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To cite this article: Daniela Requena Suarez *et al* 2021 *Environ. Res. Lett.* **16** 044014

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ENVIRONMENTAL RESEARCH
LETTERS

LETTER

OPEN ACCESS

RECEIVED
9 July 2020REVISED
22 February 2021ACCEPTED FOR PUBLICATION
24 February 2021PUBLISHED
12 March 2021

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Variation in aboveground biomass in forests and woodlands in Tanzania along gradients in environmental conditions and human use

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Disturbed African tropical forests and woodlands have the potential to contribute to climate change mitigation. Therefore, there is a need to understand how carbon stocks of disturbed and recovering tropical forests are determined by environmental conditions and human use. In this case study, we explore how gradients in environmental conditions and human use determine aboveground biomass (AGB) in 1958 national forest inventory (NFI) plots located in forests and woodlands in mainland Tanzania. Plots were divided into recovering forests (areas recovering from deforestation for <25 years) and established forests (areas consistently defined as forests for ≥ 25 years). This division, as well as the detection of year of forest establishment, was obtained through the use of dense satellite time series of forest cover probability. In decreasing order of importance, AGB in recovering forests unexpectedly decreased with water availability, increased with surrounding tree cover and time since establishment, and decreased with elevation, distance to roads, and soil phosphorus content. AGB in established forests unexpectedly decreased with water availability, increased with surrounding tree cover, and soil nitrogen content, and decreased with elevation. AGB in recovering forests increased by $0.4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ during the first 20 years following establishment. Our results can serve as the basis of carbon sink estimates in African recovering tropical forests and woodlands, and aid in forest landscape restoration planning.

1. Introduction

Tropical forests store approximately 55% of the world's forest carbon (C) stocks, acting as C sinks through a positive balance of tree growth, recruitment and mortality (Pan *et al* 2011). While forest C stocks and sinks in the tropics have primarily been studied in structurally intact, undisturbed forests in humid ecosystems (Brienen *et al* 2015, Qie *et al* 2017, Hubau *et al* 2020), disturbed and recovering forests

are both increasing in extent (Aide *et al* 2013, Lewis *et al* 2015). Given their rapid growth, recovering forests have higher instantaneous C sink capacities per unit area in comparison with capacities in old-growth forests under similar conditions (Rutishauser *et al* 2015, Poorter *et al* 2016, N'Guessan *et al* 2019).

African tropical forests and woodlands cover approximately 636 million ha, are inhabited by approximately 284 million people (FAO 2018, 2020), and experience disturbances followed by recovery

(Mitchard and Flintrop 2013, McNicol *et al* 2018). African forests and woodlands are partial sources of income and act as safety nets for rural and semi-rural communities in situations of poverty, economic instability, and/or under the effects of climate change (Chomitz 2007, Djoudi *et al* 2015). Due to their vast extent, their unique composition and their ability to support surrounding human and non-human populations, while at the same time being under constant use, understanding the role that African forests and woodlands have in climate change mitigation is of utmost importance.

The determinants of C stocks in disturbed and recovering tropical forests and woodlands in Africa remain mostly understudied (Marunda and Bouda 2010, Schimel 2010, Becknell *et al* 2012, Pennington *et al* 2018). Forest C stocks are often estimated by measuring standing aboveground biomass (AGB; Mg ha^{-1}), which in undisturbed forests is determined mainly by local environmental conditions. Across undisturbed forests and woodlands in Africa, AGB is likely to be higher in areas with low elevation and gentle slopes (Ensslin *et al* 2015, Yohannes and Soromessa 2015), high levels of water availability throughout the year (Becknell *et al* 2012, Ensslin *et al* 2015) and on older, fertile soils (Lewis *et al* 2013). In disturbed and recovering forests, AGB is additionally influenced by natural or human disturbances. AGB tends to be higher under lower intensities of human activities such as wood extraction, land conversion (Bonner *et al* 2013, Pelletier *et al* 2017, McNicol *et al* 2018), and when not affected by forest fires (Ryan and Williams 2011, Tarimo *et al* 2015). In addition, AGB in recovering forests is expected to increase with time since forest establishment (Pelletier *et al* 2018, N'Guessan *et al* 2019, Requena Suarez *et al* 2019).

Large-scale efforts such as national forest inventories (NFIs) have the potential to identify which environmental conditions and degrees of human use are associated with AGB across large areas in forest ecosystems in Africa. NFIs provide valuable *in situ* observations of AGB, covering broad gradients in environmental conditions and degrees of human use, and can therefore be used for this purpose. Although NFIs seldom provide a quantitative metric of disturbance or recovery of their plots, through the use of validated methodologies of forest cover change detection using time series of satellite images (Sexton *et al* 2013, 2015, 2016a, Feng *et al* 2016, Lembani *et al* 2019, Hamunyela *et al* 2020), it is possible to estimate time since forest establishment in recently recovered forests. The integration of AGB estimated from NFI plots, spatial datasets of environmental conditions and human use (including time since establishment) opens the opportunity to identify the major determinants of AGB stock in disturbed and recovering forests across large scales.

