showing the range of possible colours. Individual I-splines from final GDM showing the influence of (b) precipitation seasonality, (c) mean annual precipitation, (d) geographic distance and (e) mean annual temperature in predicting community dissimilarity. The maximum height of an I-spline shows the size of a predictor's effect on driving β-diversity patterns whilst the slope of the I-spline shows the rate of change at that point along the predictor's gradient. Higher and steeper I-splines show a greater and more rapid effect on β-diversity, respectively.

Comparing community composition of wet and dry miombo

Species composition differed significantly between wet and dry miombo plots (MANOVA: r^2 = 0.006, d.f. = 1, p = 0.001). However, the model had a very low R^2, suggesting that splitting the plots by wet (> 1000 mm MAP) and dry (< 1000 mm) miombo explained very little compositional variation. There was considerable overlap in composition between wet and dry plots (Figure S6). Both MAT (r^2 = 0.02, d.f. = 1, p = 0.001) and the number of frost days (r^2 = 0.01, d.f. = 1, p = 0.001) explained more of the variation in plot composition than did the split between wet and dry miombo.

Savanna woodland tree phylogenetic α- and β-diversity over environmental gradients

Patterns of phylogenetic diversity (PD) closely mirrored those of species richness. PD increased with MAP (β_{MAP} = 0.13; CI = 0.11-0.15; model R^2 = 0.09 ± 0.007; Figure 4) and plot area ($\beta_{PLOT\ AREA}$ = 0.05; CI = 0.04-0.06). PD also increased with the number of frost days, MAT, herbivore biomass, and precipitation seasonality but the size of these effects was much less than that of MAP (Figure 4). Greater fire intensity was associated with a decrease in phylogenetic diversity ($\beta_{FIRE\ INTENSITY}$ = -0.02; CI = -0.03--0.01). For the remaining variables the posterior distribution of the parameter estimates overlapped zero, meaning the model was not confident of a directional effect of these (Figure 4).

In contrast to PD, the standard effect size of PD decreased with MAP (β_{MAP} = -0.2; CI = -0.26--0.14; Figure 4) and plot area ($\beta_{PLOT\ AREA}$ = -0.12; CI = -0.15--0.09), and also decreased with greater precipitation seasonality (β_{PRECIP} = -0.12; CI = -0.16--0.09). Similarly to PD, sesPD increased with MAT, but also increased with soil P content and human footprint index (Figure 4). The model was highly confident of the direction of these effects, with 0 lying outside of the 95% CI of the posterior for each of these variables (Figure 4). All other variables had no

directional effect on sesPD, with the 95% CI of the posterior of its coefficient overlapping 0 (Figure 4).

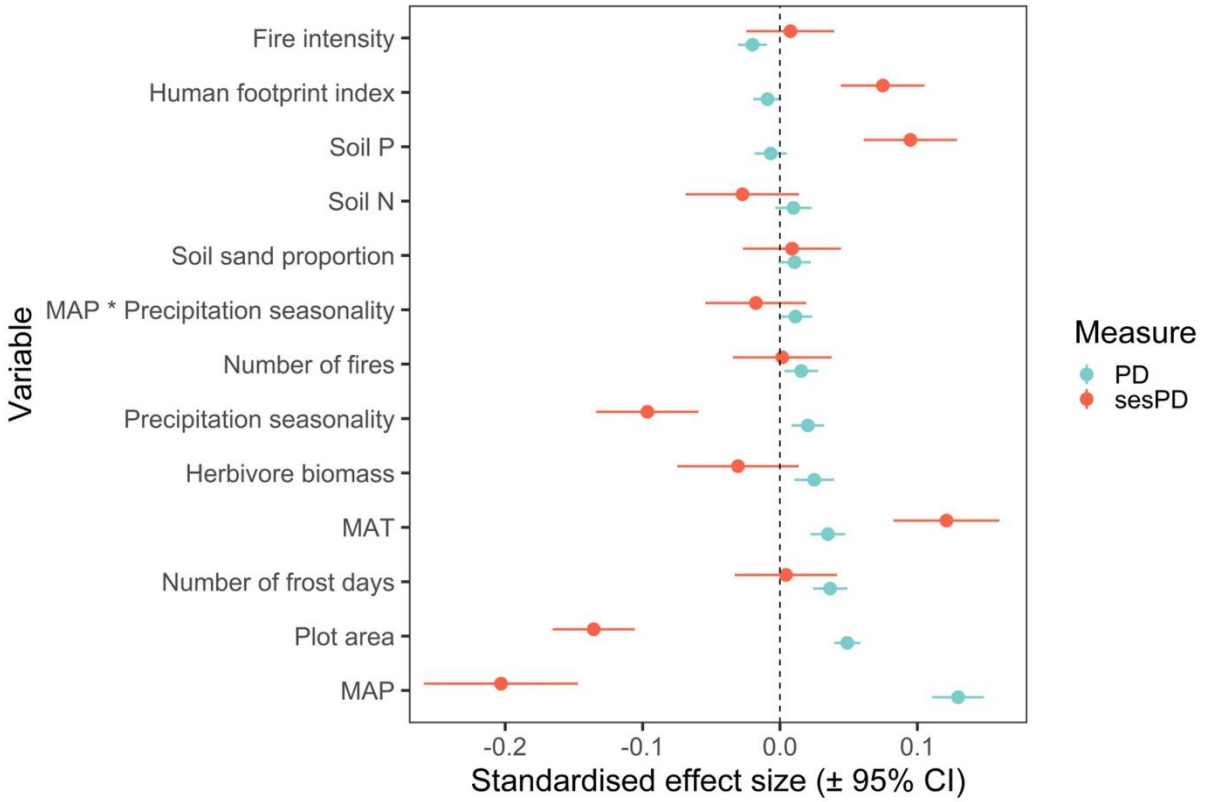

Figure 4. Determinants of tree phylogenetic diversity. Standardised effect sizes are shown for each variable in the regression models. Points and lines show the mean and 95% credible intervals respectively. Points to the left of the dashed line had a negative effect on species richness, whilst those to the right had a positive effect.

Phylogenetic β-diversity was mostly characterised by patterns of turnover ($\beta_{PHYLO\ SIM}$ = 0.35) but, in contrast to species richness, also showed signs of nestedness ($\beta_{PHYLO\ NEST}$ = 0.15). Again, precipitation seasonality was the most important predictor of phylogenetic community dissimilarity as judged by its I-spline height (Figure 5a). Fire count and MAT were then the most important predictors of phylogenetic dissimilarity (Figure 5b & c), with the effect of both becoming greater towards their upper limits. MAP, soil sand proportion, geographic distance, herbivory, soil phosphorous content, and human footprint index all had a minor influence on phylogenetic dissimilarity (Figure 5d – f). Soil nitrogen content, number of frost

days, and fire intensity had no effect on phylogenetic dissimilarity and so were not included in the final GDM.

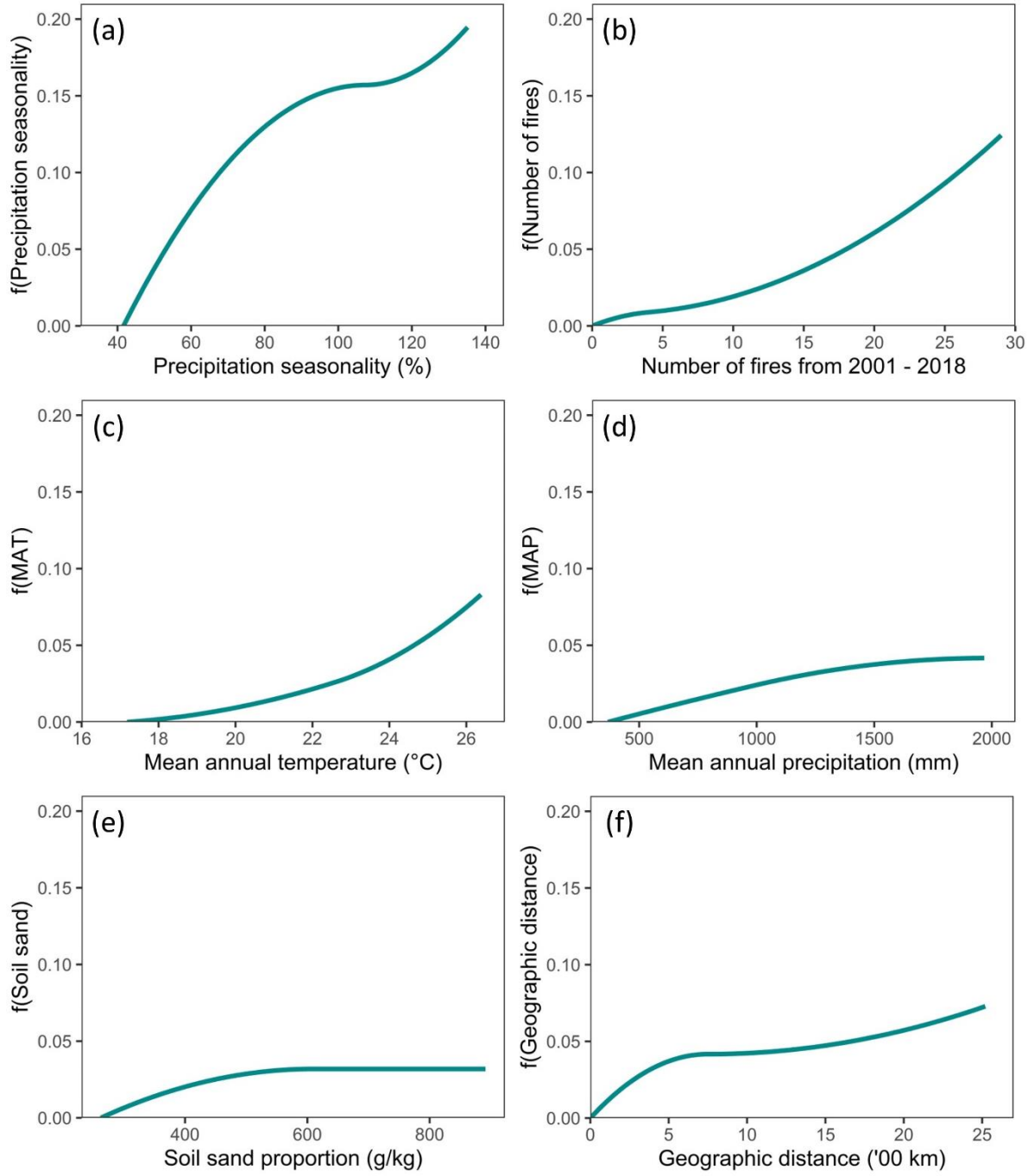

Figure 5. Individual I-splines from phylogenetic GDM showing the influence of (a) precipitation seasonality, (b) fire count, (c) MAT, (d) MAP, (e) soil sand proportion and (f) geographic distance in predicting phylogenetic community dissimilarity of trees across the woodlands of eastern and southern Africa.

2.5 Discussion

Using plot-level data, we tackled the key knowledge gap of how environmental gradients structure tree biodiversity within disturbance-driven savannas. Focusing on the eastern and southern African woodlands — the world's largest savanna — we find clear climate effects on all aspects of tree diversity with second order effects of soil, human use, and other disturbance agents. Precipitation gradients are particularly strong drivers of tree richness and community assembly in savanna woodlands, with wetter savannas containing more tree species than drier savannas, and high community turnover across the region largely driven by precipitation regimes. Patterns of phylogenetic diversity closely follow those of species richness. Phylogenetic turnover was lower than taxonomic turnover but more pronounced than phylogenetic nestedness, with these patterns again largely driven by precipitation regimes.

Climate-richness relationships in savanna

Species richness was positively related to precipitation volume, similar to observations from moist tropical forests (ter Steege et al., 2003) and previous studies of southern African woodlands (O'Brien et al., 1998; Godlee et al., 2021). Several hypotheses have been proposed to explain the mechanisms that drive this relationship, which is widely observed across taxa and biomes (Gaston, 2000; Currie et al., 2004). Previously, positive relationships between rainfall and species richness in southern Africa have been used as evidence in support of the energy-richness hypothesis (O'Brien et al., 1998). The energy-richness hypothesis suggests that greater energy availability leads to more individuals and consequently more species, but evidence for this is conflicting (Keil & Chase, 2019). Our finding that species richness increases with both MAP and MAT, proxies for energy, could support the energy-richness hypothesis in savannas. Alternatively, high turnover across the region and the greater PD of wetter plots could provide evidence in support for the physiological tolerance hypothesis

determining climate-richness patterns in savanna. Functional trade-offs to survive extremes may inhibit the ability of species found in the wettest plots of our study region from occurring in the driest plots (Vinya et al., 2013). A trait-based study could more explicitly test this, assessing whether wetter environments allow a greater range of functional strategies and therefore drive our observed climate-richness relationship (see Spasojevic et al., 2014).

Tree species richness was also weakly positively related to soil nitrogen content, MAT, herbivore biomass, and the number of frost days, and weakly negatively related to soil phosphorous content. The positive effect of soil nitrogen content is unsurprising given its role in determining miombo canopy structure (Shirima et al., 2015), whilst the negative effect of soil P on richness may be the result of a greater number of ectomycorrhizal species in nutrient-limited soils (Frost, 1996). Temperature and the lack of frost is a strong determinant of savanna phenology and productivity (Frost, 1996; Chidumayo, 2001), potentially explaining its positive relationship with species richness (Godlee et al., 2021).

Increasing species richness with herbivore biomass may result from suppression of dominant competitive plants through grazing and browsing (Pringle et al., 2016) or reduction of fire fuel resulting in less death by fire – potentially evidenced by our result of increasing fire intensity having a negative effect on species richness. Despite its importance in determining the distribution of savannas (Lehmann et al., 2011), fire frequency had no effect on the tree species richness of woodlands, repeating patterns observed after prescribed fires in the dry miombo (Furley et al., 2008). However, this could result from the coarse nature of available fire and herbivory data, which may not accurately capture the disturbance experienced by these systems as these drivers may operate on smaller spatial scales. Species richness declined with increasing human footprint index, potentially due to widespread utilisation of savannas by local people (Ryan et al., 2016) which can reduce tree diversity (Tripathi et al., 2019; 2021).

Savanna tree β- and phylogenetic-diversity responses to environmental gradients

Our results show widespread turnover in tree community composition across savanna woodlands of eastern and southern African, driven largely by precipitation patterns. High turnover is surprising given the dominance of miombo woodlands by the same genera across their range (Frost, 1996). Turnover suggests that interspecific responses to environmental filters are important in structuring communities, which is consistent with previous work highlighting strong associations between species and precipitation regimes (Engelbrecht et al., 2007). Our results mirror high taxonomic turnover observed in Panama (Umaña et al., 2021), but contradict patterns of nestedness from the Western Amazon (Esquivel-Muelbert et al., 2017). Turnover might be a characteristic of semiarid tree floras, as similar results have been found in dry forests of the Americas (DRYFLOR, 2016), and a result of our study investigating community structure over lower precipitation gradients (< 2000 mm compared to up to 3500 mm in Esquivel-Muelbert et al., 2017).

Precipitation seasonality was the primary driver of compositional turnover, showing a similar pattern to tropical forests in the Western Ghats, India (Davidar et al., 2007). The strong influence of precipitation seasonality is consistent with the role of seasonal water availability in determining miombo species' distributions (Vinya et al., 2013). MAP plays an important role in structuring community dissimilarity between 360 mm and ~800 mm of rainfall, suggesting that at large scales, composition of drier savanna woodland is structured by climate as opposed to disturbance regimes, in a similar way to woody cover (Sankaran et al., 2005). Fire, MAT, and soil nitrogen content played a limited role in determining β-diversity patterns. Fire determines savanna distributions (Lehmann et al., 2011) whilst temperature range is an important determinant of productivity in the miombo (Chidumayo, 2001), so their limited effects on community structure are surprising.

Our study provides further evidence of high, almost complete, turnover in the bistable region (700 – 1900 mm MAP) – the climatic area in which both savannas and forests are widespread - previously identified by Aleman et al. (2020). High turnover reflects the greater floristic heterogeneity of eastern and southern African savannas compared to those in the north and west (Fayolle et al., 2019). Initial classification of miombo drew a clear distinction between wet (> 1000 mm MAP) and dry (< 1000 mm) woodland (White, 1983), and whilst we did find a difference in the species composition of wet and dry miombo, there was considerable overlap in communities. However, this may result from our focus on trees, which give rise to different biogeographic divisions than analysis including herbs and shrubs (Droissart et al., 2018).

Evolutionary diversity peaks at around 1500 mm of MAP in South America (Neves et al., 2020), but we did not find such a peak. PD increased with MAP, but this pattern was reversed when accounting for species richness. This suggests that there is both an increase in species richness but also replacement of dry-adapted species with phylogenetically clustered species adapted to wetter conditions. The sesPD of wetter plots was more negative than drier plots, suggesting greater levels of phylogenetic redundancy. This redundancy could protect the long-term functioning of these plots as losses of species are less likely to lead to losses of unique evolutionary diversity (Yachi & Loreau, 1999). However, these patterns could also be explained by the negative correlation of sesPD and species richness (Sandel, 2018). As the regional species pool increases in size, absolute index values of communities increase making it difficult to compare the magnitude of environmental-biotic filtering between communities with different numbers of species (Sandel, 2018). We found very little effect of humans on PD, in contrast to patterns observed in central African rainforests where undisturbed, semi-deciduous and transition forests have greater evolutionary diversity than evergreen forests (Réjou-Méchain et al., 2021).

Caveats

One caveat to our study is that the processes that shape species' evolution and diversification in these woodlands are likely to have acted on a timescale outside of the period which our predictors cover. However, contemporary patterns of biodiversity are a result of both evolutionary processes acting on geological timescales (Mittelbach et al., 2007) and more recent climatic conditions (Currie et al., 2004). Whilst the long abiotic and evolutionary history of these woodlands is likely to have shaped their current diversity and composition, more recent climatic conditions are also strong determinants of community assembly (Field et al., 2009) and reflect measurable processes given the lack of very long-term geological and climatic data. Following this, an additional caveat is that our study only uses climatic data from 1970-2000 as this is the data freely available from WorldClim (Fick & Hijmans, 2017). Furthermore, this is the time period during which many of these trees (> 10 cm DBH) established. However, given that precipitation is a key driver of tree community composition in these woodlands, understanding how communities are responding to current, and will respond to future rainfall, offers an interesting avenue for future research.

Conclusions

We use plot-level data to show strong climate-richness relationships in savannas. Precipitation patterns play a primary role in determining savanna woodland community composition, similar to patterns observed across the moist tropics. Tree species richness and evolutionary diversity increase with rainfall, while precipitation seasonality and amount are important drivers of β-diversity patterns. Disturbance from herbivory and fire plays an important role in determining savanna physiognomy and distribution globally, but disturbance appears to play a minor role in influencing community composition and diversity in eastern and southern African woodlands. High turnover across eastern and southern African woodlands at multiple

taxonomic levels suggest that protecting woodlands across environmental gradients is necessary to maximise conservation outcomes.

2.6 Supplementary material

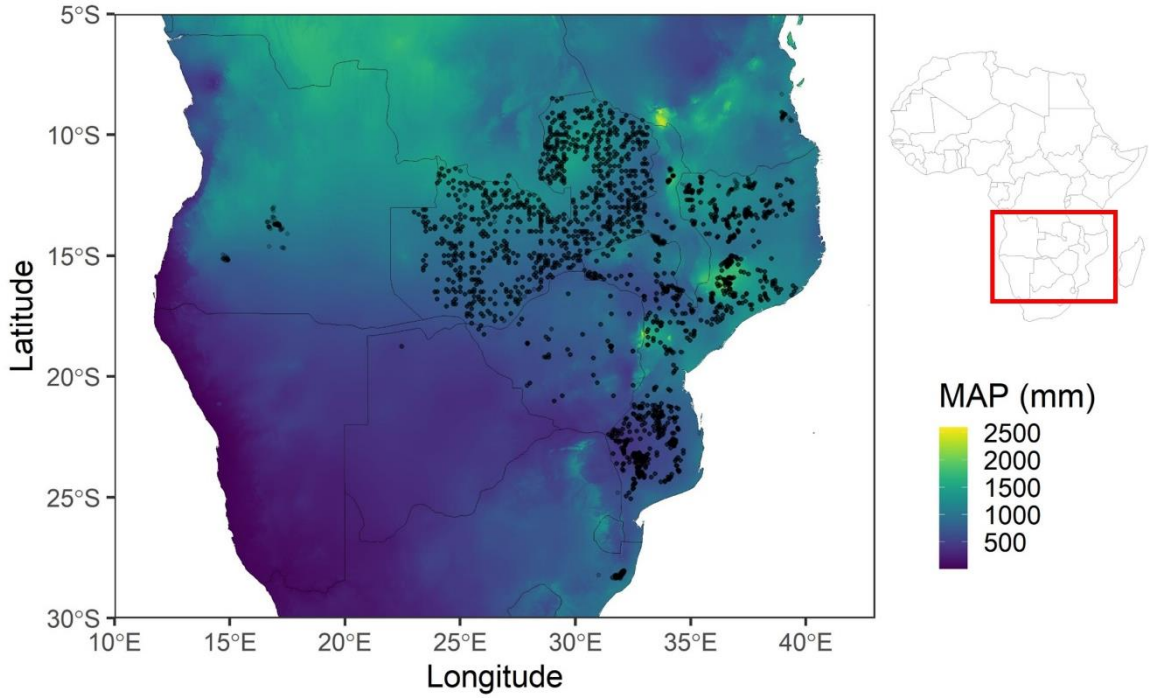

Figure S1. Map of plots from across our study region with gradient of mean annual precipitation (MAP; mm)

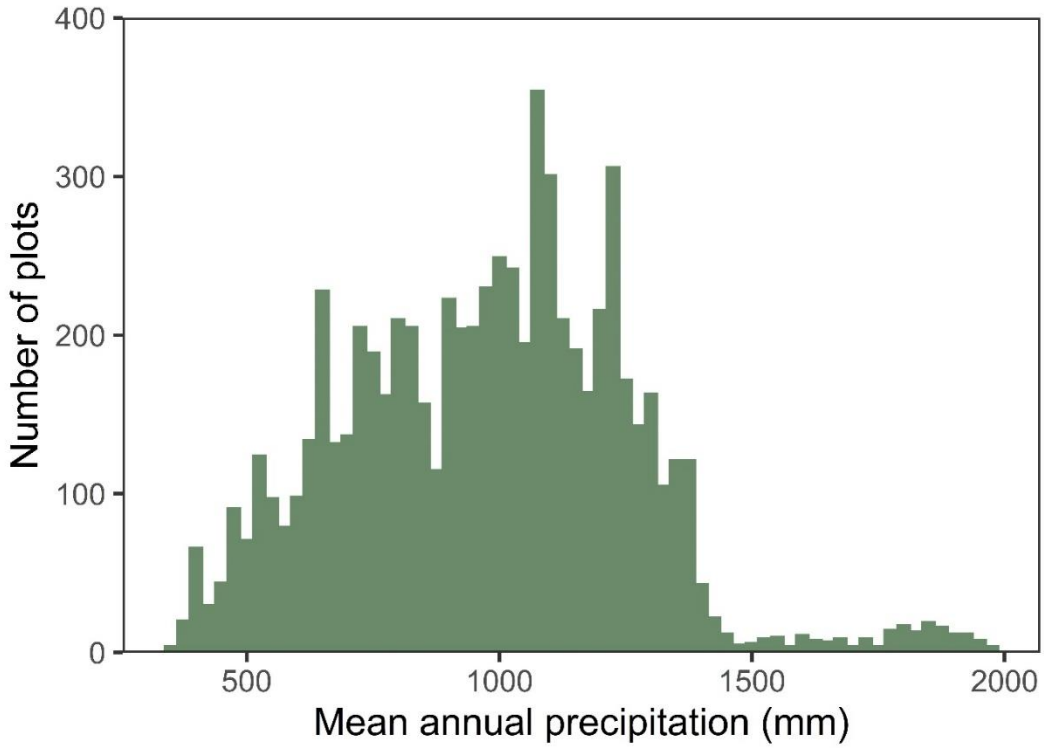

Figure S2. Histogram of spread of MAP across all our sampled plots. Minimum MAP = 367 mm, maximum MAP = 1968 mm.

Supplementary methods

Bayesian models comparing species richness and phylogenetic diversity over environmental gradients were run using the following weakly informative, non-flat priors:

$$Species\ richness \sim Negative\ binomial(\alpha, \beta)$$

α ~ Normal (2, 1)

β ~ Normal (0, 1)

ϕ ~ Gamma (0.1, 0.1)

$$PD \sim Gamma\ hurdle(\alpha, \beta)$$

α ~ Normal (6, 2)

β ~ Normal (0, 1)

ϕ ~ Gamma (0.1, 0.1)

$$sesPD \sim Gaussian(\mu, \sigma)$$

μ ~ Normal (0, 1)

β ~ Normal (0, 1)

σ ~ Normal (0, 0.1)

Table S1 – Correlation coefficient estimates between all variables included in the final models comparing species richness, PD, and sesPD over environmental gradients. Variables with correlation coefficients > 0.7 were dropped from the model following Dormann *et al*. (2013).

