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Effects of Fire, Grazing and Agriculture on Carbon Stocks and Biodiversity in the Ruaha-Katavi Landscape

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ABSTRACT

The wildlife corridor between Ruaha and Katavi National Parks is under threat from cultivation and increased fire frequencies. This study evaluated the impacts of protection, fire, and habitat conversion on carbon stocks and biodiversity in the Ruaha-Katavi Landscape. Soil carbon, above-ground woody carbon stocks, herbaceous biomass and insect species richness were determined from 87 plots across a variety of land uses. There were significant differences in carbon stocks among different soil, and land use types (p < 0.001). Sandy soils featured significantly higher woody carbon (p < 0.001) than heavy clay soils. Conversion of woodlands to croplands significantly reduced aboveground woody carbon (p < 0.001) from an average of 72.4 Mg/ha for woodlands compared to 30.9 Mg/ha for croplands. Furthermore, croplands had significantly lower woody carbon than grazed woodland remnants in Open Areas (p = 0.005). Herbaceous plants and Orthoptera species richness did not vary significantly with land use (p > 0.05). Lepidoptera species richness significantly correlated with tree species richness. This study provides some key preliminary information that may justify feasible interventions to slow down conversion of woodlands into croplands to achieve climate-related benefits mainly reduction of greenhouse gas emissions by sequestering carbon in wood and soils.

Keywords: Carbon – fire – grazing – cropland – livestock - butterflies - grasshoppers - trees, - protected areas.

INTRODUCTION

Tropical forests are a reservoir for about 25% of the global terrestrial carbon (Bonan, 2008; Santos *et al*. 2011, Sarkinen *et al*. 2011, Portillo-Quintero *et al*. 2015), thus play major roles in regulating global climate dynamics (Lewis *et al*. 2009, Zhou *et al*. 2013). However, recent findings show that tropical forests are subject to huge losses and are becoming a source of carbon emissions to the atmosphere rather than carbon sink (Holbrook *et al*. 1995, Geoghegan *et al* 2010, Jaramillo *et al* 2011, Becknell *et al*. 2012). In sub-Saharan Africa, these forests still occupy 25% of the land area despite millennia of conversion into land for crop production (FAO 2016) and serve as critical habitat for some of Earth's most threatened wildlife species, such as lion (*Panthera leo*), elephant (*Loxodonta africana*), roan (*Hippotragus equinus*) and sable antelope (*Hippotragus niger*) (Gippoliti *et al*. 2018). Historically, this habitat was sparsely populated due to soils being too poor for crop production and grasses too low in nutrients to support livestock grazing. However, transhumance movements of livestock, human population growth, easier access to fertilizers, and increased access to markets have increased conversion of these forests into croplands mixed with heavily grazed woodlands without fire (Syampungani *et al*. 2009). These conversions are likely to affect the carbon stocks, and supporting and regulating ecosystem services (Soka and Nzunda 2014, Sunderland *et al*. 2015, Siyu 2020).

Protected areas throughout the dry tropical forest zones of Africa experience high fire frequencies (Lipsett-Moore 2018) that can degrade wildlife habitat, convert woodland to grassland, and deplete organic matter in soils that are already some of the poorest on earth (Dougill 2004, Davies 2010). Consequently, simple protection from human activity may be insufficient to sustain productivity and associated wildlife populations (Veldhuis *et al*. 2019). A conservation goal is to reduce habitat conversion and manage fire to achieve more beneficial early-season burning (Archibald *et al*. 2005, Chirwa 2008, Russell-Smith *et al*. 2013, Lipsett-Moore 2018, Russell-Smith *et al*. 2021). Recent reviews suggest that miombo woodland can harbor significant amount of carbon stocks (60-100 metric tons/ha) in wood and soil to a depth of 1 m, and those excessive fires can deplete carbon stocks (Chidumayo and Kwibisa 2003; Ryan *et al*. 2011, Woollen *et al*. 2012, Chidumayo 2013, Gumbo *et al*. 2018). Moreover, intense livestock grazing can deplete organic matter in the soil, and with time may significantly reduce nutrients and water-holding capacity of the soil, thus its reproductive potential (Ellis and Swift 1988, Bollig *et al*. 2013). Slowing conversion of woodland into agricultural land and managing fire in the Ruaha-Katavi Landscape (RKL) may achieve climate-related benefits mainly reduction of greenhouse gas emissions by sequestering carbon in wood and soils. Also, may achieve sustainable production and water retention benefits in the form of productive ecosystems and sustainable hydrological cycles that support human livelihoods. For example, soil with the greater organic matter may retain water deeper during the dry season; over large watersheds such as those in the RKL this can mitigate upstream drying of the Rungwa and Ruaha River basins.

The most common human pressures causing deforestation and severe forest degradation including agriculture, unsustainable forest management, mining, infrastructure projects and the consequences of protection for fire regimes also affect biodiversity (Ntongani *et al*. 2010, Jew *et al*. 2015, Brockerhoff *et al*. 2017), but these consequence of fire on ecosystem services are understudied (Pausas and Keeley 2019) and focused mainly on plants (Gumbo *et al*. 2018). Fire plays a major role in biodiversity protection all over the world. Fire suppression can cause devastating wildfires because of an unnatural accumulation of fuel. Deliberate human suppression of fire can also have direct negative impacts on species. In forests where fire is a natural part of the system, plant and animal species are adapted to a natural fire regime and benefit from the aftermath of a fire (Dennis *et al*. 2001, Cremer 2004, Pausas and Keeley 2009). Loss of woody canopy can reduce butterfly (Lepidoptera) diversity (Jew *et al*. 2015) and fire affects species composition of wood beetles (Coleoptera) (Madoffe *et al*. 2000). Given the importance of insects in ecological food webs, crop pollination, and other ecosystem services (Losey and Vaughan 2006), and in light of their global decline (Sánchez-Bayo and Wyckhuys 2019), it is critical that impacts of protection, fire, and habitat conversion be measured and linked to ecosystem health, as indicated by carbon stocks and/or biodiversity.

The linkage between the three roles of ecosystems in providing climate benefits, supporting productive human communities, and sustaining biodiversity is unclear (Runting *et al*. 2017, Asch *et al*. 2019’ Pausas and Keeley 2019). A key question that has received relatively little attention is whether biodiversity is either positively or negatively associated with carbon. Habitats receiving more human impact are generally assumed to be reduced in biodiversity. To address these issues, we measured species diversity of grasshopper, butterfly and moth, and some soil parameters, as well as carbon in woody, tree and herbaceous plants in areas subject to different land use and management in the Ruaha-Katavi Landscape (RKL). We explored whether carbon and species diversity of selected three insect species differed among lands used for crop production and community forest management (Open Areas, OA) and protected areas that allow different human use such as Forest Reserves (FR) that allowed beekeeping and livestock grazing, Wildlife Management Areas (WMA) that allow controlled grazing and tourism/hunting, and Game Reserves (GR) that allow permitted hunting and tourism. In addition, we explored whether high carbon stock in the soil and wood in this ecosystem is associated with its high water-holding capacity (an ecosystem service associated with soil carbon that promotes productivity and potentially diversity). These measurements allowed us to evaluate the potential impact of changing land use and management on carbon stocks and biodiversity, and to assess possible negative associations between carbon stocks and biodiversity that might drive trade-offs in future land use and management between increasing carbon stocks and sequestering greenhouse gases, and in supporting miombo woodlands' key role in the conservation of biodiversity.