In this study, we use an extensive NFI dataset across Tanzania's forests and woodlands—consisting

mainly of open and closed woodlands, including miombo woodlands and degraded forests—and integrate it with spatial datasets to identify the determinants of AGB. Tanzanian forests are currently under use throughout the country (URT 2016), with fuelwood and charcoal use contributing to 92% of the country's energy consumption (Malimbwi and Zahabu 2009). At the same time, efforts for their sustainable management have been underway for at least three decades (Blomley *et al* 2011), as well as forest conservation, through the establishment of protected areas in 36% of its mainland area (Gizachew *et al* 2020). Understanding how AGB varies along gradients in environmental conditions and human use can aid forest landscape restoration planning in Tanzanian forests and woodlands as well as in similar ecosystems in other areas.

Here, we use forest cover time series to divide forest plots into established and recovering forests. For recovering forests, we used time since forest establishment—derived from satellite time series—as a quantitative indicator to assess AGB recovery and therefore the C sink capacity of Tanzania's recovering forests. We hypothesize that (a) AGB is higher in areas with low elevation and gentle slopes, with high levels of water availability, in fertile soils, and with low intensity of human use, and that (b) AGB in recently recovering forest plots increases with time since forest establishment, and therefore that recovering forests act as partial C sinks.

2. Methods

To test our hypotheses, we used a mixed-effects modelling approach to identify the main environmental and human use determinants of AGB in Tanzania's forests, which we divided into recovering and established forests. For this study, we define recovering forests as areas with forests or woodlands that have been regrowing for less than 25 years, and established forests as areas that have been consistently defined as forests or woodlands for at least the last 25 years. We used the same covariations for environmental and human use to test the first hypothesis (determinants of AGB at a specific point in time) in both types of forests. Additionally, for recovering forests, we tested the second hypothesis (effect of time on AGB) through the inclusion of time since forest establishment.

2.1. Study site and forest plot data

Forest plots were measured across Tanzania (figure 1(a)) from 2010 until 2012 as part of the NAFORMA (National Forest Monitoring and Assessment of Tanzania Mainland) project led by the Tanzania Forest Services Agency, in collaboration with the FAO-Finland forestry programme (TFS 2015). A stratified sampling design was followed to account

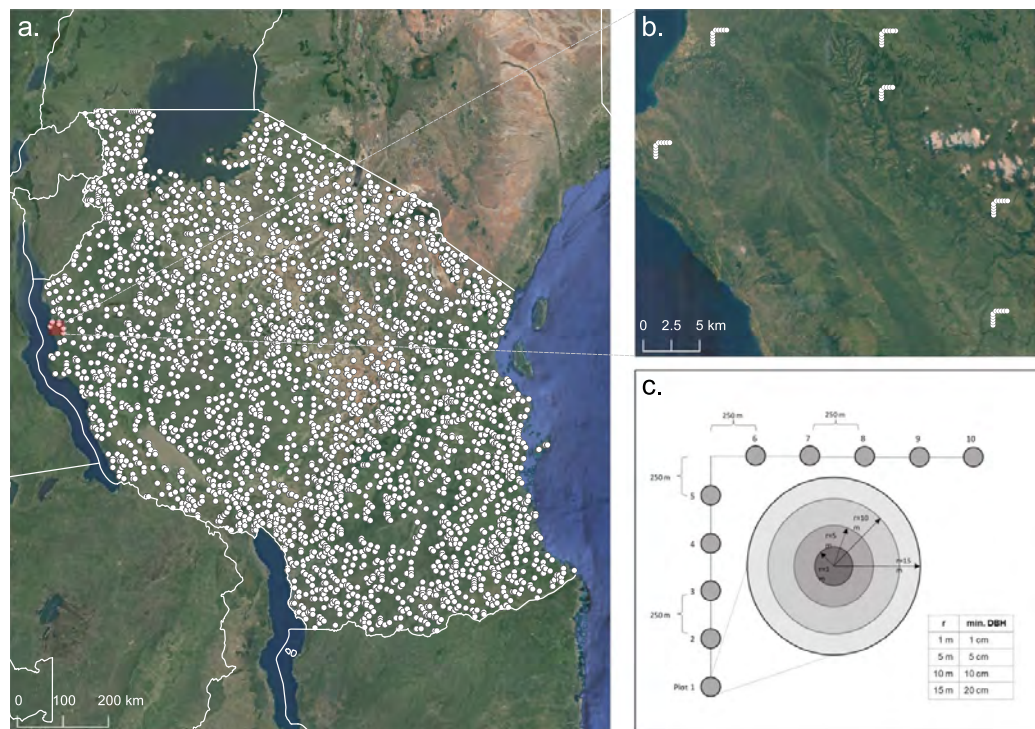


Figure 1. Distribution of NAFORMA clusters and plots. (a) White dots represent the cluster locations in Tanzania, (b) close-up of clusters (red inset in (a)) in which individual plots can be distinguished, and (c) NAFORMA cluster and plot design.

for variability in forests and land use (Tomppo *et al* 2014). Forest plots were arranged in L-shaped clusters of up to ten plots (average = 9.5), with 250 m between plots (figures 1(b) and (c)). A total of 30 382 plots grouped in 3208 clusters were measured as part of the inventory, including plots outside forests and woodlands.