	MAP	MAT	Precipitation seasonality	Number frost days	Fire count	Fire intensity	Soil N	Soil sand	Plot area	Herbivore biomass	Soil P	Human footprint
MAP	1	-0.3	0.03	0.05	0.45	0.31	0.42	-0.2	0.01	-0.7	0.28	0.1
MAT	-0.3	1	-0.24	-0.52	-0.3	-0.14	0.07	0.25	0.05	0.25	0.02	-0.04
Precipitation seasonality	0.03	-0.24	1	0.13	0.22	0.07	-0.39	0.19	-0.18	-0.26	-0.18	-0.04
Number frost days	0.05	-0.52	0.13	1	0.22	0.03	-0.15	-0.27	-0.05	-0.13	0.04	-0.03
Fire count	0.45	-0.3	0.22	0.22	1	0.31	-0.02	-0.15	-0.04	-0.37	0.05	0.06
Fire intensity	0.31	-0.14	0.07	0.03	0.31	1	0.03	0.02	0.07	-0.22	0.07	0.06
Soil N	0.42	0.07	-0.39	-0.15	-0.02	0.03	1	-0.34	0.07	-0.2	0.38	-0.03
Soil sand	-0.2	0.25	0.19	-0.27	-0.15	0.02	-0.34	1	-0.01	0.04	-0.25	0.04
Plot area	0.01	0.05	-0.18	-0.05	-0.04	0.07	0.07	-0.01	1	0.07	0.03	0.09
Herbivore biomass	-0.7	0.25	-0.26	-0.13	-0.37	-0.22	-0.2	0.04	0.07	1	-0.1	-0.02
Soil P	0.28	0.02	-0.18	0.04	0.05	0.07	0.38	-0.25	0.03	-0.1	1	0.01
Human footprint	0.1	-0.04	-0.04	-0.03	0.06	0.06	-0.03	0.04	0.09	-0.02	0.01	1

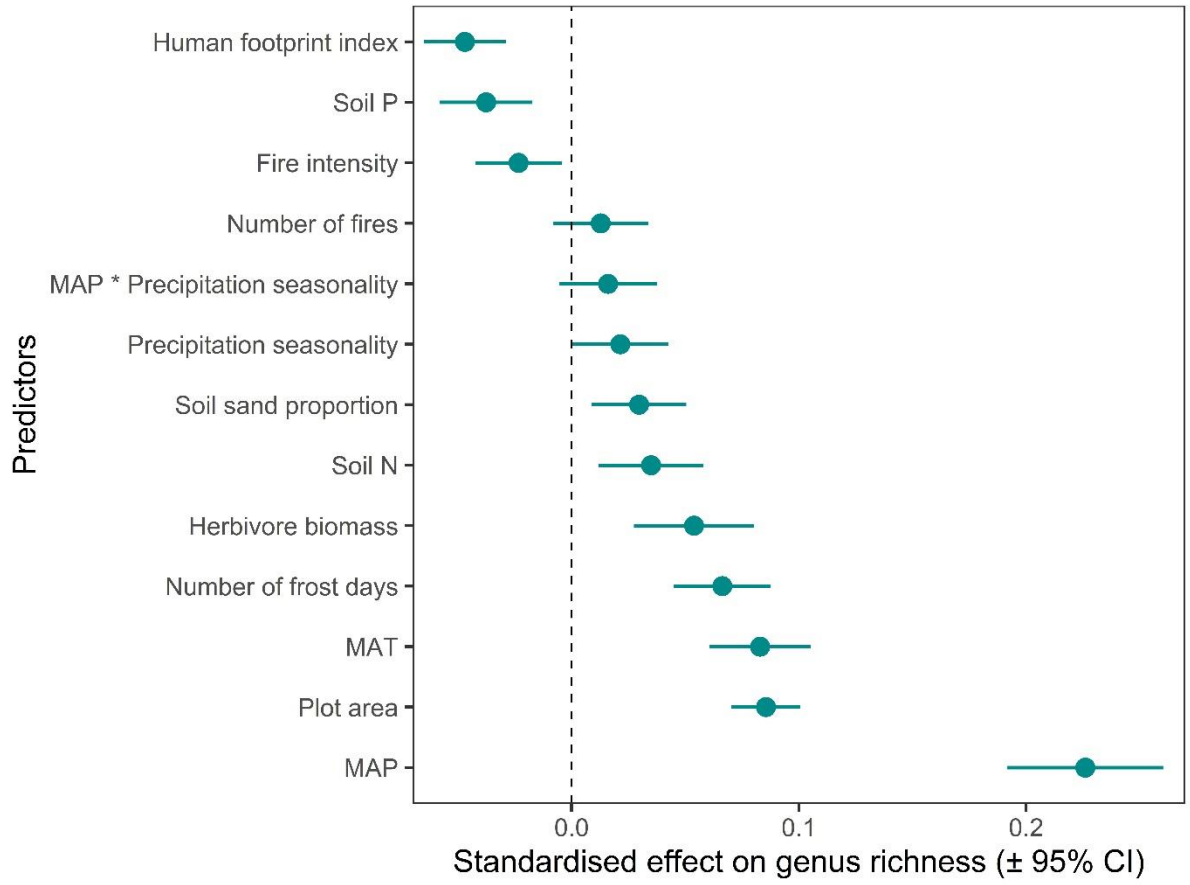

Figure S3. Determinants of tree genus richness in the woodlands of eastern and southern Africa. Standardised effect sizes are shown for each variable included in the model. Points and lines show the mean and 95% credible intervals (CI) respectively. Points to the left of the dashed line had a negative effect on genus richness, whilst those to the right had a positive effect.

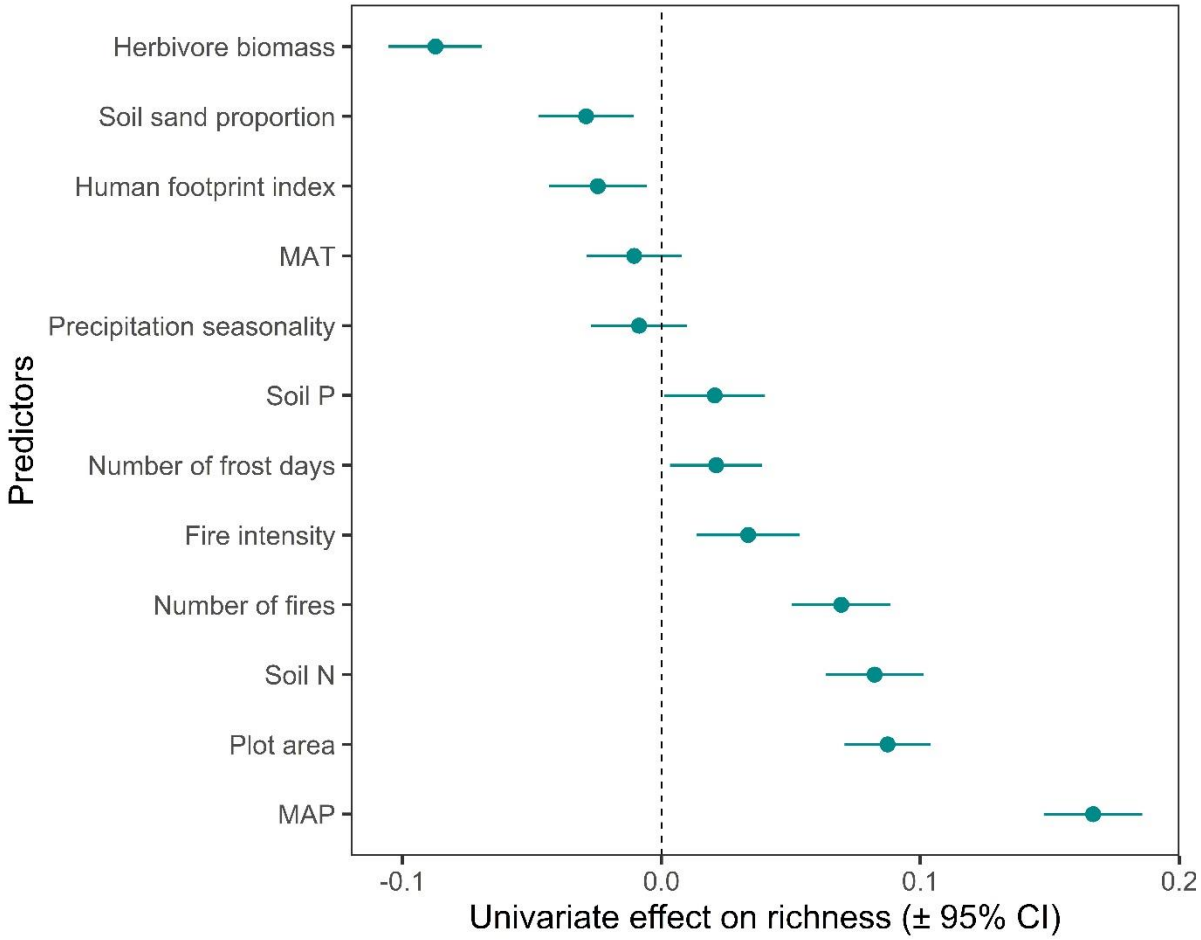

Figure S4. Coefficient estimates for each variable when each variable is included in a univariate model assessing change in species richness. Points and lines show the mean and 95% credible intervals respectively.

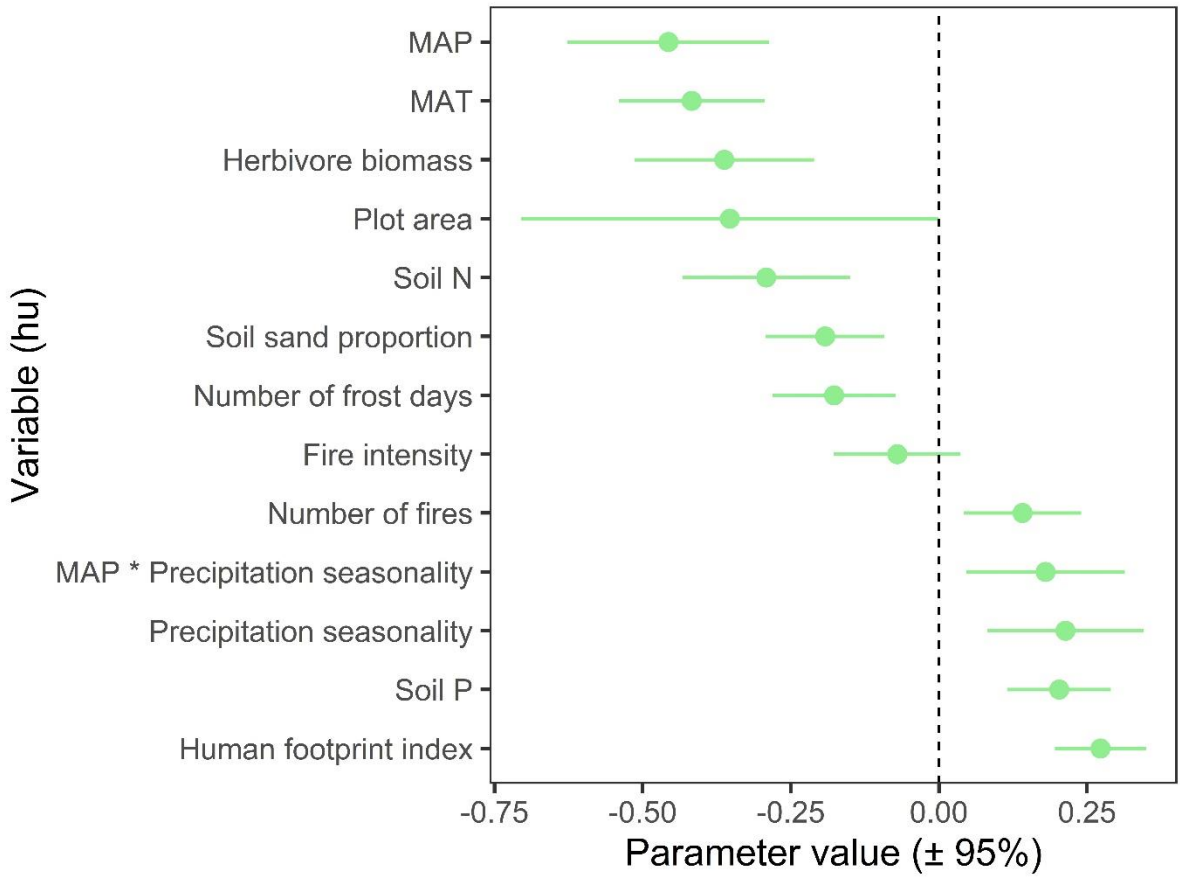

Figure S5. Coefficient estimates for each of the hu variables from the Bernoulli part of the Gamma hurdle model for PD. Points and lines show the mean and 95% credible intervals respectively.

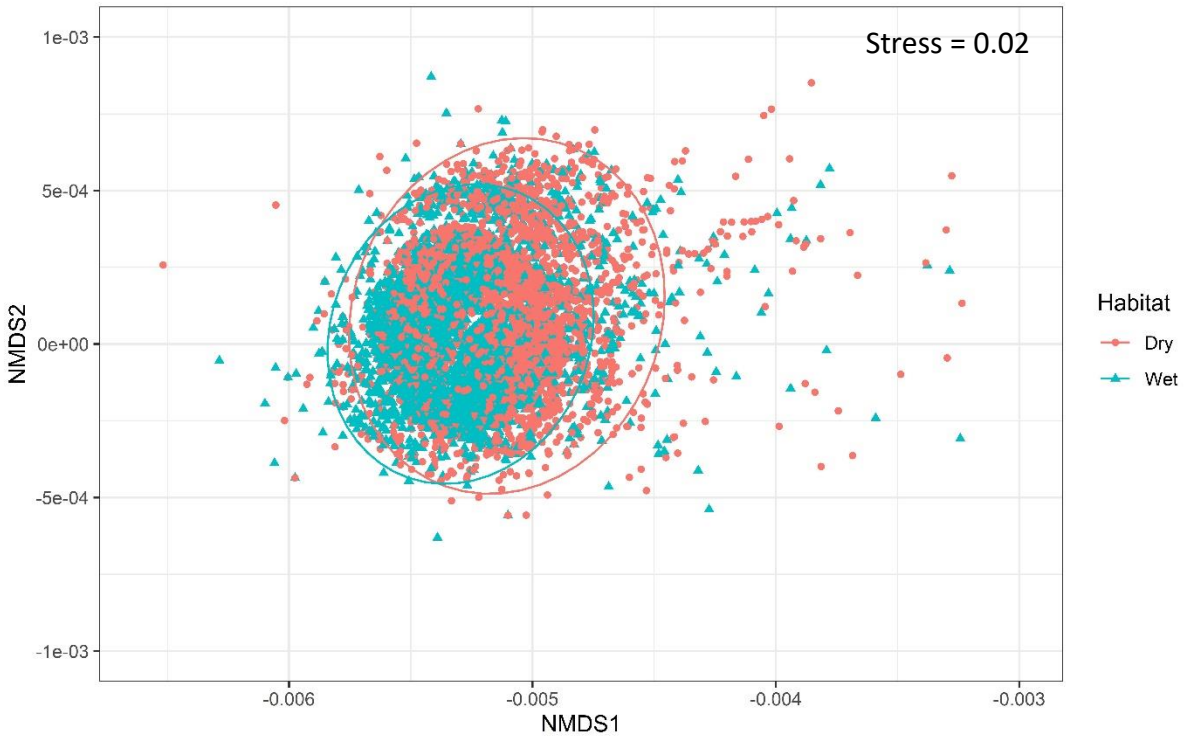

Figure S6. NMDS ordination comparing the community composition between wet (> 1000 mm MAP) and dry (< 1000 mm MAP) plots. Ellipses show 95% confidence intervals around the centroid.

Chapter 3:

Determinants of trait variation among African savanna trees

3.1 Abstract

Functional traits dictate the ability of species to persist under certain conditions and are therefore increasingly used to elucidate patterns and processes of community assembly. Savannas cover one-fifth of the Earth's surface, contribute up to 30% of primary productivity, and support the livelihoods of hundreds of millions, but understanding of the functional composition of savanna tree communities remains a key knowledge gap. We compile data on 13 important functional traits for tree species from across the savannas of eastern and southern Africa to assess how functional traits cluster across species. We combine this with plot composition data from the Socio-Ecological Observatory for Studying African Woodlands (SEOSAW) network to understand how community functional composition changes over gradients of climate, soil, fire, and herbivory. We find three distinct functional clusters characterised by: i) high wood density and slow growth, ii) thick bark and rapid growth and iii) spinescence and high leaf nitrogen. The relative basal area of these clusters show marked responses to gradients of rainfall, fire, and herbivory and so we interpret these functional syndromes as: i) dry adaptation and herbivore avoidance, ii) fire tolerance, and iii) herbivore tolerance. We find a shift from dominance of dry-adapted, herbivore-avoidant species to fire-tolerant species as rainfall increases, with herbivore-tolerant trees rarely dominant throughout. This functional shift potentially drives high species turnover across the savannas of southern and eastern Africa, with replacement of dry-adapted species by fire-adapted species over the rainfall gradient. Trait community weighted means are broadly invariant to our gradients, supporting the idea that functional syndromes help understand trait variation across savanna ecosystems. There is a need for increased trait data collection for trees in the region, given the great potential for functional traits to inform important ecological knowledge gaps and help with predictions in the face of environmental change.

3.2 Introduction

Functional traits are increasingly used to understand the ecological processes that determine community assembly (McGill *et al*., 2006) world over. Morphological and physiological traits dictate the ability of plant species to persist in a given environment and are thus likely to strongly influence patterns of composition and processes of community assembly (McGill *et al*., 2006; Westoby & Wright, 2006). Despite covering 20% of the Earth's surface (Pennington *et al*., 2018), harbouring substantial biodiversity, and supporting the livelihoods of 100s of millions of people (Ryan *et al*., 2016), mechanisms of community assembly in savannas remain understudied. Savannas experience high rates of disturbance from both herbivores and fire (Staver *et al*., 2012), have highly seasonal rainfall regimes (Lehmann *et al.*, 2011), and vary in canopy cover (Sankaran *et al*., 2005), characteristics likely to lead to unique community composition patterns and assembly processes. Assessing tree functional trait patterns could therefore provide a vital tool to help resolve fundamental ecological knowledge gaps in globally important savannas.

Environmental and biophysical constraints on species lead to trait trade-offs related to allocation of limited resources and the costs associated with this (Wright *et al*., 2004; Maynard *et al*., 2022). Global trait syntheses have described trade-offs primarily along the leaf economics spectrum, which determines tree growth rates (Wright *et al*., 2004, Reich, 2014), and secondarily along an axis related to tree size and competition for light (Maynard et al., 2022). Trees at the "fast" end of the leaf economics spectrum have traits that maximise rapid resource acquisition and growth, whilst trees at the "slow" end have increased tissue longevity but grow more slowly (Wright *et al*., 2004).

Widespread fire, herbivory, and rainfall seasonality in savannas could lead to alternative trade-offs in savanna species as tree competition for light and resources is reduced

but disturbance-driven selection pressures are intensified. Functional traits to cope with disturbances, such as thick bark and resprouting ability, allow savanna trees to occupy a unique persistence niche (Bond & Midgley, 2001), shaping savanna-forest boundaries (Hoffman et al., 2009) and differentiating savannas from thicket and forest communities in South Africa (Charles-Dominique et al., 2015). Among savanna species, herbivore pressures cluster species into three defence syndromes characterised by: i) structural and chemical defences, ii) structural defences only, or iii) chemical defences with low leaf nitrogen (Wigley et al., 2018). But wider understanding of functional clustering and trade-offs across a broader spectrum of functional traits within savanna species remains a clear knowledge gap.

Savannas in southern and eastern Africa exhibit high species turnover (Davies et al., 2023), splitting into 6 floristic clusters based on woody plant community composition (Fayolle et al., 2019). But whether species turnover translates into functional turnover is not known. Environmental filtering can determine community composition, selecting for, or against, species over environmental gradients (Cadotte & Tucker, 2017) – a process mediated by species' functional traits (McGill et al., 2006). High resource environments select for 'fast' species (e.g., high specific leaf area (SLA) and leaf nitrogen), whilst nutrient- and water-limited systems select for 'slow' species (e.g., thick leaves, dense wood; Wright *et al*., 2004; Ordoñez et al., 2009; Maynard *et al*., 2022). But associations between leaf traits and climate and soil gradients are weaker in southern African savannas than globally (Wigley *et al*., 2016).

Fire and herbivory predominate in savannas, maintaining low tree cover across savannas for millions of years (Strömberg, 2011) and filtering species based on their functional traits. Thick bark insulates trees from fire (Hoffman & Solbrig, 2003) and reduces water loss (Paine *et al*., 2010), with fire regimes explaining variation in bark thickness (Pausas, 2015; Charles-Dominique *et al*., 2017). Spinescence, a trait evolved to reduce herbivory, is associated with low rainfall, high soil nutrients, and low fire frequency (Charles-Dominique et al., 2016).

Exclosure experiments in Kruger national park, South Africa, show preferential browsing of leaves with high leaf nitrogen by herbivores, leading to changes in woody plant composition (Wigley et al., 2014). Assessing patterns of functional composition could further improve our understanding of how widespread fire and herbivory shape communities in the savannas of eastern and southern Africa.

Here, we combine species-level trait data (Table 1) with plot data from across the savanna woodlands of southern and eastern Africa —the world's largest savanna— to assess three key questions concerning community assembly in these woodlands:

i) How do the functional traits of savanna trees cluster across species?

ii) How does the relative basal area of functional clusters change over climate, soil, fire, and herbivory gradients?

iii) How does community-level functional trait composition vary over climate, soil, fire, and herbivory gradients?

3.3 Methods

Functional trait data

To understand how functional traits cluster across savanna species, and how savanna tree trait composition changes across the region, we first created a list of savanna tree species of southern and eastern Africa. We did this using plot composition data from the SEOSAW network which combines plot survey data from > 10,000 plots, across 13 countries in eastern and southern Africa (SEOSAW, 2021). Following this, we collated available trait data for the species on this list from a range of sources, making particular effort to include traits that are thought to be functionally important in savanna systems (Table 1). Trait data for maximum tree height and number of stems were mostly extracted from the SEOSAW stem dataset and supplemented from other sources, such as the African plant database (African Plant Database v4). We calculated allometric height-diameter coefficients for species for which both height and DBH data were available for >= 5 individuals using a simple linear equation (see supplementary methods). Wood density was extracted for all species from the global wood density database using the 'getWoodDensity' function from *BIOMASS* package in R (Chave *et al*., 2009).

Several traits were extracted from the TRY database (Kattge et al., 2020), including leaf nitrogen content, leaf area, specific leaf area (SLA), seed dry mass, bark thickness, and deciduousness. These traits were also supplemented by trait data provided by researchers from the region. Like height, bark thickness is an allometric trait that increases with tree size and so is typically expressed in relation to stem diameter. As we did not have enough individuals with paired bark thickness and DBH measures to calculate an allometric measure of bark thickness using linear models, we used logged bark thickness as a ratio of logged DBH to give an allometric coefficient of bark thickness (Jackson et al., 1999). Deciduousness was determined by searching plant descriptions on the African plant database (African Plant Database v4).

Spinescent genera were identified from previous work in the region by Charles-Dominique (2016) and otherwise checking species' descriptions from the African plant database for evidence of spinescence; in instances where there was no mention of spines or any synonyms (spinescent, spinescent-tipped) in species' descriptions, species were assumed to not be spinescent. Nitrogen-fixing species were identified by searching the Germplasm Resources Information Network (GRIN) for previous evidence of nodulation in species – if there was no previous evidence of nodulation, species were assumed to not be nitrogen fixers. Species' size-standardised growth rates were provided from previous work in the region by Libanda, B. (2021; see paper for methods).

Table 1 Functional traits included in our analysis

Trait	Unit(s)	Functional relevance	N species*	N plots**	Source(s)
Wood density	g/cm^3	Drought resistance and structural support (e.g. against elephants)	664 (100%)	6001 (100%)	Chave et al., 2009
Deciduousness	Yes/no	Protection from desiccation during dry seasons	445 (67%)	5891 (98%)	TRY; African Plant Database
Leaf nitrogen	mg/g	Related to maximum photosynthetic rate	241 (36%)	2745 (46%)	Co-authors; TRY
Nitrogen fixation	Yes/no	Ability to fix nitrogen in nutrient-poor soils	664 (100%)	6001 (100%)	GRIN
SLA	$mm^2\ mg^{-1}$	Investment in growth rate and resource acquisition	252 (38%)	3468 (58%)	Co-authors; TRY
Spinescence	Yes/no	Reduction of herbivory rate	664 (100%)	6001 (100%)	Charles-Dominique et al., 2015; African Plant Database
Number of stems	count	Ability to resprout following disturbance	664 (100%)	6001 (100%)	SEOSAW inventory data
Maximum height	m	Light competition and escaping fire and herbivore traps	644 (97%)	5999 (99%)	SEOSAW inventory data; Co-authors; TRY
Allometric height	Coefficient	Plant investment in growth	370 (56%)	5964 (99%)	Co-authors; TRY
Seed dry mass	mg	Plant investment in sexual reproduction	429 (65%)	5074 (85%)	Co-authors; TRY
Allometric bark thickness	Coefficient	Protection from fire, water loss, and debarking by herbivores	71 (11%)	1142 (19%)	Co-authors; TRY
Leaf area	mm^2	Interception of light and related to growth	311 (47%)	3253 (54%)	Co-authors; TRY
Growth rates	Diameter mm/year	Competition for resources and escaping browse and fire traps	277 (42%)	4965 (83%)	Libanda, B., 2021

*Number of species with trait data (% given out of total of 664 species); **Number of plots with > 80% of total plot basal area covered by species with trait data (% given as total of 6001 plots)

Study region and community composition data

To assess how the functional composition of savanna tree communities changes with respect to climatic, soil, fire, and herbivory gradients we used plot data from across eastern and southern Africa compiled by SEOSAW (SEOSAW, 2021). We selected plots from the SEOSAW database that were designated as woodland under White's vegetation map of Africa (White, 1983), including a mix of savanna types: mopane woodlands, mixed woodlands, *Acacia* (*sensu lato*) savannas, and miombo woodlands (sensu White, 1983). The latter is the most extensive tropical woodland type of Africa - covering an area of 1.9 million km^2 (Ribeiro *et al*., 2020) dominated by trees from the genera *Brachystegia, Julbernardia,* and *Isoberlinia* (Frost, 1996). We selected plots ranging in size, from 0.1 and 1 ha, representing a trade-off between coverage within our target region and sampling homogeneity. This selection process gave us tree composition data from 6001 plots, spanning eight countries across eastern and southern Africa (Figure S1). In our assessment of plot composition, we included only living stems >10 cm diameter at breast height (DBH, 1.3 m). Trees not identified to species-level were excluded from our analyses as we are unable to provide accurate trait data for these species. The basal area (BA) of each tree was calculated using individual stem DBH, with BA summed across stems for trees with multiple stems. Plot BA was calculated as the sum of the BA of all trees >10 cm DBH.

To assess how environmental conditions changed in our selected plots, we extracted climate data from the WorldClim version 2.1 database (Fick & Hijmans, 2017). Mean annual precipitation (MAP; BIO12) and mean annual temperature (MAT; BIO1) were taken as the mean value between 1970 and 2000 at 30 arc seconds resolution. Dry season length was extracted from the RADS dataset (Bombardi et al., 2019) and averaged from 1998-2016. Soil nitrogen and phosphorous content (g kg^{-1}), and soil sand proportion data were extracted from the ISRIC SoilGrids data product at 250 m resolution (Hengl *et al*., 2017). Fire count and

intensity data were extracted from the MODIS burned area product (MCD64A1; Giglio *et al*., 2015), with fire counts taken as the number of times a pixel was recorded as burned between 2001 – 2018 at a resolution of 1 km and fire intensity referring to the greatest fire radiative power value over the period. Present day herbivore biomass was extracted from maps created by Hempson *et al*. (2017) at 0.5° resolution.