MATERIALS AND METHODS

Study Area

The Ruaha-Katavi migration corridor is a vast area of upland dry tropical forest and poorly drained lowlands that provides critical corridors between wet and dry season ranges for East Africa's largest remaining elephant population (Wildlife Conservation Society 2016). The migration corridor remains one of the largest (360,000 km^2) ecologically intact savannah ecosystems in Africa - a true African stronghold, making it imperative for conservation. The landscape incorporates two national parks, three main game reserve complexes, open land and several key wildlife corridors, all of which contribute to the area's conservation integrity (Figure 1). The migration corridor also supports other threatened or vulnerable wildlife species. It also provides vital natural resources (timber, dry season forage for livestock) and ecosystem services such as beekeeping and water table replenishment to several remote, rural Tanzanian communities. The dominant natural habitat type in the migration corridor is a dry tropical forest called miombo, which features leguminous trees (e.g., genus *Brachystegia* and *Julbernardia*) (Frost 1996, Burgess *et al*. 2004) and tall grasses (e.g., *Hyparrhenia rufa*) on upland sandy soils that often contain barely detectable levels of phosphorus and other key plant and animal nutrients (Rannestad and Gessesse 2020). The eastern portion of the landscape is dominated by the Great Ruaha River which is the most economically important water course in Tanzania. Rising in the Southern Highlands, it winds north and east before merging with the Rufiji and on to the Indian Ocean having passed through the Ruaha landscape.

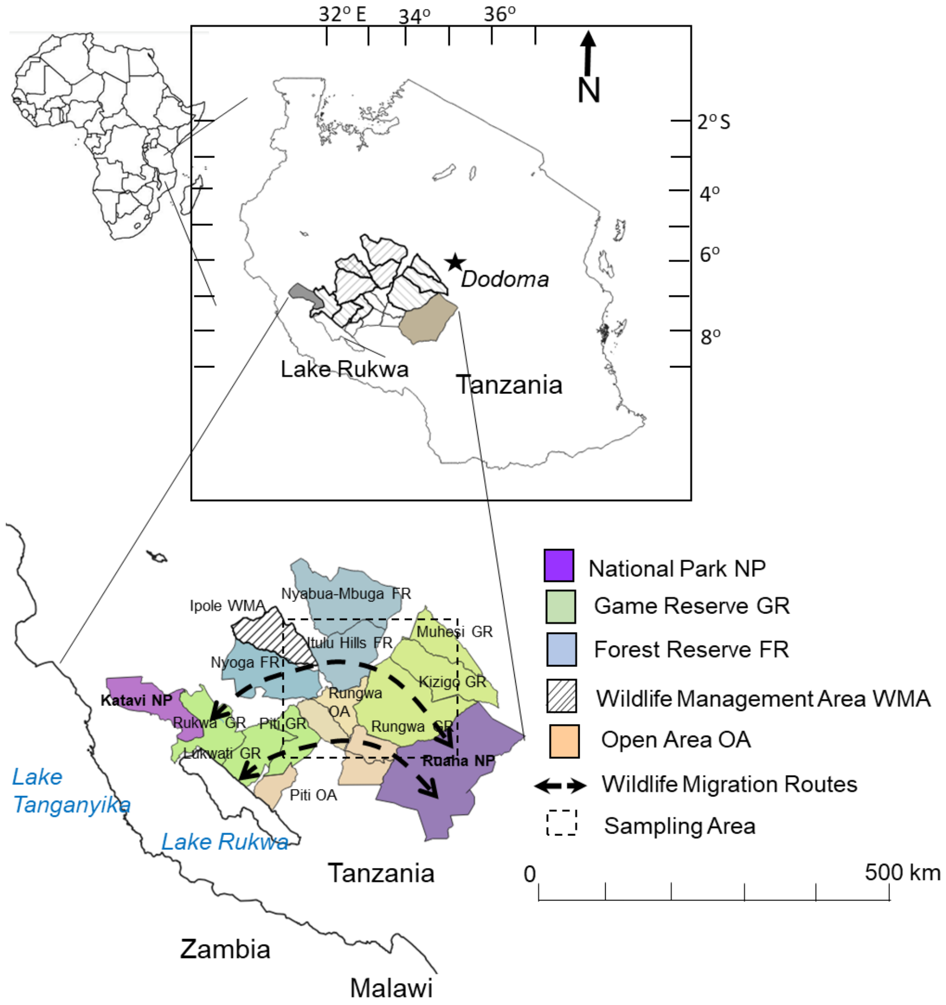


Figure 1. The Ruaha-Katavi Landscape in west-central Tanzania, consisting of multiple Open Areas (OA), various game reserves (GR) forest reserves (FR), and Wildlife Management Areas (WMA) National Parks (NP).

Sampling Design

This study involved a rapid sampling of a large number of stations across a variety of land uses (Figure 1) and, within those uses, across different fire frequencies (Figure 2). As an alternative, standardize for likely human influence, we established a 3 km buffer around mapped roads in selected jurisdictions and then selected at random from within these buffers. The buffers were oversampled to include extremes in disturbance history, e.g., fire frequency in protected areas and time since the conversion of forests to croplands and redundant points near mean disturbance history values were eliminated at random to achieve a desired 15 - 20 sampling stations per land-use x disturbance history combination (Figure 3). This replicates the most common land use x disturbance history combinations, including sandy and mbuga soils, and crop production, grazing, fire, selective timber harvest, and protected area land uses.

