Master's thesis

NTNU
Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

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Carbon stocks across the Serengeti ecosystem: Impacts of climate, land-management and woody plant cover

Master's thesis in Natural Resources Management
Supervisor: James D.M Speed
Co-supervisors: Bente Jessen Graae, Stuart W. Smith & Vegard Martinsen
May 2019

Photo: Per Harald Olsen

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Abstract

Given the current rates of human land-use change and increases in atmospheric carbon dioxide, it is crucial to ensure efficient management of ecosystems to maximise carbon storage. Specifically, protection of land is a primary conservation approach in face of land-use change, with the added potential to enhance ecosystem carbon storage. In this context, savannahs are important land areas for protection as they cover a large geographical area as well as provide a range of ecosystem services i.e., habitats for abundant wildlife, agricultural land, and grazing land for livestock. However, little attention has been given to how different land-management practices affect savannah ecosystem carbon stocks. In this thesis, we quantified ecosystem carbon stocks in protected areas and adjacent unprotected areas across varying in climatic conditions (i.e., precipitation) and soil types (i.e., soil texture) in the Serengeti ecosystem. We specifically aimed to assess the importance of direct and indirect relationships between major biotic (i.e., herbivore community, soil macro fauna, and woody encroachment) and abiotic (i.e., fire frequencies) drivers of aboveground and belowground carbon stocks. We sampled data on woody, herbaceous, dead wood, A-horizon, and mineral-horizon in a total of seven sites located across gradients of precipitation and land-use. Our results demonstrated that aboveground carbon stocks varied with contrasting land-management practices of protected areas and neighbouring unprotected areas, which remained consistent across soil types and precipitation regimes. Belowground carbon stocks displayed rather marginal percentage differences, however great quantified difference in carbon amount between protected areas and unprotected areas. Belowground, the variation in carbon stocks was more related to the direct effects of herbivore abundance (i.e., dung, trampling) rather than to herbivore foraging effects on aboveground carbon stocks that influence litter inputs into the soil. For the Serengeti ecosystem, ecosystem carbon stocks were mainly related to differences in fire frequencies and herbivore community, and not to woody encroachment. Within this thesis, we highlight the importance of investigating ecosystem carbon stocks across several predictors, to obtain a sufficient understanding of the ecosystem that allow informed management decisions. We suggest that in the Serengeti ecosystem management attention should be given to wild and domestic herbivore interactions, as well as fire impacts to enhance carbon storage inside protected areas and prevent adjacent unprotected areas from becoming depleted of carbon.

Sammendrag

Vi står i dag ovenfor enorme utfordringer med tanke på økende arealbruks- og klimaendringer. Derfor er det vesentlig å forstå hvordan man mest effektivt forvalter et økosystem med økt karbonlagring i fokus. Et tiltak som har vært benyttet for å forhindre ytterligere arealbruksendringer er arealvern – et tiltak som også har vist seg å tilrettelegge for terrestrisk karbonlagring. Savanner er viktige landområder for vern da de både dekker et stort geografisk område, og bidrar med en rekke økosystemtjenester som arbeidsplasser, gressmark for husdyr og tilholdssted for ville dyr. På tross av dette har terrestrisk karbonlagre i savanner blitt fått lite fokus, spesielt med tanke på hvordan ulike forvaltningsstrategier påvirker dem. I denne oppgaven har vi kvantifisert terrestriske karbonlagre i verneområder og omkringliggende områder uten vern, eksponert for ulikt klima og lokalisert på ulike jordtyper i Serengeti. Vår målsetning har vært å evaluere viktigheten av direkte og indirekte sammenhenger mellom biotiske (dvs., ulike grupper av beitedyr, makrofauna i jorden og økt tredekke) samt abiotiske (dvs., brannfrekvens) drivkrefter på karbonlagre både over- og under bakken. Vi samlet biomassedata for trær, gress, død ved, A-sjikt og mineral-sjikt fra syv lokaliteter som befant seg i ulike nedbørssoner og med ulikt arealbruk. Våre resultater viste at karbonlagrene over bakken varierte med arealbruksforvaltning, en variasjon som holdt seg konstant i de ulike nedbørssoner og var uavhengig av jordtype. Karbonlagrene under bakken viste en tendens til variasjon med arealbruk. Denne variasjonen viste seg å være mer relatert til direkte effekter av beitedyr (dvs., dyretråkk og møkk), enn til deres effekt på vegetasjon og dermed på tilførsel av planteavfall til jordsmonnet. Sammenhengen mellom arealbruksforvaltning og terrestriske karbonlagre var hovedsakelig relatert til brannfrekvenser og ulike grupper av beitedyr. Forskjeller i tredekke hadde ingen påvirkning på terrestriske karbonlagre. Vi belyser med dette viktigheten av å utforske flere forklaringsvariabler for å ta opplyste forvaltningsvalg med fokus på terrestrisk karbonlagringspotensiale. Vår spesifikke anbefaling i Serengeti økosystem er at forvaltningsorganer bør fokusere på interaksjoner mellom ville- og domestiserte beitedyr, samt brannfrekvenser. Dette for å kunne tilrettelegge for karbonlagring i verneområder, samt for å forhindre at omkringliggende områder uten vern akkumulerer mindre karbon.

Key words/ nøkkelord: Ecosystem carbon stocks, savannah, Serengeti ecosystem, land-management, fire frequency, herbivore community, soil texture, precipitation, woody encroachment.

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Table of Content

1 Introduction

As almost half the earth's terrestrial surface has been altered by human action (Vitousek et al., 1997), it is essential to understand the outcome and potential of different land-management practices. In addition, given current increases in atmospheric carbon dioxide (CO_2), it should be a priority to identify and efficiently manage ecosystems to enhance carbon storage potential. Addressing human land-use changes through protection of land is a primary mitigation approach within the domain of nature conservation strategies. Protection of land is commonly exercised through regulation of wildlife, hunting, grazing, logging, farming, and burning (Watson 2014). In addition, it has the potential to mitigate increasing atmospheric CO_2 by facilitating ecosystem carbon storage (Derner & Schuman, 2007).

Savannahs are not considered dense carbon stores individually (Post et al., 1982). However, they are important global carbon stores because they occupy a large geographical area (Scholes & Archer, 1997) and account for 30% of terrestrial primary production (Parr et al., 2014). At the same time, savannahs provide essential ecosystem services as they constitute important habitats for endangered megafauna and a diverse herbivore assemblage as well as house 20% of the world's human population and their livestock (Scholes & Archer, 1997). It is critical to understand how protection of land influences savannah ecosystem carbon stocks and dynamics as savannahs are amongst the ecosystems most sensitive to land-use changes (Sankaran et al., 2005; Parr et al., 2014).

Existing research suggests potentially higher ecosystem carbon stocks in protected areas compared to unprotected areas, associated with contrasting land-management practices (Derner & Schuman, 2007). Contrasting land-management practices in African savannahs reflect amongst others differences in herbivore community and fire regulations. While wild herbivore communities migrate and consist of a diverse assemblage of functional types including both grazers and browsers (McNaughton, 1985; Goheen et al., 2010), domestic herbivores have become more static, less diverse, and impose a greater and more constant grazing pressure (Hempson et al., 2017). High grazing pressure in unprotected areas reduces plant biomass, litter input into the soil, as well as amount of fuel for wildfires. Savannahs are fire prone areas that require regular fires to persist in its natural state of coexistence between trees and grasses (Scholes & Archer, 1997; Holdo et al., 2012). Therefore, fire frequencies in protected areas are often increased through active management (Smith, 2008; Veldhuis et al., 2019).

Domestic herbivore community (e.g., foraging behaviour, abundance, and grazer browser ratios), and less fire regulations (e.g., lower fire frequencies) have long been recognized as drivers of increased woody abundance (encroachment) in savannahs (Scholes & Archer, 1997; Roques et al., 2001; Holdo et al., 2009a; Venter et al., 2018). Woody encroachment on grasslands is a widespread phenomenon in African savannahs, occurring frequently in unprotected areas without mega-herbivores (Stevens et al., 2017; Venter et al., 2018). Studies have found increased soil carbon storage in the upper 10 cm of the soil below large mature savannah trees, attributed to higher litter input (Coetsee et al., 2010; Becker et al., 2017). However, severe woody encroachment can inhibit herbaceous growth and thereby decrease litter input and soil carbon storage (Hudak et al., 2003). Hence, herbivore community and fire frequencies can impact whether an ecosystem becomes a carbon sink or carbon source by changing the vegetation composition and the litter input into the soil. Changed litter input into the soil along with changed amounts of herbivore dung can furthermore alter the activity and decomposition rates of soil organisms (Schmitz et al., 2018). The outcome of these alterations appear to vary among taxa, as examples woody encroachment of grasslands has been found to reduce species richness of nematodes (Jackson et al., 2002) and ants (Abreu et al., 2017), while abundance of termite mounds appear independent of land-use (Jones, 1990).

The status of savannah protected areas as being dense carbon stores when compared to surrounding unprotected areas has recently come under some challenge. Areas surrounding protected areas have higher human population growth, and experience more rapid land-use changes than areas farther away from protected areas (Wittemyer et al., 2008; Estes et al., 2012). Veldhuis et al. (2019) found this edge effect to squeeze wildlife towards the centre of the protected area. Thereby increasing grazing pressure and reducing soil carbon storage in the central region. This highlights how vulnerable wildlife and soil carbon stocks can be to pressures from outside a protected area. Furthermore, exposing of wildlife to domestic herbivores can lead to disease transmission (Holdo et al., 2009b). Before management areas were established in the Serengeti ecosystem, rinderpest spread from domestic herbivores to wild herbivores. Rinderpest reduced the population of migrating ungulates which led to accumulation of aboveground biomass, and hence increased wildfire frequencies. Following this trophic cascade, ecosystem carbon stocks were substantially reduced (Holdo et al., 2009b). These studies both raise important questions regarding how our land-management practices adjacent to protected areas affect ecosystem carbon stocks within protected areas.

It is important to acknowledge that other factors may impact ecosystem carbon stocks as well as land-management practices. A substantial body of literature has investigated major drivers of savannah carbon stocks (Table 1). In addition to fire and herbivory, precipitation and soil texture have been shown to explain aboveground biomass patterns in savannahs (Scholes & Archer, 1997). At the same time, soil texture works as a mediator of belowground carbon by affecting the stability of soil organic matter i.e., coarser texture is expected to stabilize less soil organic matter (Paul, 1984; Six et al., 2002). In wooded savannahs, herbaceous biomass is recognized as the most important contributor to the belowground carbon pool (Pellegrini et al., 2015), which in turn is the largest terrestrial ecosystem carbon pool (Eswaran et al., 1993). Extent of herbaceous cover is largely regulated by factors such as presence of trees (Scholes & Archer, 1997), soil type (Kumar et al., 2002), and precipitation (McNaughton, 1985; Holdo et al., 2009a). Therefore, it is crucial to understand how soil type and climate affect ecosystem carbon stocks to allow effective land management strategies.

Table 1. Summary of drivers (predictor) of savannah ecosystem carbon stocks. Predictor variables are fire, herbivore community (i.e., grazing pressure, dung), soil macro fauna, woody encroachment, woody and herbaceous cover, mean annual precipitation (MAP), soil texture (sand), and soil organic nitrogen (SON). Response variables are woody and herbaceous biomass, soil organic carbon (SOC), SON, and woody encroachment. Effect of drivers are indicated by + (positive), - (negative), or 0 (neutral effect).

Predictor	Response	Effect	
Fire	Woody biomass/ woody encroachment	-	Fire reduces woody biomass and encroachment (Dublin et al., 1990; Roques et al., 2001; Bond & Keeley, 2005; Sankaran et al., 2008; Holdo et al., 2009a; Holdo et al., 2014; Skowno et al., 2017; Veldhuis et al., 2017).
	Herbaceous biomass	0/+	Herbaceous biomass is more resilient than woody biomass (Pellegrini et al., 2015). Positive effect through the effect of fire on woody biomass (Holdo et al., 2009a).
	SOC	0/-	No direct effect of fire on SOC, but indirect through its negative effect on vegetation (Savadogo et al., 2007; Coetsee et al., 2010; Holdo et al., 2012; Pellegrini et al., 2015).
Herbivore community	Woody biomass/ woody encroachment	+	Changed herbivore community from wild to domestic herbivores and altered grazer browser ratios can increase woody biomass and result in woody encroachment (Dublin et al., 1990; Roques et al., 2001; Holdo et al., 2009a; Goheen et al., 2010; Daskin et al., 2016; Seymour et al., 2016; Veldhuis et al., 2017; Morrison et al., 2018).
	SON	+	Dung increases SON content of the soil (Schmitz et al., 2018).
	SOC	-/+	Effect depends on soil texture, plant community, and MAP (McSherry & Ritchie, 2013). Mixed results (Milchunas & Lauenroth, 1993). (-)Loss of SOC with high grazing pressure (Pineiro et al., 2010; Ritchie, 2014; Veldhuis et al., 2019). (+)When dung is eaten by insects SOC gets incorporated into the soil reservoir which is less prone to burning than vegetation (Schmitz et al., 2014).
Soil macro fauna effect	SOC	-/+	Termites decompose large amounts of litter and prevent organic matter accumulation in the soil (Jones, 1990). Soil macro fauna alter carbon fluxes, however their effect on carbon stocks is still uncertain (Dungait et al., 2012; Schmitz et al., 2014).
Woody encroachment	Herbaceous biomass	-	High woody encroachment can inhibit herbaceous growth (Hudak et al., 2003)

	SOC	+/-	Increase SOC (Abreu et al., 2017), however when woody encroachment is severe, SOC starts to decrease (Hudak et al., 2003). Dry sites gained, but wet sites (MAP > 600) lost SOC with woody encroachment (Jackson et al., 2002).
Woody cover	Herbaceous biomass	-/+	Shade, nutrients, water, but also competition as herbaceous cover reduces tree seedling survival (Becker et al., 2017; Morrison et al., 2018). Positive impact of large, mature, and nitrogen fixating trees (Scholes & Archer, 1997).
	SOC	+	More SOC found beneath large trees regardless of tree species. However, no impact outside of tree canopy (Coetsee et al., 2010; Becker et al., 2017).
Herbaceous cover	SOC	+	More important for SOC than woody cover (Pellegrini et al., 2015)
MAP	Woody biomass	+	Positive when MAP < 600 (Sankaran et al., 2008).
	Herbaceous biomass	+	Positive relationship (McNaughton, 1985). However, it also depends on trees as they are competitors (Holdo et al., 2009a).
	Woody encroachment	0	Meta-analysis showed no effect (Stevens et al., 2017).
	SOC	+/-	Found to be positive through its effect on herbaceous cover (Pellegrini et al., 2015). However, also negative because it can increase decomposition due to higher microbial activity (Pineiro et al., 2010).
Sand	Herbaceous biomass	+	High infiltration increases herbaceous growth (Kumar et al., 2002).
	Woody biomass	+	High infiltration increases woody growth (Sankaran et al., 2005).
	SOC	-	Decreases with sand, increases with clay (Six et al., 2002; Hudak et al., 2003).
	Soil Nitrogen	-	Decreases with sand, increases with clay (Six et al., 2002; Hudak et al., 2003).
SON	SOC	0	SON and SOC are tightly linked. SON is important for SOC because primary productivity depends on SON, and SOC amounts depends on aboveground biomass. Meanwhile, SON availability also depends on SOC (Pineiro et al., 2010).