Statistical Analyses

Identifying functional clusters and cluster-environment relationships

To identify functional trait clusters in savanna trees, we used *k*-means clustering and pairwise comparisons of trait means (Hartigan & Wong, 1979). *K*-means clustering aims to group species into clusters that minimise intra-group variation, such that the sum of squares from points to the centre of the cluster is minimised. We clustered species using *k*-means with the Hartigan-Wong algorithm to group together species with the most similar trait profiles. We did this only for species with all 13 trait values (n_{spp} = 46, see Table 2). We assessed the optimal number of clusters to split our species into using the silhouette method. To characterise the trait profile of each cluster, we then made pairwise comparisons of trait means between clusters. We used a simple Bayesian model implemented with the R package brms (Bürkner, 2021) to give the cluster-level effect on each of the traits (see supplementary methods for more detail on models), before contrasting posterior means between clusters to identify whether estimates overlapped using the hypothesis function.

To understand how trait clusters responded to environmental conditions, we assessed how the proportion of tree BA that each cluster contributed to the total plot BA (relative BA from here) changed along gradients of climate, soil, fire, and herbivory using Bayesian linear regression. We limited this analysis to only include plots for which the species assigned to clusters contributed > 50% of total plot BA (n = 2246 plots). We included cluster as an

interaction term on all our predictors to assess how the relative BA of each of the three clusters individually responded to our gradients (See supplementary methods for more information). We modelled this using an ordered beta regression through the *ordbetareg* package to allow for our proportion data including 0s and 1s (Kubinec, 2020).

Assessing community-level functional trait-environment relationships

We assessed how savanna tree traits respond at the community-level to climatic, soil, fire, and herbivory gradients by first calculating community-weighted means (CWM) for the continuous functional traits. CWMs were calculated for each trait in each plot weighted by the proportion of each species' contribution to the total plot basal area (BA). Plots were excluded from this analysis if the BA coverage for the trait of interest was <80% of total plot BA (Table 1). For binary functional traits, we calculated the proportion of the plot basal area that was composed of deciduous, nitrogen fixing, and spinescent individuals.

We then used Bayesian linear regression to assess the effect of our gradients on the trait composition of savanna tree communities. Trait CWMs were modelled using either a log normal or gamma likelihood. We initially ran two models for each trait CWM, one using a log normal likelihood and one with gamma and determined the superior model using Leave-One-Out (LOO) cross-validation to compare the pointwise out-of-sample predictive accuracy of each model (Vehtari *et al*., 2017). Trait proportions were modelled using a beta likelihood. Since our proportion data contains 0s and 1s (instances in which none or all of the individuals in a plot were deciduous, nitrogen-fixing, or spiny), we transformed data following the method proposed by Smithson & Verkuilen (2006). This rescales the data to lie between 0 and 1, allowing modelling under a regular beta likelihood (See supplementary methods for further model details).

We found strong evidence of a phylogenetic signal in several of our functional traits (see supplementary methods and Table S1), caused by species descended from common ancestors being more likely to share similar traits (Revell et al., 2008). To control for phylogenetic autocorrelation, we added plot-level phylogenetic dissimilarity as a random effect in our models using UniFrac distance (see supplementary methods).

For all Bayesian models, predictors were standardized to zero mean and one standard deviation, prior to model fitting. Models were fit using weakly informative, regularizing priors (see supplementary methods), with four chains run for 1000 warmup and 1000 post-warmup samples. Checks of chain convergence and posterior predictive ability were performed on all models. All statistical analyses were carried out in *R* (R Core Team 2017).

3.4 Results

How do the functional traits of savanna trees cluster across species?

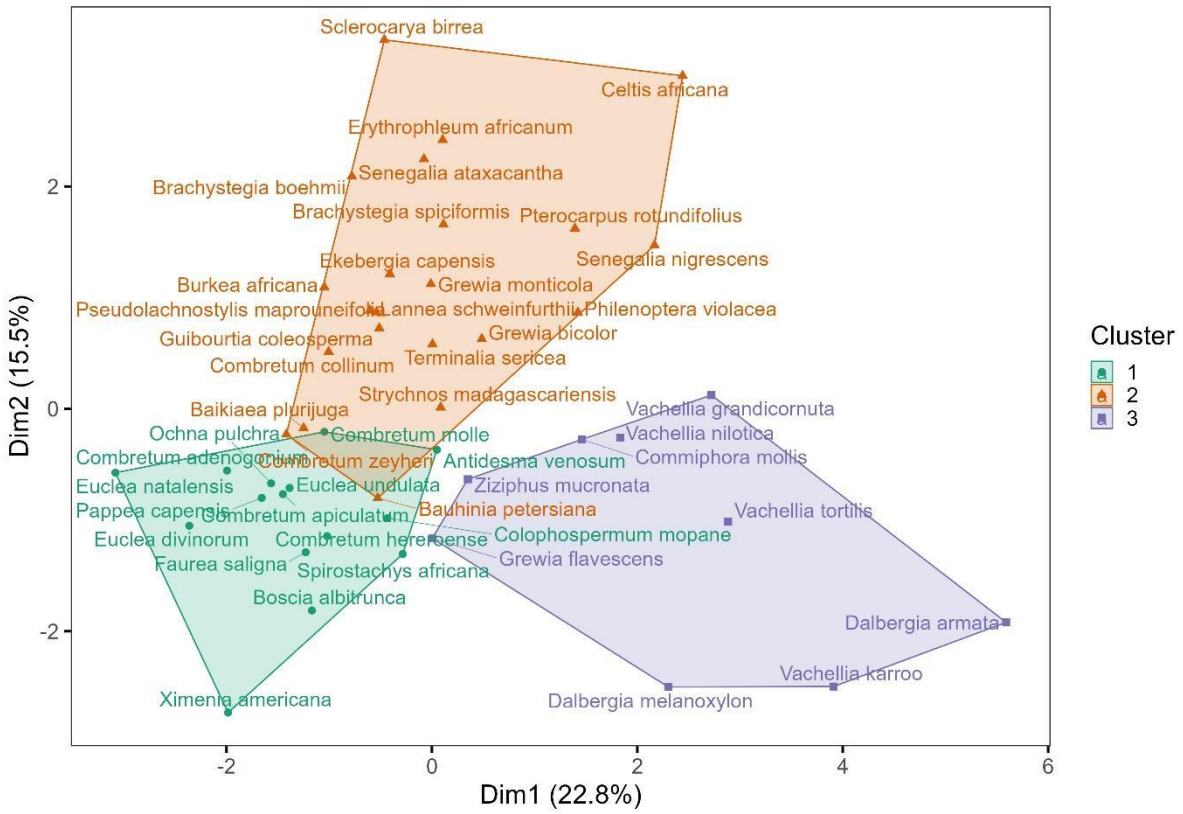

Figure 1. A) Ordination of *K*-means clustering of species, with all trait information (n = 46). Species were split into three clusters which was identified as the optimum number of clusters through the silhouette method (Figure S2).

Using the silhouette method, we identified 3 clusters as the optimum number of groups to sort our species into (Figure 1 & S2). *K*-means clustering then sorted species into one of the three groups according to their functional profiles, minimising intra-cluster variation (Figure 1; Table 2).

Comparing mean trait values among clusters, we see that Cluster #1 has significantly higher wood density and lower leaf nitrogen content than the other two (Figure 2A), suggesting it is adapted to dry environments and possibly herbivore avoidance (Figure 2B). Cluster #2 has significantly larger leaves and higher growth rates than the other two clusters (Figure 2A),

whilst also having thicker bark than Cluster #3, suggesting this cluster is suited to an acquisitive growth strategy and fire tolerance (Figure 2B). The third cluster of species is significantly more spinescent and nitrogen fixing than the other two clusters (Figure 2A), whilst also having smaller, more nitrogen dense leaves, suggesting a trait syndrome suited to tolerating herbivory (Figure 2B).

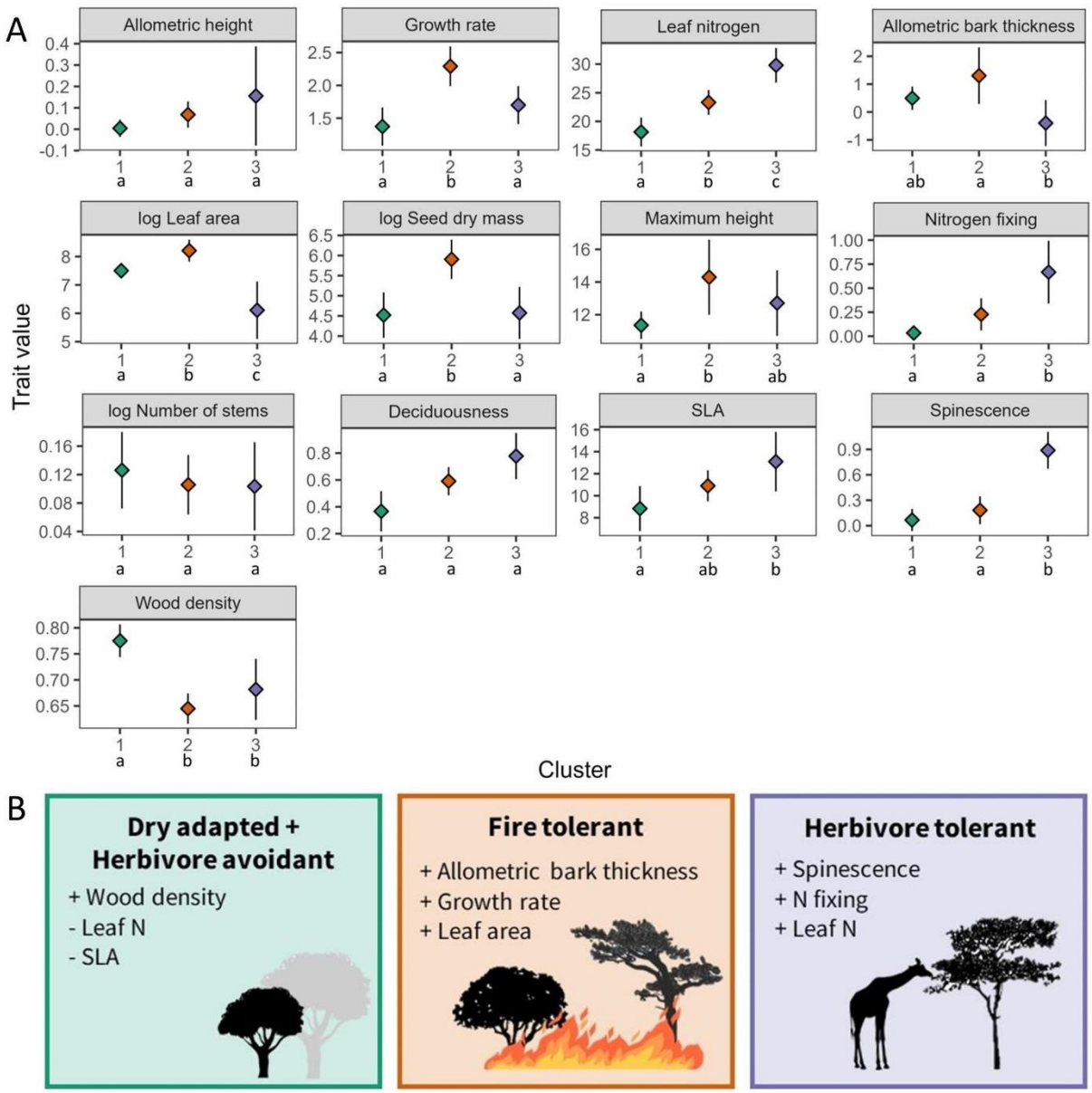

Figure 2. A) Mean trait values of each of the 3 clusters as identified by *k*-means clustering, and B) defining trait characteristics of each cluster. Diamonds show mean value, whilst lines show 95% CI. Different letters (a, b, ab) below cluster numbers indicate significant differences in trait values between clusters whilst the shared letters between groups indicate no significant difference, tested at the $p < 0.05$ level. Log leaf area, seed dry mass, and number of stems are all natural logs.

Table 2. Species included in clustering analysis and the cluster to which they are assigned

Dry-adapted & herbivore avoidant	Fire tolerant	Herbivore tolerant
Antidesma venosum	Baikiaea plurijuga	Commiphora mollis
Boscia albitrunca	Bauhinia petersiana	Dalbergia armata
Colophospermum mopane	Brachystegia boehmii	Dalbergia melanoxylon
Combretum adenogonium	Brachystegia spiciformis	Grewia flavescens
Combretum apiculatum	Burkea africana	Vachellia grandicornuta
Combretum hereroense	Celtis africana	Vachellia karroo
Combretum molle	Combretum collinum	Vachellia nilotica
Euclea divinorum	Combretum zeyheri	Vachellia tortilis
Euclea natalensis	Ekebergia capensis	Ziziphus mucronata
Euclea undulata	Erythrophleum africanum	
Faurea saligna	Grewia bicolor	
Ochna pulchra	Grewia monticola	
Pappea capensis	Guibourtia coleosperma	
Spirostachys africana	Lannea schweinfurthii	
Ximenia americana	Philenoptera violacea	
	Pseudolachnostylis maprouneifolia	
	Pterocarpus rotundifolius	
	Sclerocarya birrea	
	Senegalia ataxacantha	
	Senegalia nigrescens	
	Strychnos madagascariensis	
	Terminalia sericea	

How does the relative basal area of functional clusters change over climate, soil, fire, and herbivory gradients?

Climate, fire, and herbivory were the strongest determinants of the relative BA of our three functional clusters of species, with soil having a smaller effect (Figure 3A). Cluster #2 species, those with thick bark, rapid growth, and large leaves, had higher relative BA in wetter and cooler plots and in plots with more frequent fires (Figure 3A – D; β_{MAP} = 0.15, 95% Credible Interval (CI) = 0.09-0.22; β_{MAT} = -0.14, CI = -0.18--0.10; $\beta_{FIRE\ COUNT}$ = 0.05, CI = 0-0.09). Conversely, species in Cluster #1, those with high wood density and low leaf nitrogen, had a greater relative BA in drier and hotter plots with less fire and higher soil nitrogen content (Figure 3A – E; β_{MAP} = -0.35, CI = -0.44--0.27; β_{MAT} = 0.36, CI = 0.31-0.41; $\beta_{FIRE\ COUNT}$ = -0.08, CI = -0.14--0.02; $\beta_{SOIL\ N}$ = 0.17, CI = 0.12-0.23). Cluster #3 species, those with spines and high leaf nitrogen, had higher relative BA in plots with high herbivore biomass and low fire frequency ($\beta_{HERBIVORY}$ =0.36, CI = 0.25-0.46; $\beta_{FIRE\ COUNT}$ = -0.29, CI = -0.41--0.18), but were almost never dominant (Figure 3A – D).

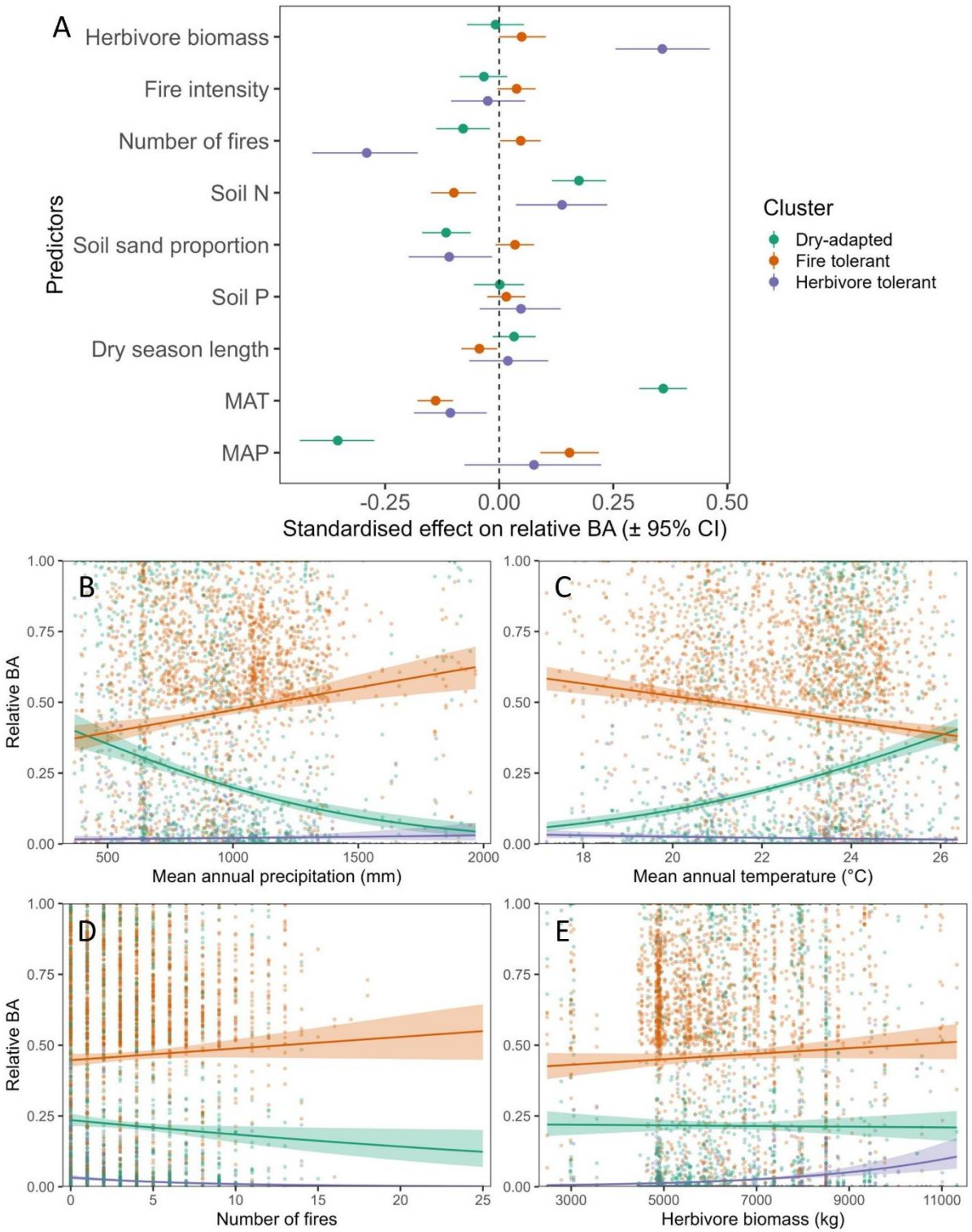

Figure 3. A) Standardised effect sizes of climate, soil, fire, and herbivory gradients on the relative basal area of each of the three clusters. Conditional effects plots of the relative BA of each cluster as a function of B) MAP, C) MAT, D) number of fires, and E) herbivore biomass. Standard effect sizes show the median of the posterior and 95% credible intervals (CI). Points to the left of the dashed line had a negative effect on relative BA, whilst those to the right had a positive effect.

How does community-level functional trait composition vary over climate, soil, fire, and herbivory gradients?

Overall, there were only a few, weak relationships between our climate, soil, fire, and herbivory gradients and trait CWMs and proportions. The CWM of seed dry mass increased with rainfall and decreased with temperature (Figure 4A & 1B; β_{MAP} = 0.15, CI= 0.10-0.19; β_{MAT} = -0.05, CI = -0.08--0.03), with cooler plots also having lower growth rates (β_{MAT} = -0.05, CI = -0.06--0.05). The CWM of allometric bark thickness decreased with increasing herbivore biomass and soil nitrogen content (Figure 4A; $\beta_{HERBIVORY}$ = -0.12, CI = -0.16--0.07; $\beta_{SOIL\ N}$ = -0.16, CI = -0.21--0.11). The relative BA of nitrogen fixing trees increased with rainfall, soil phosphorous, and with herbivore biomass (Figure 4C; β_{MAP} = 0.11, CI = 0.07-0.15; $\beta_{SOIL\ P}$ = 0.05, CI = 0.02-0.08; $\beta_{HERBIVORY}$ = 0.10, CI = 0.06-0.14), with the proportion of spinescent trees also increasing with herbivore biomass and soil phosphorous ($\beta_{HERBIVORY}$ = 0.10, CI = 0.07-0.14; $\beta_{SOIL\ P}$ = 0.06, CI = 0.03-0.08). However, trait CWM and basal area proportions were largely invariant to climate, soil, fire, and herbivory, with the 95% credible interval of the posterior overlapping 0 or the mean size of the effect being < 0.05 in the majority of instances (Figure 4A, 4D – E).

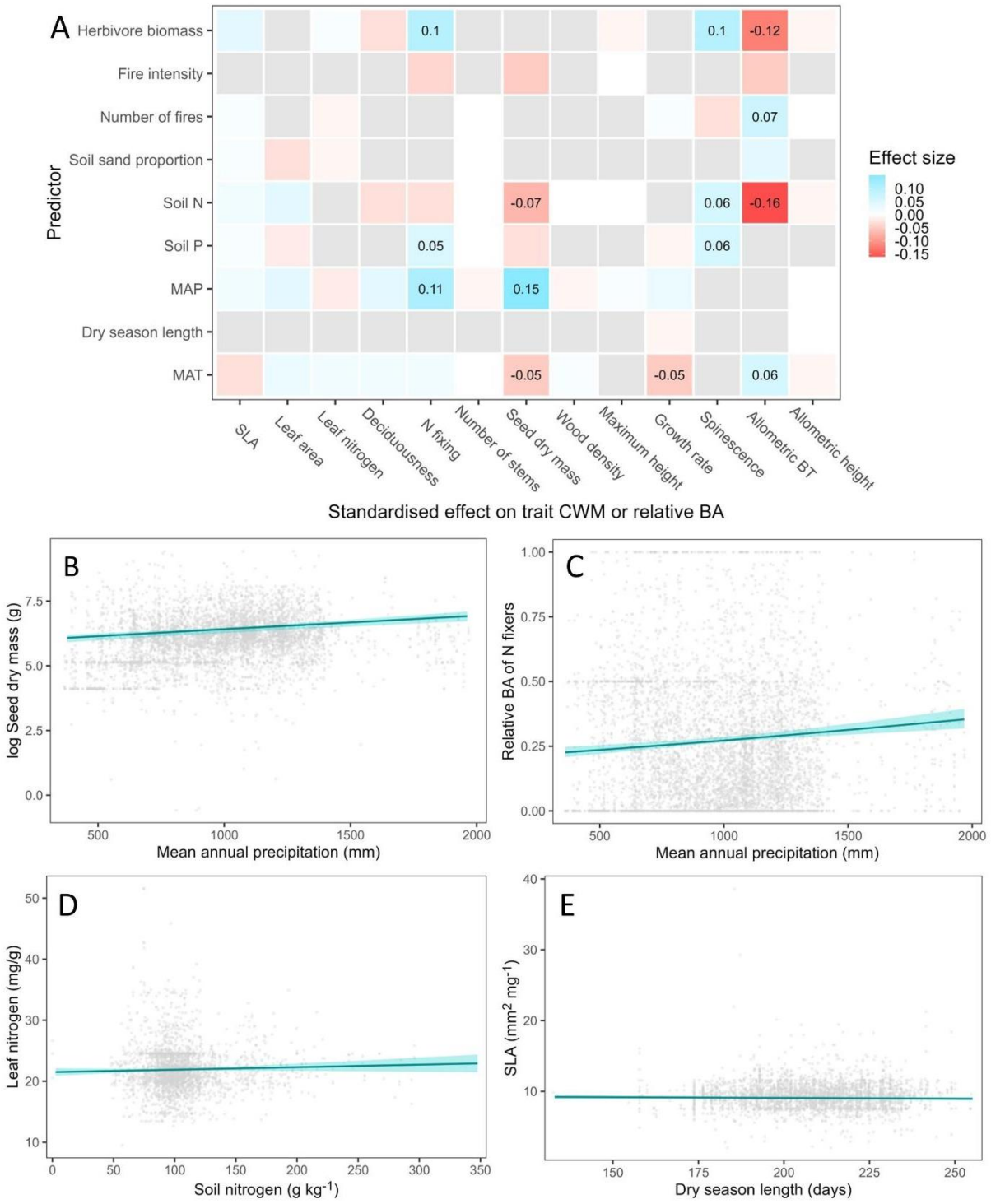

Figure 4. Determinants of savanna tree community weighted mean (CWM) across the savannas of southern and eastern Africa. A) Coefficients of the effects of predictors on the CWM or relative BA of each trait. Tiles are coloured relative to the effect size of the predictor, with blue tiles having a positive effect on a given trait and red tiles having a negative effect. Paler colours indicate smaller effect sizes, whilst grey tiles indicate where the 95% credible interval (CI) of the effect size overlapped 0. The size of the effect is given in instances where the mean effect size was > 0.05 away from 0. Conditional effect plots showing how B) the CWM of seed dry mass and C) the relative BA of N fixing individuals changes with annual precipitation volume, D) the CWM of leaf nitrogen changes with soil nitrogen content, and E) the CWM of SLA changes with increasing dry season length.

3.5 Discussion

We used species- and community-level tree functional trait variation across eastern and southern Africa to elucidate the processes governing community assembly in these diverse savannas. Species clustered into three significantly distinct functional syndromes, characterised respectively by: i) high wood density and slow growth, ii) thick bark and rapid growth, or iii) spinescence and high leaf nitrogen. The relative BAs of these clusters showed marked responses to environmental gradients, suggesting that water availability and fire and herbivore regimes help drive floristic turnover and shape community assembly in the savannas of southern and eastern Africa. However, community weighted means of traits individually showed little response to climatic, soil, fire, and herbivory gradients across the region, supporting the idea that functional syndromes help understand trait variation across savanna ecosystems.

Functional syndromes of savanna tree species

Functional clustering of 46 savanna tree species showed a clear divergence in strategies in response to water availability and fire and herbivore regimes, with species aligning into one of three distinct trait syndromes. Cluster #1 was characterized by high wood density, slow growth, and low leaf nitrogen; this cluster was dominant at low rainfall and at high temperatures, so we interpret this as primarily reflecting adaptations to low water availability. High wood density and slow growth reduce risk in terms of water use, enhancing cavitation resistance and increasing drought tolerance (Oliviera et al., 2021). This conservative growth strategy in response to water-limitation enables dominance in drier savannas but reduces the ability of this cluster to compete with more acquisitive growth strategies in wetter savannas, conforming to global analyses of the leaf and wood economics spectrums and their relative responses to environmental gradients (Wright et al., 2004; Maynard et al., 2022; Ordoñez et al., 2009). Low

leaf nitrogen also suggests low quality forage (Wigley et al., 2014), and the cluster contains species of*, e.g., Euclea* (Table 2), that are classically considered to avoid herbivory (Scogings, 2014). Thus, this cluster of species is likely also herbivore avoidant (Wigley et al., 2018). We suggest that further work to consider traits like plant secondary defensive compounds or digestible fibre might help further elucidate the ecology of this cluster.