NAFORMA uses circular forest plots of 0.0707 ha (figure 1(c)). Within these plots, the total height (H ; in m) and diameter at breast height (DBH; in cm) of all trees with a DBH above 1, 5, 10 or 20 cm—based on sub-plot radii of 1, 5, 10 and 15 m, respectively (figure 1(c))—were measured. Species-specific or regional allometric equations were used to calculate tree-level volume (m^3) (Malimbwi 1987, Haule and Munyuku 1994, Malimbwi *et al* 1998, 2000). Tree-level AGB (Mg) was calculated by multiplying tree-level volume estimates with species-specific or regional wood densities (TFS 2015). These values were used to estimate total AGB ($Mg\ ha^{-1}$) per plot. We included 16 630 plots in natural forests and woodlands, and excluded plots located in plantations, mangroves, bushlands, grasslands, cultivated land and inland water areas. In order to include a plot in the analysis, AGB estimates had to be >0 and $<400\ Mg\ ha^{-1}$ to exclude plots with AGB values higher than those expected in undisturbed

closed-canopy forests (Brown and Gaston 1995, Lewis *et al* 2013).

2.2. Estimation of time since establishment

The time since establishment (in years) of each forest plot was determined based on a time-series analysis of Landsat multispectral imagery. Time since establishment was estimated by detecting changes in the probability of forest cover derived from the estimate and uncertainty of tree-canopy cover (Sexton *et al* 2013, 2016b) at plot locations based on the full Landsat image archive at the time—from 1984 to 2018. For this region, pixels with $>10\%$ tree cover were defined as forest. This threshold was chosen due to the predominance of low-biomass tropical forests and woodlands in the study area, coinciding with Tanzania's definition of 'forest' (URT 2016). With this threshold, we generated a forest reference baseline corresponding to 2018, and plots in locations that did not exceed the threshold in 2018 were excluded from further analysis. Year of forest gain at each plot location was detected through a kernel analysis of a time-series of forest-cover, expressed as the probability of the class forest in a given pixel in a given year. A kernel spanning 7 years, including 3 years before and 3 years after a given year, was run retrospectively through the series beginning in 2018. The mean and

variance of forest probabilities in before- and after-kernel samples around the focal year (i.e. the year in which forest probability surpassed 50%) were calculated, and the difference between groups was tested using a variant of the two-sample z-test. If a statistically significant ($p < 0.05$) difference was identified between the two ascending groups, the focal year was labelled as forest gain. If multiple significant gains were detected in the series, the location was labelled with the year of most recent gain. Plots in locations for which forest gain was detected during the study period were regarded as recovering forests, and plots in locations for which the forest probability was over 50% throughout the whole period were regarded as established forests.

For plots in recovering forests, the establishment year was assumed to occur 2 years prior to the detection of forest gain. Time since forest establishment was calculated by subtracting the year of forest establishment from the year in which the plot of the given location was measured (i.e. measurement year). Two additional criteria were applied for recovering forest plots: first, the plot needed to have been measured at least one year after the year of forest establishment; second, we included plots for which the probability of forest gain was at least 20%.

2.3. Environmental and human use predictors

To test the effect of topography, water availability, soil fertility and degree of human use on AGB in the selected forest plots, we gathered ten relevant environmental and human use predictors for all plot locations (table 1). Due to the extent of the study area, plots spanned broad gradients in environmental conditions and human use.

The effect of topography was evaluated through elevation (m) and slope ($^{\circ}$) extracted or calculated from the shuttle radar topography mission digital elevation model (Jarvis *et al* 2008) at 90 m resolution. To evaluate effects of water availability, we extracted climatic water deficit (CWD; in mm yr^{-1}) from Chave *et al* (2014) at a resolution of 2.5', defined as the sum of the differences between monthly rainfall and monthly evapotranspiration in the months where evapotranspiration exceeded rainfall, thus only in periods of water deficit. To evaluate the effect of soil fertility, we included nitrogen (N) and phosphorus (P) soil content data at 0–30 cm depth (in ppm) from Hengl *et al* (2017) at a resolution of 250 m.

To test for the effect of human use, we included metrics of surrounding tree cover, forest accessibility and fire disturbances. We calculated the percent surrounding tree cover in the landscape based on percent tree cover data for 2010 (%), which was extracted from Hansen *et al* (2013) at 30 m spatial resolution within radius of 500 m of the plots' locations. Degree of forest accessibility was included as distance of plots to roads and settlements. This was done by calculating the Cartesian distance (in km) to the nearest primary,

secondary or tertiary road and to the nearest city, village or town using road and settlement vector data for Tanzania (OpenStreetMap Contributors 2019). To account for the effect of fire, we evaluated intensity of fire disturbances (Trapnell 1959, Chidumayo 1997, Kennard *et al* 2002) through the inclusion of average fire duration per month which was extracted for the 2003–2012 period from Andela *et al* (2019) at 500 m resolution.

Predictors were extracted or calculated in R v.3.4.0 (R Core Team 2017), using the *raster*, *spatiaEco*, and *rgeos* packages (Bivand and Rundel 2017, Evans 2018, Hijmans 2019). Four plots with unrealistically high soil N ($n = 1$; 5505 ppm) and soil P ($n = 3$; 2260–2455 ppm) content were excluded from further analysis.