We find that few studies have compared ecosystem carbon stocks resulting from different land-management practices (i.e., protected areas and unprotected areas), and sufficiently investigated the additional variables (i.e., climate and soil type) possibly influencing land-management outcomes. Reviews highlight the absence of studies investigating the effect of wild versus domestic herbivores on ecosystem carbon stocks (McSherry & Ritchie, 2013), as well as the functional understanding of carbon stocks in relation to management-environment interactions (Derner & Schuman, 2007). The effects of land-management practices on ecosystem carbon stocks have mostly been studied either exclusively inside protected areas or outside, by exploring the specific effects of individual variables e.g., grazing intensity by use of exclosures (Pineiro et al., 2010), or fire impact evaluated by burning treatments (Pellegrini et al., 2015).

We propose a conceptual model (Fig. 1) built on current knowledge (Table 1) as a suggestion to how land-management practices, climate, and soil type can relate to aboveground and belowground carbon stocks in a savannah ecosystem. By the use of this figure, we aim to assess the importance of direct and indirect relationships between major biotic and abiotic drivers of aboveground and belowground carbon stocks in the Serengeti ecosystem. Specifically, we quantify aboveground and belowground carbon stocks across (1) contrasting land-management practices (protected areas versus unprotected areas), and (2) climate (precipitation regime) and soil types (texture gradient).

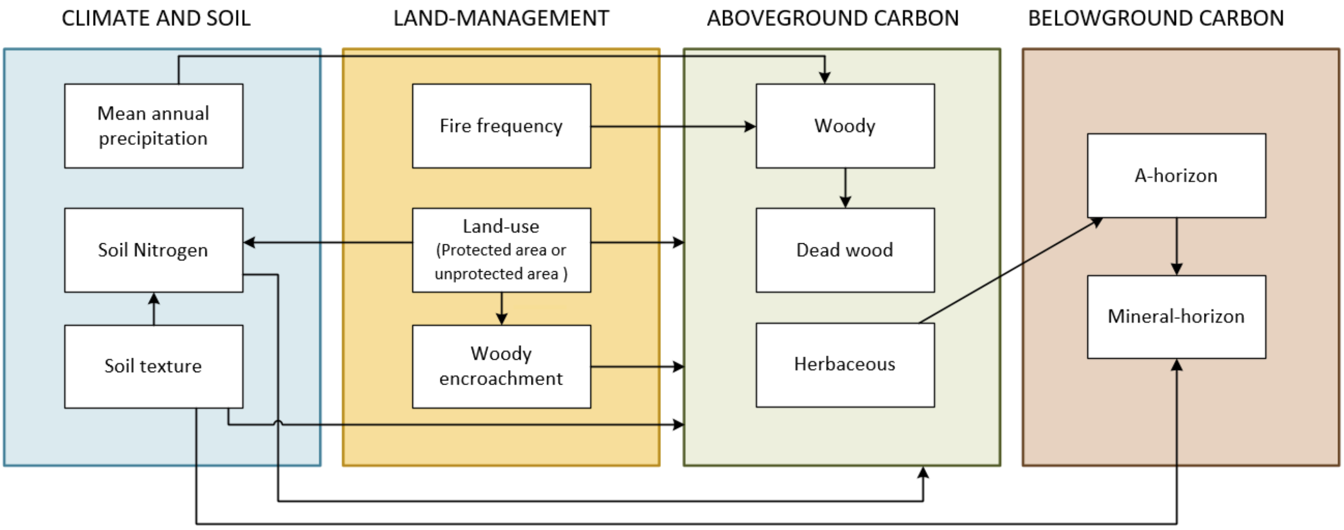

Figure 1. Conceptual model of relationships between climate and soil variables, land-management variables, aboveground, and belowground carbon stocks. Relationships are based on previous research (Table 1).

First, we hypothesize that aboveground and belowground carbon stocks will be affected by land-management differences between protected areas and unprotected areas. Specifically, we predict that unprotected areas will have lower ecosystem carbon stocks compared to protected areas. This is because unprotected areas have higher grazing pressure by domestic herbivores, less dead wood due to collection of firewood, and therefore less litter input into the soil. These ecological dynamics in combination with reduced fire frequencies, can facilitate woody encroachment in unprotected areas resulting in altered litter quality and input into the soil. In turn, altered litter and domestic herbivore dung inputs can affect the soil macro fauna activity, and hence their decomposition.

Second, we hypothesize that landscape variation in climate and soil texture will modulate the effect of land-management practices on aboveground and belowground carbon stocks. We expect the effect of land-management to be stronger in dryer sites with sandier soils, because precipitation increases aboveground biomass (McNaughton, 1985) and soil texture influences the capacity of soil to stabilize and retain organic matter (Paul, 1984; Six et al., 2002).

2 Materials and method

2.1 Study site selection

Our sampling sites were all part of the greater Serengeti ecosystem (size: 25. 000 km^2, location: 1–2° S, 34–26° E) situated in Tanzania, in eastern Africa (Fig. 2a). The Serengeti ecosystem supports a warm, tropical and mesic savannah, with two rainfall seasons occurring largely from November to December and from March to May (Frank et al., 1998). Several abiotic and biotic variables vary across the Serengeti ecosystem: precipitation and soil texture varies spatially, northwest receives > 1000 mm rainfall per year (Fig. 2b) and is dominated by clay, while southeast receives < 700 mm rainfall per year (Fig. 2b) and is dominated by silty organic matter-rich soils (McNaughton, 1985; Sinclair et al., 2007); fires occur mostly inside the protected areas since it is used as a management tool (Fig. 2c); tree densities vary from a treeless southeast to sudden *Vachellia* (formerly *Acacia*) woodlands dominating the west and stretching north to the Loita Plains (Sinclair et al., 2007); tree species vary where the most dominant species are *Vachellia tortilis* and *V. robusta*, and sub-dominant species are amongst others *V. drepanolobium*, *V. Senegal*, *Commiphora trothae*, and *Balanites aegyptica* (Anderson et al., 2015); and finally herbivore community varies from protected areas with migratory ungulates such as wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), and eland (*Taurotragus oryx*) and presence of elephants (*Loxodonta africana africana*) (McNaughton, 1985; Sinclair et al., 2007), to unprotected areas dominated by domestic herbivores such as cattle and small ruminants (goats and sheep).

In this study we investigated seven sites (four in protected areas and three in neighbouring unprotected areas, Fig. 2a) situated in wooded savannah. Two distinct land-uses were selected: protected areas dominated by wildlife, and adjacent unprotected areas dominated by domestic herbivores. Precipitation varied across sampling sites from dry (600-700 mm year^{-1}) to wet (1300 mm year^{-1}) savannah (Fig. 2b). To investigate land-management differences across equal precipitation levels we deliberately selected neighbouring sites with contrasting land-use, located in areas with similar precipitation (Fig. 2b, Table 2). Seronera was the only sampling site without a neighbouring unprotected area, located in the centre of the Serengeti National Park (Fig. 2a). Sampling **sites** of 4 km^2 were divided into four **blocks** of 2500 m^2 (referred to as block level). Within each block, four 20 m^2 circular **plots** (referred to as plot level) were randomly selected. Woody and herbaceous carbon pools were measured at block level, while dead wood and belowground carbon pools were measured at plot level.

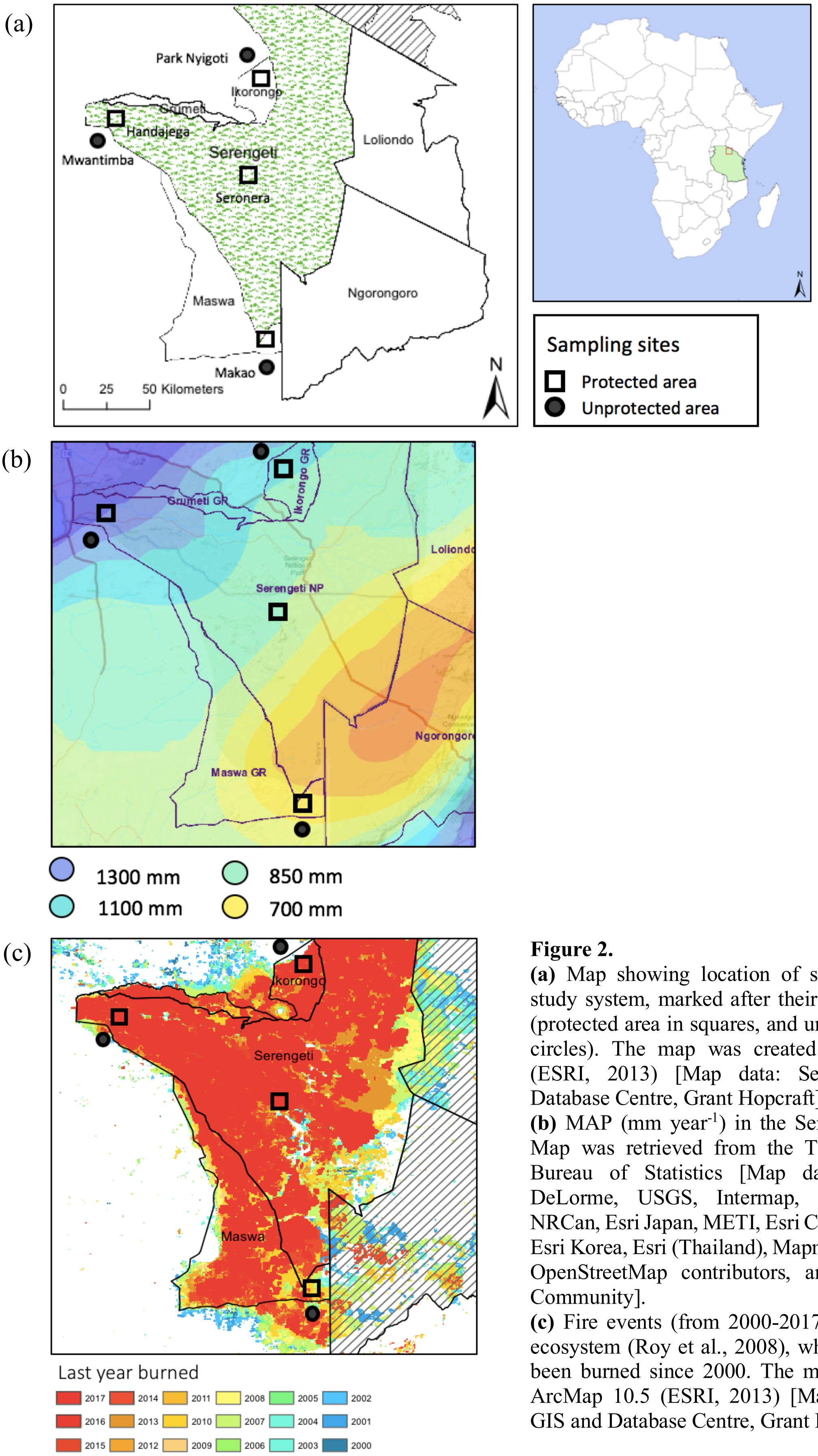

Figure 2.

(a) Map showing location of sampling sites and study system, marked after their land-management (protected area in squares, and unprotected areas in circles). The map was created in ArcMap 10.5 (ESRI, 2013) [Map data: Serengeti GIS and Database Centre, Grant Hopcraft].

(b) MAP (mm year^{-1}) in the Serengeti ecosystem. Map was retrieved from the Tanzanian National Bureau of Statistics [Map data: Esri, HERE, DeLorme, USGS, Intermap, INCREMENT P, NRCan, Esri Japan, METI, Esri China (Hong Kong), Esri Korea, Esri (Thailand), MapmyIndia, NGCC, © OpenStreetMap contributors, and the GIS User Community].