Cluster #2 was characterised by rapid growth, large leaves, and thick bark relative to tree size, with the cluster increasing its proportion of plot BA with greater rainfall. By contrast with Cluster #1, this cluster had an acquisitive growth strategy with large, pinnate leaves, maximizing light interception and allowing rapid growth (Wright et al., 2004), conferring a competitive advantage and allowing the cluster to dominate in wetter savannas. Bark insulates the cambium from high temperatures thus thicker bark coneys a survival advantage to savanna stems, reducing topkill rates from fire (Hoffman & Solbrig, 2003; Hoffman et al., 2003), whilst rapid growth possibly also enables stems to escape fire traps (Bond & Keeley, 2005). We therefore understand the trait syndrome of this cluster as a fire tolerance adaptation, allowing the cluster to dominate in wetter savannas where fires are more frequent (Staver et al., 2012; Archibald and Hempson, 2016) and water limitation is reduced favouring more acquisitive growth strategies (Oliviera et al., 2021).

A shift in dominance from Cluster #1 to #2 with increasing rainfall suggests that divergent functional strategies to deal with water availability and fire and herbivory shapes high species turnover across these savannas that we have observed previously (Davies et al., 2023). One caveat to note is that bark thickness has been very sparsely sampled for our focal species (n = 71, 11% of species) and so we highlight the need for further trait sampling, particularly of bark traits, across the region. Despite this, we are confident in the implications of our findings given that we have a full suite of trait data for several of the most dominant

species in the region (the 46 species included in our cluster analysis account for 39.5% of BA in all our study plots, and we retained plots where our coverage was > 50% of BA).

Finally, Cluster #3 contained spinescent species with high leaf nitrogen, including a high proportion of nitrogen fixers, and was positively associated with herbivore biomass and negatively associated with fire. We therefore interpret this cluster as herbivore tolerant. Leaves with high leaf nitrogen offer particularly attractive forage to browsers (Wigley et al., 2014), and thus species use spines, in combination with branching architecture, to reduce browsing rates of herbivores and limit leaf tissue loss (Charles-Dominique et al., 2016). This cluster contains several species that are known to limit browsing through structural defences, such as *Vachellia grandicornuta* and *Dalbergia melanoxylon* (Table 2). The relative BA of this cluster increases with herbivore density but decreases with fire frequency, likely reflecting the spatial segregation of these competing consumers, as areas experience intense fire or herbivory but rarely both (Staver et al., 2012; Archibald and Hempson, 2016) and so this cluster does not need to invest in fire-resistance traits like thick bark.

Community trait compositional responses to environmental gradients

Generally, trait CWMs and relative BAs showed only weak responses to environmental gradients, with some exceptions. The CWM of allometric bark thickness decreased in areas with greater herbivory, suggesting environmental filtering by a lack of fire reducing the competitive edge of thick barked species as intense herbivory and fire tend to be spatially separated (Staver et al., 2012, Archibald and Hempson, 2016). Nitrogen fixing trees increased their relative BA in wetter plots, contradicting previous evidence that aridity favours N-fixers (Pellegrini et al., 2015). This could reflect a difference in approaches to classifying nitrogen fixers, as we assign putative fixation at the species-level, demonstrating the need for more intensive work on N fixation incidence. As expected, spinescence was greater in areas with

higher herbivore density, evidencing environmental filtering of non-spinescent species (Charles-Domnique et al., 2016). Seed dry mass increased with rainfall, possibly suggesting greater reproductive tree-tree competition between species in wetter systems due to higher tree density and greater diversity (Turnbull et al., 2004; Godlee et al., 2021). Both seed dry mass and number of stems were unaffected by fire and herbivory gradients, showing no support for the shifting persistence niche concept in our savanna (Clarke et al., 2015). We found strong evidence for phylogenetic signals in several of our traits as expected (Revell et al., 2008; Wigley et al., 2016).

At the community-level, individual traits associated with acquisitive and conservative growth strategies were invariant to environmental gradients, corroborating previous work showing weak community-level leaf trait-environment relationships in savannas (Wigley et al., 2016). This also contradicts a classic dichotomy in savanna ecology that fine-leaved and broadleaved trees separate between nutrient-rich and nutrient-poor soils, respectively (Scholes, 1990). Corroborating more recent studies showing a lack of quantitative evidence for this separation in southern Africa (Wigley et al., 2018), although other soil factors, like texture, could be important determinants (Pringle et al., 2016). Limited trait-environment relationships in savannas may be due to fires changing the distribution and availability of soil nutrients (Pellegrini et al., 2015), and support assessing traits in combination to help understand variation across savanna ecosystems. One caveat to our finding of a lack of effect of soil on functional composition may be due to the coarse nature of available soil data (250 m resolution) which may overlook finer-scale changes in soil nutrient content and texture that could influence functional community composition. Strong phenotypic plasticity in savanna trees (for example: Bayonne Mboumba & Ward, 2008) may mask savanna trait-environment relationships when using species' means.

Conclusions

We find that savanna trees separate into three functionally distinct clusters of species organised around responses to climate, fire, and herbivory. We find a shift from dominance of dry-adapted, herbivore avoidant species to fire tolerant species with increasing rainfall, with herbivore-tolerant trees (spinescent and N-fixing) rarely dominant throughout. This functional shift likely drives high species turnover across the savannas of southern and eastern Africa. We highlight the need for increased trait data collection for trees in the region. The lack of trait data available for tree species in the region is concerning given the great potential for functional traits to inform important ecological knowledge gaps, help with predictions in the face of environmental change, and their importance to ecosystem service provision.

Acknowledgements

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3.6 Supplementary material

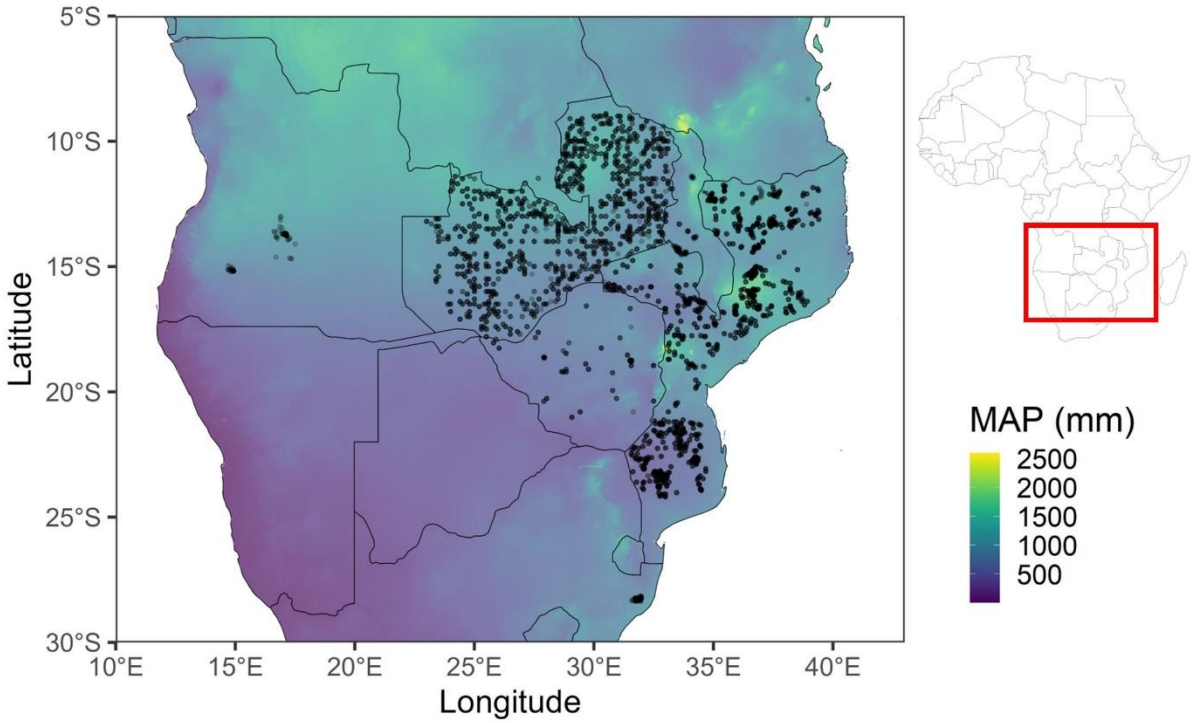

Figure S1. Map of plots from across our study region with gradients of MAP

Supplementary methods

Allometric height calculation

We calculated an allometric height coefficient for species which had > 4 individuals with paired height and DBH measures (n = 370 species). We used a simple linear equation to calculate species-level allometric height coefficients:

$$ln(height) \sim 0 + \beta_1 * ln(DBH)$$

We then took β_1, the slope of the regression between log-transformed height and DBH, for each species as the allometric height coefficient, adapting methods from (Feldpausch et al., 2011). We used a 0 intercept as this logically means a tree with 0cm DBH has 0m height, although we recognise arguments for and against this approach (Feldpausch et al., 2011).

Testing for phylogenetic signal and controlling for phylogenetic autocorrelation

To test whether closely related species share more similar trait values we checked for evidence of a phylogenetic signal in each of our 13 traits. We first used the *V.PhyloMaker* package to create a phylogenetic tree for all of our species based off a backbone provided by Open Tree of Life (Jin & Qian, 2019), with names standardised according to The Plant List (2010). We then calculated Pagel's lambda using the *phylosig* function from the *picante* package (Kembel et al., 2010), giving a measure of the strength of phylogenetic signal for each of our traits. We saw a strong phylogenetic signal in several of our traits (Table SX).

Given this phylogenetic signal, we controlled for phylogenetic autocorrelation between our plots by introducing phylogenetic dissimilarity as a random effect in our models of trait CWM and proportion. We did this by creating a UniFrac distance matrix to measure the phylogenetic dissimilarity between our plots. This matrix was then included as a random effect in each of our models of trait CWM and proportions.

Model likelihoods and priors

To make pairwise comparisons of trait means between clusters we used a simple Bayesian linear model in brms and then contrasted posteriors of cluster-level effects using the hypothesis function. 13 models were run in total, one for each trait, using one of a gamma, log-normal, gaussian, or binomial likelihood depending on the distribution of the trait. We also used the ordbetareg package to allow for our proportion data including 0s and 1s (Kubinec, 2023). We used the following weakly informative, regularizing priors in each of the models:

$$Trait\ mean \sim Gaussian\ (\mu, \sigma)$$

μ ~ Normal (0, 1)

σ ~ Normal (0, 1

$$Trait\ mean \sim Gamma\ (\alpha, \beta, \phi)$$

α ~ Normal (0, 1)

β ~ Normal (0, 1)

ϕ ~ Gamma (0.01, 0.01)

$$Trait\ mean \sim Log\ normal\ (\mu, \sigma)$$

μ ~ Normal (0, 1)

σ ~ Normal (0, 1)

$$Trait\ mean \sim Binomial\ (n, p)$$

n ~ Normal (0, 1)

p ~ Normal (0, 1)

To assess how individual traits respond we used Bayesian models to compare trait community weighted means (CWM) and proportions over climatic, soil, and disturbance gradients. These were run using the following weakly informative, non-flat priors:

$$Trait\ CWM \sim Log\ normal\ (\mu, \sigma)$$

μ ~ Normal (0, 1)

σ ~ Normal (0, 1)

$$Trait\ CWM \sim Gamma\ (\alpha, \beta, \phi)$$

α ~ Normal (0, 1)

β ~ Normal (0, 1)

ϕ ~ Gamma (0.01, 0.01)

$$Trait\ proportion \sim Beta\ (\mu, \phi)$$

μ ~ Normal (0, 1)

ϕ ~ Normal (0, 1)

Table S1. Tests for phylogenetic signal in our 12 traits

Trait	Pagel's λ	P-value
Wood density	0.99	<0.001
Growth rate	0.07	0.05
Max height	0.26	<0.001
Allometric height	0.26	<0.001
Leaf area	0.49	<0.001
Spinescence	0.99	<0.001
SLA	0.25	<0.001
Leaf nitrogen	0.49	<0.001
Number of stems	0	1
Bark thickness	0.12	0.28
Deciduousness	0.57	<0.001
Nitrogen fixing	0.97	<0.001
Seed dry mass	1	<0.001

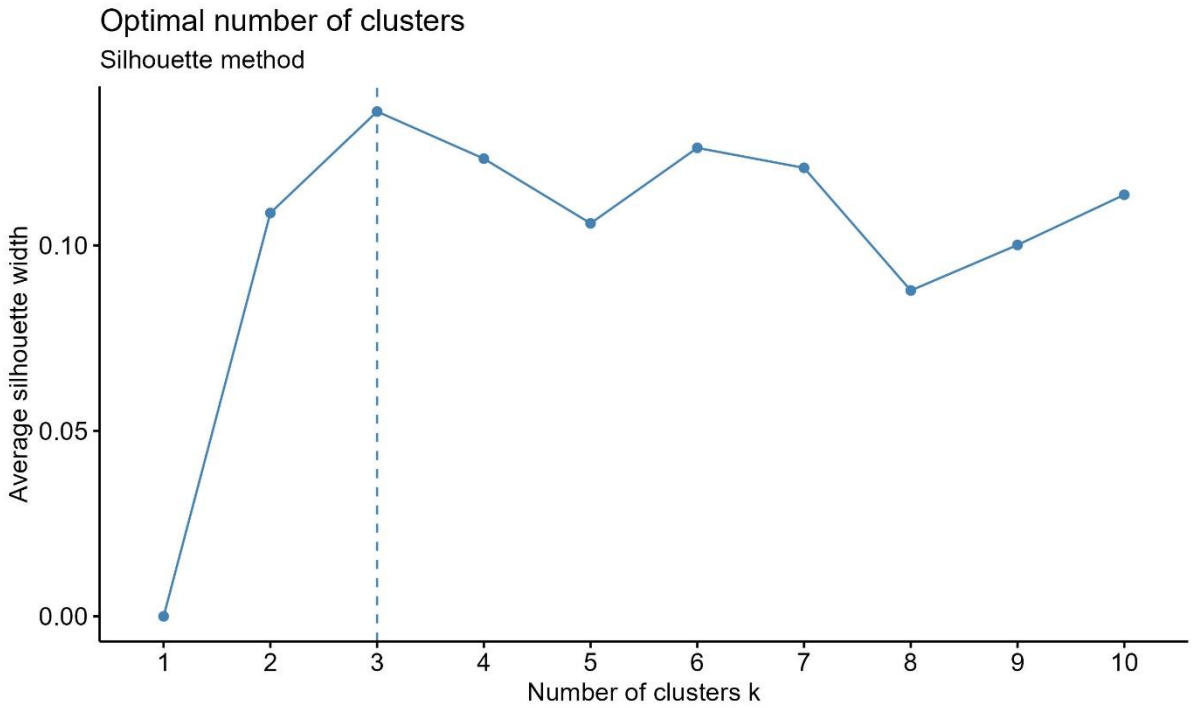

Figure S2. Silhouette plot to identify optimal number of clusters for k-means clustering analysis

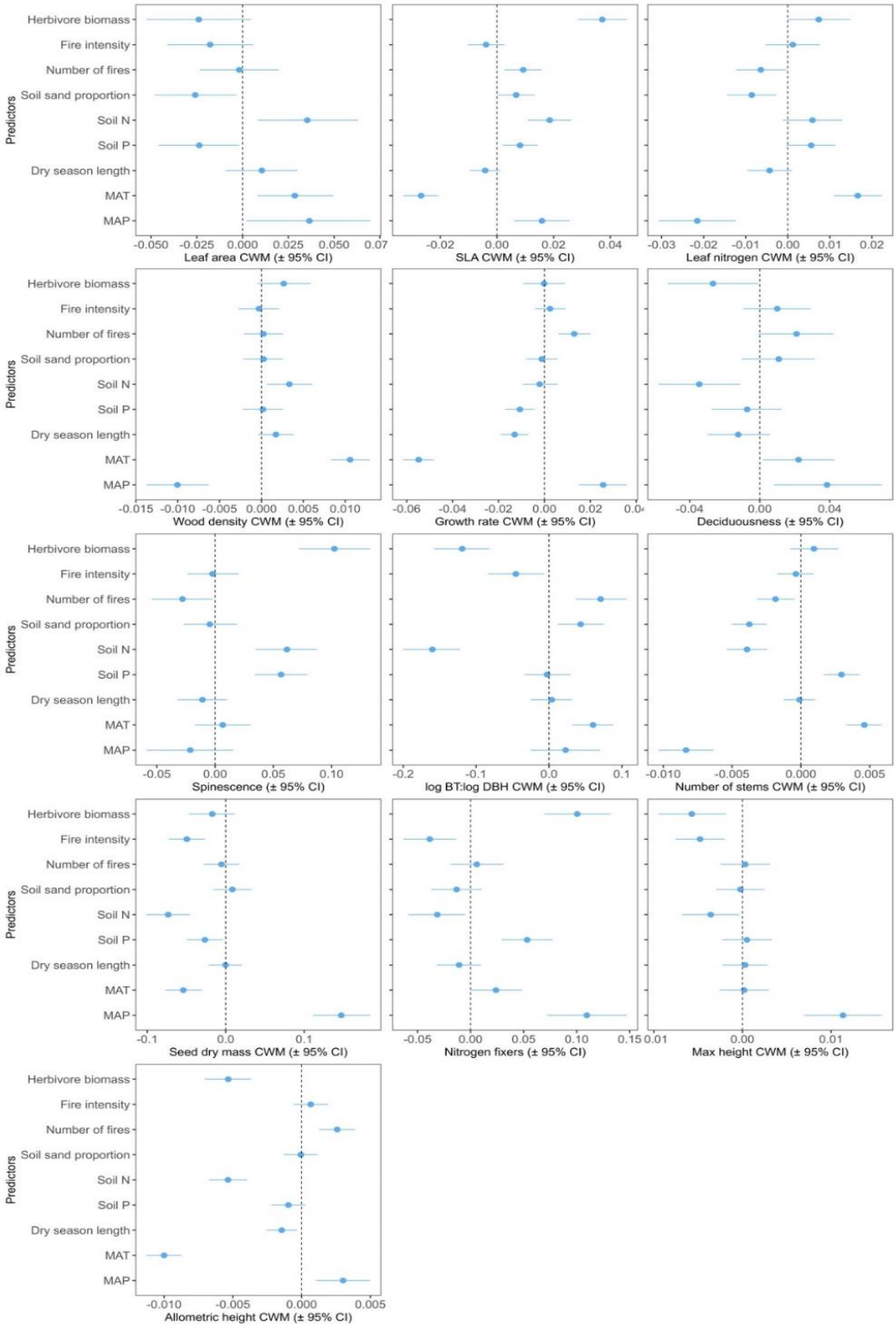

Figure S3. Coefficient plots showing the effect size of each predictor on the CWM or proportion of each of our 13 traits. Standard effect sizes show the median of the posterior and 95% credible intervals (CI). Points to the left of the dashed line had a negative effect on cluster proportion, whilst those to the right had a positive effect.

Chapter 4:

Protecting habitats in low-intensity tropical farmland using carbon-based payments for ecosystem services

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4.1 Abstract

Tropical land-use change for agricultural expansion is the primary driver of global biodiversity decline. Efforts to stem this decline often focus on protecting pristine habitats or returning farmland to forest, yet such approaches fail to protect vulnerable taxa reliant on habitats within low-intensity farmland. We assess the economic viability of carbon-based payments for ecosystem services (PES) to protect farmland trees and fallowing in Ghana, which provide vital wintering sites for imperiled Afro-palearctic migrant birds and enhance landscape-level carbon storage. We estimate the carbon breakeven prices associated with alternative agricultural management scenarios that protect existing farmland trees. Breakeven prices associated with tree protection on existing farmland were very low, ranging from US$2.49 – US$6.45 t^{-1} CO_2. Extending and reintroducing fallow periods also carried competitive breakeven prices, US$4.67 – US$15.45 t^{-1} CO_2, when combined with the protection of 50 trees per hectare. Accounting for leakage and economic uncertainty increased breakeven prices considerably, but scenarios protecting farmland trees and extending fallow periods remained below EU Emissions Trading Scheme (ETS) prices. Protecting low-intensity farmland habitats and associated biodiversity is cost-effective under carbon-based PES. Implementation should be combined with efforts to close yield gaps, providing greater local food security and resilience.

Keywords: carbon-based payments for ecosystem services, farmland habitats, opportunity cost, palearctic migrants, land sharing

4.2 Introduction

Agricultural expansion is the greatest threat to global biodiversity (Laurance, 2007). Replacement of natural habitats with crops and grazing for livestock leads to declines in biodiversity (Gibson *et al*., 2011), with disastrous consequences for ecosystem functioning and service provision (Cardinale *et al*., 2012). With global population and food demand projected to continue rising to at least 2050 (Tilman *et al*., 2011), agricultural expansion and intensification will persist, largely to the detriment of global biodiversity (Laurance *et al*., 2014).

Conservation efforts often seek to prevent or reverse tropical agricultural expansion by prohibiting the clearance of forests (Peres, 2005) or encouraging forest regrowth on abandoned agricultural land (Gilroy *et al*., 2014). For instance, sparing primary tropical forest from conversion or allowing secondary forest regrowth on abandoned farmland via agricultural intensification will conserve more biodiversity than protecting wildlife within farmland (land sharing) (Phalan *et al*., 2011; Edwards *et al*., 2021). However, boosting agricultural yields via intensification reduces 'wildlife-friendly' habitat within agricultural land (Fischer *et al*., 2008) or shortens fallow periods (Morton *et al*., 2020), which is detrimental to populations reliant on low-intensity agriculture (Pywell *et al*., 2014) or agroforestry (Bhagwat *et al*., 2008). Land-sparing is often the most effective method of conserving biodiversity (Luskin *et al*., 2018). However, in areas with a long history of human disturbance a hybrid 'three-compartment' approach, whereby some low-intensity farmland is retained alongside natural habitat on land that is spared as result of high-intensity agriculture, allows the persistence of species reliant on both natural habitat and low-intensity farmland (Feniuk *et al*., 2019).

Low-intensity farmland habitats are particularly important for migratory species (Jones *et al*., 1996). For example, low-intensity farmland provides wintering habitat for Himalayan

bird species (Elsen *et al*., 2017), whilst Afro-Palearctic migrants commonly spend the winter in farmland of sub-Saharan West Africa (Morel & Morel 1992). Long-distance Afro-Palearctic migrants have suffered greater declines than either short-distance migrants or resident species (Sanderson *et al*., 2006), and destruction of wintering habitats on low-intensity farmland in sub-Saharan Africa is one of the potential drivers of their population declines (Vickery *et al*., 2014). Isolated, mature farmland trees have a disproportionately high positive effect on biodiversity (Fischer *et al*., 2010; Douglas *et al*., 2014), whilst fallowed land provides suitable habitat for migratory bird species (Deikumah *et* al., 2017). However, farmland tree cover is declining (Gonzalez *et al*., 2014) and fallow cycles have been shortened or abandoned entirely in an effort to increase productivity (Evenson & Gollin, 2003). With food demand likely to continue to increase pressure on farmers to intensify, ensuring the protection of low-intensity farmland habitats is vital to safeguard populations of declining taxa, including migratory birds.

Given limited global conservation funding (Maxwell *et al*., 2015), a key question is whether it is economically viable to fund the retention of low-intensity farmland of particular importance to biodiversity under carbon-based payments for ecosystem service schemes. Carbon-based PES schemes used to fund conservation action often focus on preventing forest loss or returning farmland to forest. For example, raising agricultural yields on existing farmland and increasing charcoal-use efficiency in Tanzania can prevent forest conversion at US$6.50 t^{-1} CO_2 (Fisher *et al*., 2011). Similarly, abandonment of cattle pasture in the Colombian Andes and shortening of fallow periods in shifting cultivation farmland in North-east India allow forest regeneration at US$1.99 t^{-1} CO_2 and US$0.89 t^{-1} CO_2 breakeven prices, respectively (Gilroy *et al*., 2014; Morton *et al*., 2020). With agriculture now the dominant global land use (Ellis & Ramankutty, 2008), finding cost-effective ways to also protect and boost rare farmland taxa is vital to meet biodiversity conservation goals.

Here, we examine the economics of alternative agricultural land management scenarios, calculating the opportunity costs and carbon breakeven prices of protecting existing tropical farmland habitats for the benefit of migratory bird populations. We focus on Ghana, where agriculture is the mainstay in the country's economy, similar to many developing countries (Dethier & Effenberger 2012). High habitat diversity and mosaics of agriculture, grasslands, shrublands, and forests provide important habitats for palearctic migrants - particularly in the Guinea-Congolian/Sudanian transition (Mallord *et al*., 2016; Deikumah *et al*., 2017). However, population growth and increased food demand is increasing pressure on farmers to expand and intensify (Zhang *et al*., 2021), which threatens the persistence of these important habitats and the biodiversity they support.

Using secondary, nationally representative, economic data for Ghana, we simulate the cost of (i) protecting existing trees in agricultural land and (ii) extending and reintroducing fallows to farmland. We measure the potential carbon protected in these landscapes, and the future carbon accrued as trees mature over the project period, using tree inventory data from across Ghana. We simulate opportunity costs and carbon breakeven prices for multiple cropping scenarios at two tree densities - reflecting a diversity of farming practices and attitudes to farmland trees - to assess the potential for carbon-based PES schemes to protect farmland habitats.

4.3 Methods

Study area and data collection

Agriculture in Ghana has been an integral part of the country's progression towards middle-income country status (Breisinger *et al*., 2009). The country is dominated by smallholders, with over 90% of farms <2 ha (MOFA 2012), and characterized by low yields (Wongnaa *et al*., 2019) and minimal fertilizer use (Callo-Concha *et al*., 2012). Approximately 80% of land in Ghana

is under customary tenure (Pande & Udry 2005). Land-use rights are mostly granted by village chiefs, although, having cleared land for cultivation, land is customarily recognized as the property of the farmer (Chapoto *et al*., 2013). Despite steady economic growth (average growth of 6.8% from 2005-2017; GLSS7), a large proportion of the population remain below the poverty line, and recent declines in poverty incidence have been minimal – reducing by only 0.8% between 2012/13 and 2016/17 (from 24.2% to 23.4%; GLSS7).