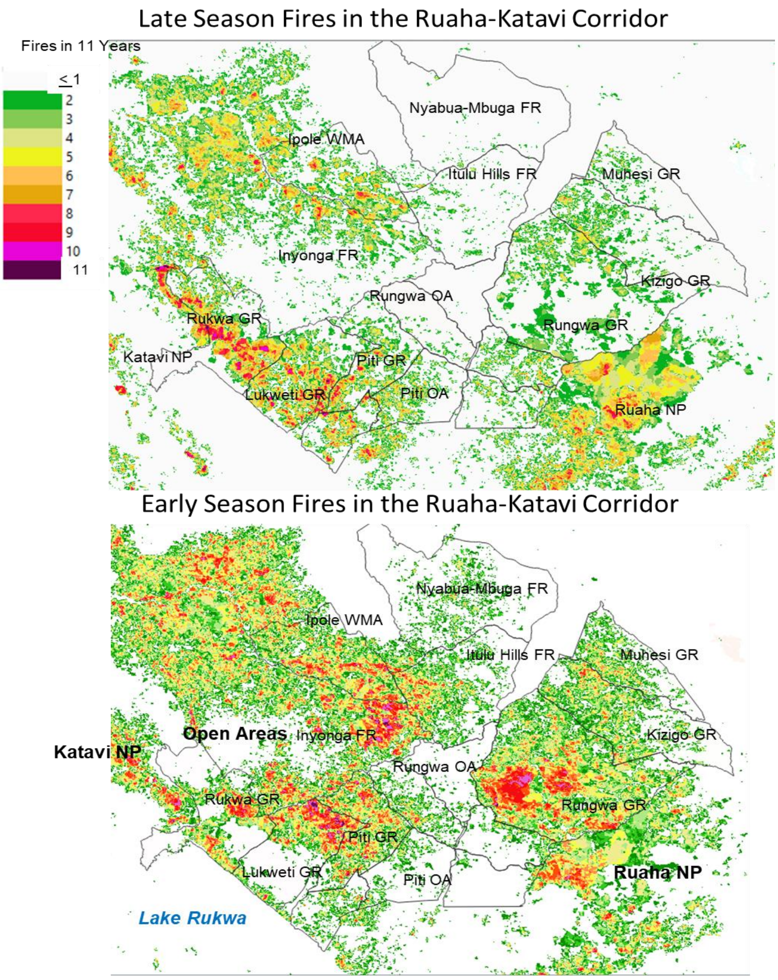


Figure 2. Distribution of fire frequency for the RKL derived from MODIS MCD64A1 Burned Area Product. A = Late season fires (August - November). B = Early season fires (June - July).

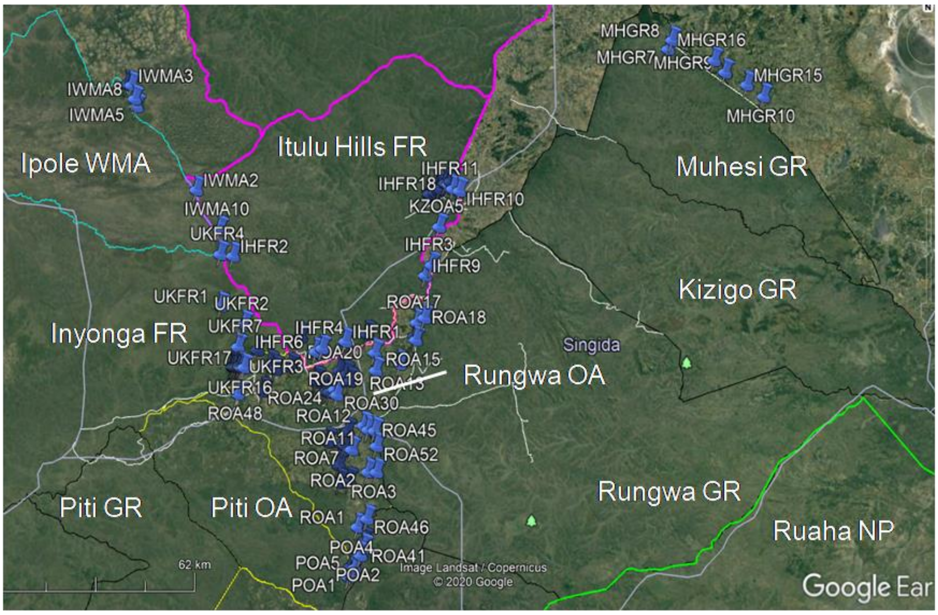


Figure 3. Distribution of sampling stations (blue pins), extending some 250 km from east to west and north to south across Muhesi Game Reserve (GR), Itulu Hills and Inyonga Forest Reserves (FR) and Rungwa and Piti Open Areas (OA)

Sampling occurred within four land use classes in the RKL: including two game reserves (GR) and forest reserves (FR), open areas that retain woodland (OA), and open areas cleared for crop production. Within each land use, we generated 10 - 20 points within 3 km of accessible roads and then randomly selected out of these 25% black cotton soil (mbuga) and 75% sandy soil points. For crop and livestock grazed points, we randomly selected 20 - 30 sandy soil points that vary in the time since they were converted from woodland to estimate soil carbon changes with time after conversion. For protected area land uses, we selected seven (7) black cotton soil points and 43 sandy soil points, with the sandy soil points varying in the frequency of fires over the last 10 years.

Fire frequency was determined with MODIS Burned Area Product (MCD64A1), which incorporates multiple visible and infrared spectra from the MODIS satellite to estimate whether vegetation has burned (Dempewolf *et al.* 2007). Monthly layers of burn dates were downloaded from http://earthdata.org LPDAAC and used to classify whether pixels had burned in that month. Monthly burn occurrences from each year were summed across years to yield a total number of fires at a site since 2009.

Time since conversion

The history of conversion was determined by tracking changes in the visual classification of woodland to cropland and uncultivated mbuga habitat to rice cultivation in annual Google Earth images (based on Landsat 8 classifications) dating back to 2000 (Figure 4).

Woody biomass and carbon density and tree diversity

At each sampling station, an 8-m radius plot (201 m^2) was selected from the initial random GPS point by a blind toss of a steel marker. Sampling was performed in the dry

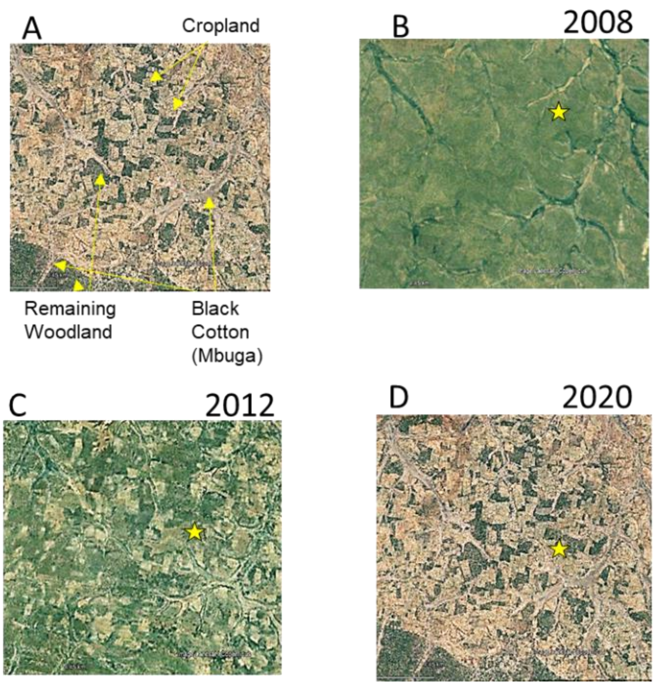


Figure 4. Example use of dated Google Earth Pro images to establish timelines of woodland clearing for sampling stations in the Open Areas. Woodland and crop and mbuga soil areas are easily visually classified. Annual images are available which allows the year in which a given point (e.g., yellow star) is converted from woodland to cropland to be determined (B - D).

season after leaf abscission, so tree canopy cover was not estimated. Stem density and diameter at breast height (dbh) was measured with a tape at 1.3 m height for each woody stem (> 5 cm) within an 8-m radius plot (201 m^2). The tree species for all stems were noted, with multiple stems from the same plant considered as independent stems. Aboveground wood biomass was estimated by incorporating each measured dbh into an allometric equation C (kg) = $0.046*dbh^{2.76}$ for each tree and then summing woody carbon over all trees in the 201 m^2 plot.

