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Carbon sink despite large deforestation in African tropical dry forests (miombo woodlands)

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Supplementary material for this article is available [online](#)

Abstract

Direct and indirect human impacts may be causing widespread vegetation changes African tropical dry forests (TDFs). This study provides the first field-based large-scale assessment of vegetation changes for the miombo region, using nation-wide re-measured permanent plots for the Republic of Zambia. Using path analysis, a technique used to describe and quantify causal relationships, we investigated the drivers of change for the 2006–2014 period, under different land-use and productivity trajectories. We assessed the change in vegetation metrics representing stand structure and tree diversity, identified causal factors for species richness, basal area, and productivity and compared the biomass change of different species. We assessed carbon emissions and absorptions from forestlands and used error propagation and sensitivity analysis to quantify uncertainty. Our results suggest that Zambia's TDFs are resilient in the face of human activities, with significant biomass gains observed in the re-measured plots over the country. However, the proximity to roads, fragmentation by other land uses, and to a lesser extent fire occurrence were found to negatively affect productivity. We found that biomass gains were concentrated in several dominant species, mostly belonging to a single subfamily of non-nodulating legumes (Fabaceae, subfamily Caesalpinioideae) characteristic of the region. Our results indicate that Zambia's TDFs have been acting as an overall carbon sink, despite large carbon emissions from land-cover change. Decline in biomass for certain dominant species signal a risk of over-exploitation. We also identified important differences in plant diversity and functional traits between miombo woodlands and other types of African savanna vegetation, signaling differences in ecological processes at play. These results illustrate the ecological complexity and diversity of Africa's vegetation, and caution against overgeneralizations of ecological processes in the context of global change and carbon management. Future research should focus on understanding the observed species-specific biomass gain and identifying its potential drivers.

Introduction

Woody ecosystems play a major role as carbon sinks [1] and provide vital ecosystems services. Human

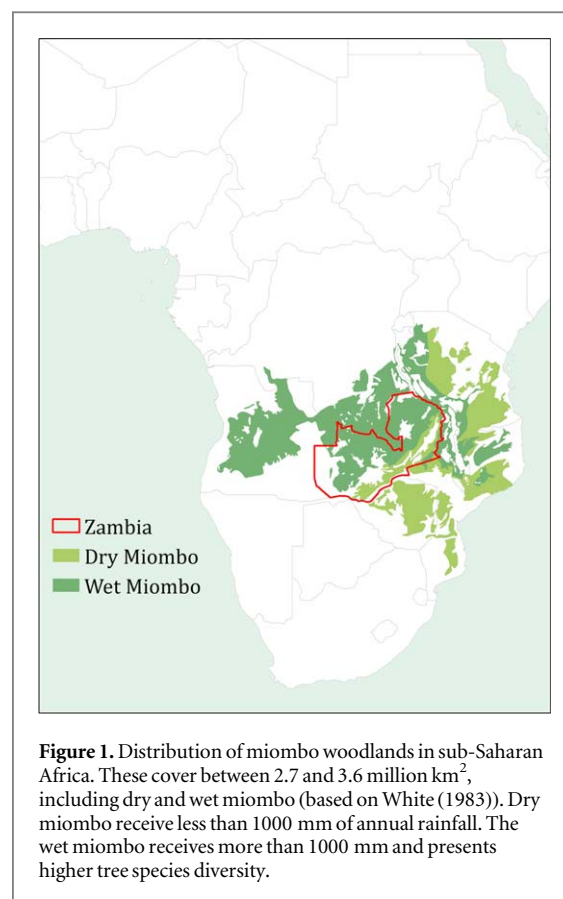
activities have pervasive impacts on vegetation world-wide. Drivers of changes include land-use and land-cover change, climate change, altered disturbance regimes, and rising atmospheric CO₂ levels [2]. Some

parts of the world including tropical dry forests (TDFs) are especially threatened by direct and indirect human activities and lack sustained attention from research [3]. The lack of long-term monitoring networks capable of recording changes in vegetation conditions for some large regions of the world, including sub-Saharan Africa, creates an important geographic bias in knowledge [4]. This lack of data constrains our ability to assess the impacts of different influences on diversity and ecosystem functions and generates large uncertainties when trying to understand ecological processes and predict future consequences of multiple interacting drivers in many developing countries. This, in turn, limits the development of adaptive management and conservation approaches. To overcome this issue, the repeated direct measurement of permanent survey plots is crucial for quantifying vegetation and biomass change to validate and complement remote sensing and modeling approaches.

The miombo woodlands have received relatively little attention, despite their significant importance for biodiversity conservation [5], the global carbon cycle [6], and for the livelihoods of millions of people [7]. The miombo woodlands, located in the mesic part of the African savanna biome [8], are the most extensive seasonally dry tropical woodland⁷ in the East and Central-South Africa region, covering about 2.7–3.6 million km² [9, 10] (figure 1). ‘Miombo’ is an indigenous term used to describe African woodlands dominated by the genera *Brachystegia*, *Julbernardia* and/or *Isoberlinia* (Fabaceae, subfamily Caesalpinioideae). Mature undisturbed miombo is a closed-canopy deciduous non-spinescent woodland over most of its range [11, 12]. For the past 55 000 years, these woodlands have experienced a long history of human influence for timber and fuel wood, shifting cultivation, and frequent anthropic dry-season fires [13]. They are also known to be highly resilient to disturbances [14–16]. However, a recent long-term field study reports a decline in biomass due to fire, harvesting and conversion to crop cultivation [17]. Given the role of this region globally, it is crucial to understand the current drivers of change on woody plant diversity and ecosystem functions in African TDFs but until recently, no empirical study existed to comprehensively assess the large-scale impacts on the vegetation.

Some remote sensing and model-based assessments show significant recent declines in canopy cover regionally [18–20] and predict increasing impacts for the future [21]. Other remote sensing studies challenge the view of a reduction in woody vegetation. Brandt, Rasmussen [22] and Andela, Liu [23] shows a gain in woody cover in African drylands and Liu, van Dijk [24]

⁷ There is still a debate about whether miombo woodlands should be classified as savanna or forests (see Frost in Campbell *et al* 1996). In this study, we adopted the national definition of forest (Zambia Forest Act 2015) which consider miombo and other woodlands as forests.



a biomass gain in tropical savanna, including in some area of the miombo region [25].

In addition to land-use change, fire is a key determinant of woody biomass in the miombo woodlands [16, 17]. Dry-season (May–November) understory fires fueled by the dry grass layer are frequent [9]. Fire is an important part of land management for preparing land for cultivation, hunting, clearing grass and livestock management with some accidental fires resulting from these activities and charcoal making [26, 27]. Fire management through prescribed burns is used in the early dry-season to reduce grass fuel loads and to avoid late dry-season fires that can kill the trees. It is a potential option to maintain woody biomass in the miombo woodlands [17].

Climate and other environmental factors, including rainfall, rainfall seasonality, and edaphic conditions, influence the distribution of tree diversity and carbon storage in African vegetation [28–32]. Inter-annual atmospheric variability, including El Niño–Southern Oscillation (ENSO) may also affect productivity through modifications in intra-seasonal rainfall variability [33].

Woody encroachment, or an increase in the area covered by woody vegetation, is a widespread phenomenon across the savanna biome [34, 35], including in Africa [19, 36–38]. Rising atmospheric CO₂ is identified as one of the most important drivers of woody encroachment due to the CO₂ fertilization effect on biomass growth [39–41]. There has been

however no evidence of woody encroachment in the miombo region.

Sustaining ecosystem functions and understanding ecosystem response to disturbances fundamentally requires understanding plant responses to different drivers. For example, the sensitivity or resistance of TDFs to changing rainfalls depends largely on plant responses to drought [42]. Tree diversity, often mediated by functional diversity, shows a positive correlation with productivity and carbon storage in forests. Globally, forests with higher relative species richness are more productive [4]. On the other hand, species dominance matters a lot for carbon storage [43–46].