(c) Fire events (from 2000-2017) in the Serengeti ecosystem (Roy et al., 2008), white areas have not been burned since 2000. The map was created in ArcMap 10.5 (ESRI, 2013) [Map data: Serengeti GIS and Database Centre, Grant Hopcraft].

Table 2. Sampling site characteristics. Land-use and protection status (game reserve (GR) or national park (NP)) according to Veldhuis et al. (2019), protection year, MAP (2015-2017), fire frequency (number of fires from 2000-2017) and year of last registered fire.

Sampling sites	Land-use	Protection year	MAP (mm year^{-1})	Fire frequency	Year of last fire
Makao	Unprotected area	-	672	6	2010
Maswa	Protected area (GR)	1969	736	2	2005
Mwantimba	Unprotected area	-	1295	0	2000
Handajega	Protected area (NP)	1951	1279	7	2015
Seronera	Protected area (NP)	1951	855	5	2016
Park Nyigoti	Unprotected area	-	1135	7	2011
Ikorongo	Protected area (GR)	1994	1135	10	2015

2.2 Data collection

2.2.1 Aboveground carbon stocks

Woody, herbaceous, and dead wood biomass (kg) data were collected in December 2017. Woody species were surveyed in every block, except for one block in Seronera, resulting in a total of 27 measurements of woody carbon (Table 3). In Mwantimba, block sizes were reduced to 400 m^2 due to high densities of small trees. First, all trees were counted and individual species determined. Second, diameter at breast height (DBH) were recorded for individuals > 1.35 m, and basal diameter and height recorded for individuals ≤ 1.35 m. Woody biomass was estimated using allometric equations ([1], [2]) developed in a wooded savannah with the same region specifics and overstory tree species, such as *Vachellia* and *Commiphora*. Biomass of small trees was estimated according to Chamshama et al. (2004):

$$\text{Biomass of trees} \leq 1.35 \text{ m} = 0.0625 \times \text{basal diameter}^{2.553}, \qquad [1]$$

and biomass of mature trees was estimated according to Luganga (2015):

$$\text{Biomass of trees} > 1.35 \text{ m} = 0.0625 \times \text{DBH}^{2.553}. \qquad [2]$$

Herbaceous vegetation was collected in five of seven sites. Sampling was undertaken in one 0.6 × 0.6 m quadrat in every block in Makao, Maswa, Mwantimba, Handajega, and Seronera, resulting in a total of 20 measurements of herbaceous carbon (Table 3). All harvested biomass was air-dried over several weeks, weighed, and calculated to dry biomass per area (kg m^{-2}).

Dead wood, both coarse woody debris (> 10 cm diameter) and fine woody debris (> 2 cm diameter, > 20 cm length), was sampled in every site at plot level. Resulting in a total of 112 measurements of dead wood carbon (Table 3). Dead wood diameter at mid-point, length, and decay class according to Pfeifer et al. (2015) (Appendix, Table A1) were assessed within each 20 m^2 circular plot across all pieces of debris. We calculated the volume (cm^3) of each dead wood piece by the volume of a cylinder. Biomass of each dead wood piece was calculated by multiplying its density (g cm^{-3}) by volume (cm^3). Dead wood density (g cm^{-3}) was obtained per decay class from Pfeifer et al. (2015) (Appendix, Table A1). All aboveground biomass quantiles namely, woody, herbaceous and dead wood were converted to carbon stocks (kg m^{-2}) by assuming that carbon constitutes 50% of biomass.

2.2.2 Belowground carbon stocks

Both surface (A-horizon, upper 0-5 cm) and deeper (mineral-horizon, upper 5-20 cm) soil data were collected at plot level in December 2017, resulting in a total of 112 measurements of both A-horizon and mineral-horizon carbon (Table 3). In each 20 m^2 circular plot, sampling took place within three quadrats of 1 m^2 that had been randomly selected. To standardize our sampling, we sampled outside any tree canopy (a minimum of 1.5 × radius of nearest tree canopy), away from large rocks, rodent holes, and termite mounds.

Within each quadrat three soil samples were taken using soil augers. First, a soil auger with an internal diameter of 2 cm was used to take a maximum 20 cm soil sample in the centre of the quadrat. Then a soil auger with internal diameter of 1.9 cm was used to take two additional soil samples of the upper 0-5 cm of the soil within every quadrat. Depth (cm) of each of the sampled horizons were recorded. If an organic layer (O-horizon) was observed, three additional samples per circle were taken of the O-horizon with the smallest auger. The 20 cm soil cores were subdivided into upper 0-5 cm, and lower 5-20 cm. Thereafter, soil cores were pooled together according to their horizon depth, per circular plot (plot level), in separate zip lock bags, resulting in 16 bags for the O-horizon, 112 bags for A-horizon, and 112 bags for the mineral-horizon. Finally, 1-3 bulk samples were taken at every site using a steel cylinder (100 cm^3) to obtain a control measure of bulk density (BD, g cm^{-3}) per site for later comparison with BD of each soil sample. A subsample of each sample was used for chemical analysis.

All soil samples were dried at 60°C for 48 hours and weighed. Prior to analyses all samples were sieved through a 2 mm steel sieve. Samples with stones were weighed again after sieving and removal of stones. BD (g cm^{-3}) of the dry fine earth was calculated for every sample by dividing the total weight of the dry soil (g) corrected for stone weight by the volume of the soil auger (cm^{-3}). A subsample of one tea spoon from each soil sample was first grinded in a Retch

RM200 electrical grinder and put in separate paper bags. 16-20 mg of soil was weighed and put in individual tin containers. Analysis of total carbon and nitrogen was then performed by a Vario Micro Cube (Elementar) analyser. The fraction of organic and inorganic carbon was estimated by loss on ignition, at 550°C and 900°C respectively. At 200-500°C organic matter is oxidized to CO^2, and at 700-900°C further loss of CO^2 from carbonate minerals (inorganic carbon) takes place (Krogstad et al., 2018). Fraction of organic carbon was calculated by (LOI550°C/LOI900°C), and inorganic by 1-(LOI550°C/LOI900°C). Volume based soil carbon stocks (kg m^{-2}) of O-horizon, A-horizon, and mineral-horizon were calculated according to Martinsen et al. (2011):

$$\text{E-stock} = \text{Depth (cm)} \times \text{BD (kg cm}^{-3}\text{)} \times \text{E-content content (\%)}, \qquad [4]$$

where E-stock is the volume-based elemental (i.e., carbon or nitrogen) stock (density, kg m^{-2}).

2.2.3 Land-management variables

The impact of different land-management practices on aboveground and belowground carbon stocks was explored by several abiotic and biotic variables that we expected to vary with land-management, including woody encroachment, fire, soil biota, and herbivore dung.

To obtain a woody encroachment measure at block level, we explored the spatial tree biomass distribution (Appendix, Fig. A1). We found a high proportion of small trees with low biomass, and some large trees with high biomass, supported by Anderson et al. (2015) and Holdo et al. (2014). Woody encroachment was therefore calculated by dividing number of trees per m^2 by median tree biomass (kg) per block to get a standardized measure, resulting in a total of 28 measures of woody encroachment (Table 3).

Fire frequencies and year of last fire were obtained from MODIS Burned Area Product from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS MCD 45A) with a pixel resolution of 500 m × 500 m (Roy et al., 2008). Fire was here recorded for each year between 2000 and 2017 as either zero (no fire) or one (at least one fire occurrence). January, February, and March 2000 were not included as the MODIS burned area product was only available from 1st April 2000. Additionally, June 2001 was excluded from our analyses due to a satellite technical failure. The cumulative fire raster layer and vector shapefile of block spatial locations were then intersected to obtain fire frequency over the 17 years for every block, resulting in a total of 28 measures of fire frequency and year of last fire (Table 3).

Information on soil macro fauna driven mass loss (%) (referred to as soil macro fauna effect) was collected at block level in four of seven sites; Makao, Maswa, Mwantimba, and Handajega. A modified Tea Bag Index approach was used (Keuskamp et al., 2013) where 16 Lipton Rooibos (recalcitrant) tea-bags were incubated in the soil for two months per block during the wet season. Eight tea-bags were enveloped with 0.3 mm aperture sized stainless metal mesh to *exclude* soil macro fauna (mainly termite species), while the other eight were *open* (non-metal mesh) and available for both soil macro fauna and soil microorganisms. Litterbags were collected, oven-dried at 60°C for 48 hours and weighted without bag (only litter). Soil macro fauna effect was then calculated as the difference between treatments by subtracting mass loss in exclosed litterbags from mass loss in open litterbags, if a negative value appeared it was set to zero. We ended up with a total of 16 measures of soil macro fauna effect, averaged per block (Table 3).

To retrieve more detail of how land-management varied within both protected areas and unprotected areas, wild and domestic herbivore dung was counted in each block in four of seven sites; Makao, Maswa, Mwantimba, and Handajega. Resulting in a total of 16 wild and 16 domestic herbivore dung counts (Table 3). All fresh dung was counted along a 4 × 50 m transect each month over a two-year period from May 2016 to May 2018. Monthly dung counts were averaged over the two-year period to get a mean monthly dung measure of both wild and domestic herbivores. We investigated dung counts as proxies of wild and domestic herbivore abundance, as Riginos and Grace (2008) found dung densities in savannah to be strongly related to the relative density of the same species.

2.2.4 Climate variable

How aboveground and belowground carbon stocks related to climate was explored by precipitation. We obtained satellite-based daily rainfall from NASA's Goddard Earth Sciences Data and Information Services Centre (Huffman & Savtchenko, 2017) and half-hourly measurements of cloud cover were taken using multi-satellite microwave data at 10 × 10 km spatial resolution. Daily rainfall estimates were taken from 2015 to 2017, and aggregated per year. This provided a measure of annual precipitation per block for all sites, resulting in a total of 28 measures of mean annual precipitation (MAP) (Table 3).

2.2.5 Soil variables

Impact of soil type on aboveground and belowground carbon stocks were explored by sand (%) and nitrogen content (kg m^{-2}) of the soil. We analysed for sand, silt and clay content of the soil at every site at block level, resulting in 28 measures of soil texture (Table 3). Nitrogen content of the soil (A-horizon and mineral-horizon) were analysed at every site at plot level, resulting in 112 measures of nitrogen for each horizon (Table 3).

Soil texture classes (clay, silt, and sand) were measured by the pipette method, and estimated by the particle size distribution. First, 10 mL deionized water and 10 mL of 35% hydrogen peroxide (H_2O_2) were added to 10 g of soil, and left over night. Second, extra 35% H_2O_2 was added, and the solution was heated until the organic material was fully oxidized. After this, water was added until the solution reached 200 mL before it was heated and reduced to 90 mL and left overnight. No hydrochloric acid (HCL) was added due to the high pH of the samples indicating that the samples could contain calcium carbonate ($CaCO_3$) (Krogstad et al., 2018). After sedimentation, water was sucked out. After pre-treatments, 25 mL deionized water was added to each sample. Sedimentation analysis was performed by the pipette method, before each sample was sieved through a 600 µm and a 63 µm sieve to decide the distribution of particles within each specific size class (sedimentation: clay and silt, sieving: sand) according to Krogstad et al. (2018). Nitrogen stocks (both A-horizon and mineral-horizon) (kg m^{-2}) were estimated by volume based E-stock calculations [4]. Nitrogen content of the soil (%) was analysed together with carbon content of the soil (method detailed above).

We analysed soil for total nitrogen and texture with the purpose of further usage in statistical analysis. pH (of all soil samples), cation exchange capacity (CEC), acid oxalate extractable phosphorous (P), aluminium (Al) and iron (Fe) (of two samples per site) were analysed to gain an extended understanding of variation in soil properties, and not with the purpose of further usage in our statistical analysis. pH was measured in soil mixed with deionized water (10 mL of soil, and 25 mL of deionized water) by a PHM210 standard pH-meter. CEC (Cmol kg^{-1}) was calculated based the sum of ammonium acetate ($C_2H_7NO_2$) extractable base cations (K^+, Na^+, Mg^{2+}, Ca^{2+}) and acidity (H^+) in the soil. The concentrations of K^+, Na^+, Mg^{2+}, and Ca^{2+} was analysed by an Agilent 5110 ICP-OES instrument (configuration: synchronous vertical dual view). Acid oxalate extractable P, Al and Fe was measured by shaking the samples with a ammonium oxalate solution (Krogstad et al., 2018).

Table 3. Sampling level of aboveground carbon pools (woody, herbaceous, and dead wood) and belowground carbon pools (A-horizon and mineral-horizon), as well as dung counts (wild and domestic herbivores), soil macro fauna effect, fire, MAP, soil texture, and soil nitrogen pools (A-horizon and mineral-horizon), B=block, P=plot.