Soil carbon density

We collected two soil cores (8.25 cm diameter) at each plot to 40 cm depth, which corresponds to the depth at which land use was most likely to affect soil carbon. Wet mass of soil (M_w) from the known volume (V) of the two cores was measured in the field following by filtering through a 2mm mesh sieve to remove rocks and pebbles. The volume of rocks, v_R, was measured by displacement of water in a graduated cylinder and wet mass, m_w of a 30 ml subsample was measured in the field with a digital scale and dry mass of the subsample, m_d, was measured in the lab following drying for 48 hrs at 105°C. Bulk density (BDg/cm^3) was estimated as:

$$BD = [M_w/(V-v_R)]*(m_d/m_w) \qquad (1)$$

A 100 g subsample was analyzed for percent organic C (SOC %) using the Walkley-Black method at the Department of Soil and Geological Sciences, Sokoine University of Agriculture (SUA) in Tanzania. Belowground soil carbon density, SOC density (Mg/ha) to a Depth = 40 cm was estimated as:

$$SOC = SOC\%*BD*(V-v_R)*Depth \qquad (2)$$

Herbaceous biomass and plant richness

Plant biomass was estimated using a rapid non-destructive assessment method. A 0.1 kg circular aluminum plate (60 cm diameter) was dropped along a graduated pole and the displacement of the plate above ground level. Herbaceous plant species richness was determined by counting the number of plant species in the 0.28 m^2 underneath the plate. These measurements were made at each of sixteen locations 1 m apart in transects along the N-S diameter of the 8 m radius tree sampling plot.

Insect diversity

A team member walked continuously within the 8-m radius tree sampling plot for 30 min, catching Orthoptera and Lepidoptera using sweep net with a 38-cm net ring, 91-cm handle, and white muslin bag. Voucher specimens of each collected morphospecies were pinned in insect trays for later identification, and probable IDs were assigned to Lepidoptera observed in plots but not caught.

Statistical analysis

Soil, woody, and total carbon, as well as tree, herbaceous plant were compared among management and land use factors using Statistical Package for Social Sciences (SPSS) version 26 Generalized Linear Models. A single model compared three predictor variables, each with two or more levels: Original Land Cover (mbuga versus woodland), Land Management Type (OA, FR, GR), and Land Use (crop, grazed, logged, or protected) plus time since clearing and fire frequency as covariates. We also related tree, herbaceous plant, and insect diversity to soil, woody, and total carbon using linear regression in SPSS 26.

RESULTS

Land Management and Fire in the Ruaha-Katavi Landscape

Fire history construction in the RKL revealed several patterns. Late season (August - November) fires 2009 - 2020 occurred primarily inside highly protected areas considerably buffered from human settlement, including Ruaha National Park and Rukwa and Lukwati Game Reserves (Figure 5). In contrast, early-season fires predominated in protected areas near human settlement, particularly in areas that allow human utilization for beekeeping, selective timber harvest, and livestock grazing. Frequencies above 8 fires in 11 years occurred in central parts of protected areas, while frequencies in zones within approximately 15 km of settled borders experienced generally less than three fires in 11 years, and most of those were early season burns (Figure 2).

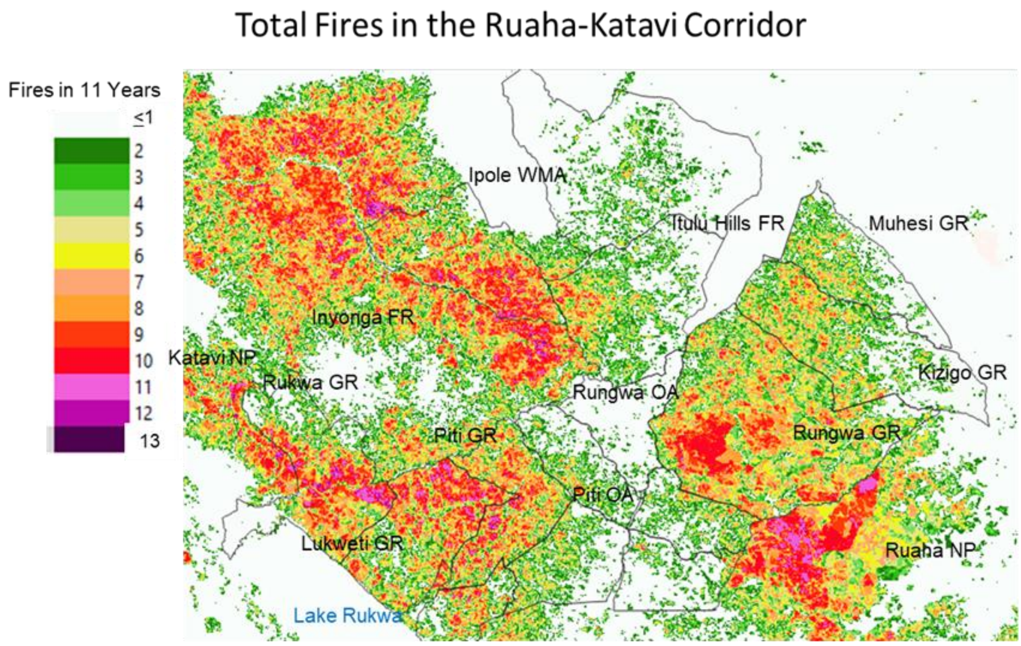


Figure 5. Total fire frequency in the RKL, aggregating across early and late fires. Note the concentration of fires in the center of protected areas (GR, FR), and low fire frequencies in protected areas near borders with settlements in Open Areas (OA).

Land Use, Management and Carbon Stocks

In a General Linear Model analysis (GLM), we detected significant differences in carbon stocks among different soil, and land use types (Table 1). Of note, sandy soils that supported miombo canopy tree species featured significantly higher woody carbon (X^2_6 = 33.28, p < 0.001) than heavy clay mbuga soils (Figure 6). Likewise, as expected, conversion of woodland to cropland significantly reduced aboveground woody carbon (X^2_6 = 33.28, p < 0.001) from an average of 72.4 Mg (metric tons)/ha for woodland habitats compared to a mean of 30.9 Mg/ha for croplands in various stages of recovery following woodland clearing and two years' crop production.