2.4. Statistical analysis

To identify the determinants of AGB in recovering and established forests, we modelled plot-level AGB (in Mg ha^{-1}) for recovering and established forests separately as a function of elevation, slope, CWD, soil P content, soil N content, surrounding tree cover, distance to roads, distance to settlements and average fire duration using a linear mixed-effects model. An interaction between CWD and average fire duration was included, in line with Lehmann *et al* (2014) who describe a strong relationship between water availability and fires affecting biomass in African sparse woodlands. For recovering forests, we additionally included time since establishment, which was ln-transformed to account for the non-linear AGB increase over time. The aforementioned predictors were included as fixed effects, and plot clusters were regarded as random effects, for which random intercepts were included. Model performance was evaluated using Akaike's information criterion and model fits were evaluated based on their marginal (fixed-effects only) and conditional (fixed and random effects) R^2 (Nakagawa and Schielzeth 2013). All predictors were standardised by subtracting the mean and dividing the difference by 1 SD (Gelman and Hill 2007) to compare effect sizes. We used the *lme4* package (Bates *et al* 2015) to fit mixed-effects models in R.

3. Results

3.1. Spatial distribution and stand age of forest plots

A total of 1479 plots in recovering forests and 479 plots in established forests were included in the analysis (figure 2). Thirty-nine percent of the plots were located within 10 km of a road and 27.4% of the plots were located within 10 km of a human settlement (figure 2(a)). Recovering forests comprised a similar percentage of the total number of plots within 10 km of roads and settlements (40.0% and 28.1%,

Table 1. Environmental and human use predictors for the NAFORMA forest plots. Time since establishment was derived from this study only for plots in recovering forests.

Code	Variable	Unit	Min	Max	Mean	SD	Original source	Original spatial resolution
<i>yrs_since_est</i>	Time since establishment (only for recovering forests)	yr	1.0	24.0	11.0	7.4	This study	—
<i>elevation</i>	Elevation	m	13.0	2123.0	1108.8	393.8	Jarvis <i>et al</i> (2008)	90 m
<i>slope</i>	Slope	°	0.0	17.2	1.4	2.1	Jarvis <i>et al</i> (2008)	90 m
<i>CWD</i>	Climatic water deficit	mm yr ⁻¹	-1312.5	-372.0	-891.4	156.1	Chave <i>et al</i> (2014)	2.5'
<i>soilP</i>	Total phosphorus (P) content of the soil fine earth fraction for 0–30 cm depth.	ppm	73.0	1163.0	255.8	123.5	Hengl <i>et al</i> (2017)	250 m
<i>soilN</i>	Total nitrogen (N) content of the soil fine earth fraction for 0–30 cm depth.	ppm	373.0	2336.0	811.7	284.8	Hengl <i>et al</i> (2017)	250 m
<i>tree_cover</i>	Surrounding tree cover in 2010 (500 m radius)	%	3.3	65.9	26.7	10.0	Hansen <i>et al</i> (2013)	30 m
<i>dist_roads</i>	Distance to nearest road	km	0.0	121.2	23.5	23.8	OpenStreetMap Contributors (2019)	—
<i>dist_settl</i>	Distance to nearest settlement	km	0.2	78.5	21.7	15.2	OpenStreetMap Contributors (2019)	—
<i>fire_duration</i>	Average fire duration per month	days	0.0	11.8	4.3	1.9	Andela <i>et al</i> (2019)	500 m