This study is the first national-scale analysis of vegetation change for the African miombo region. It is based on a network of permanent plots established nation-wide in Zambia that were measured through two national vegetation surveys in 2006–2007 and 2012–2014. Previous studies in the miombo region were for one point in time or covered relatively small areas. We evaluate the drivers of change and sustainability for Zambia's TDFs, assessing the impacts of natural and anthropogenic perturbations on woody plant diversity, stocks and productivity. We focus on three main questions: (1) Are there significant changes in stand metrics between the two vegetation surveys (including biomass, species richness, basal area, stump density, stem density, species evenness, volume)? (2) What are the main human and natural drivers of these changes under different land use and productivity trajectories? (3) What are the species mostly associated with biomass change? This study uses Zambia's national forest definition [47] which includes miombo woodlands, the dominant vegetation type occupying 70% of forestland (app. 50 million ha), as well as tropical evergreen and deciduous dry forests, mopane and undifferentiated woodlands based on White [48] classification. Zambia has one of the highest rates of deforestation in the world [18], with national analysis showing an increasing rates of $250\,000\text{ ha yr}^{-1}$ for 2000–2010 and $341\,067\text{ ha yr}^{-1}$ for 2010–2014 [49]. Given the increasing pressure on these TDFs, we expected to observe a decline in stock, productivity and woody plant diversity due to human activities, but we were somewhat surprised to find a gain in these metrics.

Methods

This study is based on the Integrated Land Use Assessment vegetation survey phase I (2006–2007) and phase II (2012–2014) for Zambia, led by the Zambia Forestry Department (ZFD) with the technical support of the Food and Agriculture Organization. During ILUA I, a network of permanent plots was established using a systematic sampling design demarcated using permanent marker, GPS coordinates and

triangulation points. For each plot, the individual tree location was taken along a central transect of 250 m and 10 m on each side of the central line (20 m by 250 m). These permanent plots were revisited during ILUA II and the first 50 m of the central transect was re-measured. Only the re-measured section of 20 m by 50 m (or 1000 m^2) was compared (figure 2). Methodological details of the ILUA surveys are provided in appendix S1 is available online at stacks.iop.org/ERL/13/094017/mmedia in supporting information and in two publicly available field manuals [50, 51].

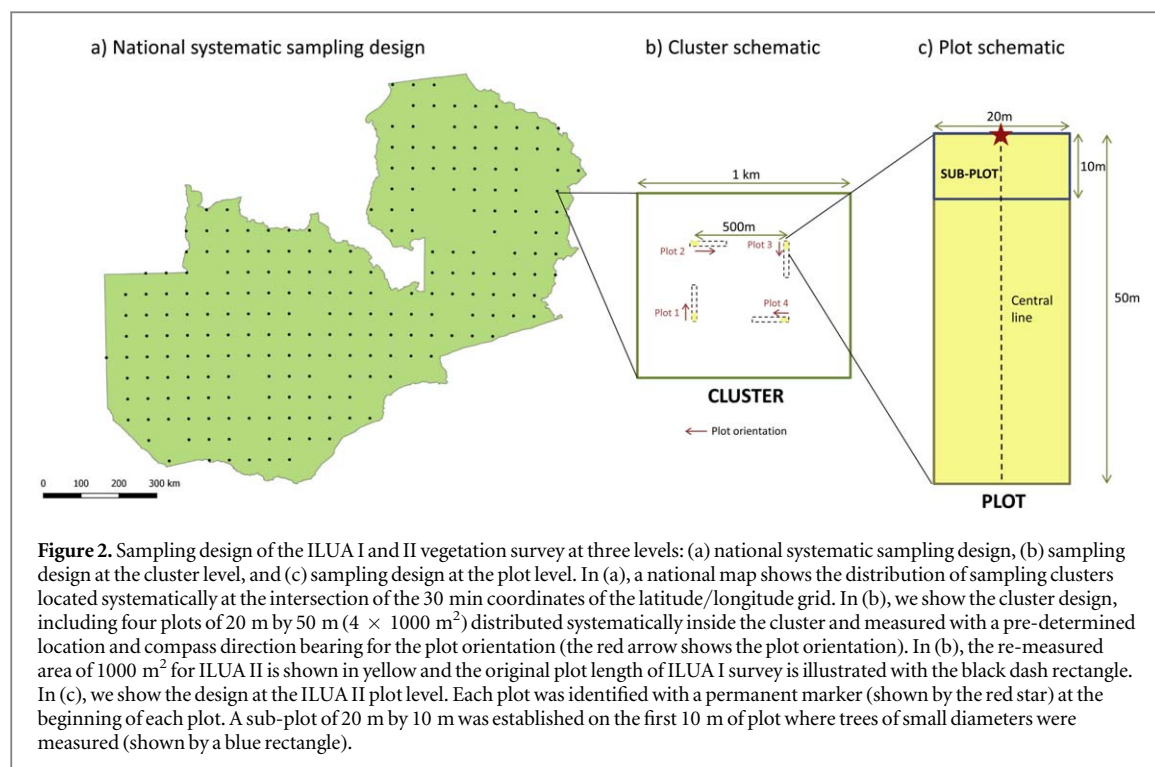
Data management strategy

For the change analysis, re-measured plots between ILUA I and ILUA II were identified through spatial overlap in a GIS in order to ensure comparison of the same location. Re-measured plots amounted to 829 out of 839 plots measured in ILUA I and included in 212 1 km by 1 km clusters of four plots (figure 2). To compare the two assessments, we selected the trees of the ILUA I survey based on their position along the central transect, namely the trees located within the first 50 m of the 250 m transect. It was not possible to perform a tree-by-tree comparison which would have required trees to be tagged with a unique identifier. The comparison is done in terms of the sampled area, on a plot-by-plot basis.

When the ILUA I and ILUA II species lists were compared, some spelling errors and species known under different scientific names were noticed. To obtain valid results in terms of woody plant diversity, an unique species list was generated from the two surveys where we removed duplications or spelling mistakes that would have affected the evaluation of change in diversity. The final list was verified and validated by a botanical curator and co-author (N.Z.) and included 238 woody species belonging to 154 genera, showing high diversity and endemism over the country.

Stand metrics

We calculated woody plant diversity indices and stand structure variables for each of the surveys, at both the cluster and the plot levels. We calculated common alpha (α) biodiversity indices including tree species richness, Shannon's entropy, Simpson's index, the Shannon and the Simpson diversity numbers, as well as the Pielou, Shannon, and Simpson evenness indices [52]. With the FD package in R [53], we calculated functional diversity indices using important life-history traits, wood density and seed mass, gathered from global data sets [54–56]. Stand structure variables included basal area, stump density, and biomass for all trees and shrubs $\geq 5\text{ cm}$ diameter at breast height (dbh) as well as stem density for all stems $\geq 1.3\text{ m}$ in height. The plot biomass was calculated by summing the individual tree biomasses estimated with the allometric models developed by Chave, Rejou-Mechain [57] using the dbh, height and wood density



(wd) of each individual. The average of the four plots was used at the cluster level. Then, we evaluated the mean difference and variation in metrics between the two repeated measurements.

The difference in aboveground biomass between the repeated measurements, hereafter called productivity, was considered a key variable to assess TDFs resilience. Because these TDFs are subjected to frequent fires as well as other disturbances, the difference in biomass can be either positive (gain) or negative (loss). Changes associated with belowground components, litter and woody debris were not accounted for because these components were not measured during the first survey.

Explanatory variables

In addition to the survey data from ILUA I and II, we extracted explanatory variables from land-cover change maps and from global data sets. The land-cover change maps were developed by the ILUA II project for years 2000, 2010, and 2014, using Landsat imagery (30 m pixel). The maps are based on the six Inter-governmental Panel on Climate Change land-cover categories (cropland, forestland, grassland, settlement, wetland and other land). It includes classes that show no change (stable class over time) and classes showing the conversion of forests (appendix S1, figure S1.1).

We calculated statistics from the land-cover change maps, using tabulated areas and zonal statistics in ArcGIS in a 1 km radius of the plot center. We also developed patch and landscape metrics to describe landscape heterogeneity with the 2014 land-cover map, using FRAGSTATS [58] in R. These fragmentation metrics (~50 metrics) were calculated using a

1 km radius from the cluster center and were developed for the forestland category. One example of fragmentation metric is the 'core area of forestland', which represents the area within a forest patch beyond some specified edge distance or buffer width [59]. We also compiled fire area from the MODIS burned area products (MCD45A1) [60] from 2006 to 2014 in order to evaluate the presence or absence of fire, the fire frequency and the time since fire (appendix S1, figure S1.2). Other variables related to human influence were assessed including the distance to roads, population within 5 km radius and distance to towns.