We gathered economic data on crop yields and prices, and agricultural input costs from the Ghana Living Standard Survey (GLSS 7). The GLSS collects information on the livelihoods and well-being of the population, including information on agricultural land use, yields, and costs, from a nationally representative sample of 15,000 households. From the GLSS we extracted yields and input costs for two staple crops: maize and cassava, and several secondary crops: groundnut, soybean, and plantain. Maize is the most important crop in Ghana, with a cropped area of 1 million ha in 2012 (MOFA 2012). Maize is commonly cropped in a fallow cycle, ranging from 1-5 years (Hansen *et al*., 2012), or intercropped with nitrifying legumes to maximise yields (Kermah *et al*., 2017). Cassava is an important source of calories across sub-Saharan Africa (De Souza *et al*., 2017) and has an important role in increasing food security as the roots can be harvested all year-round (Rahman & Awerije 2016) and potential exists to massively increase yields (Adiele *et al*., 2020).

All subsequent modelling and analyses were carried out in R version 4.0.2 (R Core Team 2020).

Agricultural management scenarios

We calculated opportunity costs (OC) and carbon breakeven prices (BEP) following similar methods to those previously used in other carbon-based PES schemes (Fisher *et al*., 2011; Morton *et al*., 2020) to allow for direct comparison. We modeled the OC and BEP associated with four different crop rotations: maize-fallow, maize-legume (groundnut and soybean),

cassava-only, and cassava-plantain, under three management scenarios. Scenarios 1 and 2 represent two of the most intense agricultural management regimes currently used in the region, whilst scenario 3 shows a potential route to reduce the intensification of these systems (Figure 1). Scenarios were modelled over a 30-year project period, a common length for PES schemes (See Fisher *et al*., 2011; Gilroy *et al*., 2014).

Scenarios 1-1.2 (Figure 1) represent a two-year fallow cycle, the most intensive form of agriculture that still utilises fallow periods, leaving 50% of land under fallow. Scenarios 1-1.2 were modelled for maize as it is uncommon to continuously grow maize on the same farmland without intercropping with legumes. Scenarios 2-2.2 represent continuous cultivation (Figure 1). We modelled scenarios 2-2.2 for maize-legume, cassava-only, and cassava-plantain crop rotations. Scenarios 3-3.2 show the conversion of both scenarios 1-1.2 and scenarios 2-2.2 to a three-year fallow cycle (Figure 1), leaving 66% of land under fallow. Scenario 3 was modelled for each of the four crop rotations, however, under the cassava-plantain system, plantain was retained in the landscape during fallow years.

Economic modelling

The net present value (NPV) of scenarios was calculated using economic models (full details of models and variables used is given in supplementary materials). Model parameters were set using GLSS data on crop yields and input costs (including hired labour, equipment, tools, transport, storage, fertilizer, seeds, irrigation, and fuel). To reflect variability in yields and input costs, we sampled parameter values from a normal distribution using the median value bounded by the upper and lower limits of the collected data, weighted by region to account for variable sampling intensity. All economic parameters were adjusted to 2019 US$. We performed 10,000 independent model runs for each scenario, sampling new model parameters each iteration.

We removed cases where farm NPV fell below US$0 (Figure S1; 33% of cases) from our calculations of OC and BEP. In these instances, we assume loss-making farmers are involved in informal markets, reflecting a survival strategy (Vorley, 2013), using crops to barter for goods and services, and so applying only economic value to the yields of these farmers is inappropriate and gave negative BEP. The OC of alternative scenarios were calculated as the difference between the NPV of the proposed scenario and the NPV of the most intensive alternative for that crop. Retaining trees in the landscape was assumed to have an OC related to an area of no production around that tree, scaled by the tree's size (see supplementary methods). We present OC per 6 ha as this allows us to compare all three farming systems to one another without having to use units < 1 ha, but our results are readily scalable to smaller or larger farm sizes.

Landscape carbon and breakeven price calculations

We calculated our carbon BEP based on the protection of existing farmland trees from removal. Trees are common features of farmland in Ghana (Hansen *et al*., 2012), but population growth, agricultural intensification, and high volatility in landscape transition has reduced tree cover across the Sahel and threatens the persistence of farmland trees (Niang *et al*., 2008; Gonzalez *et al*., 2014). For example, shea trees – a group with high economic and cultural value, and carbon sequestration potential (Takimoto *et al*., 2008) – are rapidly declining in parklands due to population growth and wood fuel demand (Okiror *et al*., 2012; Lovett & Phillips, 2018).

We populated our landscapes with randomly selected trees from an inventory sampled from three regions of Ghana: Ashanti, Brong Ahafo, and Eastern. The inventory contained information on tree species, height, diameter at breast height (DBH), and wood density for 4973 individuals of 128 species, with trees ranging from 5-190 cm DBH (Figure S2; see supplementary material for tree sampling methodology). Breakeven prices were calculated

assuming the protection of aboveground carbon contained within trees at the start of the project, plus the additional carbon sequestered over the 30-year project. The aboveground carbon held within trees was calculated using the allometric equation developed by Chave et al. (2014).

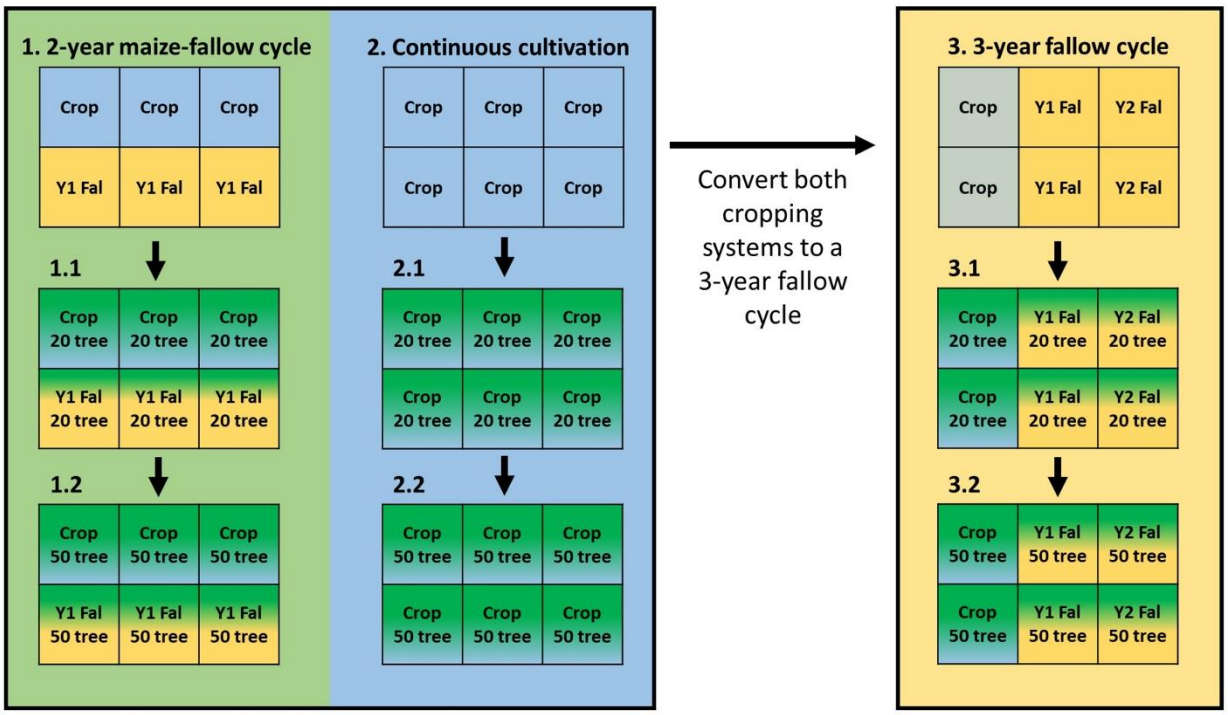

Figure 1. Current and alternative management scenarios for agricultural landscapes in West Africa. (A) Existing two-year maize-fallow cycles, with SC1.1 and SC1.2 showing the protection of 20 and 50 trees/ha, respectively. (B) Existing continuously cultivated farmland, with SC2.1-2.2 showing the protection of 20 and 50 trees/ha, respectively. Continuously cropped scenarios were modelled for three different crop types: maize intercropped with legumes, cassava-only, and cassava intercropped with plantain. (C) Conversion of both existing cropping systems to a three-year fallow cycle, with SC3.1 and SC3.2 showing the protection of 20 and 50 trees/ha, respectively. Colours represent land use: cultivated (blue), fallow (yellow), and tree density (green shading).

For scenarios 1.1, 2.1, and 3.1, we created landscapes in which tree density was set to 20 trees/ha (Figure 1), reflecting the mean tree density of the farmed parklands of the Sahel (Bayala *et al*., 2014). For scenarios 1.2, 2.2, and 3.2, tree density was set at 50 trees/ha, the average tree density of cropped land in northern Ghana (Hansen *et al*., 2012; Figure 1). Trees were randomly sampled with replacement from our inventory for each of the 10,000 model iterations we performed. Carbon accumulation over our 30-year project period was calculated by maintaining the randomly selected trees within our landscape over the project period and allowing these trees to grow each year, whilst recalculating aboveground carbon. Tree diameter

at breast height (DBH) was uniformly increased by 0.55 cm yr^{-1} for all trees - the best available estimate of annual tree growth in the region (Mbow *et al*., 2013).

Carbon breakeven prices were calculated for each of the scenarios using a modified version of the long-term certified emissions reduction scheme (lCER; see supplementary methods). Breakeven prices were calculated to offset both opportunity costs and the predicted costs of project monitoring and management. Monitoring costs were based on existing community-based monitoring schemes (Cranford and Mourato, 2011; Murtinho and Hayes, 2007; see supplementary methods).

Leakage and economic uncertainty

Preventing leakage of agricultural activity to regions with lesser restrictions (Latawiec *et al*., 2015) is likely to mean breakeven prices are higher than prices that are only equal to opportunity and management costs. Previous analysis suggests the cost of preventing leakage is likely to be equal to the opportunity costs associated with the project (Fisher *et al*., 2011). To account for this, and for potential fluctuations in discount rate, we performed a precautionary reanalysis, doubling opportunity costs and allowing discount rate to vary between 10%-25%. We also perform a reanalysis of our data with reference to a baseline of 10 trees/ha, reflecting instances whereby farmers may retain a very low density of trees on their farms given the benefits they provide (Sinare & Gordon, 2015).

Regional variations in breakeven prices

We calculated individual breakeven prices for ten regions across Ghana (Figure S3) using regionalized yield and input cost data extracted from the GLSS and regionalized inflation rates to convert these to 2019 US$ values. We compared breakeven costs between regions, and against the country-wide average, to identify the most cost-effective regions to implement alternative management scenarios.

4.4 Results

Opportunity costs of alternative management scenarios

Protecting trees in existing two-year maize-fallow (SC1) and continuous cultivation (SC2) farmland had low annual opportunity costs (Figure 2), ranging from US$14.17 to US$98.56 for 6 ha of land. Protecting trees in two-year maize-fallow carried the lowest opportunity costs, followed by continuously cultivated maize-legume, then cassava-only, with continuously cultivated cassava-plantain carrying the greatest opportunity cost.

Preventing the removal of trees from 6 ha of farmland currently under a two-year maize-fallow cycle had median annual opportunity costs of US$14.17 (SD; ±18.09) to protect 20 trees/ha (SC1.1) and US$39.41 (±38.44) for 50 trees/ha (SC1.2). Protecting trees in continuous cultivation scenarios (SC2) carried greater opportunity costs for all crop types compared to the maize-fallow system (Figure 2). Across 6 ha of continuously cropped cassava, protecting 20 trees/ha (SC2.1) cost US$33.81 (±42.43) and 50 trees/ha (SC2.2) was US$92.15 (±90.36). Maize intercropped with legumes had lower opportunity costs than both cassava crop systems at all tree densities (Figure 2), with preventing the removal of 20 trees/ha (SC2.1) costing US$31.06 (±29.18) and 50 trees/ha (SC2.2) costing US$85.03 (±57.19).

Converting existing two-year maize-fallow and continuous cultivation farmland into a three-year fallow cycle (SC3) had considerably higher opportunity costs than maintaining current regimes (Figure 2). However, extending a two-year maize-fallow cycle to a three-year maize-fallow cycle carried much lower opportunity costs than converting continuous cultivation systems to a three-year fallow (Figure 2). Extending a two-year maize-fallow cycle to a three-year cycle carried a median cost of US$57.04 (±55.90) for 6 ha of farmland. Exchanging continuous cultivation for a three-year fallow cycle (SC3) was more expensive for all crop types (Figure 2), with a median cost of converting maize-legume systems of

US$202.24 (±170.78), cassava-only systems of US$264.88 (±263.83), and cassava-plantain systems of US$217.35 (±207.36) for 6 ha of farmland.

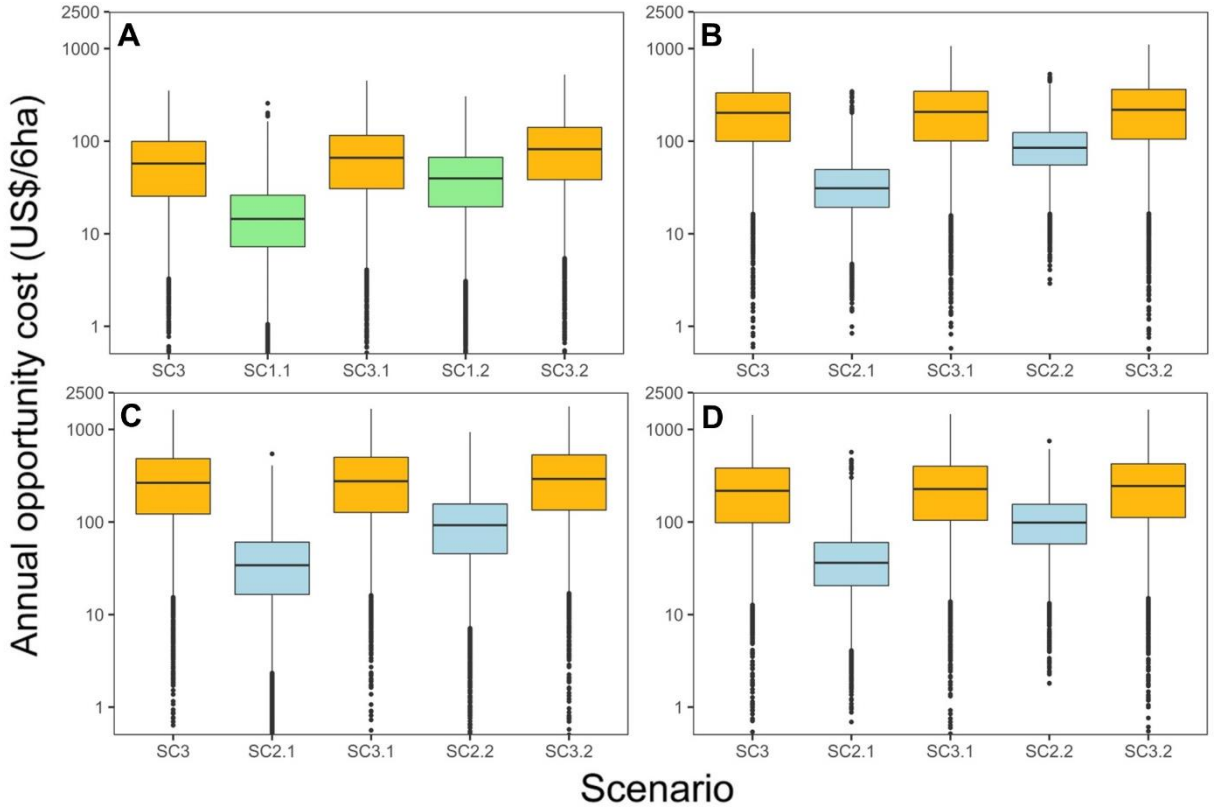

Figure 2. Annual opportunity cost of alternative landscape management over 6 ha of farmland for A) maize-fallow crop, B) maize-legume crop, C) cassava-only crop, and D) cassava-plantain crop. Box whisker plots show median, interquartile and 1.5 x interquartile ranges, and outliers. Plot colours indicate the agricultural system: two-year maize-fallow cycle (green), continuously cultivated (blue), and three-year fallow cycle (yellow). Opportunity costs are fitted to a log scale to aid clarity.

Protecting existing trees within the landscape post-conversion to a three-year fallow cycle had marginal effects on opportunity costs for all cropping systems. Over 6 ha of farmland, protecting 20 trees/ha in a three-year maize-fallow cycle (SC3.1) carried a median cost of US$65.86 (±64.42), whilst protecting 50 trees/ha (SC3.2) was US$81.70 (±77.14). Following conversion from continuous cultivation to a three-year fallow cycle, opportunity costs remained high for the other three crop types. Cassava carried the highest median costs, with protection of 20 trees/ha (SC3.1) costing US$275.48 (±273.52), and 50 trees/ha (SC3.2) costing US$291.69 (±287.60).

Carbon breakeven prices of alternative management scenarios

Carbon breakeven prices for protecting trees on farms whilst maintaining current agricultural practices were substantially lower than the breakeven prices for converting these systems to a three-year fallow cycle (Figure 3). Increasing tree density reduced breakeven prices in all scenarios and for all crop types (Figure 3). Protecting existing trees under a two-year maize-fallow regime (SC1) had the lowest breakeven price at all tree densities (Figure 3A), with a median price of US$3.22 (±1.93) t^{-1} CO_2 at 20 trees/ha (SC1.1) and US$2.49 (±1.80) t^{-1} CO_2 at 50 trees/ha (SC1.2). The breakeven price of protecting trees under continuous cultivation was lower in the maize-legume cropping regime than both the cassava and cassava-plantain regimes for all tree densities (Figure 3). The median breakeven prices for the maize-legume scenarios were US$5.61 (±2.81) t^{-1} CO_2 at 20 trees/ha (SC2.1) and US$4.96 (±2.58) t^{-1} CO_2 at 50 trees/ha (SC2.2). Both cassava regimes carried similar, but higher, breakeven prices, with cassava-only median prices of US$6.01 (±4.37) t^{-1} CO_2 at 20 trees/ha (SC2.1) and US$5.40 (±4.17) t^{-1} CO_2 at 50 trees/ha (SC2.2).

Extending existing two-year maize-fallow cycles to three-year fallow cycles (SC3) carried much lower breakeven prices than converting continuous cultivation scenarios, for all tree densities (Figure 3). Median breakeven prices for extending a two-year fallow cycle to a three-year fallow cycle were US$10.24 (±12.21) t^{-1} CO_2 at 20 trees/ha (SC3.1) and US$4.67 (±4.43) t^{-1} CO_2 at 50 trees/ha (SC3.2). Converting cassava-only continuous cultivation into a three-year cassava-fallow cycle carried the greatest breakeven prices, with median prices of US$39.88 (±54.48) t^{-1} CO_2 at 20 trees/ha (SC3.1) and US$15.45 (±18.01) t^{-1} CO_2 at 50 trees/ha (SC3.2).

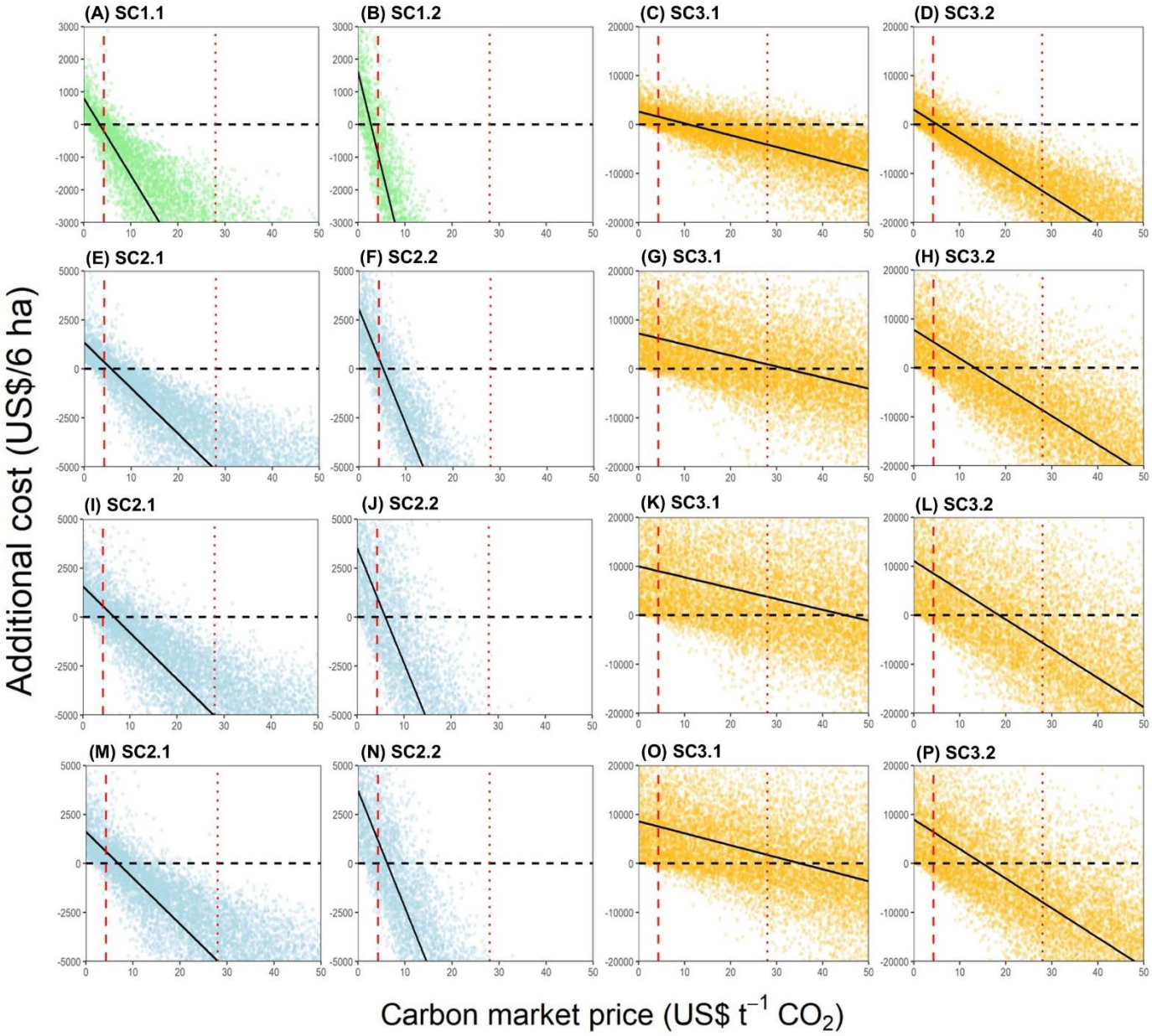

Figure 3. Carbon breakeven prices and additional costs of alternative management scenarios under a range of carbon market prices for maize-fallow (A-D), maize-legume (E-H), cassava-only (I-L), and cassava-plantain (M-P). Colours indicate the system: two-year fallow cycle (green), continuous cultivation (blue), and three-year fallow cycle (yellow). Economic models and carbon stocks were independently sampled and fitted each iteration for 10,000 unique model runs. Solid black lines show fitted linear models and dashed black lines show where no additional costs are incurred. Vertical red lines indicate global carbon prices, with the first dotted line = US$4.30 t-1CO2 (Average 2019 voluntary carbon market price), and the second dotted line = US$28 t-1CO2 (Average 2019 EU ETS carbon market price).

Leakage and economic uncertainty

Accounting for leakage and uncertainty in discount rates increased breakeven prices of protecting trees in existing cultivation scenarios (SC1.1-1.2 & SC2.1-2.2) by an average of 42%. In two-year maize-fallow systems, breakeven prices for protecting 20 trees/ha (SC1.1) increased to US$4.47 (±3.29) t^{-1} CO_2 (40% increase) and 50 trees/ha (SC1.2) increased to US$3.55 (±2.90) t^{-1} CO_2 (43% increase; Figure S5). In continuously cultivated cassava farmland breakeven prices were US$8.43 (±6.90) t^{-1} CO_2 for 20 trees/ha (SC2.1) and US$7.44 (±6.89) t^{-1} CO_2 for 50 trees/ha (SC2.2), an increase of 40% and 38%, respectively (Figure S5).

Breakeven prices of protecting trees in farmland post-conversion to a three-year fallow cycle (SC3.1-3.2) increased by an average of 46%. The breakeven price of extending a two-year maize-fallow cycle to a three-year fallow cycle and protecting 20 trees/ha (SC3.1) was US$14.56 (±20.61) t^{-1} CO_2 whilst protecting 50 trees/ha was US$6.68 (±7.13) t^{-1} CO_2, an increase of 42% and 43%, respectively (Figure S5). Converting continuously cultivated maize-legume and cassava-plantain cropping systems into a three-year fallow cycle carried breakeven prices, of US$42.29 (±55.42) t^{-1} CO_2 (46% increase) and US$45.09 (±66.50) t^{-1} CO_2 (41% increase) whilst protecting 20 trees/ha, and US$17.13 (±19.80) t^{-1} CO_2 (46% increase) and US$18.69 (±23.22) t^{-1} CO_2 (46% increase) whilst protecting 50 trees/ha (SC3.2), respectively (Figure S5).

Breakeven prices also increased when accounting for farmers optionally maintaining a very low tree density (10 trees/ha) on their land. Protecting farmland trees in existing cultivation scenarios increased by an average of 14% (Figure S6), with prices ranging from $2.59 (±1.82) t^{-1} CO_2 to $7.73 (±4.28) t^{-1} CO_2. Whilst extending fallow cycles from 2 to 3 years increased BEP by an average of 64% (Figure S6), with prices ranging from $5.38 (±5.33) t^{-1} CO_2 to $83.88 (±137.97) t^{-1} CO_2.

Regional differences in breakeven prices

The Northern region of Ghana had the lowest breakeven prices for alternative management scenarios for both maize-fallow and continuously cropped systems (Figure 4). The median breakeven prices of protecting trees in existing maize-fallow (SC1.2) of the Northern, Upper West, Central, and Brong Ahafo regions of Ghana were all below the country-wide median (Figure 4). For continuously cropped cassava systems, breakeven prices of protecting trees in the Northern, Central, and Brong Ahafo regions of Ghana were all below the country-wide median (Figure 4). Extending existing maize-fallow to a three-year cycle (SC3.2) carried breakeven prices lower than the national median in Northern, Upper West, Central, Eastern, and Brong Ahafo regions (Figure 4). Converting continuously cropped cassava to a three-year fallow cycle (SC3.2) was lower than the national median in Northern, Central, and Brong Ahafo regions (Figure 4).