Sampling site	Woody	Herba-ceous	Dead wood	Soil carbon	Dung	Soil macro fauna	Fire	MAP	Soil texture	Soil nitrogen
Makao	4 B	4 B	16 P	16 P	4 B	4 B	4 B	4 B	4 B	16 P
Maswa	4 B	4 B	16 P	16 P	4 B	4 B	4 B	4 B	4 B	16 P
Mwantimba	4 B	4 B	16 P	16 P	4 B	4 B	4 B	4 B	4 B	16 P
Handajega	4 B	4 B	16 P	16 P	4 B	4 B	4 B	4 B	4 B	16 P
Seronera	3 B	4 B	16 P	16 P	-	-	4 B	4 B	4 B	16 P
Park Nyigoti	4 B	-	16 P	16 P	-	-	4 B	4 B	4 B	16 P
Ikorongo	4 B	-	16 P	16 P	-	-	4 B	4 B	4 B	16 P

2.3 Statistical analyses

To determine the impact of land-management, soil type, and climate on aboveground and belowground carbon stocks, we used mixed effect models, model averaging, and path analysis. As a starting point for visualizing, and understanding covariation between variables, we created correlation matrices. We investigated several variables, and selected only non-colinear variables to include in the models the (Appendix, Table A2, Table A3). To avoid problems arising from collinearity, we never used variables with a Pearson's r > 0.50 in the same model. Soil texture parameters of sand, silt and clay content were highly correlated, thus we selected only sand content to include in the models (Appendix, Table A2). We ended up with four groups of variables: (1) land-management represented by land-use (protected areas versus unprotected areas), fire frequency, woody abundance (encroachment), wild and domestic herbivore dung, and soil macro fauna effect; (2) climate represented by MAP and soil by its sand and nitrogen content; (3) aboveground carbon and biomass represented by woody, herbaceous and dead wood, and finally; (4) belowground carbon represented by A-horizon and Mineral-horizon carbon. To be able to compare variables, they were all centred by subtracting the mean and scaled by dividing by the standard deviation, before analyses. An outlier (one block in Handajega) was removed after running analysis with and without this outlier (see Appendix, Fig. A2 for model average analysis with outlier).

We created *two* mixed effect models for every carbon pool (referred to as full models and subset models). The full models contained all sites, and all the response variables where we had obtained data from each site (i.e., without herbivore dung, Table 3). The subset models however, only included four sites (Makao, Mawsa, Mwantimba, and Handajega), but all variables outlined above. For the subset models we aggregated all soil data to block level because the additional variables (herbivore dung and soil macro fauna effect) where taken at the block level. In addition we wanted to avoid the risk overlooking underlying biotic drivers of ecosystem carbon stocks due to generally high spatial variation in soil. The random structure in the models reflected the experimental design. The random effect for woody and herbaceous carbon (data on block level, Table 3) was region, while for dead wood, A-horizon, and mineral-horizon (data on plot level, Table 3), it was individual block number nested within region.

Model averaging was used on a model selection object returned from dredge (Barton & Barton, 2015). First, we dredged each mixed effect model and restricted it (by "subset") not to include covarying variables (Pearson's $r > 0.50$) (Appendix, Table A2, Table A3) in the same model. We included interactions between land-use and MAP, and land-use and sand, to investigate our second hypothesis. Thereafter, we built a model selection table where each row represented a model and each column contained information about the models (e.g., coefficients, df, Akaike weights, AICc). Finally, we averaged all models to retrieve information about the relative importance of each predictor variable investigated, and their estimated conditional average coefficients. The relative importance of a variable is calculated as a sum of the Akaike weights, and is interpreted as the probability of that variable being a component of the best model. Each variable's estimated conditional average coefficient is averaged over all models where the variable appear, and weighted according to the probability of each model (Barton & Barton, 2015). Coefficients were centred and scaled so they would be directly comparable, and 95% confidence intervals were calculated. We used the importance of each variable and their estimated conditional average coefficients to rank variables according to their importance and give directions of how variables were driving aboveground and belowground carbon stocks. Model averaging treats each individual carbon pool in separate models. However, we were also interested in exploring relationships between carbon pools, and between drivers of carbon pools (i.e., how aboveground carbon stocks relate to belowground carbon stocks, or how woody encroachment varies with land-use).

We used path analysis to increase our knowledge of relationships between carbon pools, and between drivers of aboveground and belowground carbon stocks. We were interested in testing our hypotheses, and did an exploratory path analysis where we first started with a global model based on our conceptual model (Fig. 1). We specifically wanted to investigate possible causal pathways between climate and soil texture variables, and land-management variables.

Thereafter, investigate how these related to ecosystem carbon stocks directly and indirectly in the Serengeti ecosystem. Path analysis provides a means to examine a variable as a response and a predictor in the same system. Therefore, this approach allows for testing of more complex causal pathways with direct, indirect, and cascading effects by including several response and predictor variables in one global model (Grace, 2008; Shipley, 2009; Lefcheck, 2016).

Prior to our path analysis, we put restrictions to our global models. MAP, soil texture, and land-use were always predictor variables as we assumed none of the other variables (i.e., woody encroachment, fire frequency, herbaceous biomass) could explain their variation. Soil nitrogen and soil carbon are strongly positively correlated (Appendix, Table A2). Nevertheless, it is hard to define a causal relationship between them (Table 1), and if included this could overshadow other potential drivers of soil carbon stocks. Therefore, we prevented our global model from assessing the relationship between soil carbon and soil nitrogen stocks. In addition, we restricted our global model not to assess relationships between woody encroachment and woody biomass as these variables are related.

We fitted *two* piecewise structural equation models, one for all full-models and one for all subset-models, including all arrows from Fig. 1. We evaluated the global model fit by comparing the Fisher'C value against a Chi-square distribution to test the probability of the model *not* missing any relationships. If $P > 0.05$, the model is said to be a good fit of the data. We further evaluated each sub-model fit by looking at the proportion of variation explained by the fixed factors (marginal R-squared value) (Lefcheck, 2016). To get the most parsimonious global model, we removed and added variables according to their significance and contribution to the marginal R-squared values. Our final global model, based on the full-models, provided a good fit of the data (Fisher's $C = 91.778$ with $P = 0.216$) with 12 significant paths ($P < 0.05$), and two non-significant paths ($P > 0.05$). Our final global model based on the subset-models also provided a good fit of the data (Fisher's $C = 87.096$ with $P = 0.947$) with 13 significant paths ($P > 0.05$, Table 7). We used standardized estimates of each relationship to examine the complexity of variables driving aboveground and belowground ecosystem carbon stocks both directly and indirectly.

All statistical analysis were conducted in R version 3.5.2 (R Core Team, 2015). Mixed effect models were tested by ´nlme´ for model averaging and ´lme´ for path analysis, in their respective package lme4 (Bates et al., 2015) and nlme (Pinheiro et al., 2013). Model averaging, ´model.avg´, was run on a ´mod.sel´ object returned from ´dredge´ in the package MuMIn

(Barton & Barton, 2015), and piecewise structural equation models was fitted by ´psem´ in the package PiecewiseSEM (Lefcheck, 2016). The correlation matrices were created by ´pairs´ in the package Hmisc (Harrell Jr & Harrell Jr, 2019).

3 Results

3.1 Impact of land-management

Carbon stocks were substantially higher belowground (97.5% of total ecosystem carbon) than aboveground (2.5% of total ecosystem carbon) in the Serengeti ecosystem. Total ecosystem carbon stocks were slightly higher in protected areas (PA) compared to unprotected areas (UPA). Specifically, we found 2.5 times more herbaceous carbon (PA 0.02 ± 0.005, UPA 0.008 ± 0.002), 16 times more dead wood carbon (PA 0.06 ± 0.02, UPA 0.004 ± 0.001), 6 times more woody carbon (PA 0.07 ± 0.02, UPA 0.01 ± 0.005), slightly more A-horizon carbon (PA 1.49 ± 0.09, UPA 1.37 ± 0.07), and slightly more mineral-horizon carbon (PA 3.10 ± 0.23, UPA 2.76 ± 0.27) in protected areas compared to unprotected areas (Fig. 3).

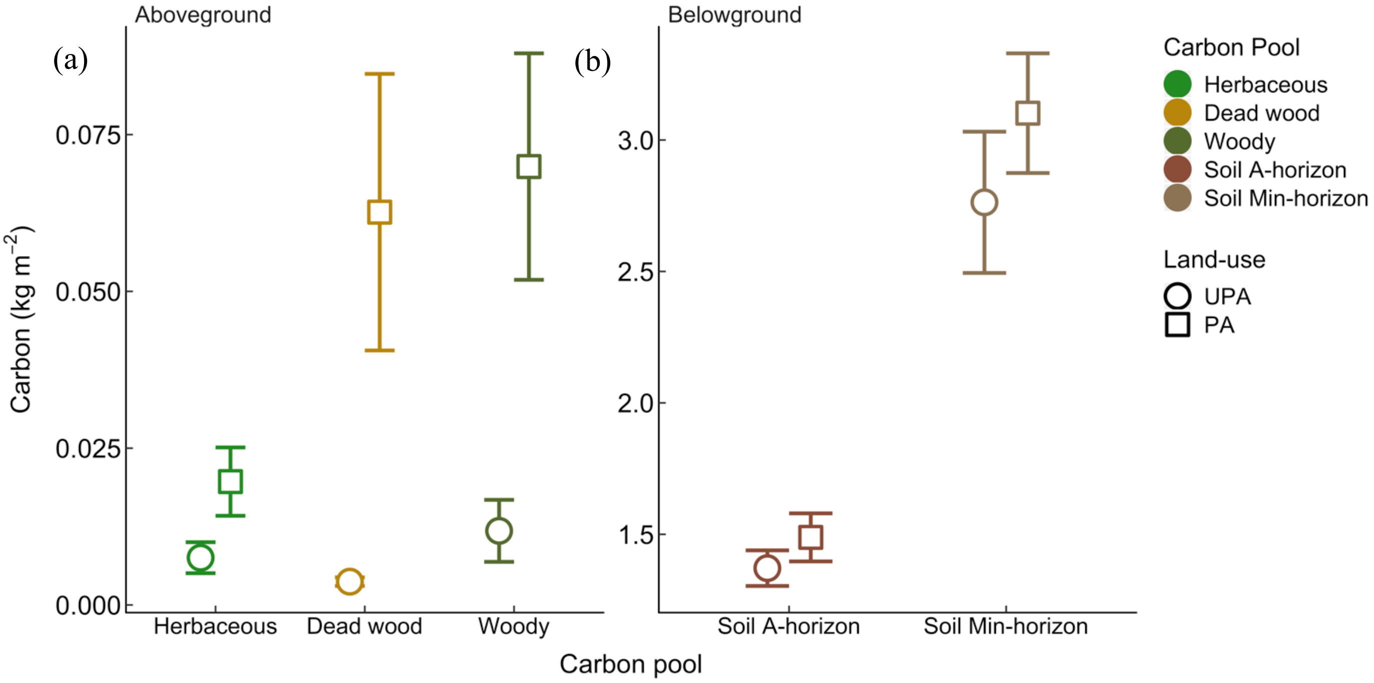

Figure 3. Carbon stocks (kg m^{-2}) (mean ± SE) of (**a**) aboveground (herbaceous (n=20), dead wood (n=112) and woody (n=27)), and (**b**) belowground (A-horizon (n=112) and Mineral-horizon (n=112)) carbon pools of unprotected areas (UPA) and protected areas (PA) in the Serengeti ecosystem.

Land-use was an important predictor of aboveground carbon stocks (Fig. 4a,c,e), however not of the belowground carbon stocks (Fig. 5a,c). Specifically, protected areas had more woody carbon (Fig. 4b), more herbaceous carbon (Fig. 4d), and more dead wood carbon (Fig. 4f). These findings were supported by the path analysis (Table 6, Fig. 6), except for land-use predicting herbaceous carbon. In the path analysis, fire frequency had a negative effect on herbaceous carbon which was also supported by the model averaging (Fig. 4c,d), here fire frequency was the most important variable with a relative variable importance (RVI) score of 0.67. Fire frequencies greater than one in every second year were associated with smaller herbaceous carbon stocks, while fire frequencies lesser than one every fourth year were associated with larger herbaceous carbon stocks. When including the outlier for Handajega, fire frequency had a positive effect on woody carbon (Appendix, Fig. A2a,b) however this relationship was not present when the outlier was removed (Fig. 4a,b). Otherwise, fire frequency was positively related to mineral-horizon carbon (RVI=0.883, Fig. 5c), where areas with higher fire frequencies had larger mineral-horizon carbon stocks (Fig. 5d), this relationship was not supported by the path analysis. Woody encroachment was neither predicting aboveground nor belowground carbon stocks.

We found no support for a path from aboveground carbon stocks to belowground carbon stocks. The carbon pools we found relating to each other were A-horizon carbon increasing mineral-horizon carbon ($P < 0.05$), and woody biomass indirectly relating to herbaceous carbon (Table 6, Fig. 6). Fire frequencies increased with increasing woody biomass ($P < 0.05$) which further had a negative impact on herbaceous carbon ($P < 0.05$), expressing a possible negative relationship between woody biomass and herbaceous biomass. Woody properties varied with land-use (Table 4). Average tree biomass per block was higher while average number of trees per block were lower in protected areas compared to unprotected areas. This resulted in a slightly lower woody abundance per m^2 in protected areas compared to unprotected areas (referred to as woody encroachment). Even so, our path analysis did not find a relationship between land-use, fire frequency, and woody encroachment (Table 6, Fig. 6).

Table 4. Woody properties per land-use (protected area (PA), unprotected area (UPA)) (mean ± SE), given in total tree biomass (kg block^{-1}), number of trees per block (n), woody encroachment (# trees m^{-1}/ median tree biomass), and dominant tree species.