Bioclimatic variables derived from monthly temperature and rainfall data were extracted at the plot center to represent annual trends, seasonality and limiting environmental variables relevant to tree distributions [61]. We also used soil organic carbon, bulk density, and pH collected at the cluster level through the soil assessment performed in ILUA II. The clay/sand ratio and the total sand were extracted from soil GIS layers provided by the ZFD.

Statistical analysis

To understand the impacts of different drivers on woody plant diversity and ecosystem functions, we used a structural equation modeling, called path analysis. This statistical approach is a straightforward extension of multiple regression, but in addition to merely explaining variation in a response variable, path analysis attempts to describe and quantify causal relationships [62]. This analysis aimed to provide estimates of the magnitude and significance of hypothesized relationships between sets of variables to understand the impacts of different trajectories of

change and capture the main drivers. We first developed a directed acyclic graph (figure S1.3), laying out the different sets of variables and the hypothetical directed links. We used correlation tables to select the most important variables for our set of descriptors. Using the lavaan package in R, we developed a series of models for different trajectories of change based on the field information, including biomass gain over time, biomass loss over time, forestland plots remaining forestland, and forestland plots converted to non-forestland, at the cluster and the plot level.

To compare plot woody plant diversity and stand structure metrics between ILUA 1 and ILUA 2, we used paired t-tests when the variables could be normalized to approximately obey a Gaussian distribution (e.g. with log-transformation); otherwise we used the Wilcoxon paired-sample test (or Wilcoxon Signed-Rank Test).

The fact that the individual trees were not tagged is a limitation of the data set, and we adopted a conservative approach to account for this. This limitation made it more difficult for us to identify potential measurement errors in the data set (e.g. inclusion or exclusion of a tree at edge of a plot). Because we have quantified a biomass increment over the time period, we have purposefully removed sites showing a higher gain that could potentially be due to the inclusion of trees in the second survey that were not measured during the first survey. To ensure robust results for statistical analysis, we have established a threshold to remove the plots with biomass gain $>50 \text{ Mg ha}^{-1}$ over the period, which is equivalent to an increment of about $3.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. We evaluated that the plots with $>50 \text{ Mg ha}^{-1}$ biomass gain have a higher probability to be affected by measurement error. We report summary statistics for the whole data set. For statistical analysis, including path analysis, t-tests, and Wilcoxon paired-sample tests, we have excluded the sites with higher biomass gain for a final sample size of 754 plots. We used growth rates with and without applying the threshold to test for sensitivity of this parameter on carbon absorptions.

To identify which species contributed the most to biomass changes, we ranked the 50 most dominant tree species based on the total biomass for ILUA 1 and for ILUA 2 and compare the difference in biomass for each species for all the plots ($n = 754$) and also by separating between plots showing a biomass increment ($n = 400$) and those with no change or a loss ($n = 354$) during the period.

Carbon emissions and absorptions from forestlands

We compared emissions from deforestation and absorptions by forestlands, contrasting different sensitivity scenarios for biomass increment in forestlands. We used error propagation to account for the different sources of error in land areas, carbon stocks and

growth rates and quantify the overall uncertainty around final estimates. For carbon emissions, we used estimates for the period 2000–2010 and 2010–2014 published by the Republic of Zambia [49], in table 6, that we converted from CO_2 into C. To account for carbon sequestration from forestlands, we used the stable forestland area from 2000–2014 published in ILUA II [63] that we multiplied by the biomass increment or growth rate values calculated from the difference between ILUA I and ILUA II. We used sensitivity analysis to test the effect of different growth rates estimates. We included the mean and the median biomass increment for plots of ‘forestland remaining forestland’ between the two surveys and the mean and median by removing all sites with a productivity higher than $3.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. These growth rates include forestland plots with degradation or disturbances, but excluded plots that have undergone conversion from forestland to other land use. Then, we calculated the difference between emissions and absorptions for the 2000–2014 period.

Results

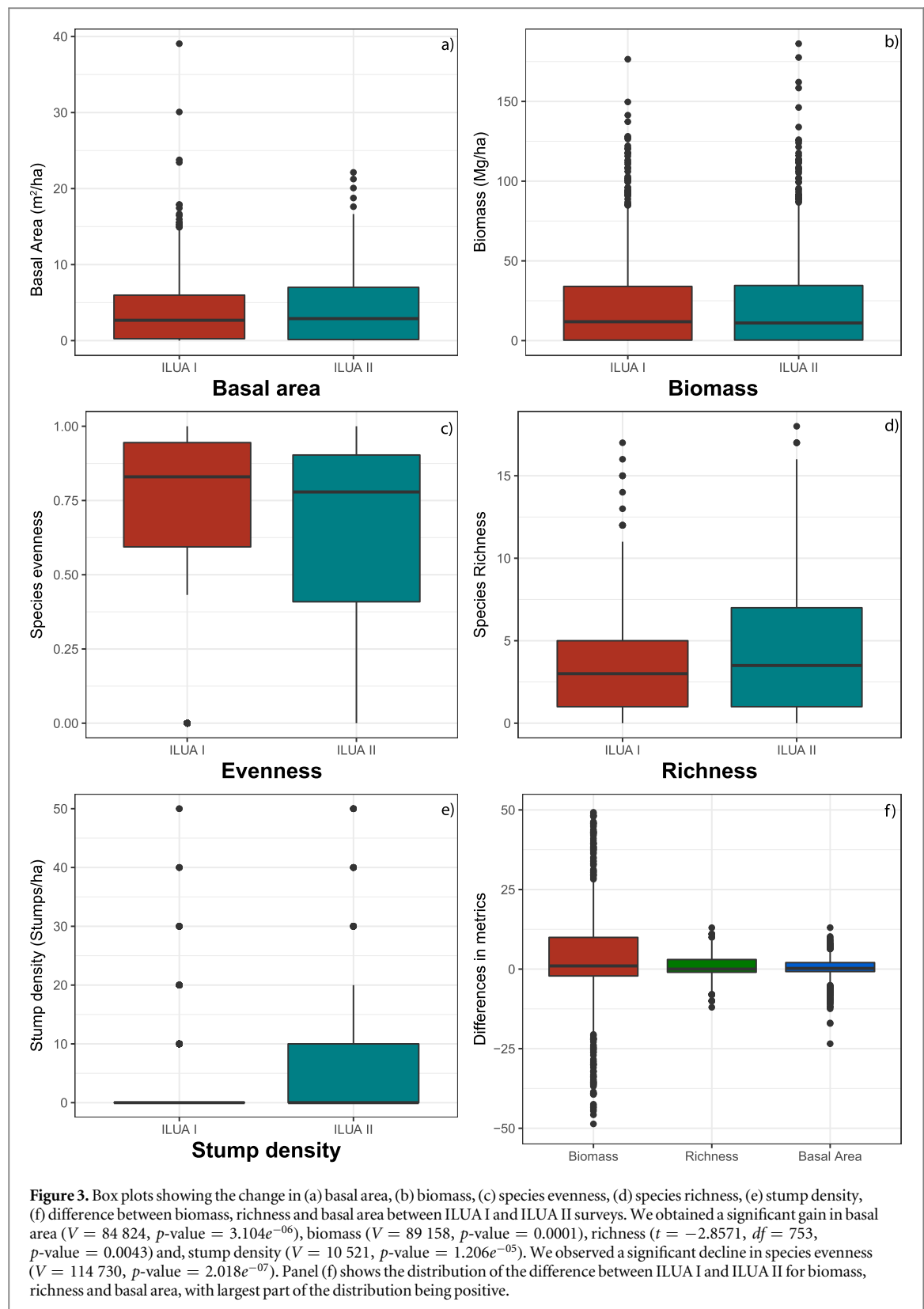
Changes in vegetation conditions

The comparison over time showed statistically significant differences between the ILUA I and II, with a gain in richness, basal area, biomass, and stump density (figure 3). The annual difference between those metrics was positive, with a mean difference of 0.15 ± 0.02 and 0.16 ± 0.03 species per year for richness, 0.12 ± 0.02 and $0.13 \pm 0.03 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ for basal area, 1.00 ± 0.17 and $1.17 \pm 0.27 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ mean annual biomass gain and $0.26\text{--}0.31 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ median annual biomass gain, for the plot and the cluster level respectively (table 1). We also noticed a statistically significant decline in evenness (figure 3) and found no significant difference in stem density ($V = 109\,830$, $p\text{-value} = 0.8229$).