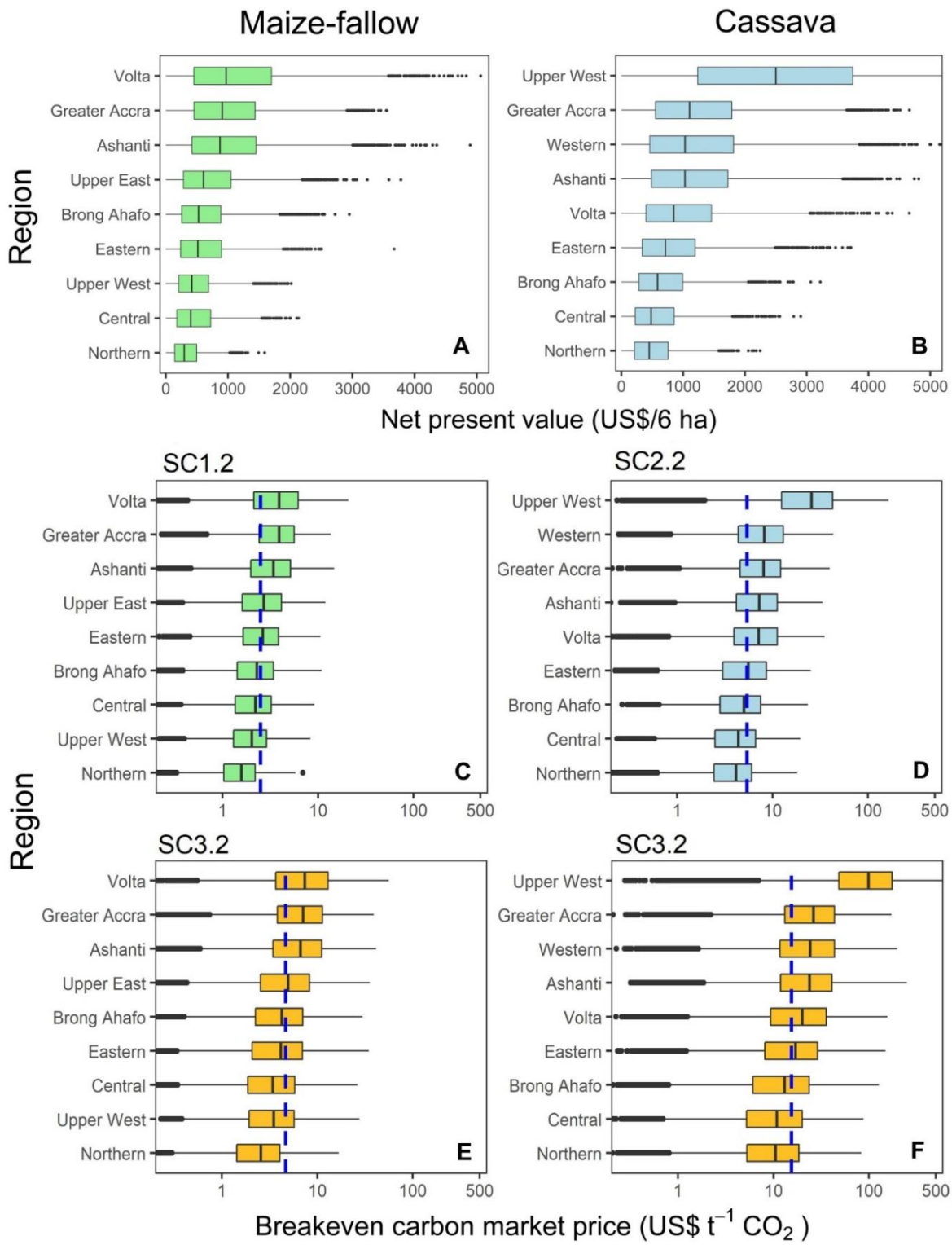

Figure 4. Regional net present value of existing A) maize-fallow and B) cassava farmland and carbon breakeven prices for alternative management scenarios for maize-fallow C) SC1.2 and E) SC3.2, and cassava D) SC2.2 and F) SC3.2. Box whisker plots show median, interquartile and 1.5 x interquartile ranges, and outliers. Plot colours indicate the agricultural system: two-year maize-fallow cycle (green), continuously cultivated (blue), and three-year fallow cycle (yellow). Breakeven prices are fitted to a log scale to aid clarity. Vertical, dashed blue lines indicate median breakeven prices from the country-wide analysis: maize-fallow SC1.2 = US$2.49 $t^{-1}CO_2$ and SC3.2 = US$4.67 $t^{-1}CO_2$, cassava SC2.2 = US$5.40 $t^{-1}CO_2$ and SC3.2 = US$15.45 $t^{-1}CO_2$.

4.5 Discussion

Low-intensity farmland provides important habitats for a variety of taxa, including migrant bird species, but is under increasing pressure of intensification to meet growing food demand. We show that protecting existing farmland trees using carbon-based PES schemes offers a cost-effective method to conserve important tropical farmland habitats. Additionally, opportunity costs incurred by introducing and extending fallow periods, which provide important habitat for vulnerable migratory bird species, can be offset using carbon-based PES when combined with tree protection.

Economic viability of alternative management scenarios

Opportunity costs of protecting trees in current farmland were very low for all cropping rotations and tree densities (US$14.17 - US$98.56 over 6 ha). Protecting isolated mature trees in farmland is vital given their disproportionate biodiversity value (Fischer *et al*., 2010) and positive influence on forest-specialist bird species (Deikumah *et al*., 2017). Introducing and extending fallow periods carried much greater opportunity costs (US$57.04– US$264.88 over 6 ha) but provides important habitats for migratory bird species (Deikumah *et al*., 2017). Encouraging the use of fallow periods and protecting farmland trees offers a win-win by protecting at-risk species and reducing carbon emissions associated with agricultural expansion and intensification.

Using carbon-based PES to protect trees in existing farmland carried low breakeven prices for all crop types and tree densities (US$2.48 – US$6.45 t^{-1} CO_2). These breakeven prices are comparable to those for forest protection through agricultural intensification (Fisher *et al*., 2011) and returning abandoned farmland to forest (Gilroy *et al*., 2014). Extending two-year fallow to a three-year cycle carried low breakeven prices when combined with tree protection (US$4.67 – US$10.24 t^{-1} CO_2). Breakeven prices for converting continuous cultivation

scenarios were much higher (US$11.75 – US$39.88 t^{-1} CO_2) due to the greater area of cultivation foregone. Despite this, breakeven prices for the protection of 50 trees/ha in a three-year fallow cycle are competitive compared to the average 2019 EU emissions trading system (ETS) carbon market price (US$28 t^{-1} CO_2). However, voluntary carbon market prices are often much lower (2019 average: US$4.30), with only the protection of trees in existing two-year maize-fallow systems competitive.

Northern regions of Ghana had the lowest breakeven prices for both maize- and cassava-based scenarios. Profit efficiency of Northern maize farmers is the lowest in Ghana (Wongnaa *et al*., 2019), hence the lower opportunity costs of alternative management scenarios. However, interventions in Northern Ghana should be taken with care as these regions are expected to experience the worst of climate effects on crop yields (Nyuor *et al*., 2016). Using payments to increase access to irrigation (Nyuor *et al*., 2016) and encouraging farmers to grow more cassava may counteract this, since cassava can be grown in marginal soils under irregular rainfall patterns (Howeler, 2017) and produces greater yields (Figure S1). Maximizing investment to these areas is the most cost-effective use of scarce conservation resources. However, the reduced growth rate of trees in the drier North may increase the time and area needed to achieve the same carbon sequestration as the wetter South. Future research could expand on our regional analysis and carry out more explicit spatial optimization, including an assessment of the carbon sequestration abilities of farmland over latitudinal and precipitation gradients and the implications of this for carbon-based PES.

Protecting 50 trees/ha carried lower breakeven prices than protecting 20 trees/ha due to the increased carbon protected (Figure S4). Low breakeven prices for tree protection are likely driven by low opportunity costs associated with maintaining trees in farmland, as the carbon protected in these landscapes is considerably lower than that accrued through forest succession (Morton *et al*., 2020) and primary forest protection (Fisher *et al*., 2011). However, our results

further demonstrate the potential of African agroforestry systems to deliver cost-effective carbon sequestration (Takimoto *et al*., 2008), whilst evidence from Mexican tropical dry forests suggests that short fallow cycles may enhance landscape-level carbon stocks (Salinas-Melgoza *et al*., 2017). We focused solely on the aboveground carbon stored in farmland trees, neglecting high soil organic carbon stored in even the most intensively managed shifting cultivation farmland (Bruun *et al*., 2020). Accounting for the additional carbon stored in soils with the introduction of a three-year fallow cycle would reduce breakeven prices. Whilst we did not consider carbon enhancements under REDD+, there is potential to increase the rates of tree recovery, growth, and carbon sequestration in shifting cultivation landscapes by optimizing fallow cycle lengths (Salinas-Melgoza *et al*., 2017) and restricting livestock browsing to certain areas of these landscapes (Morales-Barquero *et al*., 2015).

Combining the protection of low-intensity farmland habitats and the introduction of fallows with increased yields is necessary to ensure that lost production is not displaced to regions with lesser restrictions (i.e. leakage; Latawiec *et al*., 2015). Incorporating leakage and economic uncertainty into analyses increased breakeven prices considerably, but prices for protecting trees within existing farmland and in three-year fallow systems remained competitive compared to EU ETS prices (Figure S5). The sensitivity analysis to account for farmers preferentially maintaining very low tree density on their land (10 trees/ha), making fewer trees eligible for protection under a PES scheme, had a similar effect on BEP as the leakage analysis (Figure S6).

Ghanaian maize yields are far below the global average (Wongnaa *et al*., 2019), whilst fertilizer use in sub-Saharan Africa is amongst the lowest globally (Callo-Concha *et al*., 2012). Government targets for increasing fertilizer use have been consistently missed (currently 35.75 kg/ha compared with the Abuja Declaration on Fertilizer for an African Green Revolution which set 50 kg/ha as the primary target (MOFA, 2012; NEPAD, 2011)), with

potential for fertilizers to increase yields of maize and cassava (MacCarthy *et al*., 2018; Adiele *et al*., 2020). Interventions to reduce leakage would be best focused on increasing fertilizer use (Ragasa & Chapoto, 2017), introducing high-yielding varieties of crops (Walker & Alwang, 2015), and promoting mechanization (Diao *et al*., 2014). Policies that tie the provision of yield increases to the continued protection of farmland habitats as yield potential increases (Phalan *et al*., 2018) is important to safeguard vulnerable farmland bird populations. Additionally, with more people experiencing malnutrition in sub-Saharan Africa (OECD, 2018), relative to other regions, and with climate change expected to exacerbate food supply issues (Wheeler & von Braun, 2013) and socio-economic challenges such as educational attendance (Agamile & Lawson, 2021), improving food security for local people is paramount to long-term project success.

Land-sparing overwhelmingly remains the most effective method to protect global biodiversity (Luskin *et al*., 2018), however, the need to support species reliant on low-yielding farmland points towards a hybrid 'three-compartment' approach, combining high-intensity farmland with low-intensity (conservation) farmland and spared natural habitat blocks (Feniuk *et al*., 2019). The effectiveness of sparing is determined by its ability to minimize the externalities associated with intensification and to free land for nature (Balmford et al., 2018). For example, over-reliance on external inputs (agrochemicals) incurs large carbon emissions – although their widespread use is a long way off in sub-Saharan Africa (Vitousek et al., 2009). Maintaining trees in farmland provides several ecosystem services, including water regulation, nutrient cycling, and reduced soil erosion (Bayala et al., 2014), as well as benefits for open-country species (Douglas *et al*., 2014). However, trees may compete with crops for resources or provide refuge for pests, with the effect of trees on crop yields in the region remaining unresolved (Bayala et al., 2012).

Our study points to the potential for carbon funding to support the retention of low-intensity farmland. Furthermore, such actions would intersect with Forest and Landscape Restoration (FLR) projects aiming to protect and enhance carbon stocks within farmland (Sabogal *et al*., 2015), whilst reversing landscape degradation that impacts food security.

Study caveats

Firstly, we used uniform growth rates for all trees, regardless of age and species, due to limited species-specific tree growth data from the region. Tree growth and carbon sequestration is likely to be non-linear and species-specific (Stephenson *et al*., 2014). Instead, we applied a uniform DBH growth rate of 0.55 cm yr^{-1}, an average for West African savanna tree growth (Mbow *et al*., 2013), recalculating tree carbon annually using the allometric equations of Chave et al. (2014). This likely generates conservative estimates of carbon accrual since large, old trees fix large amounts of carbon annually (Stephenson *et al*., 2014) and DBH growth rates for middle-aged and mature trees is likely greater than 0.55 cm yr^{-1} (Groenendijk *et al*., 2017).

Secondly, fallowed land and mature trees could provide alternative income to farmers. Forest and non-forest environmental products can provide up to 38% (Appiah *et al*., 2007) and 13-23% (Pouliot *et al*., 2012) of household income, respectively. Incorporating this alternative income source into our opportunity cost models could drive breakeven prices down further, while adding extra security to farmer's livelihoods (Weston *et al*., 2015).

Thirdly, data errors or high variance in market prices (Table S2) and discount rates could influence our BEP, therefore a sensitivity analysis was undertaken (Figures S6-S13) to test for potential effects on our BEP. Additionally, in excluding NPV below US$0 (33% of cases), our BEP is only applicable to profit-making farmers. The large number of loss-making and subsistence farmers in our data is reflective of agriculture in sub-Saharan Africa (AGRA 2017), where a high proportion of farmers are not involved in formal markets. Likewise,

unreliable rainfall, extreme climatic events, and invasive species decimate crop yields, incurring heavy losses to farmers (Pratt *et al*., 2017) and accentuating negative socio-economic impacts (Agamile & Lawson, 2021). As a result, many farmers may be reliant on off-farm activities (Pouliot *et al*., 2012) and non-timber forest products to supplement their incomes (Appiah *et al*., 2007). Loss-making farmers are usually more engaged in informal markets – trading food for education, transport, etc. – making it difficult to quantify economic yields from their land and give accurate OC and BEP. In these instances, increasing access to education and other vital goods and services may be a more appropriate method of compensation for farmers.

Land tenure systems in Ghana are mostly customary and extremely diverse (Lambrecht & Asare 2016), with land rights granted by village chiefs (Chapoto *et al*., 2013). Carbon rights in Ghana have yet to be defined, with community-based resource management areas designated as the preferred method of PES implementation (Asare & Kwakye 2013). Hence, project implementation may be reliant upon the support of village leaders and the wider community as opposed to just that of individual farmers, compounding the need for wide stakeholder involvement in project development. Finally, whilst we lack local-level data on farmer's management of farmland trees, we simulate multiple cropping scenarios with two different farmland tree densities using globally accepted secondary data. This forms the basis for further investigation in the region, which may consider the rationale and trends behind farmer's attitudes to farmland trees.

Conclusions

Previous analyses of the viability of carbon-based PES schemes have largely focused on returning tropical farmland to forest or protecting remaining forests. Whilst these measures conserve forest biodiversity, they do not protect rare taxa within low-intensity farmland, including many migratory bird species. We demonstrate that use of carbon-based PES to protect

farmland habitats offers a cost-effective method of conserving such species. Combining the re-introduction of fallow periods with the protection of farmland trees offers competitive breakeven prices, comparable to those associated with forest protection and regeneration. Measures taken to protect farmland habitats, however, must be integrated with actions to boost yields, preventing leakage and providing increased food security for local people.

Acknowledgements

We thank the Ghana Forest Department for granting permission to carry out the work, Ghana Wildlife Society for logistical assistance with the fieldwork, and all landowners and farmers who allowed access to their land.

4.6 Supplementary Material

Supplementary methods

Net present value calculations

The net present value (NPV) of each scenario was calculated using economic models (supplementary table 1). NPV was calculated for a 6 ha landscape for all scenarios, with yield and input cost data acquired from the Ghana Living Standards Survey (GLSS7) and converted to 2019 US$/ha. All NPV calculations were discounted annually at 12%. We performed a precautionary reanalysis that included the assumed costs of leakage (by doubling OC) and allowed discount rate to vary between 10% and 25% to reflect uncertainty.

The NPV of 6 ha of farmland under scenario 1 (maize-fallow crop in a two-year cycle) was calculated as the yield of 3 ha of maize cultivation minus the agricultural costs of cultivating 3 ha of maize. For scenario 2, continuously cultivated crops (maize-legume, cassava, and cassava-plantain), the NPV was calculated as 6 ha of cultivated land minus the 6 ha of associated input costs. For cassava-plantain crop rotations, crop proportions were kept constant, with cassava covering 80% of cultivated land and plantain 20%. For the maize-legume cropping rotation, the proportion of maize was kept at 60% of cultivated area, but the relative proportions of groundnut and soybean were allowed to vary each iteration. 10,000 unique dirichlet distributions were used to ensure that the varying proportions of groundnut and soybean = 40% of cultivated land each iteration. For scenario 3, all systems were converted to a three-year fallow cycle. Therefore, the NPV of 6 ha of farmland under scenario 3 was calculated as the yield of 2 ha of cultivated land minus the cost of cultivating 2 ha. For the cassava-plantain crop rotation, plantain was maintained during the fallow period. Meaning the net present value of cassava-plantain in scenario 3 was as described above, with an additional 0.8 hectares of plantain yield (20% of 1 ha = 0.2ha, 0.2 ha x 4 = 0.8 ha).

When calculating the NPV of scenarios that protect trees in the landscape (scenarios 1.1, 1.2, 2.1, 2.2, 3.1, and 3.2) the same formulae as described above was used, however, we assumed a yield cost of retaining trees in the farmland. The yield cost was calculated as a circle of no production around the tree, with the radius of no production given as 10x the tree's DBH (*PC*). As with the calculation of carbon accrual, tree DBH was uniformly increased by 0.55 cm yr^{-1}, with the area of no production around each individual tree recalculated each year to account for growth. Trees were randomly sampled with replacement for each of the 10,000 model iterations, with the same trees used in the carbon accounting calculations.

Tree Sampling

Tree sampling took place in five study areas along the border of the Eastern Guinean Forest and Guinean forest-savanna ecoregions in the Eastern, Ashanti, and Brong Ahafo Regions of Ghana. Sampling areas were separated by at least 30km, with sampling conducted from November 2017 to March 2018.

At each sampling point we established 5 plots to record tree measurements. The plots consisted of a 25m radius circle surrounding the central point, and four 10m radius circles centred 50m away from the central point in the cardinal directions. The DBH and height of all trees (≥5 cm DBH) was measured, with trees identified to species where possible by a local expert.

Breakeven price calculations

Breakeven prices were calculated as US$ t^{-1} CO_2 that was equal to the opportunity cost of our management scenarios and the associated costs of project management and monitoring over the project's 30-year period. Management and monitoring costs were taken from Cranford and Mourato (2011), and Murtinho and Hayes (2007), and inflation adjusted to 2019 US$. Project costs were independently sampled each iteration from a normal distribution bounded between

$0.52 and $18.36 for management costs, and $3.13 - $5.63 for community-level monitoring costs. It is important to note that these prices are estimates, and there is a high degree of variation to be expected over a project's lifespan and dependent on the monitoring method of choice (Böttcher *et al*., 2009).

We used a modified version of the long-term Certified Emissions Reduction (lCER) methodology to calculate carbon breakeven prices (Equation 1). Under lCER carbon credits are issued every 5 years for the project's 30-year duration. We discounted carbon accumulation at an annual rate of 2.5%. For deforestation and reforestation analyses a 12% carbon discount rate is often used. However, lower discount rates are used for avoided deforestation (AD) PES schemes due to the lower risk of carbon loss and the fact that carbon is already present in the landscape (Morton *et al*., 2020).

$$\sum_{1}^{n} \frac{lCER}{(1+AD_r)^n} = \frac{3.67*C^5}{(1+AD_r)^5} + \frac{(3.67*C^{10})-(3.67*C^5)}{(1+AD_r)^{10}} + \cdots + \frac{(3.67*C^{30})-(3.67*C^{25})}{(1+AD_r)^{30}}$$

where AD_r is the carbon discount rate of avoided deforestation (0.025)

Equation 1

Sensitivity analysis

To assess the effect changes in agricultural prices and other market trends would have on our breakeven prices we performed an elasticity-based sensitivity analysis. We used median parameter values multiplied by values from an elasticity index (*Elasticity index ~ U(1-4)*) to assess the potential for future changes in yields and input costs to influence our breakeven prices. In addition to this we allowed discount rate to vary between 10%-25% to reflect discount rate uncertainty.

Supplementary table 1. Models used to calculate NPV of all scenarios

Model	Applicable scenarios
$\sum_{t}^{n} \frac{(C_n * Y_{1,2}) - (C_n * I_{1,2})}{(1+r)^n}$	1, 2, 3
$\sum_{t}^{n} \frac{[C_n * (aY_2 + bY_3)] - (C_n * I_2)}{(1+r)^n}$ where a = 0.8 and b = 0.2	2, 3
$\sum_{t}^{n} \frac{[C_n * (cY_1 + dY_4 + eY_5)] - (C_n * I_1)}{(1+r)^n}$ where c = 0.6; 0 < d, e < 0.4; and d + e = 0.4	2, 3
$\sum_{t}^{n} \frac{[(C_n * Y_{1,2}) * \{1 - PC\}] - (C_n * I_{1,2})}{(1+r)^n}$	1.1, 1.2, 2.1, 2.2, 3.1, 3.2
$\sum_{t}^{n} \frac{C_n * [(aY_2 + bY_3) * \{1 - PC\}] - (C_n * I_2)}{(1+r)^n}$ where a = 0.8 and b = 0.2	2.1, 2.2, 3.1, 3.2
$\sum_{t}^{n} \frac{C_n * [(cY_1 + dY_4 + eY_5) * \{1 - PC\}] - (C_n * I_1)}{(1+r)^n}$ where c = 0.6; 0 < d, e < 0.4; and d + e = 0.4	2.1, 2.2, 3.1, 3.2

Supplementary table 2. Economic parameters for crop yields and input costs

Parameter	Variable	Median (US$/ha)	Lower value (US$/ha)	Upper value (US$/ha)
Maize yield	Y_1	129.12	0	8254
Cassava yield	Y_2	134.50	0	10759.68
Maize input cost	I_1	81.41	0	4429.40
Cassava input cost	I_2	80.88	0	5408.89
Plantain yield	Y_3	134.50	0	6379.26
Soybean yield	Y_4	80.70	0	2636.12
Groundnut yield	Y_5	184.24	0	7173.12

Supplementary table 3. Additional parameter values

Parameter	Variable	Value
Number of cultivated squares	C_n	2-6
Discount rate	r	0.12
Avoided deforestation discount rate	AD_r	0.025
Production cost of trees	PC	Variable (See supplementary methods)
Proportion of cassava	a	0.8
Proportion of plantain	b	0.2
Proportion of maize	c	0.6
Proportion of soybean	d	0 – 0.4
Proportion of groundnut	e	0 – 0.4

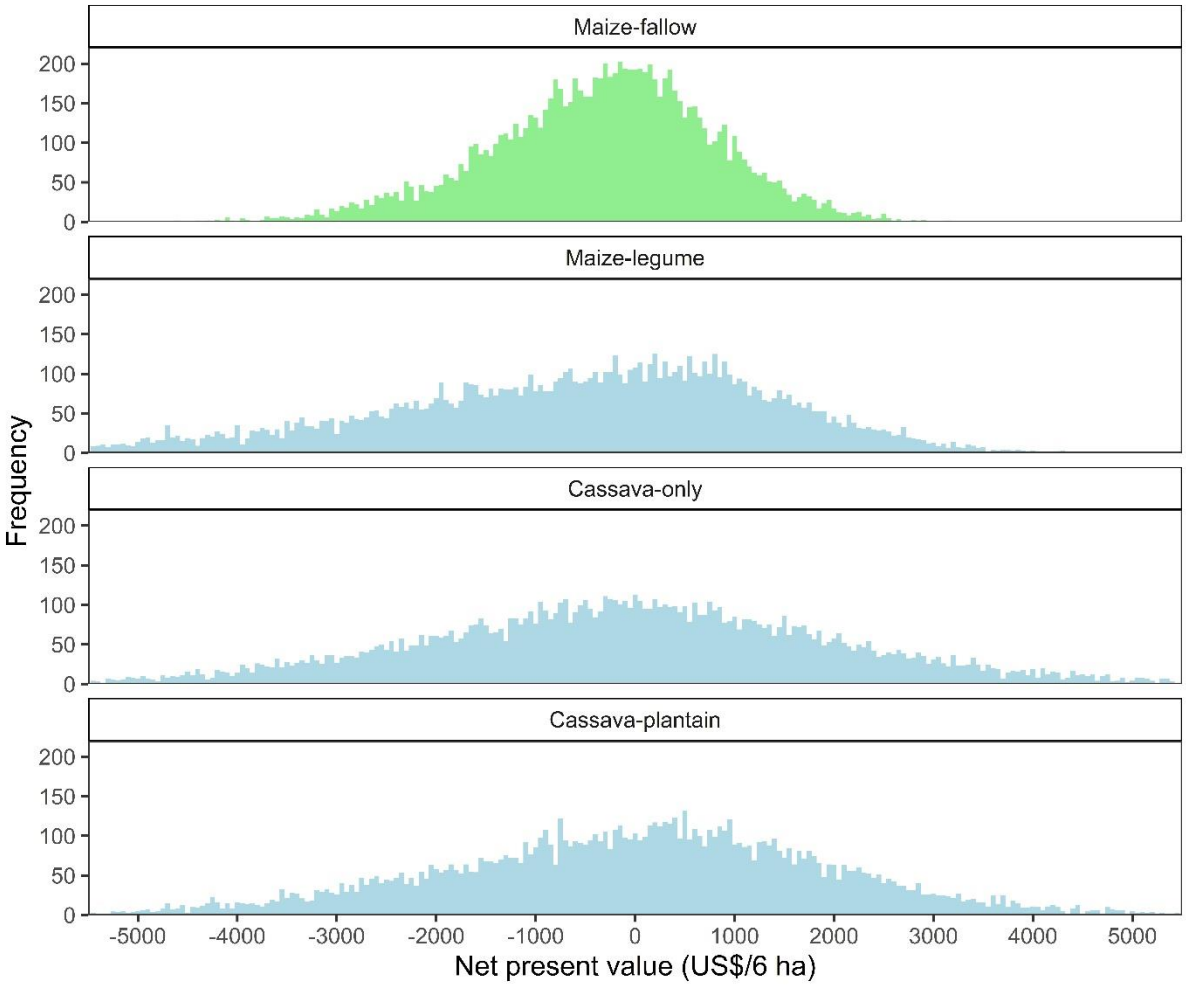

Figure S1. Net present value (NPV) of current cropping systems in Ghana. Frequencies of values is the result of 10,000 unique model runs using a normally distributed range of crop prices and farming costs. Bar colours indicate the agricultural system: two-year fallow cycle (SC1; green) and continuous cultivation (SC2; blue).