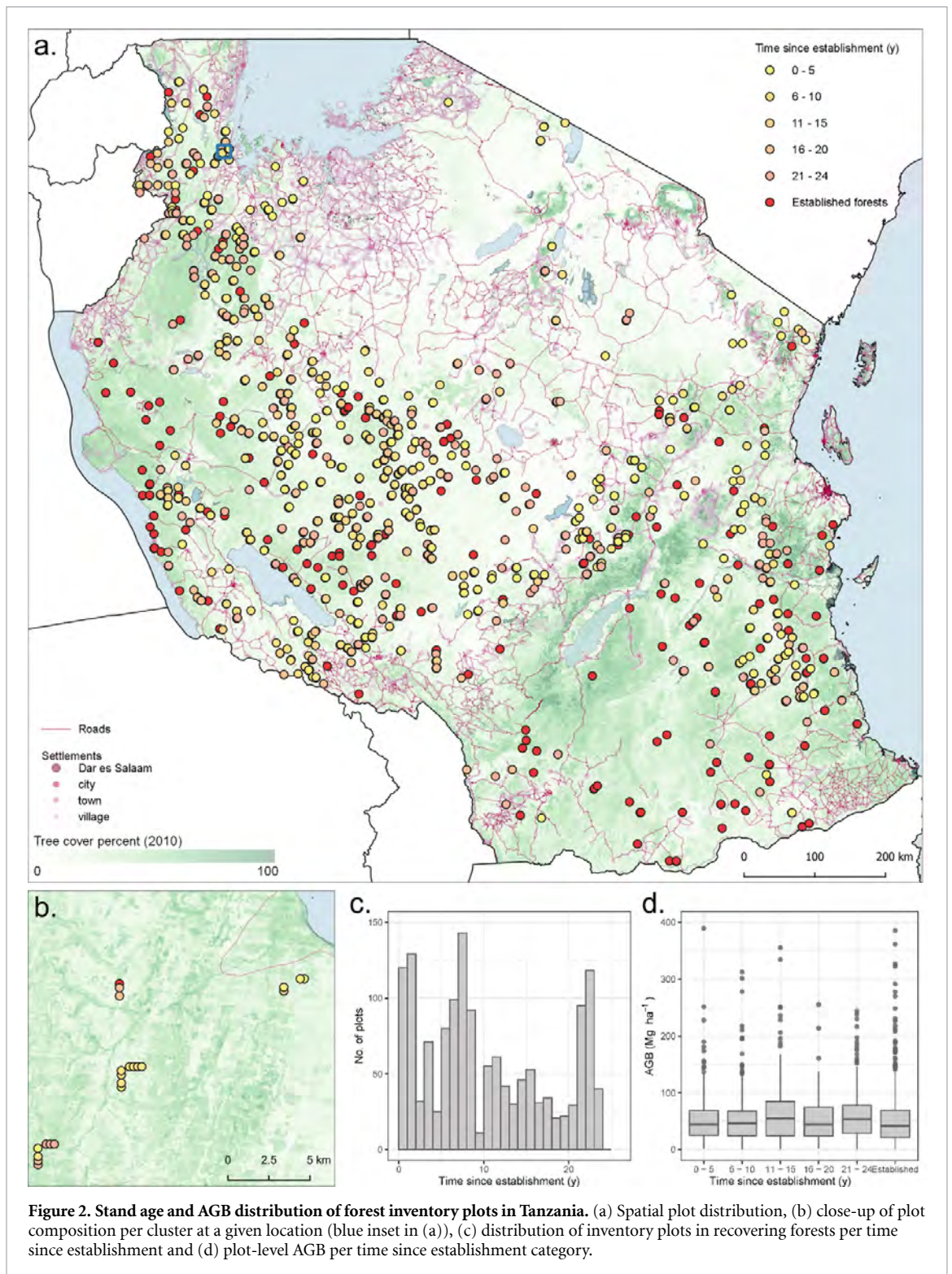


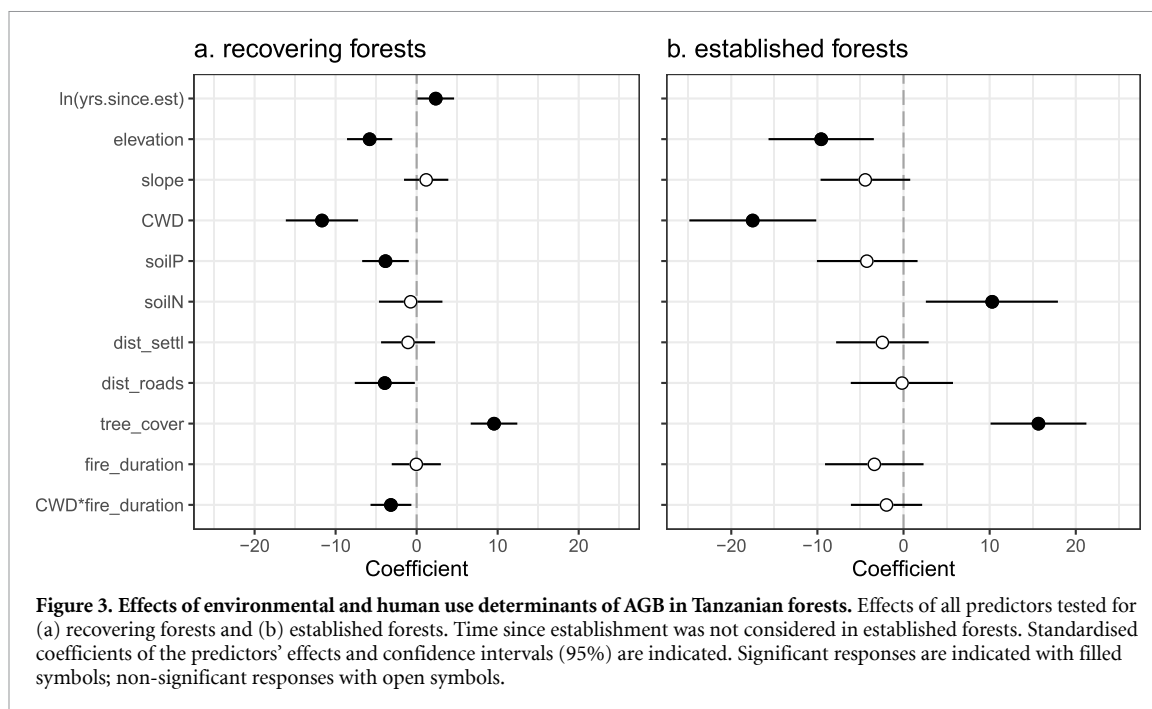
Figure 2. Stand age and AGB distribution of forest inventory plots in Tanzania. (a) Spatial plot distribution, (b) close-up of plot composition per cluster at a given location (blue inset in (a)), (c) distribution of inventory plots in recovering forests per time since establishment and (d) plot-level AGB per time since establishment category.

respectively) as plots in established forests (36.1% and 25.3%, respectively).

For plots in recovering forests, time since establishment varied from 1 to 24 years (figure 2(c)), with the majority (54.2%) established 1–10 years before field measurement. The majority (88.5%) of AGB values for recovering and established forests did not exceed 100 Mg ha^{-1} . The overall mean AGB for established forests (56.0 Mg ha^{-1}) was 0.5 Mg ha^{-1} higher than for recovering forests.