Causal factors for different trajectories of change

Trajectories of change were statistically explained by different human drivers and natural factors. Models results were consistent at the cluster and plot levels. We found persistent patterns amongst trajectories. One commonality was the positive relationship between basal area in the second survey and species richness or productivity. Richness was negatively affected by the temperature in the warmest quarter of the year. Productivity was negatively affected by species evenness (or positively with dominance) and by functional richness. Climatic and edaphic variables had no significant impact on basal area.

When all plots were included, the core area of forestland (a fragmentation metric) and the distance to road variables had a positive effect on basal area and richness, which means that plots located in continuous,



non-fragmented forestland and away from roads showed higher richness and basal area, also having an indirect positive effect on productivity (figure 4(a)).

In plots exhibiting biomass gain between the two surveys, we identified more significant factors than in other trajectories, including environmental, diversity and anthropogenic (or human-proxy) variables

(figure 4(b)). Fire occurrence decreased basal area of plots gaining biomass but was not identified to be a key variable under other trajectories. Core area of forestland was positively linked to richness. The distance to roads was related to higher basal area and productivity. We saw a positive effect of functional richness on basal area. Evenness was most strongly negatively associated

Table 1. Annualized change for woody vegetation metrics quantified at the cluster level and the plot level.

	Δ^a Biomass Mg ha^{-1} yr^{-1}	Δ Species richness Number of species	Δ Stem density $\text{ha}^{-1} \text{yr}^{-1}$	Δ Basal Area $\text{m}^2 \text{ha}^{-1}$ yr^{-1}	Δ Stump density $\text{ha}^{-1} \text{yr}^{-1}$	Δ Evenness	Δ Volume $\text{m}^3 \text{ha}^{-1}$ yr^{-1}
<i>Cluster level (N = 212)</i>							
Mean difference	1.17	0.16	253.12	0.13	0.34	−0.01	0.31
Standard error of the mean	0.27	0.03	181.84	0.03	0.13	0.003	0.24
Clusters with gain	120	134	95	129	87	68	116
Clusters with loss	83	60	108	74	48	133	87
Clusters without change	9	18	9	9	77	11	9
25th percentile	−0.36	−0.04	−104.02	−0.07	0.00	−0.03	−0.74
Median	0.31	0.11	−1.25	0.09	0.00	−0.01	0.13
75th percentile	2.23	0.39	129.77	0.37	0.71	0.01	1.77
<i>Plot level (N = 829)</i>							
Mean difference	1.00	0.15	258.51	0.12	0.33	−0.01	0.21
Standard error of the mean	0.17	0.02	110.33	0.02	0.09	0.002	0.18
Plots with gain	470	428	329	470	192	255	441
Plots with loss	259	221	402	260	84	425	289
Plots without change	100	180	98	99	553	149	99
25th percentile	−0.35	−0.14	−91.44	−0.07	0.00	−0.04	−0.71
Median	0.26	0.14	0.00	0.07	0.00	0.00	0.17
75th percentile	2.06	0.43	82.79	0.38	0.00	0.01	2.08

^a Δ indicates difference between ILUA 2 and ILUA 1 ($t_2 - t_1$).

with basal area and productivity than in any other trajectory of change. Soil organic carbon was also linked to higher productivity. The explained variation in species richness was lower for this trajectory, indicating that other factors not accounted for are also important.

Under the trajectory ‘*Forestland remaining forestland*’, we found causal links for environmental factors with richness and productivity as well as the effect of evenness and functional richness on productivity, but no human-related drivers were significant (figure 4(c)). We found that productivity was enhanced on sites with higher clay to sand ratio.

The opposite was identified for ‘*Forestland converted to non-forestland*’ where only a human-proxy variable was significant and where the core area of woody vegetation was negatively related to biomass loss (figure 4(d)). We also developed models for plots with biomass loss but the models did not succeed in converging, possibly due to lower sample size ($n = 90$).

Species associated with the biomass gain and loss

For plots characterized by a gain in biomass, we looked more closely into what species were responsible for this biomass increment. We found that dominant species, those having the largest biomass stock, also show the largest absolute biomass increment. The species showing the highest biomass gain are *Julbernardia paniculata*, *Brachystegia spiciformis*, *Brachystegia longifolia*, *Erythrophleum africanum* and *Colophospermum mopane* (figure 5(a)). Since we found no significant change in stem density in the

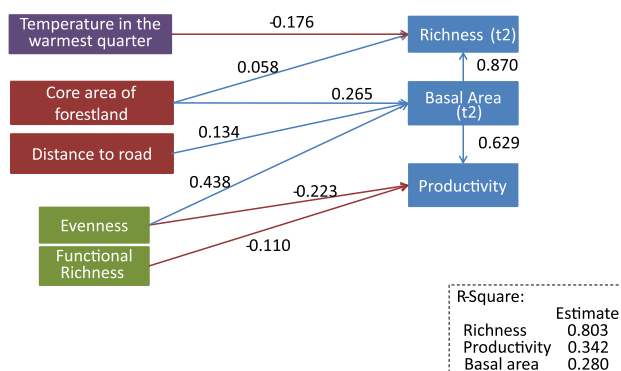
re-measured plots, it can be considered that this biomass increment is dominantly linked to the growth of individual stems rather than recruitment.

On the other hand, we also looked at plots showing no change or biomass loss to determine which species are the most affected by human activities or other disturbances (figure 5(b)). The greatest losses, in order of importance, are for *B. spiciformis*, *C. mopane*, *Isoberlinia angolensis*, *J. paniculata*, and *B. boehmii*. Then, overall plots, *C. mopane*, *I. angolensis*, and *B. spiciformis* reveal a biomass loss despite of the gains, while *B. longifolia* and *J. paniculata* show an overall gain.

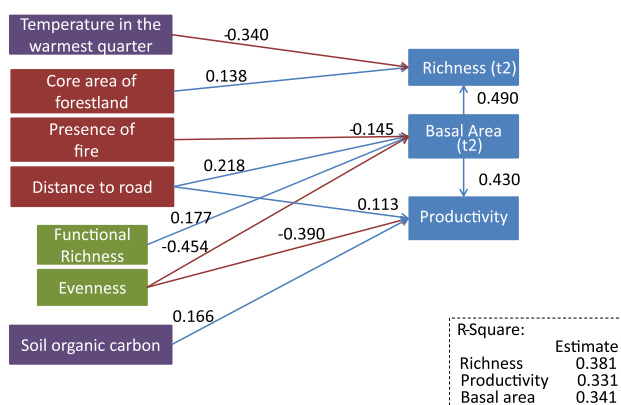
Carbon balance from land-cover change

We found that for the 2000–2014 period and accounting for different sources of uncertainty, the carbon absorptions from stable forestlands largely surpass the carbon emissions from deforestation, thus creating a carbon sink for all the sensitivity scenarios tested (figure 6). This carbon sink from forestlands in Zambia goes from −136 618 to −607 172 GgC (table S1.1), showing that these estimates are very sensitive to the growth rate used to quantify carbon absorptions from stable forestlands. We can also note a high uncertainty around emission estimates, which is driven by the uncertainty around the deforestation area estimates. Emission and absorption estimates are presented in table S1.1 in appendix S1 as well as the distribution of the carbon stock change for the subset of plots of stable forestlands (forestlands remaining forestlands) used in sensitivity analysis figure S1.4.