Land-use	Tree biomass (kg block^{-1})	# Trees (No block^{-1})	Woody encroachment	Dominant tree species
PA	538 ± 185	5.93 ± 1.06	0.002 ± 0.001	*Vachellia tortilis* *Commiphora Africana* *Vachellia senegal*
UPA	42 ± 25	6.42 ± 0.92	0.005 ± 0.002	*Ormocarpum trachycarpum* *Vachellia drepanolobium*

3.2 Impact of soil type and climate

The effect of land-use on the aboveground carbon stocks was neither mediated by sand content of the soil nor MAP. Both land-uses had similar soil properties (Table 5). Belowground carbon stocks were not significantly related to land-use. However, A-horizon carbon tended to decrease with MAP ($P > 0.05$), but the negative slope of A-horizon carbon against MAP was less steep (less negative) in protected areas compared to unprotected areas (Fig. 5b). For the mineral-horizon we found the opposite, mineral-horizon tended to increase with MAP ($P > 0.05$), but the positive slope of mineral-horizon carbon against MAP was less steep (less positive) in protected areas compared to unprotected areas (Fig. 5d). Of sand and MAP, sand was the most important driver of the system (Table 6, Fig. 6). Sand did not directly modulate the effect of land-use in the belowground carbon stocks (Fig. 5). Nevertheless, components of land-management and carbon pools were strongly influenced by sand (all P-values < 0.05). Sand negatively influenced woody encroachment, soil nitrogen (A-horizon and mineral-horizon), woody carbon, and mineral-horizon carbon. In addition sand positively influenced herbaceous carbon by its negative effect on woody carbon driving fire frequency, which finally had a negative effect on herbaceous carbon (Table 6, Fig. 6).

Table 5. Soil characteristics, averaged over A-horizon and mineral-horizon (mean ± SE) per land-use (protected area (PA), unprotected area (UPA)). Sand content (%), BD (g cm^{-3}), pH, CEC (Cmol kg^{-1}), acid oxalate extractable Al, Fe and P content (g kg^{-1}).

Land-use	Sand (%)	BD (g cm^{-3})	pH	CEC (Cmol kg^{-1})	P (g kg^{-1})	Al (g kg^{-1})	Fe (g kg^{-1})
PA	43.83 ± 4.85	1.33 ± 0.02	6.71 ± 0.05	33.94 ± 4.41	0.59 ± 0.07	1.47 ± 0.17	2.72 ± 0.27
UPA	46.96 ± 3.98	1.24 ± 0.02	6.73 ± 0.05	33.10 ± 2.23	0.59 ± 0.12	1.14 ± 0.06	3.45 ± 0.56

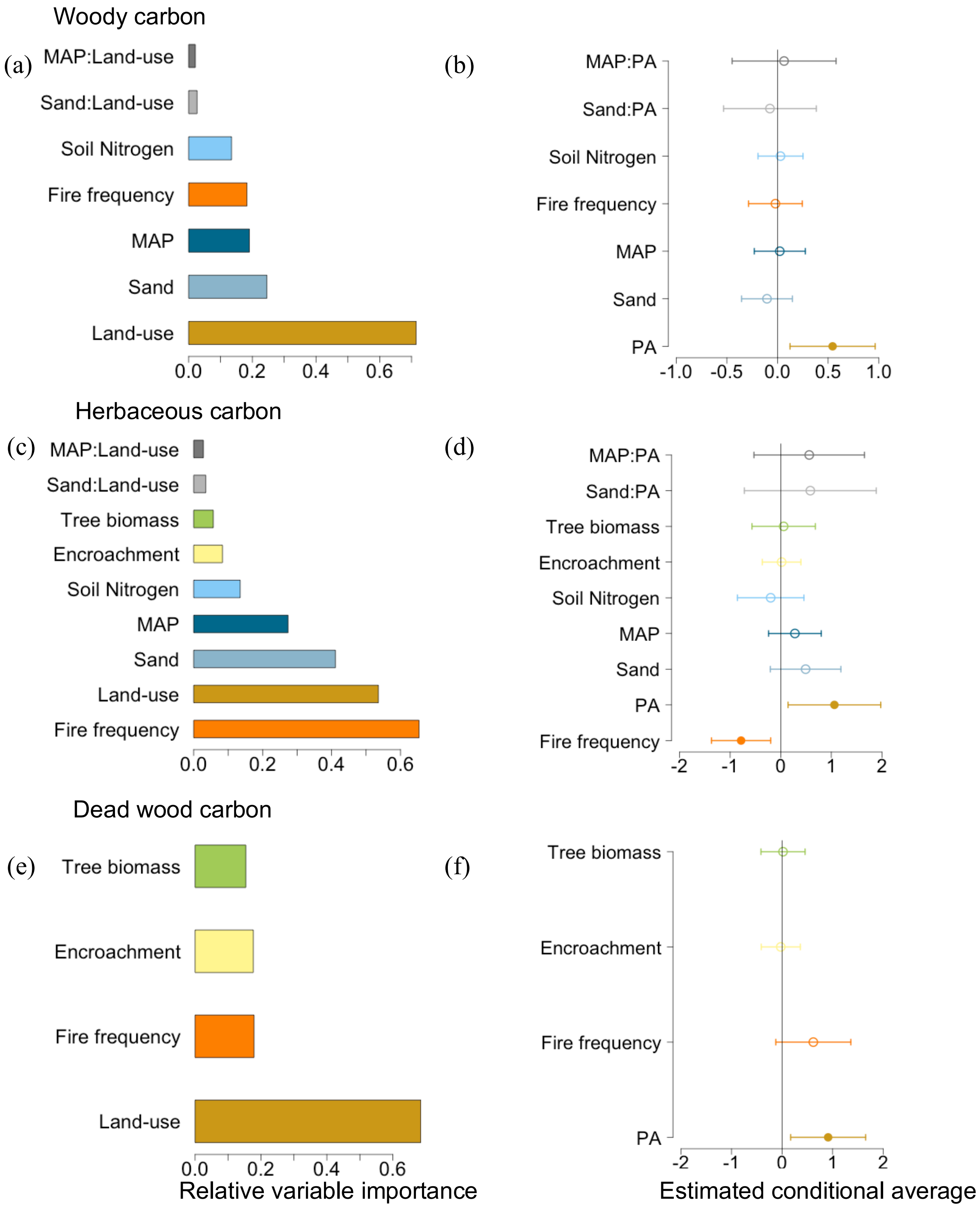

Figure 4. Model averaging analysis of linear mixed effect models of all data at block level. Land-management variables are coloured in yellow tones, climate and soil in blue, aboveground carbon pools in green, and interactions in grey. **(a,c,e)** Relative variable importance (ranked according to importance) of climate, soil, and land-management variables as predictors of woody, herbaceous, and dead wood carbon stocks. **(b,d,f)** Estimated conditional average of predictors of aboveground carbon stocks, PA is protected area. All predictor variables are centred and scaled to be directly comparable. Coefficients were averaged across all models where they appeared, means and 95% confidence intervals are shown. Closed points are coefficients with 95% confidence interval not overlapping zero ($P < 0.05$), and open points coefficients with 95% confidence interval overlapping zero ($P > 0.05$).

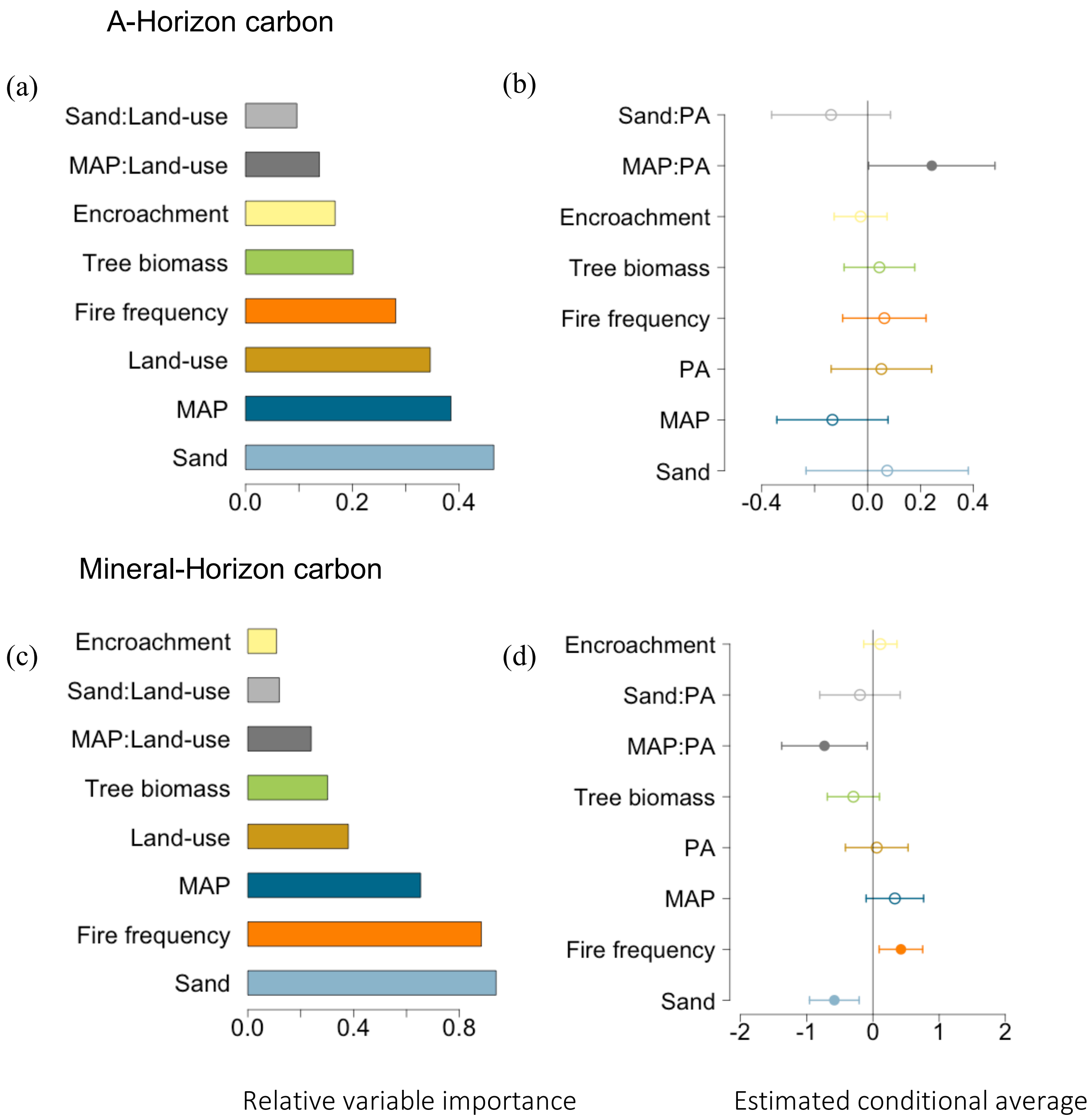

Figure 5. Model averaging analysis of linear mixed effect models of all data at plot level. Land-management variables are coloured in yellow tones, climate and soil in blue, aboveground carbon pools in green, and interactions in grey. **(a,c)** Relative variable importance (ranked according to importance) of climate, soil, and land-management variables as predictors of A-horizon and mineral-horizon carbon stocks. **(b,d)** Estimated conditional average of predictors of belowground carbon stocks, PA is protected area. All predictor variables are centred and scaled to be directly comparable. Coefficients were averaged across all models where they appeared, and means and 95% confidence intervals are shown. Closed points are coefficients with 95% confidence interval not overlapping zero ($P < 0.05$), and open points coefficients with 95% confidence interval overlapping zero ($P > 0.05$).

Table 6. Partial regression coefficients (raw and standardized (Std.)) from full path analysis exploring the direct and indirect effects of land-management, climate and soil on above and belowground carbon stocks. Standard error (SE) of std. estimate, degrees of freedom (DF), P-value, and significance (Sig.) level (*P < 0.05;** P < 0.01;***P < 0.001) is given. PA is protected area.