3.2. Environmental and human use determinants of AGB

AGB varied along environmental and human use gradients in both recovering and established forests. In recovering forests (figure 3(a)), in decreasing order of importance, AGB decreased with increasing CWD, increased with higher percentages of surrounding tree cover, decreased with elevation, distance to roads, soil P content, with the interaction between CWD and average fire duration, and increased with



time since forest establishment. In established forests (figure 3(b)), in decreasing order of importance, AGB decreased with increasing CWD, increased with surrounding tree cover and with soil N content, and decreased with elevation. The effects of slope, distance to settlements and average fire duration were not significant for either forest category. The marginal (fixed effects only) and conditional (both fixed and random effects) R^2 were 0.08 and 0.24, respectively, for the model describing recovering forests and 0.10 and 0.19 for the model describing established forests.

The effects of CWD, elevation and surrounding tree cover were significant and similar in direction in both recovering and established forests (figures 4(a)–(c)). The unexpected negative effect of CWD on AGB, which suggests that lower water deficit results in lower AGB, was the largest absolute effect in both forest categories, followed by the expected effects of surrounding tree cover (positive) and elevation (negative).

In recovering forests, the effect of time since forest establishment was small yet significant (figure 4(d)). Based on the predicted AGB at 1 and 20 years after forest establishment, and keeping all other predictors constant, the overall AGB recovery rate during the first 20 years was $0.4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$.

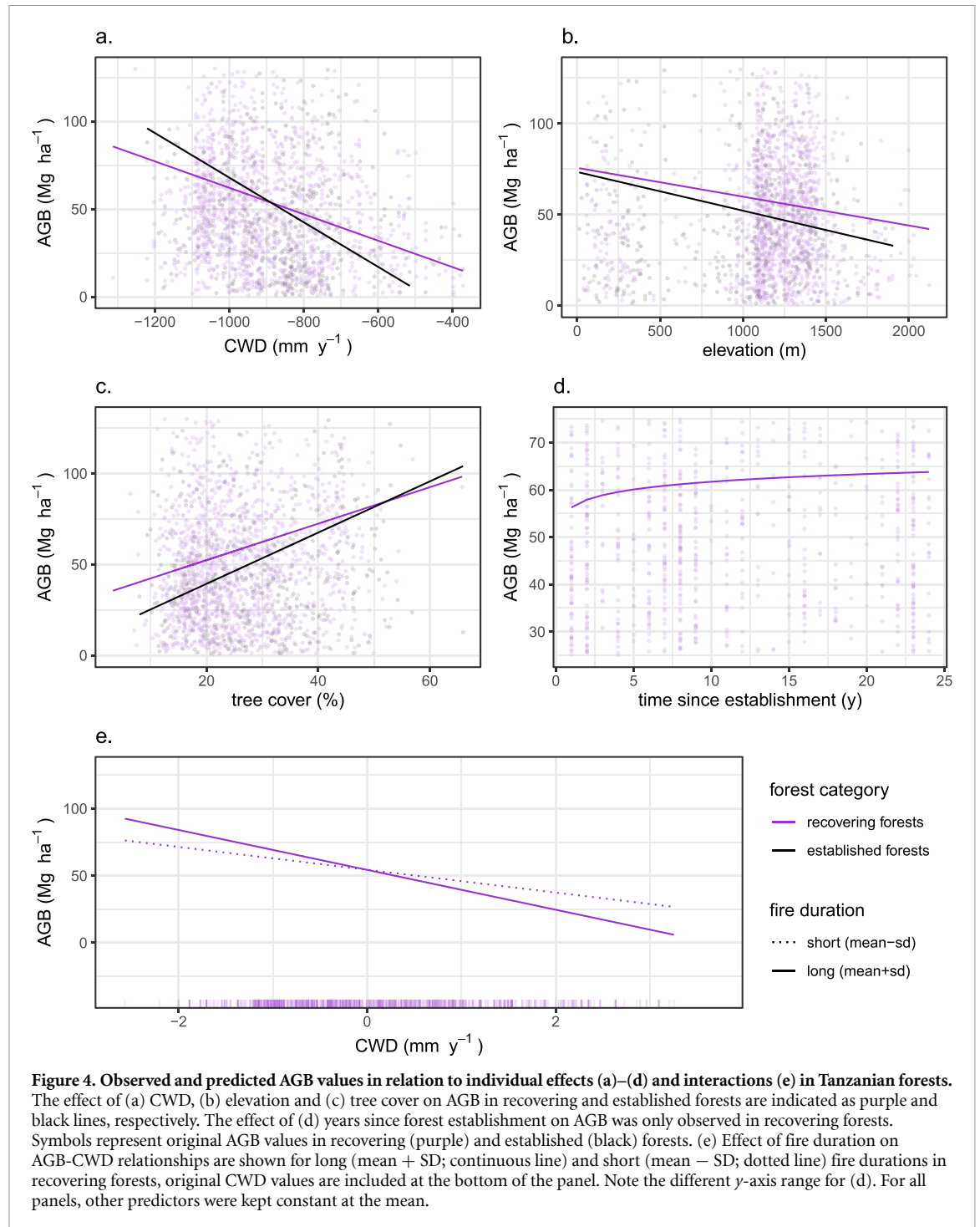
4. Discussion

4.1. Environmental and human use determinants of AGB in Tanzanian forests

Forests and woodlands in Tanzania occur mostly in areas with highly seasonal rainfall, and are subject to dryland-specific ecological, environmental and anthropogenic dynamics (Timberlake *et al* 2010).