Table 1. General Linear Model analysis of carbon stocks across soil, management and land use types in the RKL. Effect sizes are shown relative to the bottom class in each category

A		Woody Carbon				Soil Carbon			
Factor	**Level**	**Effect Size**	**SE**	**X^2**	***p***	**Effect Size**	**SE**	**X^2**	***p***
Soils	Mbuga	-58.46	14.46	16.337	**0.000**	5.35	3.46	2.694	0.122
	Sandy								
Management	FR	-0.166	22.62	0.02	0.997	1.39	5.40	0.066	0.797
	GR	52.44	28.25	3.404	0.065	7.92	6.81	1.354	0.245
	OA	-33.8	22.23	2.312	0.128				
	WMA								
Land Use	Crop	-57.700	5.0700	26.97	**0.000**	-2.30	2.16	0.560	0.445
	Grazed	-12.260	8.5000	2.06	0.227	3.90	2.21	1.880	0.287
	Protected								
B		**Total Carbon**							

Factor	Level	Effect Size	SE	X^2	P
Soils	Mbuga	55.680	15.0280	13.731	**0.0001**
	Sandy				
Management	FR	0.784	46.8842	0.000	0.987
	GR	56.350	29.5380	3.640	0.056
	OA	-31.998	23.0000	1.919	0.166
	WMA				
Land Use	Crop	-58.531	22.467	5.125	**0.032**
	Grazed	-26.5	5.126	15.213	**0.0001**
	Protected				

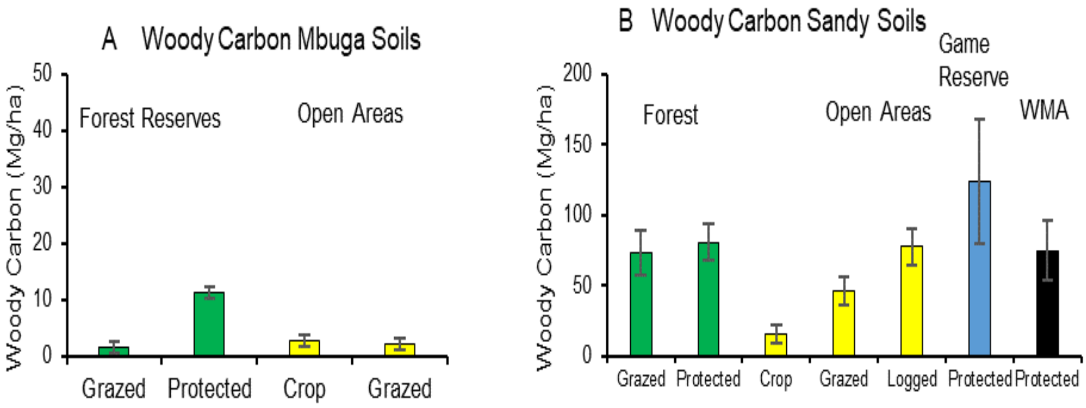


Figure 6. Mean (+ SE) woody carbon densities (Mg (metric tons)/ha) on A = mbuga and B = sandy soils in protected and open areas subject to different land uses. Note the different scales in the dependent variable between A. and B., reflecting that mbuga soils support relatively little woody carbon compared to sandy soils.

Muhesi Game Reserve featured an approximately 50 Mg/ha higher woody carbon density than other protected areas and woodland remnants in Open Areas subject to selective logging and/or livestock grazing. However, stocks were highly variable among sampling stations within the Reserve and this difference is not significant (p = 0.1). Land use had significant effects on woody carbon in Open Areas (X^2_2 = 16.33, p = 0.005), with croplands significantly lower than grazed woodland remnants, and grazed remnants significantly lower than remnants or still unsettled woodland areas subject to selective harvesting. We did not analyze herbaceous biomass stocks as these contributed negligibly (2 - 4 Mg/ha, or about 1 - 2%) to total carbon stocks (Figure 7).

Soil carbon stocks were not on average significantly different among soil types (X^2_5 = 4.639, p = 0.46), land management types (GR, FR, WMA, and OA) or land uses (cropland, grazing, selective logging, or protection) (Table 2). Measured soil carbon densities to 40 cm depth were not significantly different (X^2_5 = 0.863, p = 0.86) from measurements, corrected to 40 cm depth. Total carbon (soil + woody carbon) patterns reflected those of woody carbon (Figure 8), which reflects the relative invariance of soil carbon across the landscape and the influence of human impacts on woodlands and thus aboveground woody carbon.

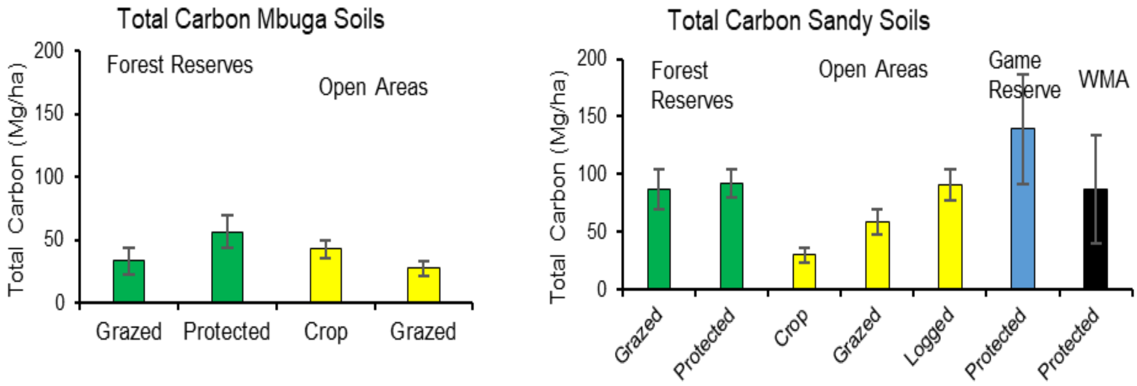


Figure 7. Mean (+ SE) total (soil + wood) carbon densities (Mg (metric tons)/ha) on A = mbuga and B = sandy soils in protected and open areas subject to different land uses. Note the different scales in the dependent variable between A. and B., reflecting that mbuga soils support relatively little woody carbon and human activity has relatively little impact compared to sandy soils.

Table 2. Carbon stocks (Mg = metric ton) on different soil, management types and land use in the RKL

Type	Use	N	Woody Carbon Mg/ha		Soil Carbon Mg/ha		Total Carbon Mg/ha	
			Mean	SE	Mean	SE	Mean	SE
Mbuga Soils								
Forest Reserves	Grazed	4	1.5	1.3	29.5	10.1	33.3	10.5
	Protected	4	11.3	7.4	31.9	5.3	56.7	24.6
Open Areas	Crop	5	2.7	2.2	36.3	3.7	42.8	22.4
	Grazed	2	2.2	2.2	21.9	4.5	27.5	13.0
Sandy Soils								
Forest Reserves	Grazed	5	73.4	16.1	29.0	3.3	87.3	8.3
	Protected	16	80.9	12.8	23.2	2.7	92.1	6.0
Open Areas	Crop	17	15.1	6.4	31.3	5.1	29.9	3.3
	Grazed	12	46.3	10.3	26.8	3.3	58.3	5.1
	Logged	10	77.7	12.7	22.6	2.7	91.2	6.3
Game Reserves	Protected	6	123.5	44.2	28.1	5.3	139.6	22.4
WMA	Protected	6	75.1	21.3	23.9	3.9	86.7	22.0