Response	Predictor	Raw estimate	Std. Estimate	SE	DF	P-value	Sig.
Woody	PA	0.058	0.484	0.033	5	0.142	
Woody	Sand	-0.022	-0.376	0.009	100	0.019	*
DW	PA	0.060	0.434	0.014	5	0.009	**
Herbaceous	Fire	-0.019	-1.018	0.002	65	0.000	***
Herbaceous	Min-horizon N	0.020	0.118	0.010	65	0.041	*
Min-horizon C	A-horizon C	0.555	0.209	0.224	80	0.015	*
Min-horizon C	Sand	-0.360	-0.342	0.160	19	0.037	*
Fire	Woody	2.453	0.159	0.843	95	0.005	**
Fire	DW	-1.829	-0.136	0.560	95	0.002	**
Woody encroachment	MAP	0.696	0.692	0.381	99	0.071	
Woody encroachment	Sand	-0.534	-0.540	0.133	99	0.000	***
A-horizon N	Sand	-0.014	-0.439	0.004	18	0.002	**
A-horizon N	MAP	-0.010	-0.307	0.004	18	0.025	*
Min-horizon N	Sand	-0.051	-0.502	0.015	19	0.002	***

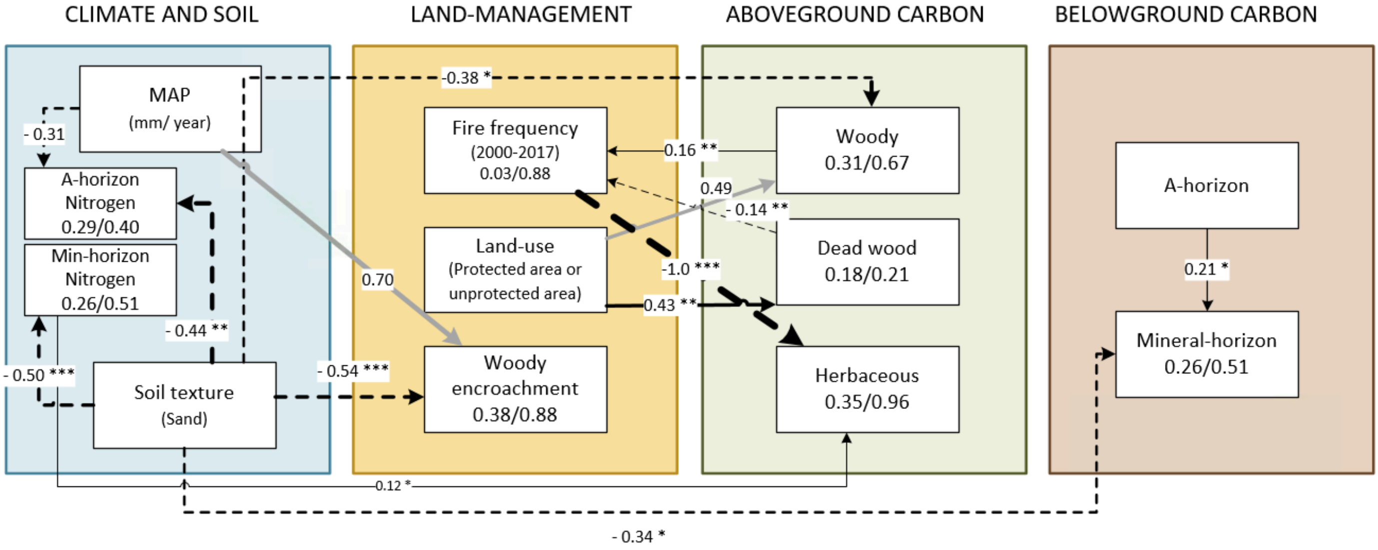

Figure 6. Full-model exploratory path analysis. Solid and dotted lines represent positive and negative relationships respectively, their standard estimates and significance levels are given (*P < 0.05;** P < 0.01;***P < 0.001), and lines are scaled according to these. Grey lines indicate non-significant relationships (P > 0.05). R-squared values (marginal/conditional) are given for each response variable.

3.3 Impact of biotic drivers

For our subset-models we included the four sites (Makao, Maswa, Mwantimba, and Handajega) where we had data on biotic drivers, namely wild herbivore dung, domestic herbivore dung, and soil macro fauna effect (Table 3). These variables were included to assess major biotic drivers of aboveground and belowground carbon stocks with differentiating land-management practices. Model averaging (Fig. 7a,b) and path analysis (Table 7, Fig. 8) supported that both wild and domestic herbivore dung were drivers of A-horizon carbon stocks ($P < 0.05$). A-horizon carbon decreased with domestic herbivore dung, and increased with wild herbivore dung (Fig. 7a,b). Over an increasing range of livestock dung (0-30), A-horizon carbon stocks decreased by 25% (Fig. 9a). While over an increasing range of wildlife dung (0-13), A-horizon carbon stocks increased by 23% (Fig. 9b). Woody carbon decreased with wild dung (Table 7, Fig. 8), but otherwise wild and domestic herbivore dung were not related to mineral-horizon or aboveground carbon stocks. Neither aboveground carbon stocks nor belowground carbon stocks were related to soil macro fauna effect in our analysis.

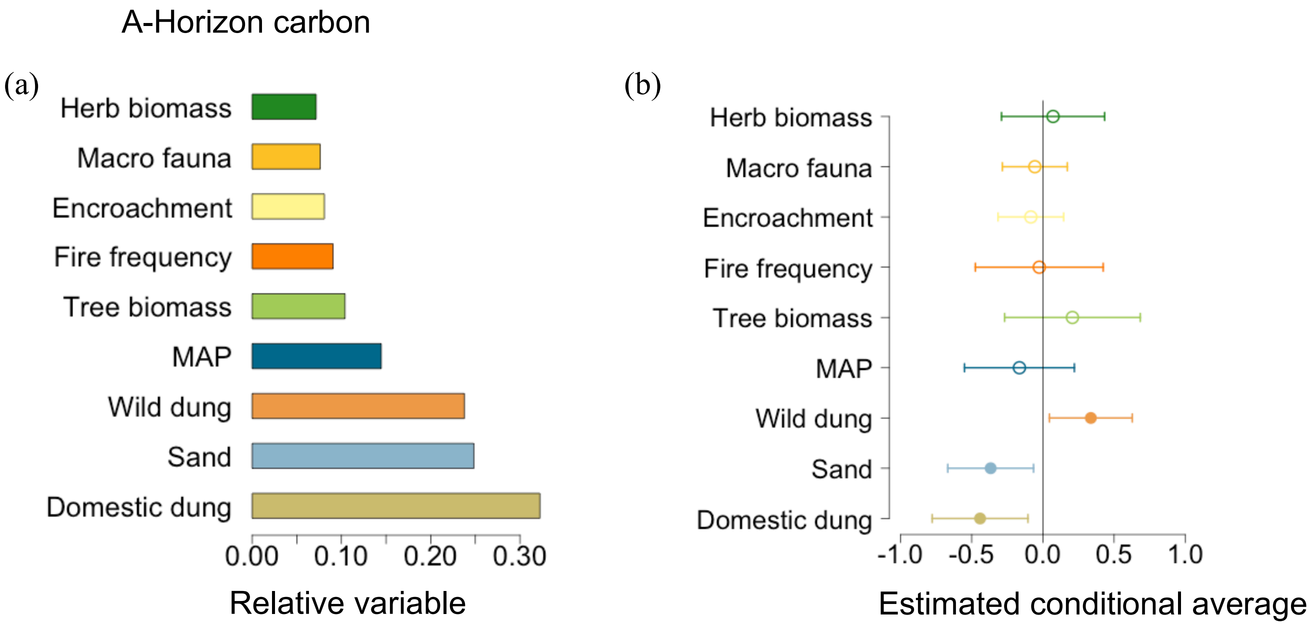

Figure 7. Model averaging analysis of linear mixed effect model of subset dataset at block level. Land-management variables are coloured in yellow tones, climate and soil in blue, and aboveground carbon stocks in green. **(a)** Relative variable importance (ranked according to importance) of climate, soil, and land-management variables as predictors of A-horizon carbon stocks. **(b)** Estimated conditional averages of predictors of A-horizon carbon stocks. All predictor variables are centred and scaled to be directly comparable. Coefficients are averaged across all models where they appeared, and means and 95% confidence intervals are shown. Closed points are coefficients with 95% confidence interval not overlapping zero ($P < 0.05$), and open points coefficients with 95% confidence interval overlapping zero ($P > 0.05$).

Table 7. Partial regression coefficients (raw and standardized (Std.)) from subset path analysis exploring the direct and indirect effects of biotic drivers of above and belowground carbon stocks. Standard error (SE) of std. estimate, degrees of freedom (DF), P-value, and significance (Sig.) level (* P < 0.05;** P < 0.01;***P < 0.001) is given.

Response	Predictor	Raw estimate	Std. Estimate	SE	DF	P-value	Sig.
Woody	Fire	0.044	0.490	0.017	9	0.031	*
Woody	Domestic dung	-0.060	-0.826	0.014	9	0.002	**
Dead wood	Herbaceous	2.921	0.664	0.975	10	0.013	*
Herbaceous	Fire	-0.016	-0.858	0.005	10	0.007	**
A-horizon C	Domestic dung	-0.111	-0.547	0.033	9	0.009	**
A-horizon C	Wild dung	0.096	0.481	0.033	9	0.016	*
Min-horizon C	A-horizon C	2.457	0.693	0.928	10	0.024	*
A-horizon N	Sand	-0.019	-0.735	0.003	9	0.000	***
A-horizon N	MAP	-0.009	-0.391	0.003	9	0.014	*
Min-horizon N	Sand	-0.076	-0.817	0.015	10	0.000	***
Macro fauna	Wild dung	0.559	0.575	0.221	10	0.030	*
Wild	Domestic dung	-0.726	-0.713	0.113	9	0.000	***
Wild	MAP	-0.759	-0.929	0.092	9	0.000	***

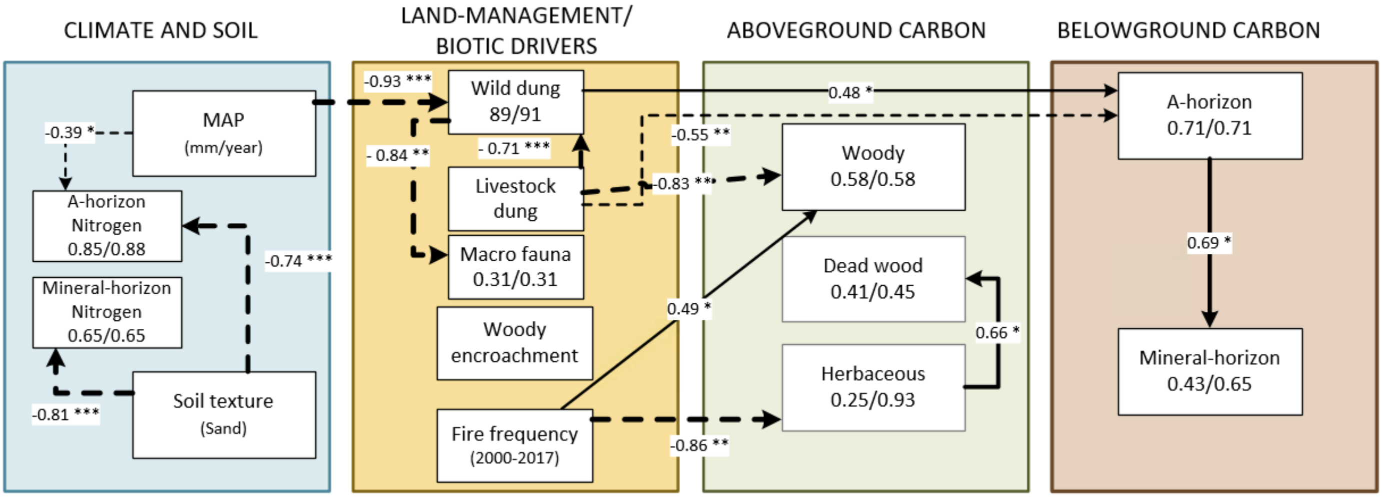

Figure 8. Subset model exploratory path analysis on block level. Solid and dotted lines represent positive and negative relationships respectively, their standard estimates and significance level are given (*P < 0.05;** P < 0.01;***P < 0.001), and lines are scaled according to these. R-squared values (marginal/conditional) are given for each response variable.

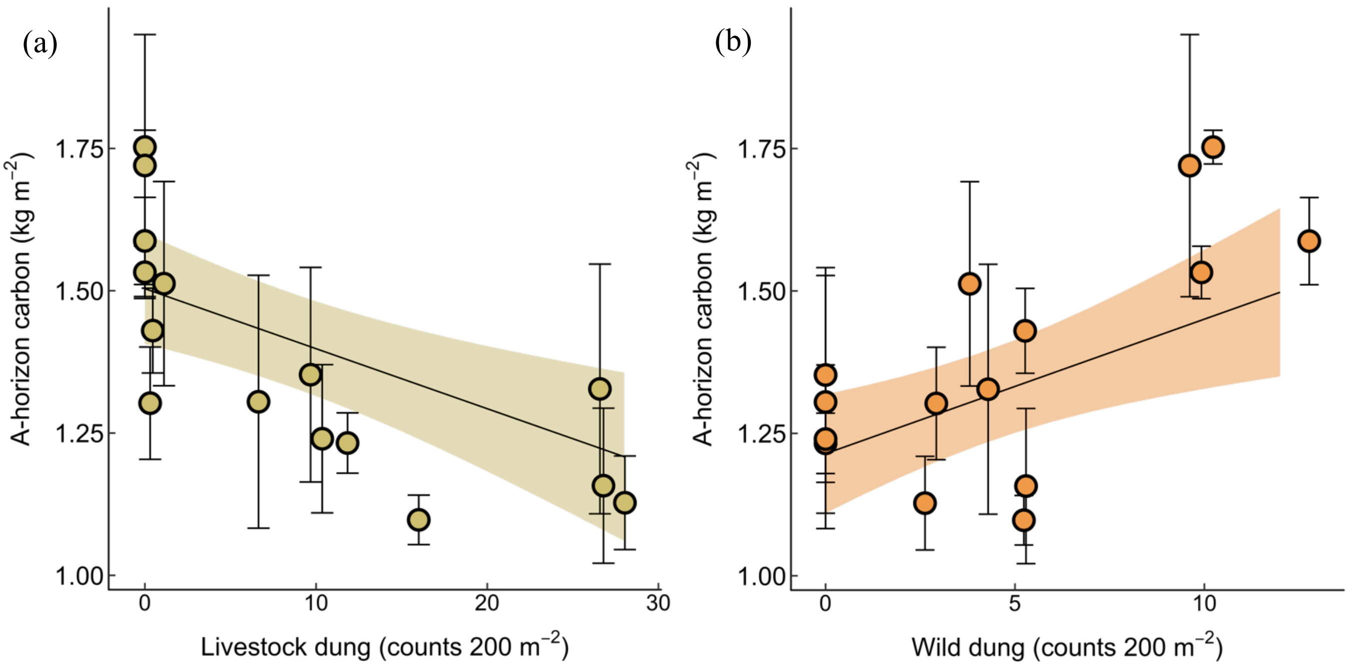

Figure 9. A-horizon carbon (mean per block ± SE) as a function of (**a**) domestic herbivore dung counts (200 m^2) from 0 to 30, and (**b**) wild herbivore dung counts (200 m^2) from 0 to 13, in the Serengeti ecosystem. Mixed effect model prediction lines and 95% confidence intervals are shown.