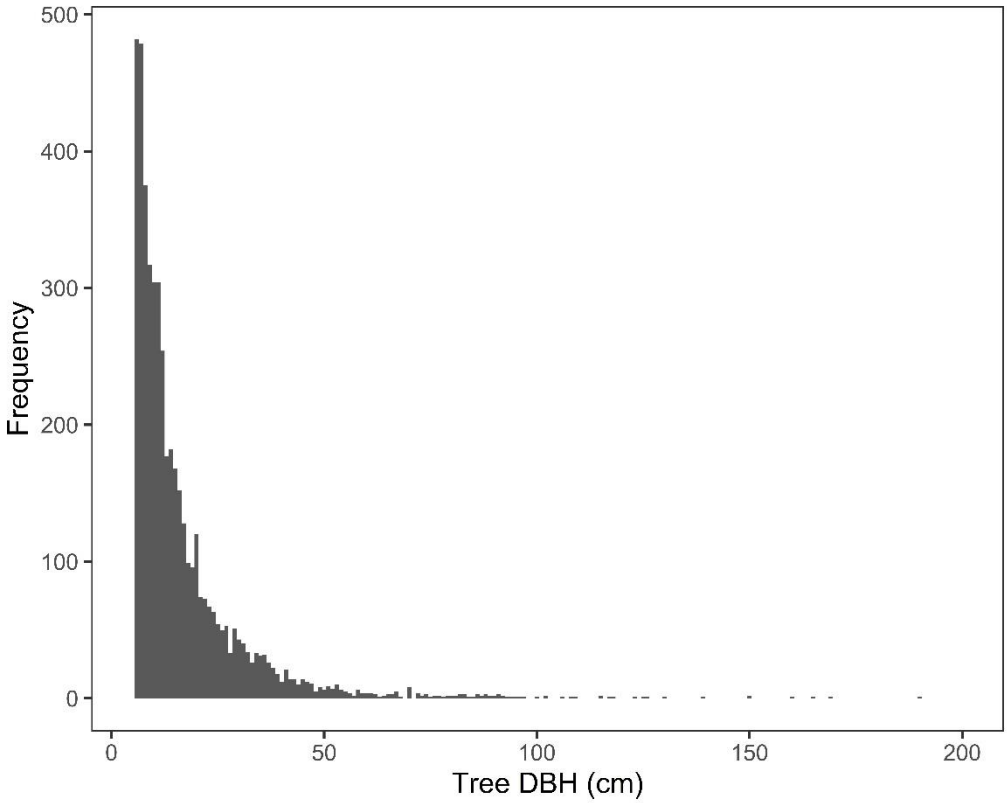

Figure S2. Distribution of tree size used to populate landscapes

Figure S3. Map of regions in Ghana

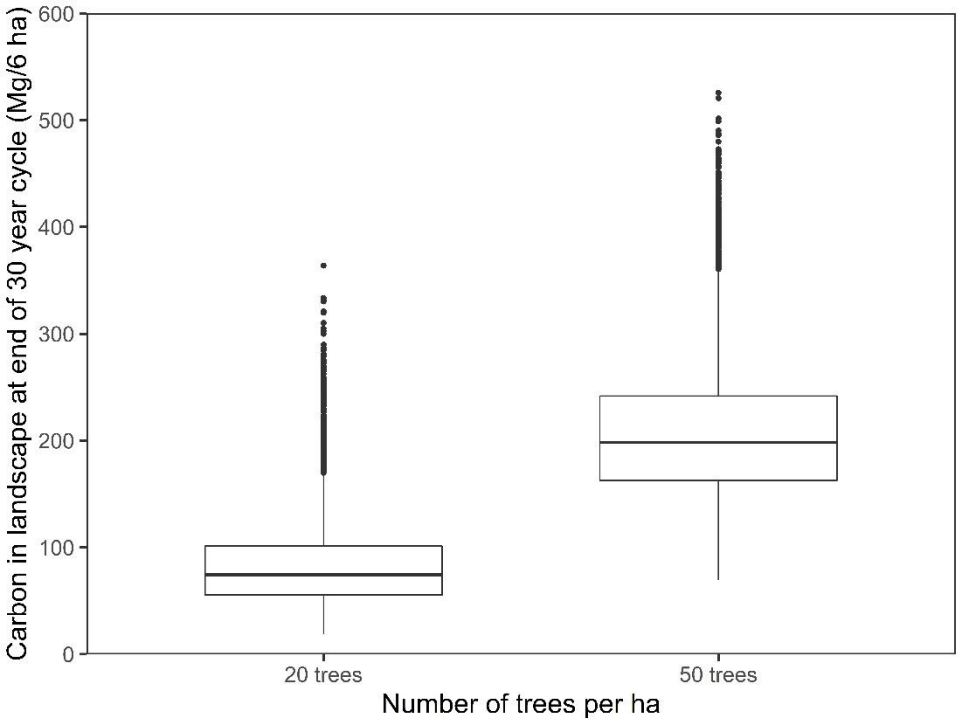

Figure S4. Carbon retained in the landscape when protecting 20 trees (SC1.1, SC2.1, and SC3.1) and 50 trees (SC1.2, SC2.2, and SC3.2) per ha. Box whisker plots show median, interquartile and 1.5 x interquartile ranges, and outliers.

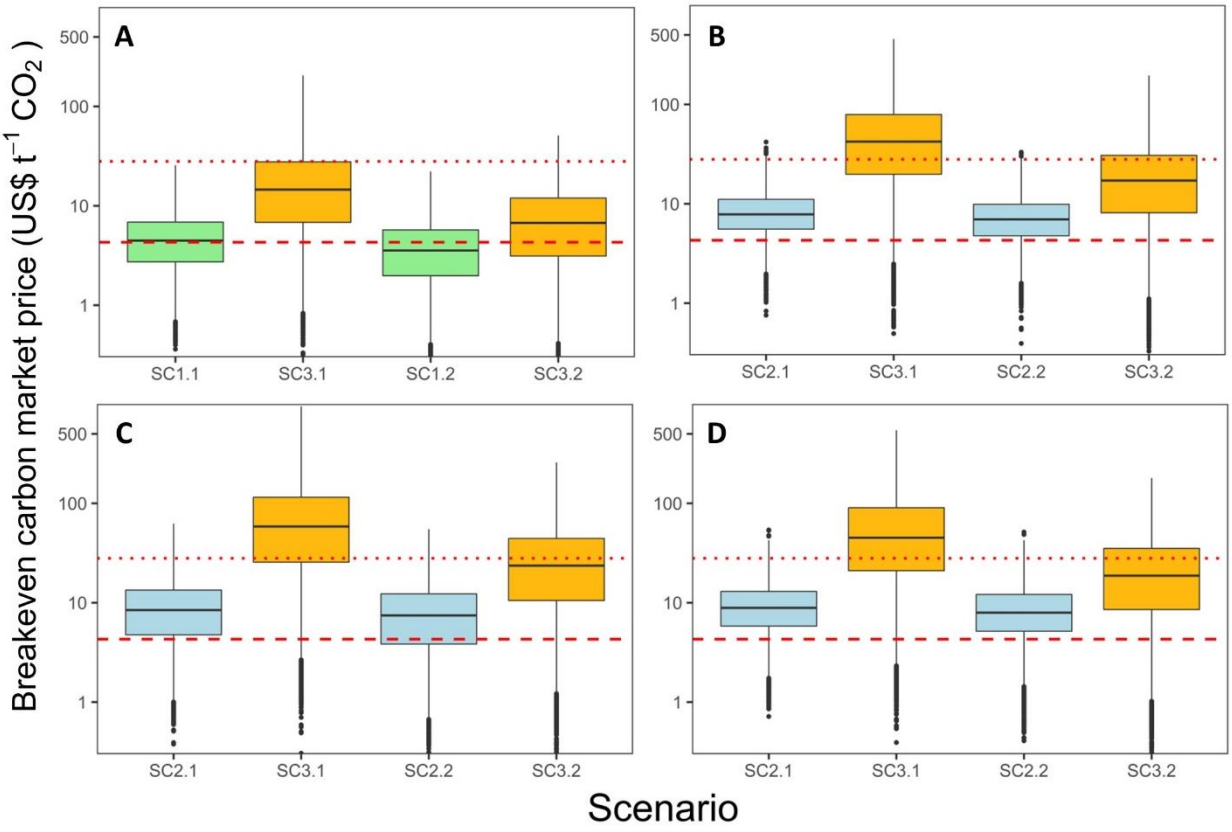

Figure S5. Breakeven prices of alternative management scenarios for existing A) maize-fallow, B) maize-legume, C) cassava, and D) cassava-plantain cropping systems accounting for leakage and economic uncertainty. Box whisker plots show median, interquartile and 1.5 x interquartile ranges, and outliers. Plot colours indicate the agricultural system: two-year maize-fallow cycle (green), continuously cultivated (blue), and three-year fallow cycle (yellow). Breakeven prices are fitted to a log scale to aid clarity. Horizontal red lines indicate global carbon prices, with the lower dotted line = US$4.30 $t^{-1}CO_2$ (Average 2019 voluntary carbon market price), and the upper dotted line = US$28 $t^{-1}CO_2$ (Average 2019 EU ETS carbon market price).

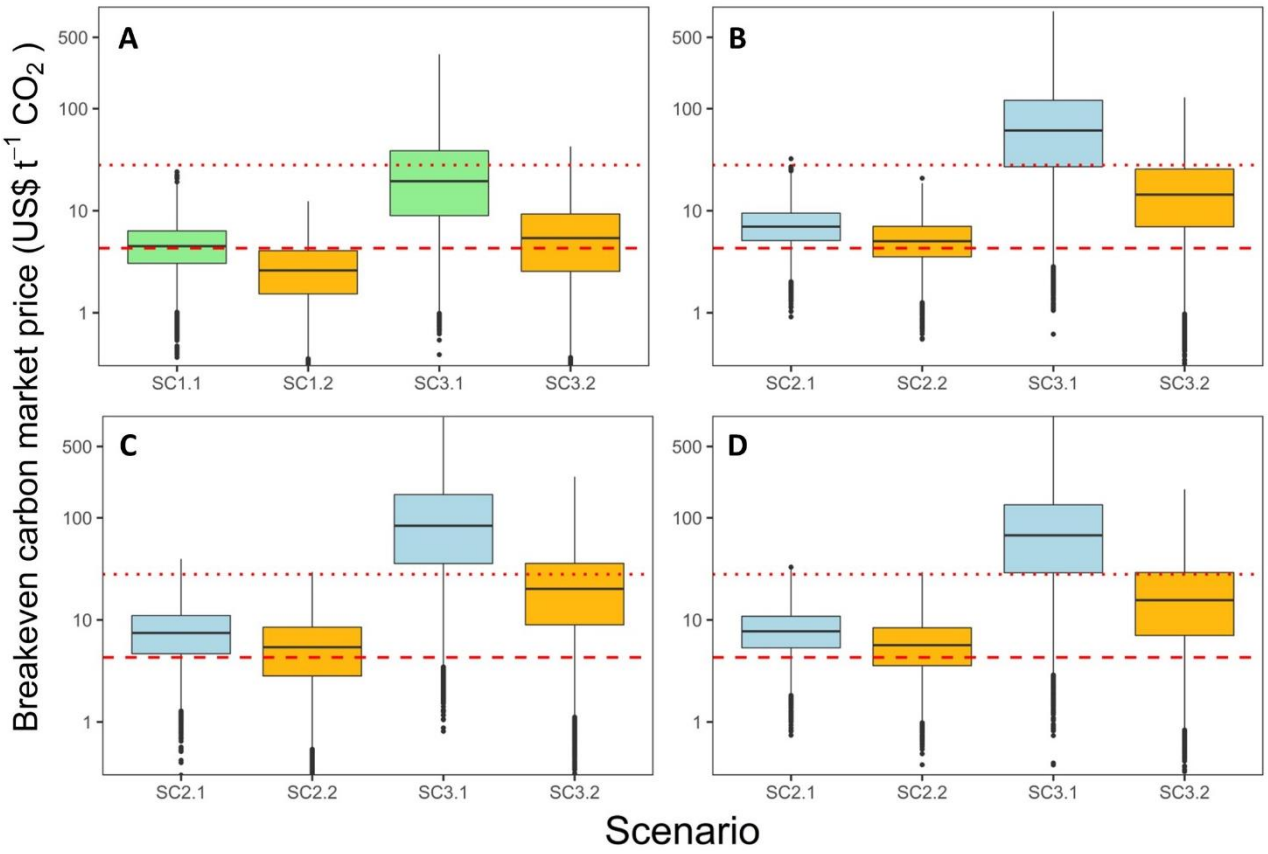

Figure S6. Breakeven prices of alternative management scenarios for existing A) maize-fallow, B) maize-legume, C) cassava, and D) cassava-plantain cropping systems assuming farmers would maintain a baseline of 10 trees/ha. Box whisker plots show median, interquartile and 1.5 x interquartile ranges, and outliers. Plot colours indicate the agricultural system: two-year maize-fallow cycle (green), continuously cultivated (blue), and three-year fallow cycle (yellow). Breakeven prices are fitted to a log scale to aid clarity. Horizontal red lines indicate global carbon prices, with the lower dotted line = US$4.30 $t^{-1}CO_2$ (Average 2019 voluntary carbon market price), and the upper dotted line = US$28 $t^{-1}CO_2$ (Average 2019 EU ETS carbon market price).

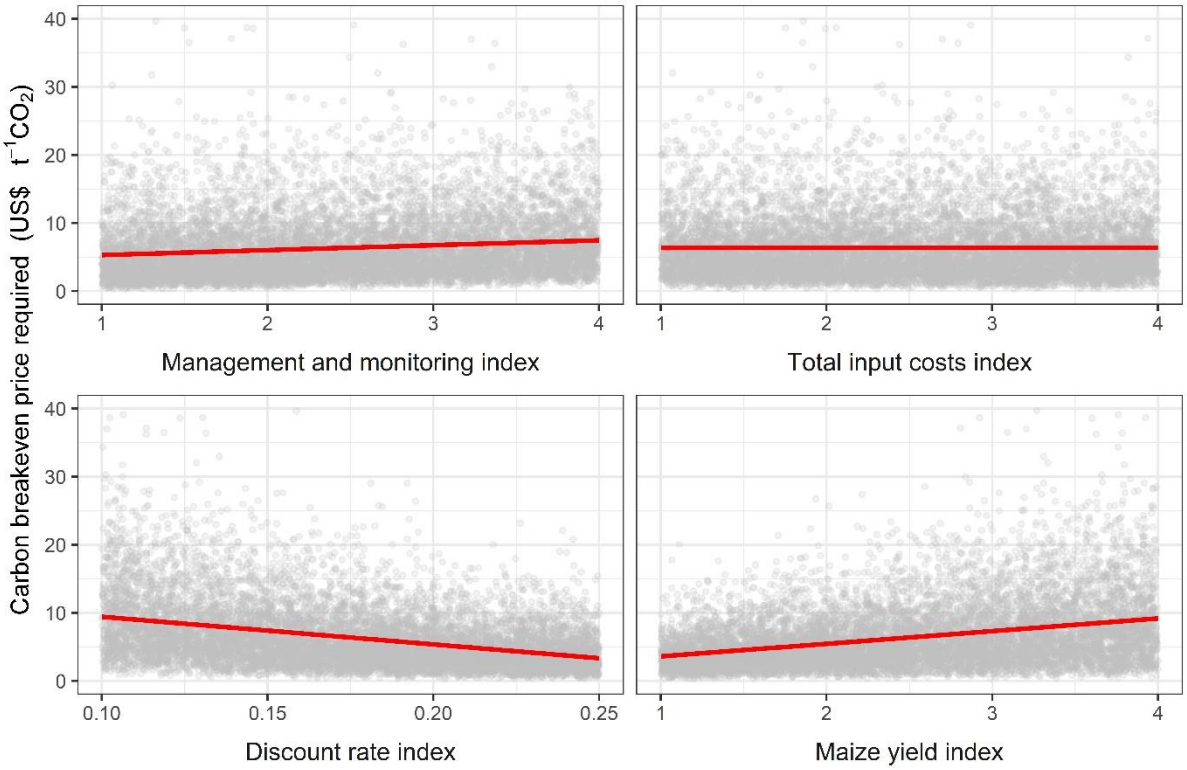

Figure S7. Sensitivity analysis of parameter variables' effect on the breakeven price of maize cultivation under scenario 1.1. Sensitivity analysis response is shown for the following variables: A) Management and monitoring costs, B) total input costs, C) discount rate, and D) maize yield index. 10,000 model runs were performed whereby parameter variables were multiplied by an index between 1 and 4, with each dot representing the breakeven price of one model run. The red lines show linear models relating index to the breakeven price.

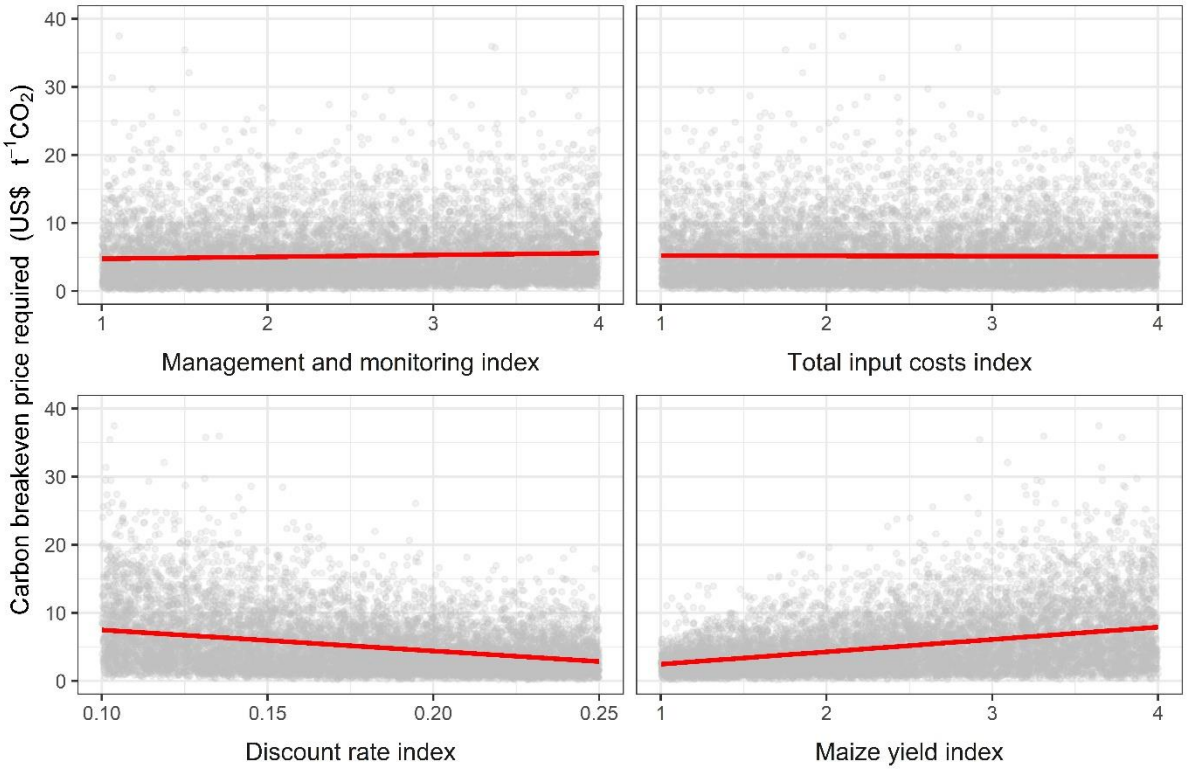

Figure S8. Sensitivity analysis of parameter variables' effect on the breakeven price of maize cultivation under scenario 1.2. Sensitivity analysis response is shown for the following variables: A) Management and monitoring costs, B) total input costs, C) discount rate, and D) maize yield index. 10,000 model runs were performed whereby parameter variables were multiplied by an index between 1 and 4, with each dot representing the breakeven price of one model run. The red lines show linear models relating index to the breakeven price.

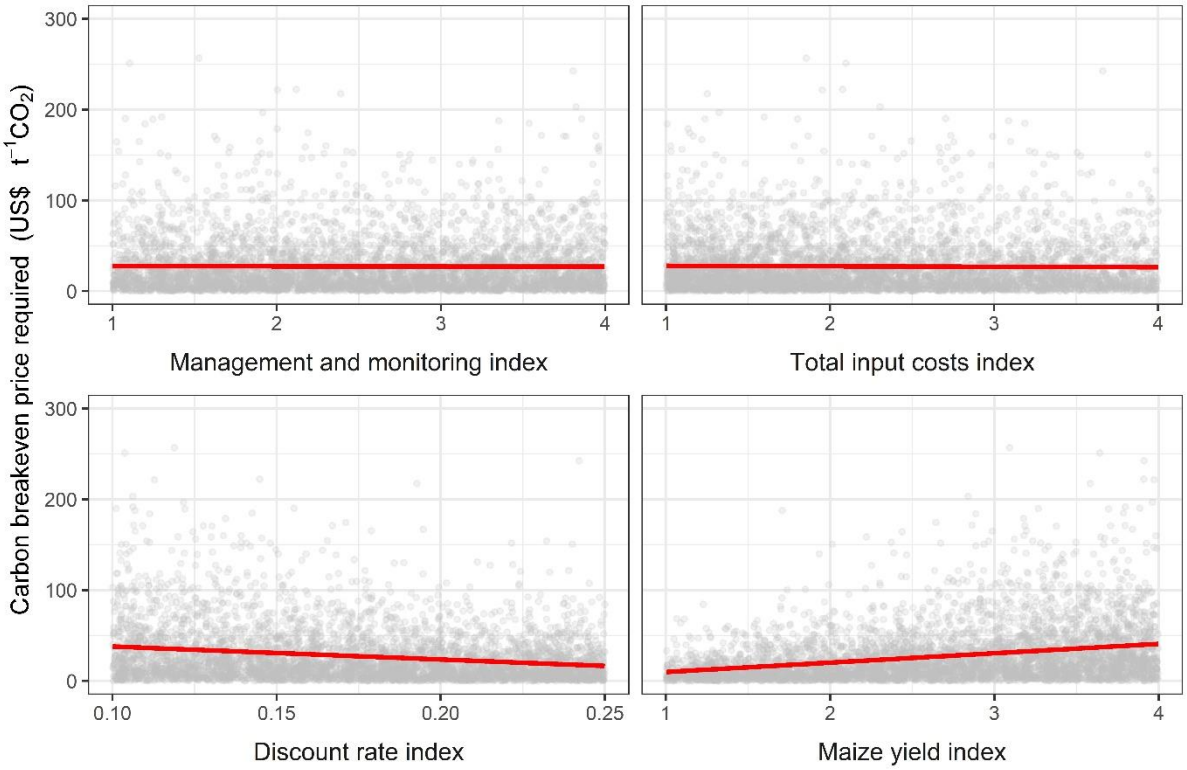

Figure S9. Sensitivity analysis of parameter variables' effect on the breakeven price of maize cultivation under scenario 3.1. Sensitivity analysis response is shown for the following variables: A) Management and monitoring costs, B) total input costs, C) discount rate, and D) maize yield index. 10,000 model runs were performed whereby parameter variables were multiplied by an index between 1 and 4, with each dot representing the breakeven price of one model run. The red lines show linear models relating index to the breakeven price.

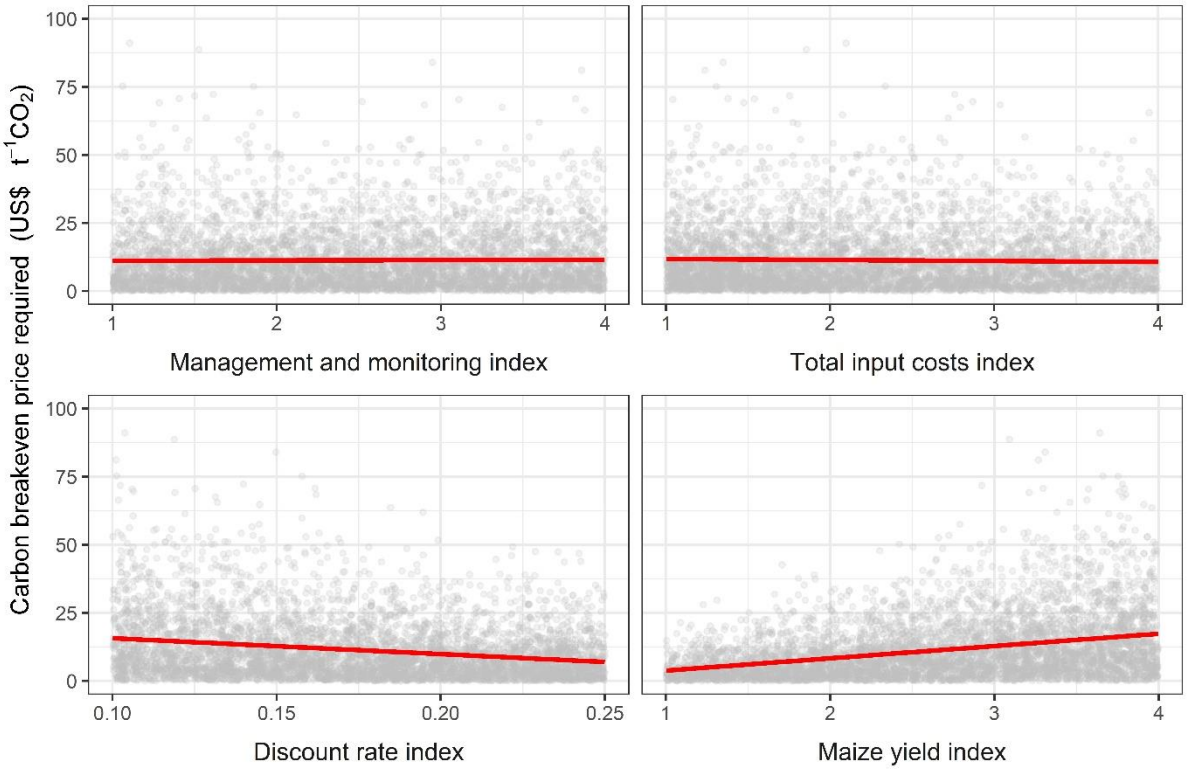

Figure S10. Sensitivity analysis of parameter variables' effect on the breakeven price of maize cultivation under scenario 3.2. Sensitivity analysis response is shown for the following variables: A) Management and monitoring costs, B) total input costs, C) discount rate, and D) maize yield index. 10,000 model runs were performed whereby parameter variables were multiplied by an index between 1 and 4, with each dot representing the breakeven price of one model run. The red lines show linear models relating index to the breakeven price.