Because of this, AGB values in this study greatly varied, aligning with AGB estimates for miombo forests, which overlap with the western part of the Tanzanian forest area covered in this study, which range from 1.3 to 95.7 Mg ha^{-1} (Gumbo *et al* 2018), and with AGB estimates in seasonally dry tropical dry forests in Africa, which range from 39 to 334 Mg ha^{-1} (Becknell *et al* 2012). The aforementioned studies evaluated how climate and disturbance affect AGB in these regions, but they are complicated by combining limited plot data from different methodologies. The spatial extent and methodological consistency of the NAFORMA dataset allowed consistent evaluation of AGB stocks along environmental and human use gradients.

For both recovering and established forests, the selected environmental and human use predictors determined less than 24% and 19% of the variation, respectively. Among these predictors, AGB was most strongly determined by, unexpectedly, a negative effect of CWD. While dry periods are a major AGB-limiting factor (Eamus 1999), the negative effect of CWD on AGB in both forest categories, surprisingly, suggests that seasonality characterised by very dry periods might positively influence AGB. This might be due to increasing periods of water deficit inhibiting the proliferation of herbaceous species, which could potentially limit forest establishment in dry forests and woodlands (Vieira and Scariot 2006, Bhadouria *et al* 2017); however to test this hypothesis, more studies on the initial stages of forest establishment are needed. Moreover, given that, overall, effects of environmental conditions and human use evaluated in this study were weak, additional research on determinants of AGB is needed. The significant interaction between CWD and fire duration in recovering forests suggests



that tree establishment in recovering forests might be positively affected by recurrent, longer fires and very dry periods. This interaction was not significant for established forests, and while fires might benefit seedling establishment (Khurana and Singh 2001), consistently recurring fires ultimately simplify the composition of a forest community (Viciera and Scariot 2006), causing further forest degradation.

As expected, elevation had a negative effect on AGB for both forest categories. The effect of slope, on the other hand, was not significant. While Tanzania has broad elevational gradients across its territory, gentle slopes are common, with steeper

slopes mostly found in the Eastern Arc Mountains, which transect Tanzania from northeast to southwest. The great majority of plots (93.2%) used in this study had a slope of 0° – 5° , suggesting that small changes in gentle slopes have little to no effect on AGB.

The effect of soil fertility, which we hypothesised to be positive, varied for both recovering and established forests, suggesting that higher AGB is found in recovering forests on soils with lower P content and in established forests on soils with higher N content. While the positive effect of soil N content on AGB was expected (Davidson *et al* 2007), this was not

observed for recovering forests, indicating that AGB during the first years is not significantly determined by the amount of soil N. Soil P content, considered a limiting nutrient in tropical forests growing on weathered soils (Murphy and Lugo 1986, Ceccon *et al* 2006, Davidson *et al* 2007), had a negative effect on AGB in recovering forests. Soils may have weathered, and/or further degraded due to lack of soil moisture, current and previous land use, recurrent resource extraction, constant herbivory and recurrent human-induced fires. Furthermore, recent local studies have suggested that AGB stocks are more strongly related to soil hydromorphy rather than to soil fertility (Gourlet-Fleury *et al* 2011). Lastly, these confounding relationships could be a consequence of using gridded spatial predictions for assessing soil nutrient effects, as opposed to using field data, which were not available.

Overall, our results reveal a complex underlying relationship between human activity and forest recovery, which has been reported previously in African forests and woodlands (Timberlake *et al* 2010). For both forest categories, the predictor of human use which mainly drove AGB was surrounding tree cover, an indicator of the extent of land conversion. This is expected, as the presence of nearby forests benefits tree establishment through natural regeneration and tree growth; however, high rates of degradation and deforestation in African woodlands (McNicol *et al* 2018) limit this effect. In recovering forests, distance to roads had a negative effect on AGB, suggesting that forest recovery tends to occur in more accessible areas (Malimbwi *et al* 2005). Land conversion is often done through induced fires, which on their own did not have a significant effect on either recovering or established forests.

Other determinants, for which no spatially explicit information was available are influencing forest recovery and degradation in Tanzania's forests. The effect of herbivory, be it by wildlife or livestock, could provide insight into tree establishment and mortality (Sankaran *et al* 2013), tree cover and forest structure (Asner *et al* 2009), as well as competition with herbaceous (grass) species (Riginos 2009). Megafauna has also been linked to the proliferation of fires (Foster *et al* 2020) and competition with herbaceous species (Bhadouria *et al* 2017). Prevalence of natural regeneration through tree resprouting, common in dry forest ecosystems (Ewel 1980, Timberlake *et al* 2010), and its interaction with constant human use (Vieira and Scariot 2006), might also provide insight into recovery from degradation. Finally, local information on previous land use preceding forest establishment, as well as current levels of forest use, both of which have proven to determine AGB stocks in miombo forests (Jew *et al* 2016, Pelletier *et al* 2017), could also provide insight into the varying levels of AGB in both recovering and established forests.