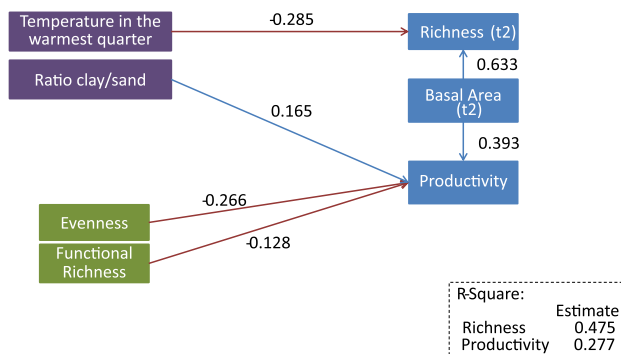
(a) All plots



(b) Plots with biomass gain



(c) Plots - Forestland remaining forestland



(d) Plots - Forestland converted to non-forestland

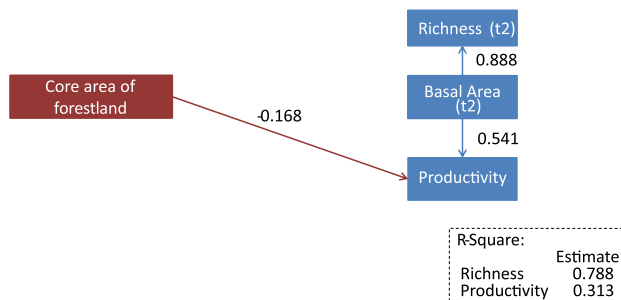
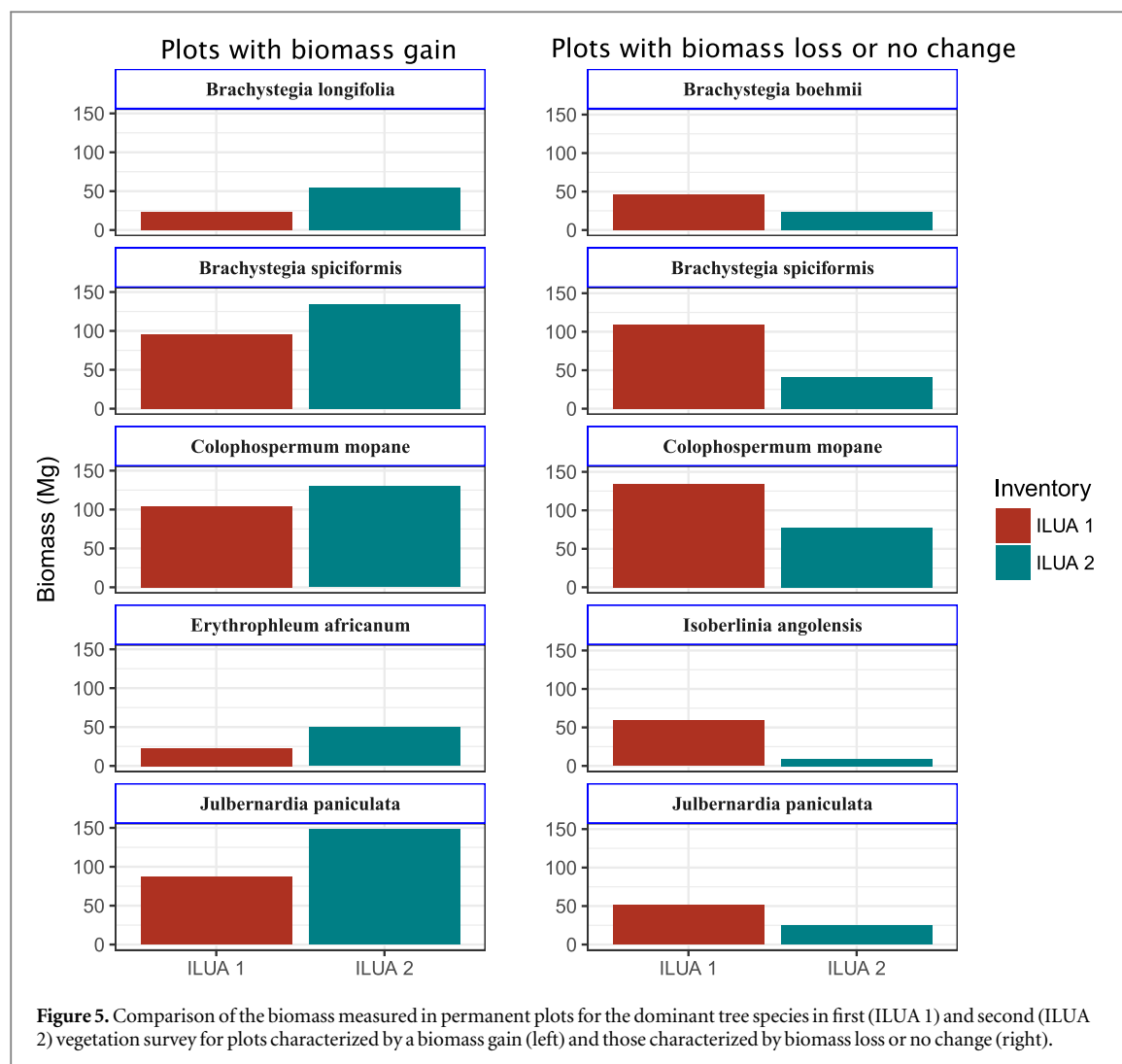


Figure 4. Path diagrams with coefficients derived from path analysis of (a) all plots together, (b) plots showing a gain in biomass from ILUA I to ILUA II, (c) plots found as forestland in ILUA I and that remained forestland in ILUA II, and (d) plots found as forestland in ILUA I and converted to other land use for ILUA II. Causal factors are classified as environmental factors (purple), diversity (green), human-proxy or anthropogenic (red) and response variables (blue). Red arrows indicate a negative effect and the blue arrows indicate a positive effect. Coefficients are standardized. All of these explanatory variables were significant. The *R*-square value for each response variables is shown in the dashed rectangle for each model. Core area of forestlands refers to the area within a forestland patch beyond a 100 m buffer width.



Discussion

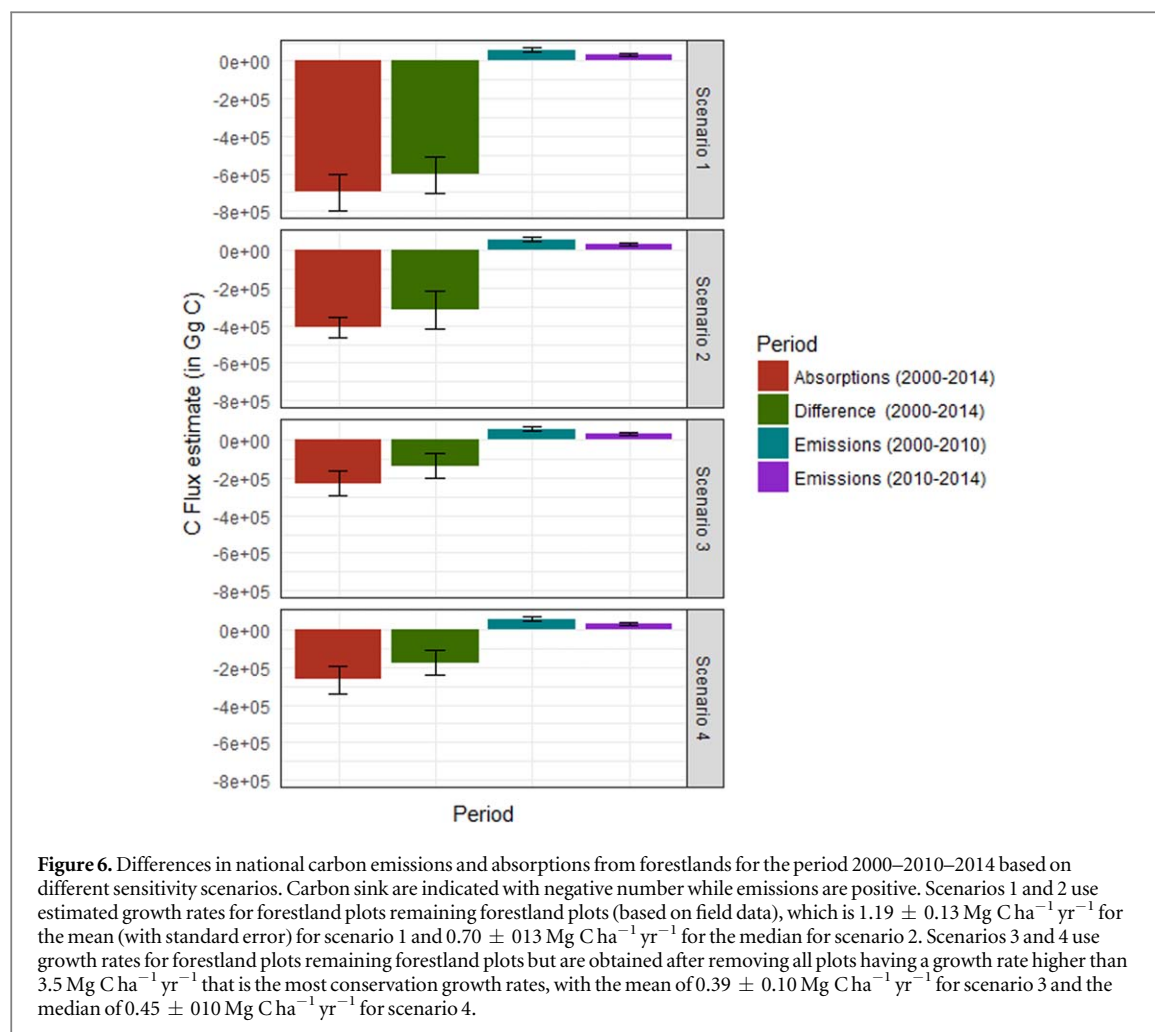
The re-measurement of permanent plots in Zambia allows for the first large-scale analysis of vegetation change for an area representative of the miombo region. It fulfills an important knowledge gap about African TDFs which remain understudied. We found overall gains in biomass and species richness at the sampled sites. This was despite significant human land use and land-cover change, and suggests that Zambia's TDFs have been acting as a carbon sink rather than a source.