4 Discussion

4.1 Land-management

Our results demonstrate that aboveground carbon stocks are greatly influenced by different land-management practices in protected areas contrasted to neighbouring unprotected areas in the Serengeti ecosystem. The substantially higher aboveground carbon stocks in protected areas, compared to unprotected areas, were mainly driven land-use and fire frequencies. Variation in belowground carbon stocks with different land-management practices were less pronounced than we predicted. It is important to notice that total carbon stocks were substantially higher and more variable belowground than aboveground. Therefore, detecting changes in the greater belowground carbon pools can be much more challenging than detecting changes in the aboveground carbon pools. On the other hand, quantified belowground carbon stocks differences across contrasting land-management practices had a greater order of magnitude than quantified aboveground carbon stocks. We show that belowground carbon stocks were on average 460 g higher per m^2 in protected areas than adjacent unprotected areas, while aboveground carbon stocks were on average 130 g higher per m^2. The Serengeti National Park is a large protected area with high spatial heterogeneity. Therefore, the strong effect of land-management practices on aboveground carbon stocks and the marginal effect, but large quantified difference in belowground carbon stocks suggest that land-management is important. Our results demonstrate that protected areas in savannahs can be considered dense carbon stores compared to surrounding unprotected areas where ecosystem carbon stocks are being depleted.

Previous studies have found soil carbon to be higher under tree canopy compared to outside tree canopy (Coetsee et al., 2010; Becker et al., 2017). In this study, we were interested in whether total woody abundance in an area (hence woody encroachment) related to ecosystem carbon stocks *outside* tree canopies. We show that woody encroachment has a neutral effect on herbaceous biomass and belowground carbon stocks. This result contrasts to previous studies (e.g., Hudak et al. (2003)) that found SOC to decrease in severely encroached sites due to inhibition of herbaceous growth. Perhaps none of our sampling sites can be categorized as severely encroached since our study sites differ greatly from the semi-arid cattle grazed savannah study sites of Hudak et al. (2003). Furthermore, the study sites they categorized as severely woody encroached had up to 9.4 kg of woody biomass per m^2, while our most heavily encroached site had 0.03 kg per m^2. Even though we cannot provide evidence for heavy encroachment in the Serengeti ecosystem, we clearly observed advances of woody encroachment in our sampling sites (pers. obs). The Serengeti ecosystem spans a rainfall gradient from arid to wet. Considering that wet areas have been found to be more sensitive to belowground carbon loss when encroached (Jackson et al., 2002), we highlight that if woody encroachment continues in the Serengeti ecosystem, soil carbon stocks may become depleted more easily, specifically in wet areas.

Woody encroachment and fire frequencies tended to differ between protected areas and neighbouring unprotected areas. Previous studies have found a dramatic increase in woody encroachment with human settlement, cattle grazing, and reduction in fire frequencies (Scholes & Archer, 1997; Roques et al., 2001). In our study, these differences were therefore less consistent than predicted i.e., Mwantimba was the only unprotected sampling site that has not been burned since 2000, and the second most woody encroached site was situated in a protected area (Handajega). In the Serengeti ecosystem, border zones between protected areas and unprotected areas have a particularly high human population growth (Estes et al., 2012), and experience illegal grazing (Veldhuis et al., 2019). Hence, we question if our sampling sites were located too close to the borders. If so, the majority of them could be situated in a buffer zone neither being "truly" protected nor "truly" unprotected, frequently being grazed by both wild and domestic herbivores and frequently being burned by human regulated fires spreading across the borders. This inconsistency could explain why our results do not support herbivore community and fire frequency to be drivers of woody encroachment.

Our results show no relationship between aboveground carbon stocks and belowground carbon stocks even though it is a common understanding that alterations in the aboveground biomass affects the belowground carbon stocks (e.g., Jackson et al. (2002)). We attribute this to our study design as we did a snapshot study. We certainly expected woody, dead wood and belowground carbon stocks to remain more or less the same throughout the year. However, herbaceous biomass has been shown to vary more, due to annual differences in precipitation and annual ungulate migrations (McNaughton, 1985). Previous studies have found litter from herbaceous biomass to be the largest contributor to the belowground carbon pools (Pellegrini et al., 2015). Because primary productivity is highly stochastic in the Serengeti ecosystem (McNaughton, 1985), we acknowledge that variation in herbaceous biomass throughout the year (i.e., averaged across each month) could be a preferred measure, presumably relating to soil carbon stocks.

4.2 Soil type and climate

Our results establish that the difference in aboveground carbon stocks between land-management practices is, contrary to our predictions, consistent across soil types and precipitation regimes across the Serengeti ecosystem. These results are supported by previous findings of savannah woody cover to depend on disturbance rather than precipitation when MAP is above 650 mm (Sankaran et al., 2005; Sankaran et al., 2008). All our study sites had high annual precipitation (MAP > 650, Table 2), therefore consistency in woody biomass across precipitation differences is justifiable. Additionally, woody biomass reduced herbaceous biomass by positively driving fire frequency. Thus, homogeniety in herbaceous biomass across varying precipitation regimes can also be explained by the dominant role of disturbances. Given sufficient precipitation in all our sites, it is not surprising that disturbance is such a strong determinant of woody and herbaceous cover in the Serengeti ecosystem.

Our results indicate that precipitation effects on belowground carbon stocks differ with depth. Surface soil carbon (A-horizon) decreased with precipitation, while carbon in the deeper soil layers (mineral-horizon) increased with precipitation. Interestingly, the precipitation effect on surface and deeper soil layers was less apparent in protected areas. This indicates that belowground carbon stocks are less influenced by precipitation in protected areas compared to neighbouring unprotected areas. Otherwise, we found A-horizon carbon stocks to be remarkably unaffected by surroundings considering the location in the soil surface (0-5 cm). Previous research has found the soil surface to be greatly influenced by vegetation, e.g. Coetsee et al. (2010) found large trees to affect savannah soils to a depth of 7 cm, however not deeper. Instead, we found the deeper soil horizon (5-20 cm) to be driven by its surroundings as A-horizon carbon stocks, fire frequency, and soil texture affected the mineral-horizon carbon stocks. Considering that the general perception seems to be either a neutral or negative effect of fire on soil carbon stocks, through its effect on vegetation (Savadogo et al., 2007; Coetsee et al., 2010; Holdo et al., 2012; Pellegrini et al., 2015), we found it surprising that fire frequency was positive for mineral-horizon carbon stocks. We question if this relates to transformation of organic matter to black (pyrogenic) carbon, however we did not investigate this further.

We investigated soil texture and climate independently, as we consider them to be unrelated to land-management practices. Nevertheless, it is necessary to acknowledge that land-management might be related to specific soil types and climatic conditions. For instance, the Serengeti National park borders were established with the intention of encompassing annual movements of large ungulates attracted to this specific geographical area (Frank et al., 1998).

These animal movements could have originally been triggered by certain local features, such as soil types or favourable climatic conditions. Other protected areas may have been created on less favourable soil types, i.e. not fertile enough for agricultural purpose or alpine habitats dominated by rocks and ice. Hence, a protected area may be situation on a specific soil type with climatic conditions that have allowed wildlife to either thrive or decline. We did not find climate and soil type to modulate the effect of land-management on aboveground and belowground carbon stocks nor did soil properties vary with land-use. Even so, soil texture emerged as a key regulator of both aboveground and belowground carbon stocks. We argue that when assessing the potential of ecosystem carbon storage in protected areas compared to its surroundings, it is crucial to account for soil type and precipitation differences.

4.3 Biotic drivers

Our results underline the importance of identifying mechanisms that link animal abundance with changes in ecosystem carbon stocks discussed by Schmitz et al. (2014). Our work demonstrates that while there was no relationship between A-horizon carbon and land-management difference (land-use, fire frequency, and woody encroachment), A-horizon carbon certainly related to herbivore abundance. Because we found wild herbivores to avoid domestic herbivores, supported by Veldhuis et al. (2019), we argue that the site with the highest wild herbivore abundance could be referred to as the “most protected area” while the site with the highest domestic herbivore abundance the “least protected area”. Over a range of protection degree from least protected to most protected, we found A-horizon carbon stocks to increase.

We found no direct link between aboveground and belowground carbon stocks in our analysis. However, we found a direct link between herbivore abundance and belowground carbon stocks. Therefore, we suggest that land-management effects on soil carbon stocks are more related to the direct effect of herbivores, such as trampling, rather than herbivore foraging effects on litter input into the soil. Our field observations of larger areas with bare soil, more cracks in the soil surface, and more signs of animal trampling in unprotected areas compared to protected areas support this suggestion. Furthermore, cattle grazing has been found to increase soil compaction in wooded savannah (Savadogo et al., 2007). These direct effects of herbivores can result in changes in the soil, such as soil being less able to infiltrate water and becoming more vulnerable to erosion. Furthermore, herbivory can increase soil temperature due to sun exposure after reduced vegetation cover, thereby boosting decomposition. All these effects may subsequently reduce belowground carbon storage (Schmitz et al., 2018).

Protected areas do not have fenced borders in the Serengeti ecosystem, so both wild and domestic herbivores can cross the borders. We acknowledge that highly productive areas located close to the border could attract both wild and domestic herbivores, and do not necessarily reflect degree of human disturbance in this area. Accordingly, investigating wild and domestic herbivore abundance in isolation may not reflect protection degree properly, and these results should therefore be interpreted with some caution. Future investigation of differences in soil carbon stocks in savannah protected and unprotected areas should sample along ratios of wild and domestic herbivores. Thereby investigating a gradient from sites with wild herbivores exclusively, to exclusively domestic herbivores.

Neither fire frequency nor woody encroachment were drivers of soil macro fauna effect. Nevertheless, we found that soil macro fauna effect decreased with wild herbivore abundance, suggesting a reduced macro fauna effect in areas with high wild herbivore abundance. In addition, we found that regardless of land-management, soil macro fauna effects do not impact aboveground and belowground carbon stocks in the Serengeti ecosystem. Firstly, this indicates that soil macro fauna effect may differ with land-use, contrary to previous findings (e.g., Jones (1990)). Secondly, it indicates that soil macro fauna activity has neutral impacts on ecosystem carbon stocks. Soil macro fauna can alter carbon fluxes (Jones, 1990; Schmitz et al., 2014; Schmitz et al., 2018). However, how these alterations impact carbon stocks, and whether they reduce or increase them long term, is currently under debate (Dungait et al., 2012). Again, the snapshot design of our study assesses soil macro fauna effect on these specific sampling dates. Hence, our results cannot contribute to the debated long term role of soil macro fauna in shaping belowground carbon stocks.

4.4 Management implications

The evidence that we present indicates that even though highly variable, total ecosystem carbon stocks were on average 600 g carbon per m^2 higher in protected areas compared to neighbouring unprotected areas in the Serengeti ecosystem. We extrapolated these findings to the whole of Serengeti National Park (~15 000 km^2) to better understand the order of magnitude of these differences. Protection of the Serengeti National Park has resulted in a total ecosystem carbon storage of 9 million tonnes more compared to if the same area had stayed unprotected. This is, assuming that the Serengeti National Park is homogenous and can be represented by our study sites. Our results show that soils are less affected by land-management changes than vegetation, which may also imply that soil carbon gains take longer time. It is critical to consider that the Serengeti ecosystem is a large geographical area with protected areas created to maintain its ecological function. Veldhuis et al. (2019) highlight that observed differences in soil carbon stocks in the Serengeti ecosystem are a result of a maximum of 66 years of protection (Table 2), and may be even more pronounced for smaller and more fragmented savannah ecosystems.

Savannahs are starting to be recognized as important carbon sinks (Jobbágy & Jackson, 2000). Nevertheless, most public attention and conservation efforts are still given to forests and their importance for carbon storage. As a consequence, initiatives meant to increase carbon sequestration through afforestation and fire suppression are frequently initiated in savannahs, for example by Reducing Emission from Deforestation and forest Degradation (REDD+) (Parr et al., 2014; Fernandes et al., 2016). Abreu et al. (2017) investigated ecosystem carbon stock differences between forest and open savannah in a wet savannah-forest transition location. Indeed, the forest area that had been woody encroached over a long time period due to fire suppression had gained more ecosystem carbon when compared to the open savannah. These gains were attributed to increases in woody carbon, and small increases in soil carbon (upper 20 cm of the soil). However, increased woody abundance also introduces deeper roots into a system with substantial soil carbon stocks below the upper 20 cm. This intrusion of roots could expose previous inaccessible carbon stores to decomposing soil organisms (Schmidt et al., 2011). Jobbágy and Jackson (2000) found savannahs to have great carbon stores to a depth of 3 m. Therefore, quantifying carbon stocks differences in the upper 20 cm of the soil may not be sufficient when investigating the impact of increased woody abundance on belowground carbon stocks.

We argue that greater attention should be given to protection of savannahs rather than to tree planting initiatives if the goal is to promote ecosystem carbon storage. Land-management practices should aim to maintain the balance of wild and domestic herbivores, as well as fire frequencies in protected areas and buffer zones surrounding them. Regulating herbivore, and fire events on savannah ecosystems is important to avoid depletion of ecosystem carbon stocks. Increased woody abundance in savannahs reduce land available for agriculture and grazing livestock. Furthermore it has been found to reduce biodiversity (Jackson et al., 2002; Abreu et al., 2017). Additionally, grasses have a higher albedo than trees and might be helpful against the current global warming trend (Schmitz et al., 2014). Therefore, land-management should strive to preserve the savannah natural state of coexistence between trees and grasses, and the many benefits it provides.