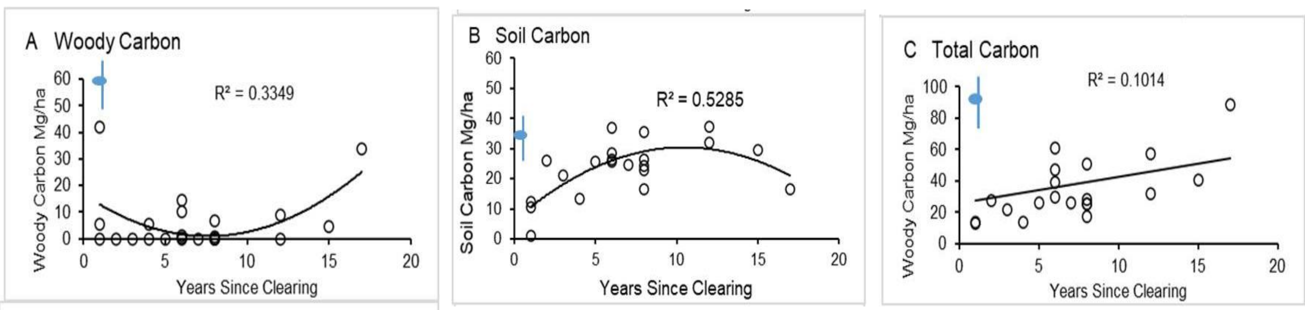


Figure 8. Relationships between measured carbon densities from 20 cropland sampling stations and years since woodland clearing, as estimated from sequential analysis of Google Earth images. Quadratic relationships are fit to the data for A. woody carbon and B. soil carbon because they are substantially superior to linear fits (sample size corrected Akaike Information Criteria was at least a value of three). Blue circles represent reference means (+ SE) of protected remnant woodlands in Open Areas influenced only by selective timber harvest.

Carbon stocks in wood, soils, and in both combined (total carbon) were not associated with total, early or late fire frequency ($X^2{}_1 <$ 1.99, p = 0.16). Fire frequency (total, early, or late season) included as a covariate in statistical analyses never yielded a better-fitting model or a significant correlation independent of other factors (p = 0.46).

Time-dependent changes in carbon stocks in cleared woodlands

Both soil and woody carbon densities exhibited significant relationships with time since the clearing of woodlands (Figure 8A & B). Total carbon exhibited a positive, though not significant relationship with time since clearing, indicating recovery of about half of the total carbon in reference areas after 15 years. The regression suggests an annual mean carbon sequestration rate in abandoned fields of 1.667 Mg C/ha. These data imply that woodland with carbon density equivalent to human-impacted dry forest might recover in approximately thirty years. A longer period would likely be required to achieve mean carbon densities found in fully protected areas such as game reserves (Figure 7).

Land Use and Management and Biodiversity

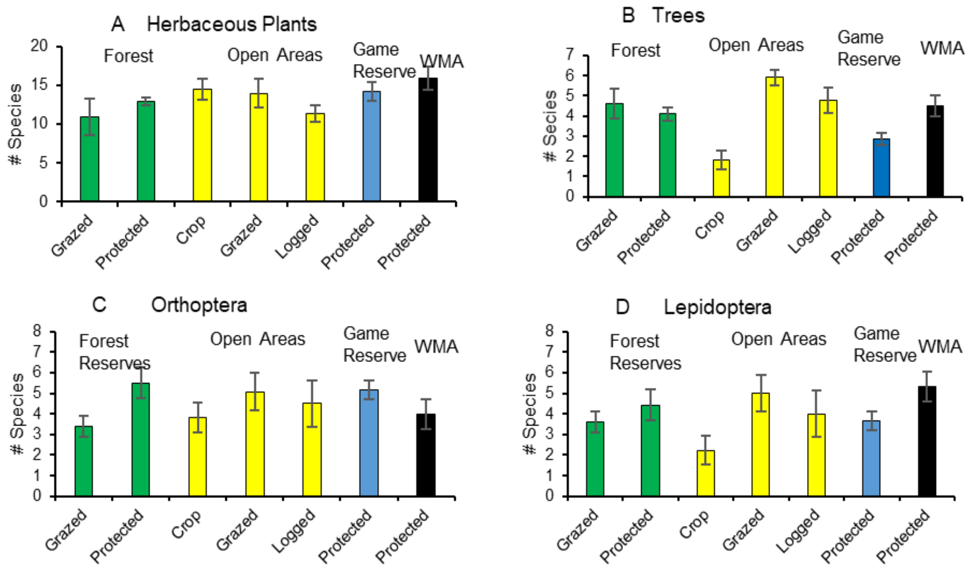
We found that species richness of herbaceous plants and trees responded differently to land management type and land use. However, Orthoptera and Lepidoptera show similar pattern for different land management and land use (Figure 9). Sampling stations did not vary substantially in species evenness, so we report here only the results for species richness, as results for calculated diversity indices are similar to those for species richness. Herbaceous plant and Orthoptera species richness did not vary significantly with land management type or land use. Woody species show significant difference with soil and land use particularly with crop production, but did not show significant difference with land management as well as grazing. Lepidoptera species richness showed significant difference only with land use particularly crop production and not with other variables (Table 3). Tree species richness was highest in grazed, wooded Open Areas, reflecting the high diversity of thorny understory trees, while richness was lowest in cropland (Figure 9). WMA and FR tree species richness were higher than that found in Muhesi Game Reserve. Lepidoptera species richness showed similar patterns (Figure 10). Indeed, Lepidoptera species richness was significantly correlated with tree species richness in both protected and open areas (Figure 9). Species richness in protected areas was not associated with fire frequency for any groups (p = 0.22).

Table 3. General Linear Models' analysis of four biodiversity measures, A. plant species richness for trees and herbaceous plants, and B. insect species richness for two orders, Lepidoptera and Orthoptera

A		**Woody Species Richness**				**Herbaceous Species Richness**			
Factor	**Level**	**Effect Size**	**SE**	**X^2**	***p***	**Effect Size**	**SE**	**X^2**	***p***
Soils	Mbuga	-2.050	0.5654	13.14	**0.000**	-2.153	1.3118	2.694	0.101
	Sandy								
Management	FR	0.686	0.9501	0.52	0.470	-3.213	2.2010	2.131	0.144
	GR	-0.908	1.2168	0.56	0.455	-1.056	2.9242	0.130	0.718
	OA	1.223	0.8912	1.88	0.170	-2.781	2.0727	1.800	0.180
	WMA								
Land Use	Crop	-2.696	0.6544	16.97	**0.000**	2.020	1.5126	1.783	0.182
	Grazed	0.425	0.5524	0.59	0.441	0.613	1.2929	0.225	0.635
	Protected								
B		**Lepidoptera Species Richness**				**Orthoptera Species Richness**			
Factor	**Level**	**Effect Size**	**SE**	**X^2**	***p***	**Effect Size**	**SE**	**X^2**	***p***
Soils	Mbuga	-0.450	0.4436	1.031	0.310	0.265	1.0845	0.060	0.807
	Sandy								
Management	FR	-1.117	0.7453	2.248	0.134	-0.455	1.3096	0.121	0.728

	GR	-1.584	0.9546	2.752	0.097	-1.370	1.6557	0.685	0.408
	OA	-0.636	0.6992	0.828	0.363	-1.907	1.5928	1.434	0.231
	WMA								
Land Use	Crop	-2.421	0.5133	22.240	**0.000**	1.212	0.8812	2.126	0.291
	Grazed	0.083	0.4333	0.037	0.848	-1.167	0.9489	1.073	0.449
	Protected								

Figure 9. Mean (+SE) species richness **of four different taxa sampled from sandy soil stations (N**



= 76) in the RKL for different land management types and land uses. Differences in means among types and uses were significant for trees and Lepidoptera.