Evidence of biomass increment and carbon sink

The biomass accumulation rates in 'forests remaining forests' quantified in this study ($1.19 \pm 0.13 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ mean and s.e.m. or $0.39 \pm 0.10 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$), is higher than the one quantified by Chidumayo [17] of $0.10 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for old growth permanent plots of Zambia. These are expected to have lower productivity, however the author indicates that the rates could have been up to about $2.0 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ if degradation due fire impacts and

harvesting was avoided. Other studies have quantified similar or higher rates but are not strictly comparable in their methodology and in the type of vegetation they measured. For example, Chidumayo [64] found an increment of 0.97 and $0.82 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (range of 0.20 – $1.42 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) for coppiced plots of age 3–29 and 48–49 years old in Zambia, respectively. McNicol, Ryan [14] found an average of $0.83 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for the miombo woodland following shifting cultivation abandonment in Tanzania. In Zambia, Kalaba, Quinn [65] obtained 0.98 and $1.42 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in agriculture and charcoal fallows respectively.

Woody plant diversity, and more specifically species dominance, appears to play a key role in this carbon sink. With our path analysis results, we found that productivity is negatively associated to species evenness, which has significantly decline between ILUA I and II. Chidumayo [17] indicates that an increase in evenness in miombo woodlands is a good indicator of forest degradation, so our findings may be indicative of overall resilience. Dominant species of the miombo and mopane woodlands played a particularly influential role in this biomass gain, and thus carbon absorptions. Our results point to biomass increment by



individual growth in these species and/or species replacement rather than recruitment, since stem density has not significantly changed for the period.

Our study provides evidence for a significant gain in biomass and a carbon sink across Zambia, but we cannot determine if there is an enhancement in carbon uptake, as we have only two points in time. The most likely interpretation for these results is that Zambia TDFs cover a large area compare to the deforested area, explaining why the absorptions surpass the emissions. While many studies have quantified deforestation in Zambia, we do not know of any study that has looked at the absorptions from TDFs at national-scale. Other countries, including Mexico [66], also show high rates of deforestation but because of their large forests extent, absorptions surpass emissions.

Other hypothetical factors that could explain this biomass gain Zambia's TDFs include changes in local drivers such as land use and management, regional changes in rainfall, in disturbance regimes (fire, grazing), or CO_2 fertilization effect. Based on recent estimates, we know that land conversion has increased between 2000–2010 and 2010–2014. The rainfall amounts in Zambia were variable over the period, showing increases in some areas and decreases in others [67], and therefore are unlikely to be the cause of

observed biomass gain. Future study should explore the potential effect of inter-annual atmospheric variability (e.g. ENSO) and intra-seasonal rainfall variability on woody productivity.

Recent human-driven decline in global burned area, including in the African woodland [68], may potentially be linked to the biomass increment that we measured. However, a recent study in Tanzania, a country with comparable vegetation and drivers, shows a consistent fire regime over time for the past ~40 years [69]. More evidence would be needed to link our results to a potential change in fire patterns.

CO_2 fertilization could be promoting the dominant species growth leading to biomass gain. Species-specific responses to elevated CO_2 concentration have been demonstrated [70], and may depend on the functional traits of woody plants [71]. Some savanna woody species have shown a strong yet different response to elevated CO_2 in experimental studies [41]. Benefits of CO_2 for tree growth and recruitment promote growth of root systems, providing stored energy for re-sprouting after fire and herbivory [72] and favoring clonal reproduction through coppicing and root suckering [73]. Most miombo dominants have the ability to coppice [74, 75]. This capacity is supported by extensive root systems, which spread

vertically, with tap roots reaching depths of at least 5 m, and producing root suckers horizontally once the aboveground parts have been removed [74]. CO₂ fertilization generally enhances water use efficiency, possibly lengthening the growing season [70]. This increased water use efficiency has been recently shown for African trees in drier areas [76].

The possibility exists that dominant trees of the miombo woodlands are responding positively to rising atmospheric CO₂ level. However, Stevens, Lehmann [34] suggest that plant nitrogen-fixing ability is critical in predicting woody encroachment in African savannas which is likely caused by rising CO₂ levels. From the encroaching species list in African dry savanna provided by Stevens, Lehmann [34], only *Colophospermum mopane* is common to the dominant trees gaining biomass in Zambia. The top weight gainers in Zambia are dominated by non-nodulating species. *Julbernardia-Brachystegia-Isobertia* species are characterized by ectomycorrhizal symbiosis [77–79], providing better capacity to respond to adverse conditions through enhanced nutrients and water uptake [79] and promoting the growth of host species [80–82]. Future research should use long tree-ring chronologies to directly assess the potential effect of atmospheric CO₂ on growth of dominant tree species.

The new national-scale repeated measurements conducted at more the 800 sites across Zambia highlights the unique species diversity and functional traits of the miombo woodlands relative to drier African savanna. Most prior research in the African savanna biome has taken place in South Africa, and researchers have commonly considered this biome to be homogenous [30]. Findings from the drier savanna biome are not generalizable to the mesic part where key differences in ecological processes and drivers exist.

Human impacts through land-use change and fire

Impact from human activities on TDFs were noticeable. We found higher productivity at sites located further away from roads and in relatively unfragmented forests. Ninety plots of forestland were cleared between the two surveys. Road expansion stimulates deforestation and forest degradation [83–87] by providing access to agricultural expansion and markets.

The effect of fragmentation in this region showing heterogeneous landscape patterns has rarely been addressed. The effect of fragmentation in closed humid tropical forest is well understood, with the edge effect increasing tree mortality caused by microclimatic changes, wind damage and invasive species near the forest edges, with associated impacts on biomass [88–90]. In the miombo woodlands, the exact mechanisms that can affect ecological processes other than the direct impact of land-use change are unknown.

Fire had only a significant negative impact on basal area in plots showing biomass gain, indicating that other factors are more important for degrading stands. Under controlled experiments, fire impact on aboveground biomass has been demonstrated by several studies in the miombo woodlands [16, 17, 91]. Fire would act as a demographic bottleneck by disproportionately affecting smaller trees (<2 m in height) and favoring grass layer development. Trees that have survived and reached a certain height are less susceptible to fire-induced mortality [72]. For both ILUA I and II survey, there is an overwhelming presence of surface fires, with very little presence of more damaging crown fire [45]. Future work should build a more fine-resolution long-term fire history (e.g. Landsat 30 m resolution, see Tarimo, Dick [69]) in order to assess the effects of fire and predict its long-term influence on diversity and ecosystem functions.

Heavy wood extraction for charcoal production and construction materials appear to show a negative balance for some of the most productive and dominant species in Zambia. This decline in biomass for *B. spiciformis*, *C. mopane* and *I. angolensis* indicates that despite their high productivity, these species are heavily extracted, a practice that could be unsustainable over time.

Conclusion

Although TDFs in Zambia are being heavily used to fulfill livelihood needs, we find that they have played an important role as carbon sink and that a significant biomass increment is observed at the re-measured sites. Similar to other areas in the tropics, absorptions from forests surpass emissions from deforestation. If the deforestation rates keep increasing however, this sink could be converted into a source in the next coming years. Using these new large-scale data from Zambia, our results highlight that the ecological complexity and diversity inside the African savanna biome should not be underestimated and warns against overgeneralizations in the context of global change and in terms of appropriate management response.