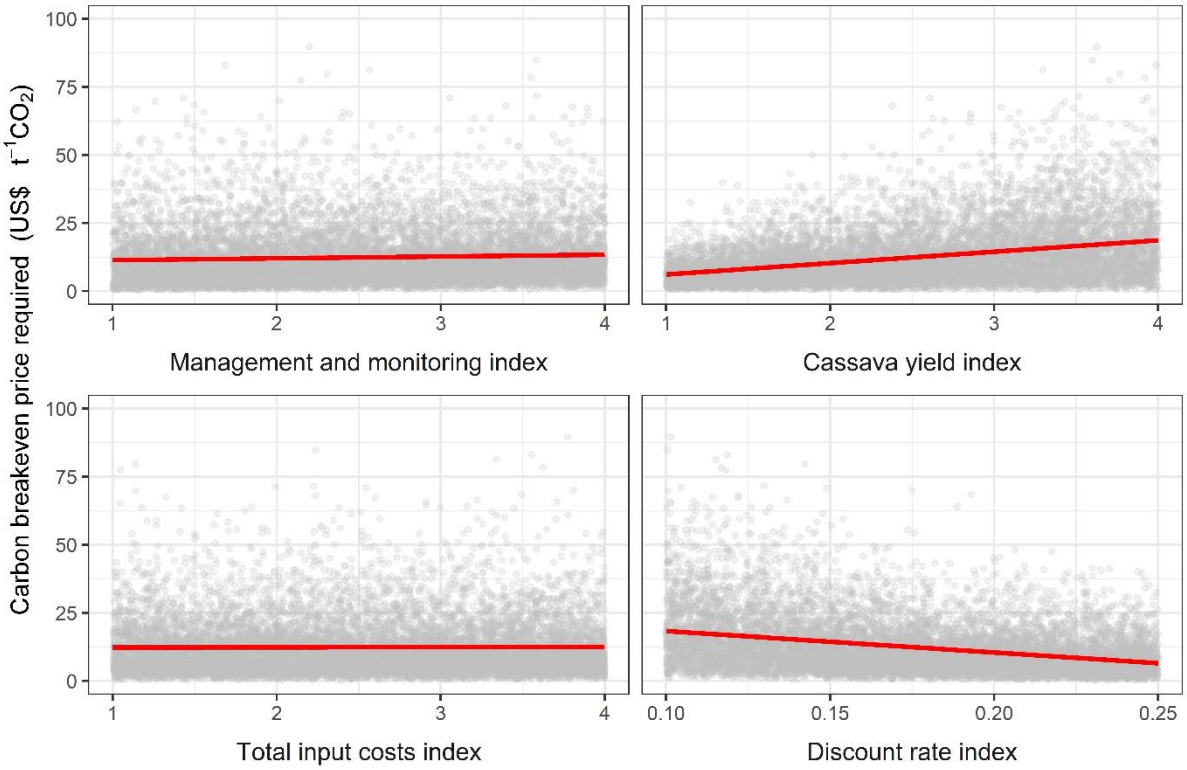

Figure S11. Sensitivity analysis of parameter variables' effect on the breakeven price of cassava cultivation under scenario 2.1. Sensitivity analysis response is shown for the following variables: A) Management and monitoring costs, B) cassava yield index, C) total input costs, D) discount rate. 10,000 model runs were performed whereby parameter variables were multiplied by an index between 1 and 4, with each dot representing the breakeven price of one model run. The red lines show linear models relating index to the breakeven price.

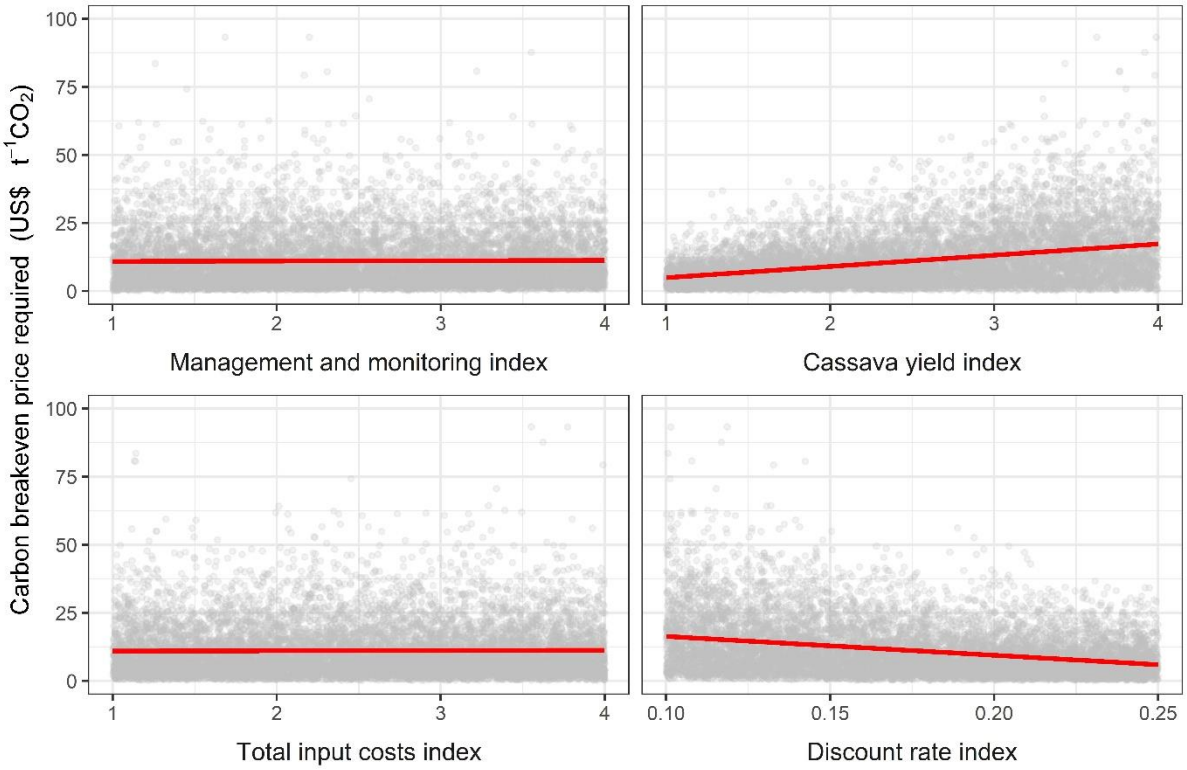

Figure S12. Sensitivity analysis of parameter variables' effect on the breakeven price of cassava cultivation under scenario 2.2. Sensitivity analysis response is shown for the following variables: A) Management and monitoring costs, B) cassava yield index, C) total input costs, D) discount rate. 10,000 model runs were performed whereby parameter variables were multiplied by an index between 1 and 4, with each dot representing the breakeven price of one model run. The red lines show linear models relating index to the breakeven price.

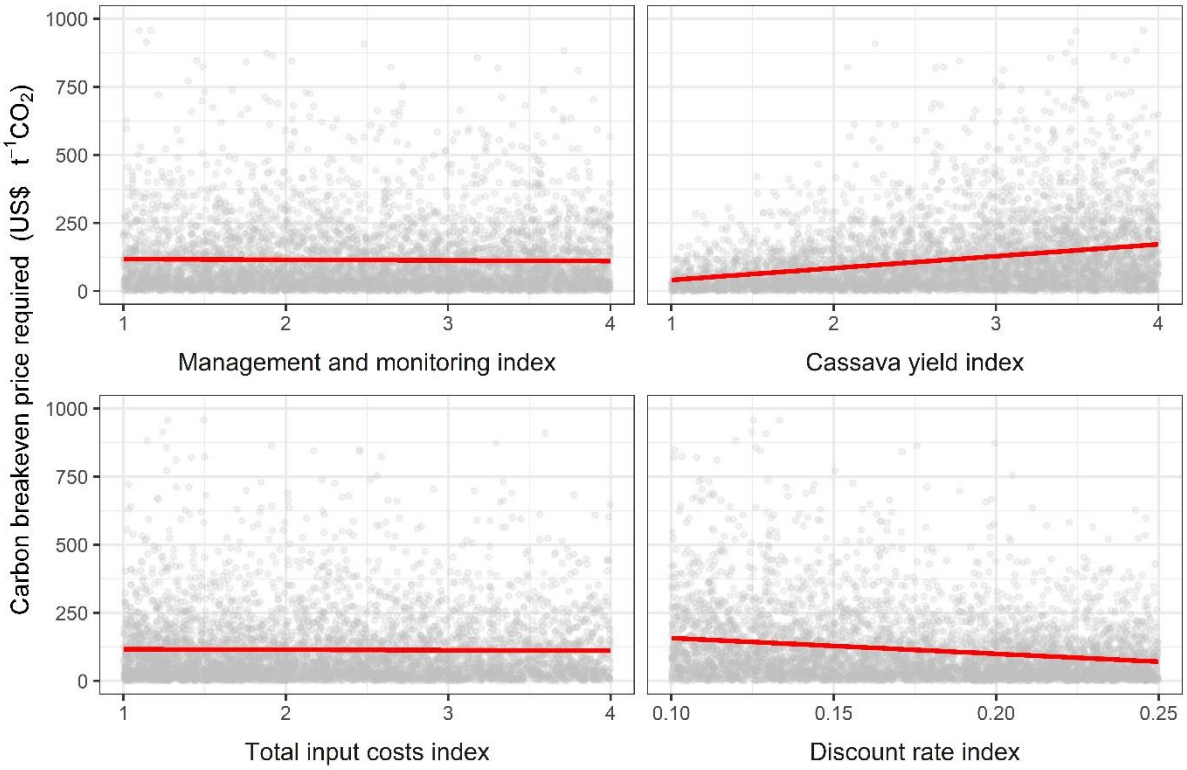

Figure S13. Sensitivity analysis of parameter variables' effect on the breakeven price of cassava cultivation under scenario 3.1. Sensitivity analysis response is shown for the following variables: A) Management and monitoring costs, B) cassava yield index, C) total input costs, D) discount rate. 10,000 model runs were performed whereby parameter variables were multiplied by an index between 1 and 4, with each dot representing the breakeven price of one model run. The red lines show linear models relating index to the breakeven price.

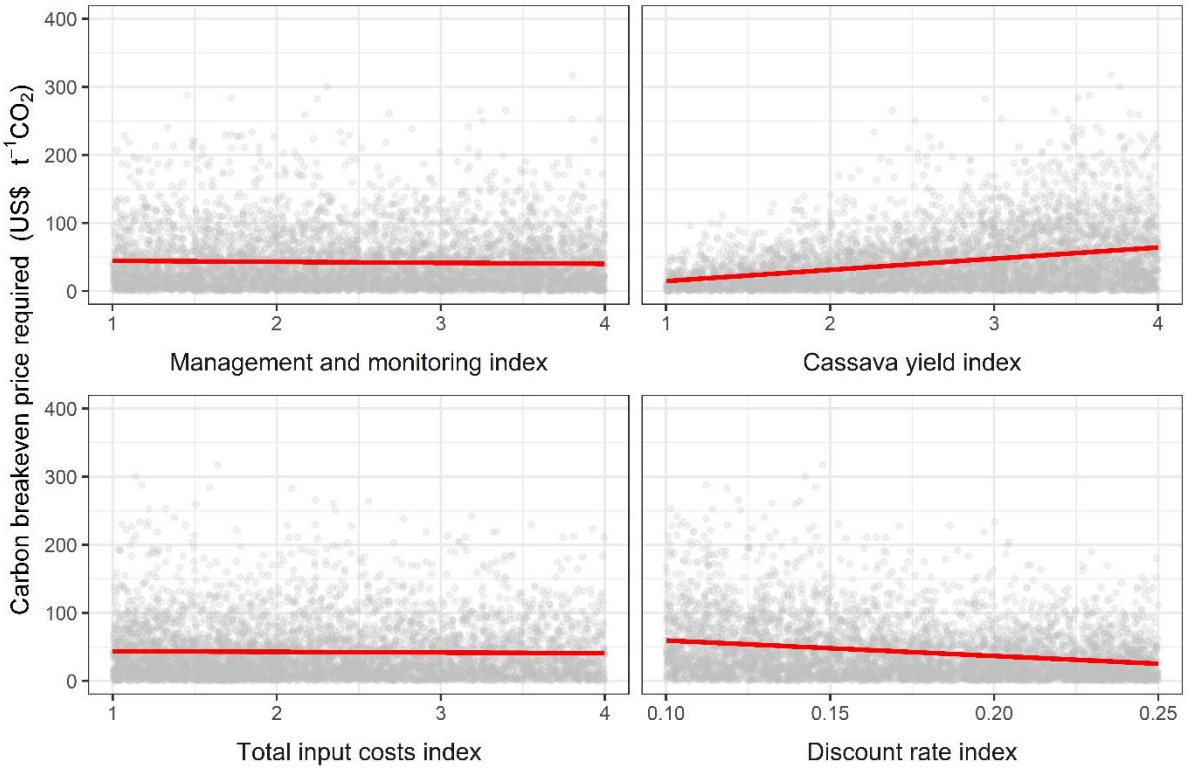

Figure S14. Sensitivity analysis of parameter variables' effect on the breakeven price of cassava cultivation under scenario 3.2. Sensitivity analysis response is shown for the following variables: A) Management and monitoring costs, B) cassava yield index, C) total input costs, D) discount rate. 10,000 model runs were performed whereby parameter variables were multiplied by an index between 1 and 4, with each dot representing the breakeven price of one model run. The red lines show linear models relating index to the breakeven price.

Chapter 5:

General discussion

5.1 Summary

Rapidly increasing economic activity, resource use, and anthropogenic alteration of landscapes through the 20th century has led us into a human-dominated ecological epoch, the Anthropocene. The release of massive amounts of carbon into the atmosphere, biosphere, and oceans will cause significant changes to climate patterns, leading to more frequent and extreme weather events, affecting global food production and the habitability of large swathes of terrestrial land. Simultaneously, extensive land-use change, overexploitation of resources and species, and climate change have led to the wholesale loss of habitats and subsequent precipitous declines in species and continue to do so.

We are therefore facing a confluence of both a global climate and biodiversity crisis. In response, great efforts are being made to increase our understanding of ecosystem processes, protect remaining habitats and species, and restore and regenerate deforested and degraded landscapes. In order to identify effective conservation actions and ways in which landscapes can help us to mitigate climate change it is vital to understand patterns of biodiversity and the processes that maintain and produce these.

In chapter two, I investigated how tree diversity is structured over environmental and disturbance gradients in the savannas of eastern and southern Africa using plot data from across the region (SEOSAW, 2021). I found that wetter savannas contain greater tree species richness and phylogenetic diversity, whilst high turnover across the region is driven by precipitation regimes (Davies et al., 2023). These results suggest that low-water availability places distributional limits on species, creating climate-richness relationships in savannas that are common in other systems (Currie et al., 2004) regardless of savannas experiencing frequent disturbances and prolonged dry seasons. Despite their importance in determining savanna distribution and structure fire and herbivory had little effect on tree diversity patterns. High

turnover suggests that to maximise the conservation of unique tree communities, savannas from across the regional rainfall gradient should be protected.

In chapter three, I compiled functional trait data for tree species from across the savannas of eastern and southern Africa to assess how functional traits cluster across species and to investigate how functional traits respond to climatic, soil, and disturbance gradients. I find that species cluster into three unique functional syndromes that differ in their functional characteristics. Cluster one had high wood density and slow growth, cluster two was characterised by thick bark and rapid growth, whilst cluster three species were spinescent and had high leaf nitrogen. We interpret these functional syndromes as: i) dry adaptation and herbivore avoidance, ii) fire tolerance, and iii) herbivore tolerance. We see that the relative dominance of these clusters changes over environmental and disturbance gradients, particularly with increasing rainfall, suggesting that functional turnover may be what drives the taxonomic turnover observed in chapter 2.

In chapter four, I assessed whether carbon-based payments for ecosystem (PES) services could be used to protect important habitats on low-intensity farmland in Ghana. Trees and fallow fields provide vital wintering habitats to imperilled Afro-palearctic migratory birds (Morel and Morel, 1992), but protection of farmland habitats is often overlooked in favour of conservation of pristine habitats and returning farmland to forest (Peres, 2005). I show that protection of trees on existing farmland can be achieved at very low carbon breakeven prices (BEP), ranging from US$2.49 - US$6.45 t^{-1} CO_2 (Davies et al., 2021). Reintroduction and extension of fallowing periods can also be achieved at competitive BEP, US$4.67—US$15.45 t^{-1} CO_2, when combined with tree protection. Here, we show that protection of farmland habitats is cost-effective under carbon-based PES but suggest that implementation should be combined with efforts to close yield gaps, providing greater local food security and resilience.

5.2 The future of savanna landscapes

5.2.1 Growing threats to savannas

Savannas face a multitude of threats in the face of growing resource demand, often driven by perverse market interests, and climatic change. Given the relatively recent incorporation of Africa into global markets and increasing interest of foreign investment in Africa, the woodlands of southern African are seen as an agricultural frontier (Lambin & Meyfroidt, 2011). Expansion of commercial agriculture poses significant threats to biodiversity and carbon storage within savannas (Searchinger et al., 2015). Finding alternative, sustainable ways to meet food demands is pivotal to protecting savanna landscapes and ensuring equitable benefits to the millions of people reliant on these landscapes for a wealth of services and products (Ryan et al., 2016). Likewise, developed nations have a responsibility to increase their own food sovereignty to avoid exporting their growing needs to commercial agricultural ventures in savannas, as has happened in South America and Southeast Asia (Gibbs et al., 2010).

Low-intensity farmland provides vital habitats to species (Pywell et al., 2014) and enables movement of species between patches of habitat, allowing population mixing and species to track climatic changes (McGuire et al., 2016; Senior et al., 2019). It is also the primary source of food for many in the savanna ecoregion (Dethier & Effenberger, 2012). Chapter four demonstrates one option to conserve habitats on low-intensity farmland, however, whilst protecting farmland habitats is important, their protection should not come at the cost of clearance of extant natural habitats, such as woodlands and forests. Clearance of natural habitats for the expansion of agriculture is the greatest threat to biodiversity (Laurance, 2007). Most woodland and forest specialist are unable to survive in agricultural habitats and so minimising farm footprints to maximise the extent of natural habitats – land sparing – is often the most effective management technique to maximise biodiversity conservation (Phalan et al.,

2011; Luskin et al., 2018). To make this viable at scale yield gaps need to be closed and their needs to significant investment in sustainable agricultural development that minimises farm footprints.

Climate change is likely to have profound impacts on ecosystem processes and therefore vegetation across savannas. Rainfall is expected to become less predictable, with increasingly severe and frequent droughts (Seth et al., 2013; Niang et al., 2014), leading to changes in fire and herbivore regimes which are also influenced by anthropogenic driven changes to land use (Andela et al., 2014). The results of chapters two and three show how important precipitation, fire, and herbivore regimes are in determining patterns of biodiversity and community composition across the savannas of eastern and southern Africa (Davies et al., 2023). We can therefore expect that changes to these regimes under future climates will have significant effects on tree community composition. It may be that increases or decreases in fire frequency lead to biotic homogenisation as those species adapted to fire either dominate or are outcompeted (Socolar et al., 2016). Extended dry seasons may favour those species which are better able to cope with water-limitation whilst species already at their water-limitation bounds may experience declines, again leading to a loss of diversity and the homogenisation of communities. However, predictions of savanna vegetative community responses to climate change remain sparse and should be a priority of future work in the region and across other savanna landscapes.

Mass planting of trees has been proposed as a method to tackle climate change, conserve biodiversity, and promote the recovery of woody ecosystems (Griscom et al., 2017). Large areas of savanna have been identified as degraded and earmarked for restoration through tree planting (Bastin et al., 2019). However, low tree cover in savannas has been maintained by a complex interaction of rainfall, herbivory, and fire regimes for millions of years (Strömberg, 2011). Increasing tree cover in savannas could further endanger species already

threatened by the conversion of savannas into low-diversity forests through fire-exclusion and afforestation (Abreu et al., 2017). Additionally, whilst trees sequester carbon through their lifetimes, these would also be prone to carbon loss from fire and may serve to reduce soil organic carbon content (Berthrong et al., 2009). In savannas where tree planting is identified as an effective restoration action, there is a need for caution to ensure the right trees are planted in the right place at the right densities to avoid the potential negative consequences associated with tree restoration.

5.2.2 Conservation in savanna landscapes

Carbon-based PES can offer pathways through which to protect carbon stored in landscapes, fund conservation efforts, and to improve local livelihoods. However, PES must not be used as an excuse for large multinationals to avoid properly reducing their massive carbon emissions or to "greenwash" environmentally and socially damaging practices. Carbon stored in biomass is impermanent (Balmford et al., 2023a), the most effective way to halt climate change is to rapidly reduce global carbon emissions – carbon-based PES must not take impetus away from this central goal. Recently, the credibility of carbon-based PES has come under increased scrutiny as evidence of massive inflation of carbon credits is uncovered, leading to a lack of additionality from carbon credits schemes (Balmford et al., 2023b). Central to viable carbon-based PES is accurate carbon accounting, whereby threats are properly assessed to ensure that carbon sold under offset schemes are true offsets.

Carbon-based PES schemes, and other conservation actions for that matter, must ensure that local communities are involved in decision-making processes and that payments and other benefits are equitably shared between stakeholders. Central to these goals is often the issue of land ownership and tenure. In Africa and Asia, for example, forests are public property (Sunderlin et al., 2008), with rural communities and indigenous people exercising customary

rights of access, extraction, and inheritance. This potentially raises the issue then that governments who have ownership of the land are the ones who collect PES from the carbon protected on that land, despite local stakeholders being the actors who have potentially suffered opportunity costs (Karsenty et al., 2014). These issues need to be avoided and treated with care under PES schemes to avoid furthering inequality in these communities and to align with sustainable development goals (UN DESA, 2022).

5.2.3 The need for more research in savannas

Savannas are ubiquitous across the tropics, dominating land cover in Africa, harbouring highly charismatic and threatened fauna and flora, and supporting the livelihoods of hundreds of millions of people (Ryan et al., 2016). These important services are underpinned by the biodiversity held within these savannas (Godlee et al., 2021) and so understanding patterns of this biodiversity is of great value. Chapter three used functional trait data for species from across eastern and southern Africa to elucidate trait trade-offs between savanna species and understand patterns of functional trait composition. The work presented in this chapter uncovered a lack of available trait data for savanna tree species in the region. Traits can help to elucidate ecological processes, help make predictions under changing climates, and are important to the maintenance of ecosystem service provision and resilience. We therefore highlight the need for increased data collection, particularly of traits, across the region in an ecosystem that has already been identified as systematically undervalued and underappreciated in the ecological and conservation literature (Parr et al., 2014).

Chapter two and three rely heavily upon plot data collected from across eastern and southern Africa and compiled by the SEOSAW network to understand community composition patterns (SEOSAW, 2021). Plot data provides the best resource to investigate ecological processes, expanding and maintaining a network of vegetative monitoring plots across

savannas is vital to further understanding of their ecology. Additionally, an increase in the abundance of long-term, vegetation monitoring plots in the region would be an incredibly valuable asset to properly understand how savannas respond to changes through time. Long-term monitoring plots would allow these patterns to be assessed temporally, as well as spatially, to see how vegetation responds to the multiple potential changes induced under future climates.

5.3 Conclusions and recommendations

This thesis aims to increase understanding of how tree community composition is structured in savannas and how important habitats in savanna landscapes may be effectively conserved. There are three primary findings from this work. Firstly, precipitation gradients are important determinants of tree diversity patterns and high taxonomic turnover across the savannas of eastern and southern Africa. Wetter savannas contain more species and greater evolutionary diversity, suggesting that low water availability limits the distribution of species creating observed climate-richness patterns. Likewise, high taxonomic turnover across the region demonstrates the need for complementarity in the planning of reserves to maximise the protection of unique tree communities. Secondly, savanna trees split into three distinct functional clusters, which are inferred to be: i) dry-adapted and herbivore avoidant, ii) fire tolerant, iii) herbivore tolerant. Across precipitation, fire, and herbivory gradients there is a shift from communities dominated by dry-adapted, herbivore avoidant species to fire tolerant species with increasing rainfall, with herbivore-tolerant trees rarely dominant throughout. Thirdly, the use of carbon-based PES to protect important habitats on low-intensity farmland in savanna landscapes is a cost-effective conservation action, costing only US$2.49 - US$6.45 t^{-1} CO_2 to protect extant trees or US$4.67—US$15.45 t^{-1} CO_2 to prolong or reintroduce fallowing. Given increasing food demand across the region, however, carbon payments must be combined with policies that enable sustainable intensification to close yield gaps and improve local food security and resilience to prevent leakage.

Future research should focus on i) continuing to expand plot and species' trait data collection across savannas, ii) develop predictions of how savanna tree composition may be influenced by projected changes in climate and disturbance regimes, and iii) find methods for smallholder agriculture to sustainably intensify production without threatening important farmland habitats. Beyond research, governments, particularly of those nations which have been responsible for the greatest carbon emissions, need to make good on promises to rapidly reduce their emissions. Carbon offsets are not a panacea to net-zero, they will only be effective in concert with emissions reductions. Increased funding of ecological research and conservation actions by in-situ researchers and conservationists is also a priority for governments and policy makers. Local actors are best placed to maintain monitoring networks and enforce conservation actions, but they need financial backing from those nations and companies largely responsible for the human-dominated epoch we find ourselves in.

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