Carbon Stocks and Biodiversity

The four groups varied in their association with carbon stocks. In protected areas, the species richness of the two insect groups, but not the two plant groups, was positively associated with woody plant carbon (Figure 10). None of the species richness of four different taxa showed any indication of negative relationships with carbon density. In Open Areas, tree and Lepidoptera species richness showed highly significant positive associations with woody carbon concentration (Figure 10).

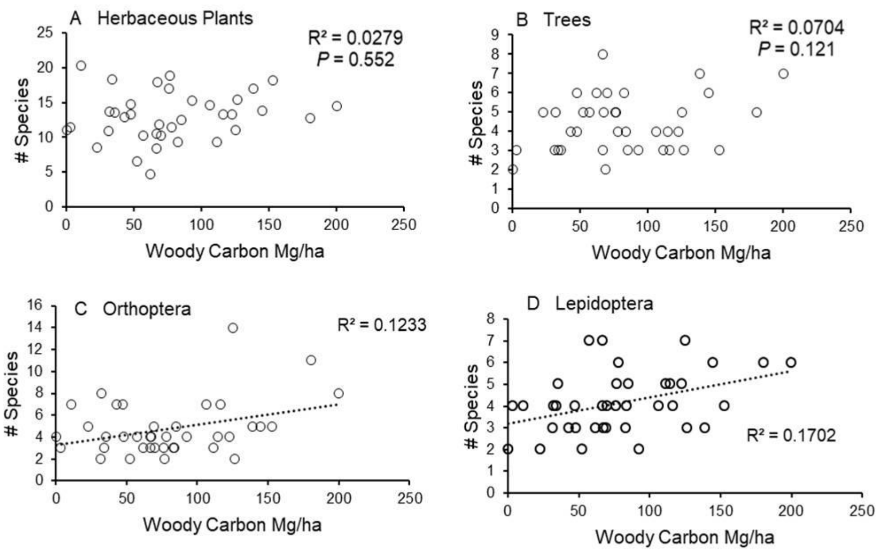


Figure 10. Relationships between species richness and total carbon density in protected areas in the RKL.

Soil Moisture and Carbon Density

An often-overlooked hypothesized benefit of higher soil carbon is greater water holding capacity and water retention. We tested this hypothesis by exploring the relationship between soil moisture and the percent of soil as organic carbon (SOC %) (Figure 11). We found a highly significant relationship for both mbuga and sandy soils. These relationships suggest that every 1% increase in soil organic carbon should be associated with a 4% increase in soil moisture.

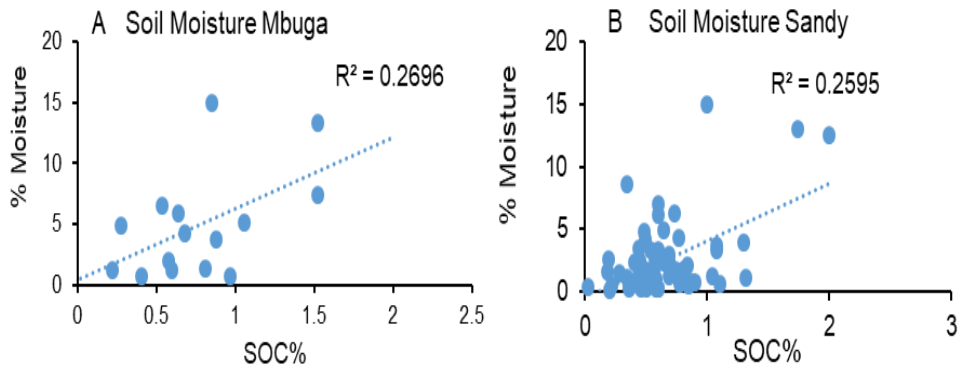


Figure 11. Relationship between gravimetric soil water content to 40 cm depth (% Moisture) and percent of soil as organic carbon (SOC %) for A. mbuga and B. sandy soils. Both relationships are significant (*p* = 0.03 for mbuga soils (N = 15); *p* < 0.001 for sandy soils (N = 72).

DISCUSSION

Land management and the type of use of land had marked effects on both soil and wood carbon stocks and biodiversity. As expected, woodland clearing for crop production dramatically reduced carbon stocks from a mean of 92 metric tons/ha total carbon in remnant woodlands and selectively logged and/or grazed woodlands in protected areas to an estimated 19 metric tons/ha in recently cleared and farmed lands. Woody carbon was initially higher than expected in the first few years because farmers frequently left large commercially valuable canopy trees, such as *Pterocarpus angolensis* and *Pericopsis angolensis* standing following clearing. Usually, these were harvested within 8 years and regeneration of canopy trees mostly yielded seedlings and very small saplings by this point. Within 10 years, regeneration yielded saplings with dbh > 5 cm leading to measurable increases in woody carbon. In contrast, soil carbon was initially 80% lower than in reference woodland soils but increased steadily to near reference levels by year 10 (Figure 8B). Though sample sizes are small, the overall pattern suggests that soil carbon declines after year 10 as trees with less biomass allocation belowground begin to establish. Soil carbon declined nearly to zero following 1 - 2 years of crop production but increased over time as croplands were abandoned. Accumulation of soil carbon in the first 15 years after field abandonment and increase in forest regeneration over time suggested that pre-clearing levels of carbon stocks might be achieved in 30 years. Grazing was not associated with any differences in carbon stocks but enhanced tree diversity, mostly of thorny sub-canopy species. Game Reserves are generally not subject to livestock grazing or selective logging, and the presence of large trees spared from selective logging may contribute to that higher mean.

Land use change had differing effects on biodiversity. Conversion of woodland to cropland was associated with reduced diversity of trees and Lepidoptera. However, richness of other taxa, namely herbaceous plants and Orthoptera, exhibited little response to conversion. One explanation is that sets of functional groups of these two taxa are replaced by others following woodland conversion, such as woodland fauna and flora being replaced by equivalent numbers of species of annual grasses and herbs and common agricultural grasshopper species. Lepidoptera, which are in general much more likely to specialize on particular plant taxa than are Orthoptera, may be more sensitive to the loss of mature canopy trees, and thus more likely to be affected by land use change. This admittedly incomplete measure of insect biodiversity is still important because these are two indicator taxa in monitoring land management effects on arthropod diversity.