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References

- [1] Pan Y *et al* 2011 A large and persistent carbon sink in the worlds forests *Science* **333** 988–93
- [2] Lehmann C E R and Parr C L 2016 Tropical grassy biomes: linking ecology, human use and conservation *Phil. Trans. R. Soc. B* **371** 20160329
- [3] Sunderland T *et al* 2015 Global dry forests: a prologue *Int. Forestry Rev.* **7** (Suppl. 2) 1–9
- [4] Liang J *et al* 2016 Positive biodiversity-productivity relationship predominant in global forests *Science* **354** aaf8957
- [5] Mittermeier R A *et al* 2003 Wilderness and biodiversity conservation *Proc. Natl Acad. Sci.* **100** 10309–13
- [6] Valentini R *et al* 2014 A full greenhouse gases budget of Africa: synthesis, uncertainties, and vulnerabilities *Biogeosciences* **11** 381–407
- [7] Campbell B, Angelsen A, Cunningham A, Katerere Y, Sitoe A and Wunder S 2007 *Miombo Woodlands—opportunities and Barriers to Sustainable Forest Management* (Bogor, Indonesia: CIFOR) (http://cifor.cgiar.org/miombo/docs/Campbell_BarriersandOpportunities.pdf) (4 November 2008)
- [8] Ratnam J *et al* 2011 When is a ‘forest’ a savanna, and why does it matter? *Glob. Ecol. Biogeogr.* **20** 653–60
- [9] Frost P 1996 The ecology of the miombo woodlands *The Miombo in Transition: Woodlands and Welfare in Africa* ed B Campbell (Bogor, Indonesia: Center for International Forestry Research) p 11–58
- [10] Dewees P A *et al* 2010 Managing the miombo woodlands of Southern Africa: policies, incentives and options for the rural poor *J. Nat. Resour. Policy Res.* **2** 57–73
- [11] Campbell B (ed) 1996 *The Miombo in Transition: Woodlands and Welfare in Africa* (Bogor: Center for International Forestry Research)
- [12] Chidumayo E N and Gumbo D J 2010 *The Dry Forests and Woodlands of Africa: Managing for Products and Services* (London: Earthscan)
- [13] Chidumayo E N 2017 Biotic interactions, climate and disturbance underlie the distribution of two Julbernardia tree species in miombo woodlands of Africa *J. Trop. Ecol.* **33** 1–11
- [14] McNicol I M, Ryan C M and Williams M 2015 How resilient are African woodlands to disturbance from shifting cultivation? *Ecol. Appl.* **25** 2320–36
- [15] Chidumayo E N and Bakker J P 2004 Development of Brachystegia-Julbernardia woodland after clear-felling in central Zambia: evidence for high resilience *Appl. Veg. Sci.* **7** 237–42
- [16] Ryan C M and Williams M 2011 How does fire intensity and frequency affect miombo woodland tree populations and biomass? *Ecol. Appl.* **21** 48–60
- [17] Chidumayo E N 2013 Forest degradation and recovery in a miombo woodland landscape in Zambia: 22 years of observations on permanent sample plots *For. Ecol. Manage.* **291** 154–61
- [18] Hansen M C *et al* 2013 High-resolution global maps of 21st-century forest cover change *Science* **342** 850–3
- [19] Mitchard E T and Flintrop C M 2013 Woody encroachment and forest degradation in sub-Saharan Africa’s woodlands and savannas 1982–2006 *Phil. Trans. R. Soc. B* **368** 20120406
- [20] Mayes M T, Mustard J F and Melillo J M 2015 Forest cover change in miombo woodlands: modeling land cover of African dry tropical forests with linear spectral mixture analysis *Remote Sens. Environ.* **165** 203–15
- [21] Aleman J C, Blarquez O and Staver C A 2016 Land-use change outweighs projected effects of changing rainfall on tree cover in sub-Saharan Africa *Glob. Change Biol.* **22** 3013–25
- [22] Brandt M *et al* 2017 Human population growth offsets climate-driven increase in woody vegetation in sub-Saharan Africa *Nat. Ecol. Evol.* **1** 0081
- [23] Andela N, Liu Y Y, van Dijk A I J M, de Jeu R A M and McVicar T R 2013 Global changes in dryland vegetation dynamics (1988–2008) assessed by satellite remote sensing: comparing a new passive microwave vegetation density record with reflective greenness data *Biogeosciences* **10** 6657–76
- [24] Liu Y Y *et al* 2015 Recent reversal in loss of global terrestrial biomass *Nat. Clim. Change* **5** 470–4
- [25] Baccini A, Walker W, Carvalho L, Farina M, Sulla-Menashe D and Houghton R A 2017 Tropical forests are a net carbon source based on aboveground measurements of gain and loss *Science* (<https://doi.org/10.1126/science.aam5962>)
- [26] Stromgaard P 1992 Immediate and long-term effects of fire and ash-fertilization on a Zambian miombo woodland soil *Agric., Ecosyst. Environ.* **41** 19–37
- [27] Chidumayo E N 1997 *Miombo Ecology and Management: an Introduction* (Intermediate Technology Publications)
- [28] Sankaran M *et al* 2005 Determinants of woody cover in African savannas *Nature* **438** 846–9
- [29] Staver A C, Archibald S and Levin S 2011 Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states *Ecology* **92** 1063–72
- [30] Lehmann C E *et al* 2014 Savanna vegetation-fire-climate relationships differ among continents *Science* **343** 548–52
- [31] Murphy B P and Bowman D M 2012 What controls the distribution of tropical forest and savanna? *Ecol. Lett.* **15** 748–58
- [32] Lehmann C E R, Archibald S A, Hoffmann W A and Bond W J 2011 Deciphering the distribution of the savanna biome *New Phytol.* **191** 197–209
- [33] Guan K *et al* 2018 Simulated sensitivity of African terrestrial ecosystem photosynthesis to rainfall frequency, intensity, and rainy season length *Environ. Res. Lett.* **13** 025013
- [34] Stevens N, Lehmann C E, Murphy B P and Durigan G 2017 Savanna woody encroachment is widespread across three continents *Glob. Change Biol.* **23** 235–44
- [35] Pellegrini A F, Hoffmann W A and Franco A C 2014 Carbon accumulation and nitrogen pool recovery during transitions from savanna to forest in central Brazil *Ecology* **95** 342–52
- [36] Mitchard E T *et al* 2011 Measuring biomass changes due to woody encroachment and deforestation/degradation in a forest-savanna boundary region of central Africa using multi-temporal L-band radar backscatter *Remote Sens. Environ.* **115** 2861–73
- [37] Buitenwerf R, Bond W, Stevens N and Trollope W 2012 Increased tree densities in South African savannas: >50 years of data suggests CO₂ as a driver *Glob. Change Biol.* **18** 675–84
- [38] Wigley B J, Bond W J and Hoffman M 2010 Thicket expansion in a South African savanna under divergent land use: local versus global drivers? *Glob. Change Biol.* **16** 964–76
- [39] Sitch S *et al* 2008 Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs) *Glob. Change Biol.* **14** 2015–39
- [40] Scheiter S and Higgins S I 2009 Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach *Glob. Change Biol.* **15** 2224–46