5 Conclusions

This study demonstrates that land-management practices influence ecosystem carbon stocks in savannahs, a pattern that is consistent across soil types and precipitation regimes. Protection of the Serengeti ecosystem has resulted in greater carbon stocks within wildlife protected areas compared to neighbouring unprotected areas. In particular, aboveground carbon pools display substantially higher carbons stocks in protected areas, while belowground carbon pools display rather marginal differences between protected areas and unprotected areas. Nevertheless, belowground carbon pools show great differences of total quantified carbon amount between protected areas and unprotected areas (460 g higher per m^2 in protected areas). Fire frequency, herbivore community, and advance of woody encroachment all tend to differ with land-management practices. However, our results for the Serengeti attribute land-management impacts on ecosystem carbon stocks mainly to differences in fire frequencies and herbivore community, and not to woody encroachment. In contrast to aboveground carbon stocks, belowground carbon stocks seem to be more driven by the direct effect of herbivore abundance, such as dung and trampling, rather than herbivore foraging effects on aboveground carbon stocks that influence litter input into the soil. These results have implications for management of ecosystems and can contribute to integrated management of protected areas and its surroundings in savannahs. We recommend that more attention should be given to efficient management of savannah ecosystems – not only to enhance carbon storage inside protected areas, but also to decelerate carbon depletion in surrounding unprotected areas. Because the Serengeti is a rather wet savannah ecosystem, we suggest that attention should be given to wild and domestic herbivore interactions as well as fire impacts in order to maximize the carbon storing capacity of this ecosystem.

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Appendix

Table A1. Woody density (wd, g cm^{-3}) (mean ± SE) of each decay class (dc) according to Pfeifer et al. (2015).

dc	Description	wd
1	Little decay, bark cover extensive, leaves and fine twigs present	0.40 ± 0.03
2	No leaves and fine twigs, bark starting to fall off, logs relatively undecayed	0.58 ± 0.08
3	No bark and few branch stubs (not moving when pulled), sapwood decaying	0.37 ± 0.03
4	No branches and bark, outer wood case hardened, inner wood decomposing	0.26 ± 0.02
5	Wood often scattered across the soil surface, logs elliptical in cross-section	0.16 ± 0.06

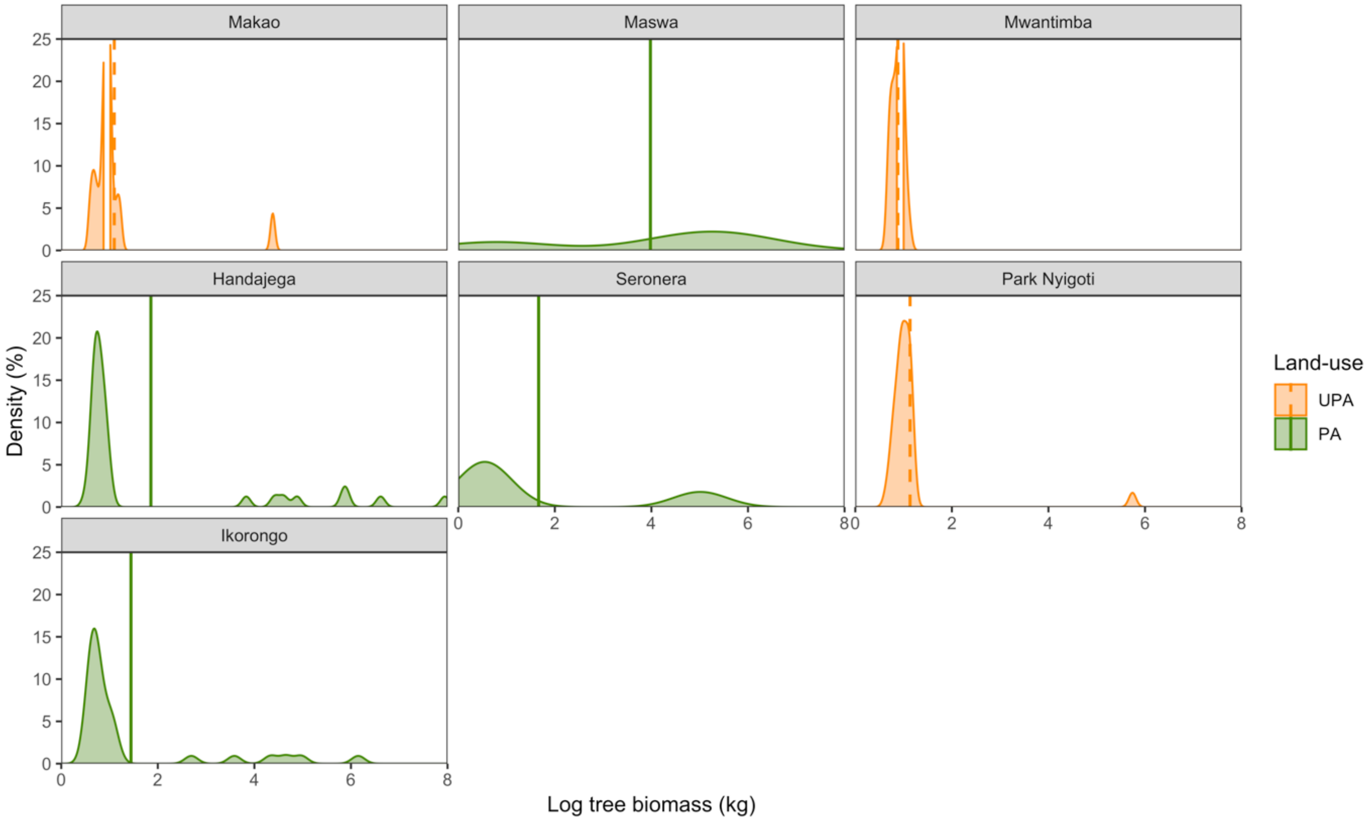

Figure A1. Distribution of tree biomass across land-uses (unprotected areas (UPA) and protected areas (PA)). Distribution of tree biomass in pastureland is shown in brown and wildlife protected areas in green. Mean tree sizes for different tree functional types are shown with dashed line for pastureland and solid line for wildlife protected areas.

Table A2. Correlation matrix (Pearson's r) of explanatory variables for data on plot level for every site. MAP, soil texture (sand and clay), year of last registered fire, fire frequency (total amount of fires from year 2000 – 2017), woody encroachment (WE, # trees m^{-1} median tree biomass^{-1}), tree biomass (Tree bm, kg m^{-2}), A-horizon (A-hor) and mineral-horizon (Min-hor) nitrogen (N) and carbon (C).

	MAP	Sand	Clay	Silt	Last Fire	Fire freq	WE	Tree bm	A-hor N	Min-hor N	Min-hor C	A-hor C
MAP	1.00	0.02	-0.11	-0.25	-0.10	-0.01	0.55	0.00	-0.31	-0.14	0.18	0.19
Sand		1.00	-0.87	-0.85	0.19	-0.01	0.04	-0.25	-0.52	-0.62	-0.61	-0.53
Clay			1.00	0.65	-0.30	-0.24	0.05	0.30	0.54	0.53	0.40	0.35
Silt				1.00	-0.42	-0.46	-0.03	0.413	-0.32	0.56	0.58	0.51
Last Fire					1.00	0.74	-0.56	0.13	-0.24	-0.10	0.08	0.01
Fire freq						1.00	-0.38	-0.03	-0.14	0.01	0.31	0.24
WE							1.00	-0.17	-0.21	-0.08	-0.03	-0.11
Tree bm								1.00	0.24	0.12	0.00	0.23
A- hor N									1.00	0.39	0.24	0.73
Min-hor N										1.00	0.84	0.36
Min-hor C											1.00	0.54
A-hor C												1.00

Table A3. Correlation matrix (Pearson's r) of explanatory variables for subset data at block level. MAP, soil texture (sand and clay), fire frequency (total amount of fires from year 2000 – 2017), woody encroachment (WE, # trees m^{-1} median tree biomass^{-1}), tree biomass (Tree bm) and herbaceous biomass (Herb bm) (kg m^{-2}), A-horizon (A-hor) and mineral-horizon (Min-hor) nitrogen (N) and carbon (C), year of last registered fire, domestic (Dom.) and wild herbivore dung, and macro fauna effect.

	MAP	Sand	Clay	Fire freq.	WE	Tree bm.	Herb bm.	A-hor N	Min-hor N	A-hor C	Min-hor C	Last fire	Dom. dung	Wild dung	Macro fauna
Macro fauna	-0.30	-0.43	0.31	-0.30	-0.29	0.37	-0.13	0.47	0.39	0.36	0.29	-0.16	-0.28	0.57	1.00
Wild dung	-0.67	-0.61	0.48	0.12	-0.64	0.47	-0.27	0.80	0.56	0.70	0.40	0.24	-0.39	1.00	
Dom. dung	-0.37	0.54	-0.45	0.38	0.01	-0.64	-0.39	-0.30	-0.36	-0.74	-0.41	0.06	1.00		
Last fire	-0.22	0.43	-0.41	0.83	-0.60	0.36	0.32	-0.15	-0.40	-0.04	-0.45	1.00			
Min-hor C	-0.09	-0.71	0.64	-0.46	0.10	0.27	-0.16	0.62	0.93	0.71	1.00				
A-hor C	-0.12	-0.75	0.66	-0.25	-0.30	0.60	0.08	0.76	0.66	1.00					
Min-hor N	-0.33	-0.82	0.75	-0.41	-0.06	0.30	-0.33	0.75	1.00						
A-hor N	-0.61	-0.86	0.83	-0.24	-0.43	0.30	-0.40	1.00							
Herb bm.	0.63	0.37	-0.37	-0.09	0.04	0.21	1.00								
Tree bm.	0.03	-0.41	0.37	0.18	-0.25	1.00									
WE	0.64	0.05	-0.03	-0.41	1.00										
Fire freq.	-0.34	0.49	-0.45	1.00											
Clay	-0.25	-0.95	1.00												
Sand	0.29	1.00													
MAP	1.00														

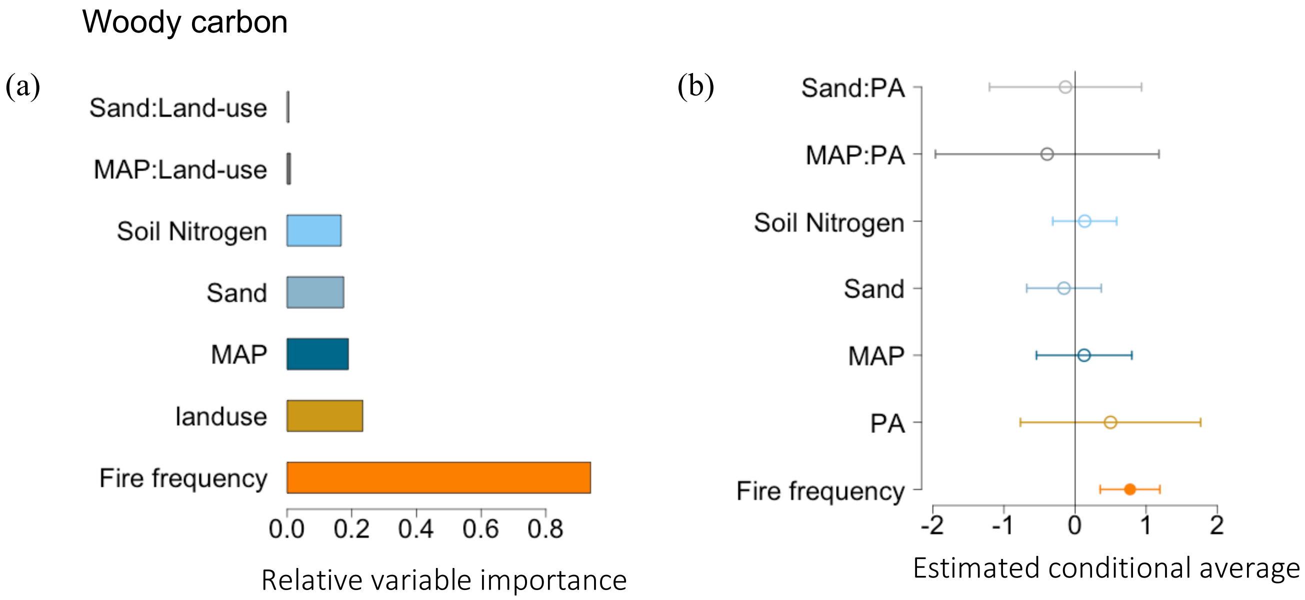

Figure A2. Model averaging analysis of a linear mixed effect model of woody carbon stocks with outlier. Land-management variables are coloured in yellow tones and climate and soil in blue. **a:** relative variable importance (ranked according to importance) of climate, soil, and land-management variables as predictors of woody carbon stocks **b:** Estimated conditional averages of predictors of woody carbon stocks. All predictor variables are centred and scaled to be directly comparable. Coefficients are averaged across all models where they appeared, and means and 95% confidence intervals are shown. Closed points are coefficients with 95% confidence interval not overlapping zero (P < 0.05), and open points coefficients with 95% confidence interval overlapping zero (P > 0.05).

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