A major outcome of the study was that fire history, spanning a gradient from very infrequent (0 to 2 burns in the past 15 years) to 1 fire every other year, exhibited little association with either carbon or biodiversity measures. Accessible sampling areas in the project experienced mostly early-season fires, with frequently burned areas occurring mostly in the Inyonga Forest Reserve and the Ipole WMA. Frequent late burns occurred in Rukwa and Lukwati Game Reserves and in Ruaha National Park, all areas well outside our access. There was no associated change in soil or woody carbon stocks, or in any of the biodiversity measures with fire frequency. This may be expected because fires in the stations we sampled were primarily early in the season, and early burning is expected to have relatively little impact on mature trees (Archibald, 2005; Russell-Smith *et al.*, 2013). Associations with late fires could have been weak because there was relatively little variation in late fires and late fires were uncommon in the study area. Frequent late fire areas deep in protected game reserves and national parks were outside our sampling area.

The substantial reduction in fire frequency in remnant woodlands in Open Areas, driven likely by reduction of fuel loads by livestock grazing, is recent, judging from the high frequency of woody stems > 5 cm in community forests and mbuga habitat. These patterns are consistent with the impact of livestock grazing by animals originating in border settlements and early fires set by beekeepers. Beekeepers often set fires accidentally from smoking bees from hives but also may set early burns purposefully to discourage the use of hive areas by livestock that have been sprayed with pesticide to deter tsetse flies. In contrast, deeper in protected areas, grass fuels in the dry season routinely exceed 300 g/m^2, as we observed in some areas of Inyonga Forest Reserve and Ipole WMA, and such biomass is sufficient fuel to carry fires. Opportunities to avoid greenhouse gas emissions by managing fire would seem to be mostly in Ruaha and the game reserves north of Lake Rukwa.

There was lack of canopy trees in mbuga soils, which instead support much smaller woody plants with bushy growth forms, such as *Vachellia drepanolobium*. Effects of this bush encroachment are unknown, but it may attract wildlife, including carnivores, deeper into human-dominated parts of Open Areas. “Laddering” of fuels from the ground to mature canopy trees may increase the possibility of catastrophic canopy fires in drought years. The formation of thickets may reduce the accessibility and utility of remnant woodland areas in providing ecosystem services like drought grazing refuges, beekeeping, and sustainable tree harvest, similar to phenomena observed in open areas surrounding Serengeti National Park (Veldhuis *et al*. 2019, Ritchie 2020).

The results are also generally consistent with the hypothesis that biodiversity increases with wood and soil carbon stocks and a key ecosystem consequence associated with higher soil carbon - greater soil moisture during the dry season in miombo woodland. A major question is whether conservation solutions face trade-offs between promoting biodiversity versus avoiding emissions or sequestering carbon in wood and soil (Thomas *et al*. 2013). In this landscape, the highest carbon stocks do not preclude a productive grass and herb understory that may support substantial herbaceous plant and insect diversity. The association of soil carbon with soil moisture suggests that higher carbon stocks may feedback on water resources in ways that increase resources (soil nutrients and water) and thus production and biodiversity. These patterns may contrast with those seen in pure grassland habitats where carbon sequestration is associated with higher production, an increase in competition for light and soil resources and a decline in plant biodiversity (Walker and Desanker 2004, Becknell *et al*. 2012).

Overall, the results suggest that substantially reduced emissions of carbon can be achieved by the conservation of miombo woodlands, especially in the areas most directly threatened by humans and most critical to maintaining wildlife corridors in the region. In addition, biodiversity and carbon appear to be complementary in this ecosystem, with Lepidoptera potentially being a key indicator taxon (Jew, 2015; Sánchez-Bayo and Wyckhuys, 2019). Over much of the region, where fire occurs it happens early in the season, perhaps due to the officially allowed influx of beekeepers into protected areas (other than GR) in June each year. Early fire frequency was not associated with any changes in carbon stocks or species richness of four different taxa, and so may not represent a high priority target in FR and WMA protected areas (Russell-Smith *et al*. 2021). Thus, conservation focus should be on finding incentives to increase the duration of farm use to reduce the rate of woodland conversion. Carbon densities which correspond to those commonly observed in Game Reserves and WMAs, species richness of trees and Lepidoptera declined, suggesting that the establishment of canopy trees and the decline of soil carbon may be associated with lower species richness. Overall, these results suggest that there is no trade-off between promoting biodiversity and protecting or generating high carbon stocks, except perhaps in the case of high carbon densities (mature canopies) in more human-disturbed (selectively logged and grazed) woodlands.

Extrapolated to the landscape scale, the mean bulk density for sandy soils is approximately 1, so comparing soil carbon from the point of abandonment of crop production (~ 10 Mg/ha) to reference levels (~30 Mg/ha), suggests that avoiding deforestation will retain 80,000 liters/ha of water in the top 40 cm of soil in both mbuga and sandy soils. Across a landscape of 100,000 ha of conserved canopy miombo, that would amount to 8 billion additional liters of water stored in soils by the middle of the dry season (we measured soil moisture in mid-September). These relationships and speculative calculations feature substantial uncertainty (Figure 11), but they provide a glimpse of the potential (and largely underappreciated) magnitude of ecosystem services provided by miombo woodlands in the form of water conservation.

CONCLUSIONS

Ruaha-Katavi Landscape plays an important role in terms of biodiversity conservation, harboring unique and species that are particularly adapted to the extreme environmental conditions. They also provide essential ecosystem goods and services, livelihoods, and well-being of its residents. Despite these and other related significances, virtually all of the remnant forests are currently exposed to various threats, largely resulting from anthropogenic activities. Consequently, these ecosystems are caught in a spiral of deforestation, fragmentation, degradation, and desertification. Livestock grazing in forest remnants and into protected areas other than game reserves resulted in an almost complete lack of fire within forested or cropland open areas. Woody carbon stocks decreased between game reserves and wildlife management areas to community forest reserves. Conversion of woodland into cropland reduced carbon stocks by 80%, but carbon in both soil and wood recovered to 50% of the level of community and forest reserves after 15 years. Fire frequency in any season was not strongly associated with carbon stocks or biodiversity. Biodiversity, especially of an indicator taxon, butterflies and moths, was generally associated with higher woody carbon, indicating these are complementary objectives in conservation activities. This study provides some key preliminary information that may justify feasible interventions to improve their retention and farmlands and overall livelihoods. Such changes may derive from the diversification of revenues from carbon finance to communities, and increased agricultural productivity. Their strong culture poses significant conservation challenges, and incentive-based programs financed by carbon (and possibly water) markets may be essential in changing attitudes to innovation and sustainability in the Ruaha-Katavi Landscape.

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