- [41] Kgope B S, Bond W J and Midgley G F 2010 Growth responses of African savanna trees implicate atmospheric [CO₂] as a driver of past and current changes in savanna tree cover *Austral Ecol.* **35** 451–63
- [42] Allen K *et al* 2017 Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes? *Environ. Res. Lett.* **12** 023001
- [43] Fauset S *et al* 2015 Hyperdominance in Amazonian forest carbon cycling *Nat. Commun.* **6** 6857
- [44] Poorter L *et al* 2015 Diversity enhances carbon storage in tropical forests *Glob. Ecol. Biogeogr.* **24** 1314–28
- [45] Pelletier J, Siampale A, Legendre P, Jantz P, Laporte N and Goetz S J 2017 Human and natural controls of the variation in aboveground tree biomass in African dry tropical forests *Ecol. Appl.* (<https://doi.org/10.1002/eap.1550>)
- [46] McNicol I M, Ryan C M, Dexter K G, Ball S M J and Williams M 2017 Aboveground carbon storage and its links to stand structure, tree diversity and floristic composition in south-eastern Tanzania *Ecosystems*
- [47] Parliament of Zambia. The Forest Act (<http://parliament.gov.zm/sites/default/files/documents/acts/The%20Forest%20Act%202015.pdf>) Lusaka, Republic of Zambia 2015
- [48] White F 1983 *The Vegetation of Africa* (Paris: UNESCO)
- [49] Republic of Zambia. Zambia's forest reference emissions level submission to the UNFCCC 2016 (http://redd.unfccc.int/files/2016_submission_frel_zambia.pdf)
- [50] FAO 2005 *Integrated Land Use Assessment of Zambia: Field Manual* (Rome: Food and Agriculture Organization of the United Nations (FAO))
- [51] Forestry Department 2014 *Integrated Land Use Assessment Phase II, Zambia: Biophysical Field Manual* (Lusaka: Forestry Department, Ministry of Lands, Natural Resources and Environmental Protection, Food and Agriculture Organization (FAO)) Contract No.: Project: GCP/GLO/194/MUL (FIN) ILUA II
- [52] Borcard D, Gillet F and Legendre P 2011 *Numerical Ecology with R* (Berlin: Springer)
- [53] Laliberté E, Legendre P and Shipley B 2014 FD: measuring functional diversity from multiple traits, and other tools for functional ecology R Package Version 10–2
- [54] Zanne A E *et al* 2009 *Data from: towards a worldwide wood economics spectrum*
- [55] Tree Functional Attributes and Ecological Database: Wood Density, (<http://db.worldagroforestry.org/wd>) (Accessed: 2017)
- [56] Kew RBG 2017 Seed Information Database (SID). Version 7.1. (<http://data.kew.org/sid/>) (October 2017)
- [57] Chave J *et al* 2014 Improved allometric models to estimate the above ground biomass of tropical trees *Glob. Change Biol.* **20** 3177–90
- [58] McGarigal K, Cushman S A and Ene E 2012 FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst (<http://umass.edu/landeco/research/fragstats/fragstats.html>)
- [59] McGarigal K 2015 *Fragstats Help* (Amherst: University of Massachusetts)
- [60] Roy D P, Boschetti L, Justice C O and Ju J 2008 The collection 5 MODIS burned area product—global evaluation by comparison with the MODIS active fire product *Remote Sens. Environ.* **112** 3690–707
- [61] Hijmans R J, Cameron S E, Parra J L, Jones P G and Jarvis A 2005 Very high resolution interpolated climate surfaces for global land areas *Int. J. Climatol.* **25** 1965–78
- [62] Shipley B 2016 *Cause and Correlation in Biology: a User's Guide to Path Analysis, Structural Equations, and Causal Inference* (Cambridge: Cambridge University Press)
- [63] ILUA II 2017 *Integrated Land Use Assessment Phase II—Report for Zambia* Lusaka, Zambia: The Food and Agriculture Organization of the United Nations and the Forestry Department, Ministry of Lands and Natural Resources
- [64] Chidumayo E N 1990 Above-ground woody biomass structure and productivity in a Zambezian woodland *For. Ecol. Manage.* **36** 33–46
- [65] Kalaba F K, Quinn C H, Dougill A J and Vinya R 2013 Floristic composition, species diversity and carbon storage in charcoal and agriculture fallows and management implications in Miombo woodlands of Zambia *For. Ecol. Manage.* **304** 99–109
- [66] Skutsch M *et al* 2017 Adapting REDD+ policy to sink conditions *For. Policy Econ.* **80** 160–6
- [67] Chabala L M, Kuntashula E and Kaluba P 2013 Characterization of temporal changes in rainfall, temperature, flooding hazard and dry spells over Zambia universal *J. Agric. Res.* **1** 134–44
- [68] Andela N *et al* 2017 A human-driven decline in global burned area *Science* **356** 1356–62
- [69] Tarimo B, Dick Ø B, Gobakken T and Totland Ø 2015 Spatial distribution of temporal dynamics in anthropogenic fires in miombo savanna woodlands of Tanzania *Carbon Balance Manage.* **10** 1–15
- [70] Norby R J and Zak D 2011 Ecological lessons from free-air CO₂ enrichment (FACE) experiments *Annu. Rev. Ecol., Evol., Systematics* **42** 181–203
- [71] Temme A A, Liu J C, Cornwell W K, Cornelissen J H C and Aerts R 2015 Winners always win: growth of a wide range of plant species from low to future high CO₂ *Ecol. Evol.* **5** 4949–61
- [72] Bond W J and Midgley G F 2012 Carbon dioxide and the uneasy interactions of trees and savannah grasses *Phil. Trans. R. Soc. B* **367** 601–12
- [73] Wakeling J L and Bond W J 2007 Disturbance and the frequency of root suckering in an invasive savanna shrub, *Dichrostachys cinerea* *Afr. J. Range Forage Sci.* **24** 73–6
- [74] Luoga E J, Witkowski E T F and Balkwill K 2004 Regeneration by coppicing (resprouting) of miombo (African savanna) trees in relation to land use *For. Ecol. Manage.* **189** 23–35
- [75] Syampungani S, Tigabu M, Matakala N, Handavu F and Oden P C 2017 Coppicing ability of dry miombo woodland species harvested for traditional charcoal production in Zambia: a win-win strategy for sustaining rural livelihoods and recovering a woodland ecosystem *J. Forestry Res.* **28** 549–56
- [76] Wils T H G, Robertson I, Woodborne S, Hall G, Koprowski M and Eshetu Z 2016 Anthropogenic forcing increases the water-use efficiency of African trees *J. Quaternary Sci.* **31** 386–90
- [77] Bauman D, Raspé O, Meerts P, Degreef J, Muledi J I and Drouet T 2016 Multiscale assemblage of an ectomycorrhizal fungal community: the influence of host functional traits and soil properties in a 10 ha miombo forest *FEMS Microbiol. Ecol.* **92** ffw151
- [78] Högborg P and Pearce G 1986 Mycorrhizas in Zambian trees in relation to host taxonomy, vegetation type and successional patterns *J. Ecol.* **74** 775–85
- [79] Bâ A M, Duponnois R, Moyersoen B and Diédhiou A G 2012 Ectomycorrhizal symbiosis of tropical African trees *Mycorrhiza* **22** 1–29
- [80] van der Putten W H 2017 Below ground drivers of plant diversity *Science* **355** 134–5
- [81] Bennett J A, Maherali H, Reinhart K O, Lekberg Y, Hart M M and Klironomos J 2017 Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics *Science* **355** 181–4
- [82] Teste F P *et al* 2017 Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands *Science* **355** 173–6
- [83] Geist H J and Lambin E F 2002 Proximate causes and underlying driving forces of tropical deforestation *Bioscience* **52** 143–50
- [84] Rudel T K 2005 *Tropical Forests: Regional Paths of Destruction and Regeneration in the Late Twentieth Century* (New York: Columbia University Press)

- [85] Pfaff A *et al* 2007 Road investments, spatial spillovers, and deforestation in the Brazilian Amazon *J. Regional Sci.* **47** 109–23
- [86] Laurance W F *et al* 2014 A global strategy for road building *Nature* **513** 229–32
- [87] Perz S *et al* 2008 Road building, land use and climate change: prospects for environmental governance in the Amazon *Phil. Trans. R. Soc. B* **363** 1889–95
- [88] Laurance W F, Delamonica P, Laurance S G, Vasconcelos H L and Lovejoy T E 2000 Conservation—rainforest fragmentation kills big trees *Nature* **404** 836
- [89] Laurance W F, Ferreira L V, Rankin-De Merona J M and Laurance S G 1998 Rain forest fragmentation and the dynamics of Amazonian tree communities *Ecology* **79** 2032–40
- [90] Laurance W F, Laurance S G, Ferreira L V, Rankin-De Merona J M, Gascon C and Lovejoy T E 1997 Biomass collapse in Amazonian forest fragments *Science* **278** 1117–8
- [91] Furley P A, Rees R M, Ryan C M and Saiz G 2008 Savanna burning and the assessment of long-term fire experiments with particular reference to Zimbabwe *Progress Phys. Geography* **32** 611–34