4.2. AGB recovery in Tanzanian recovering forests

Time since establishment had a significant, positive effect on AGB in recovering forests, indicating that, even though recovering forests in Tanzania experience disturbance, through biomass accumulation over time they can act as partial C sinks. Our estimate ($0.4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) is comparable to, albeit lower than, local estimates obtained through repeated remeasurements in permanent plots in the woodlands of south-eastern Africa. For example, coppiced miombo woodland in Mutupa, Zambia, evaluated during 1982–1988, had a mean annual increment (MAI) of $1.97 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (range: 0.41 – $2.91 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) for woodlands aged 3–29 years (Chidumayo 1990). In miombo woodlands in Kitulungalo, Tanzania, for the period of 3 years (1996–1999), MAI was estimated as $2.35 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ (Malimbwi *et al* 2005), which roughly translates to $1.18 \text{ Mg ha}^{-1} \text{ yr}^{-1}$. In Kilwa, Tanzania, regrowing forests after land disturbance accumulated AGB at a rate of $0.83 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (McNicol *et al* 2015). A recent national study of vegetation change for all forests and woodlands in Zambia (Pelletier *et al* 2018) estimated annual biomass gain rates of $1.17 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (mean) and $0.31 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (median). While our rate is lower, it accounts for varying types of disturbance during recovery, such as fires and extraction of wood, which is not fully the case in the aforementioned studies, which either account for specific disturbances, or select sites with no signs of disturbance after abandonment.

Our AGB accumulation rate estimate was one-tenth as large as the 2019 continent-level IPCC Tier 1 estimate for African recovering tropical dry forests ($3.9 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) which is based on values estimated for Central and South American dry forests due to limited data availability in Africa; however it aligns with AGB accumulation estimates suggested for African recovering tropical shrublands (0.2 – $0.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) (IPCC 2019). Continent-level estimates, which are being used for national greenhouse gas reporting of C sinks, are based on a limited number of locations in tropical dry forests and woodlands, with a major gap in Africa (Requena Suarez *et al* 2019). Region-level estimates are usually based on sites with recovery pathways with little to no disturbance during the first years, and while this could be a common pathway for recovering humid forests (Chazdon *et al* 2007, N'Guessan *et al* 2019), this is not the case for African recovering dry forests and woodlands, which are under constant use. While reporting on the C sinks in African dry forests and woodlands, recurrent disturbance of recovering forests must be taken into consideration.

4.3. Methodological implications and next steps

Given the predominance of low-biomass, sparse forests and woodlands in the study area, the use

of dense time series to detect forest cover gain is challenging. Nevertheless, Landsat-derived dense time series have been used before in this region for detection of forest cover change (Lembani *et al* 2019, Hamunyela *et al* 2020). The Tanzanian NFI plot size (15 m radius; 0.0707 ha) and spacing within clusters (250 m) allowed us to derive this metric per plot; however we can expect some error estimating AGB due to the small plot size (Tomppo *et al* 2008, Kachamba *et al* 2017), as well as the pixel-level uncertainty in forest establishment year.

For recovering forests, we used a space-for-time substitution to estimate AGB recovery. This chronosequence approach has been used elsewhere in the tropics (Chazdon *et al* 2007, Poorter *et al* 2016, N'Guessan *et al* 2019) and, since it requires plots to be measured only at a single point in time, it is a practical way to estimate AGB recovery without having to remeasure forest plots over several decades. In this study, we have employed this approach by detecting time since establishment in forest plot locations, thus deriving information on time since recovery based on 1479 plots embedded in 543 clusters treated as chronosequences.

Chronosequences require having field AGB measurements at known times since major disturbances or abandonment. Time has to be estimated in a precise, consistent, and straightforward manner, and usually relies on interviews with land owners or occasionally on aerial images (Ruiz *et al* 2005, Chazdon *et al* 2007, Piotta *et al* 2009). This greatly limits the number of forest plots that can be used, as many forest plots do not have information on the beginning of recovery or on land use history, unless they have been measured for the main purpose of studying recovery or regrowth. However, as remote sensing technologies improve, and satellite image archives become available, monitoring forest cover dynamics over several years enables the use of forest plots measured for different purposes, for which time since establishment in recovering forests is unknown. With this, using the first round of NFIs to assess forest recovery across large scales becomes possible. Since NFIs strive to systematically sample large forest areas, they are a valuable source of on-the-ground data, which, in combination with satellite time series, can be utilised to study AGB stocks in recovering forests at a national scale. Studies that use remeasured NFIs, such as the case of Pelletier *et al* (2018), offer the opportunity to examine AGB accumulation into more detail.

Satellite-based estimates of time since forest establishment, critical to assess forest recovery, can be applied to other forest inventories for which no field data on stage of recovery is available. As countries refine their estimates of forest C stocks through the implementation of NFIs, satellite time series can serve as an alternative method for repeated measurements over time to estimate

C sinks in recovering forests. Many countries with (sub)tropical forests have recently conducted, or are currently in the process of designing or carrying out NFIs (Romijn *et al* 2015), generating large-scale field data which could be appropriate for this approach.

5. Conclusions

AGB in Tanzanian forests and woodlands is partially determined by gradients in environmental conditions and human use. We found that, in spite of constant use, recovering forests have the potential to act as partial C sinks through biomass accumulation. In this respect, recovering forests in Tanzania have a climate change mitigating value, in addition to the already-essential ecosystem services that they provide to surrounding communities. Carefully planned ecosystem restoration, designed with awareness of the particularities of forest and woodland ecosystems in Africa, could assist with climate change mitigation and sustainable development. In this respect, considering only environmental determinants such as climate and topography is not enough; human use determinants of biomass, such as forest accessibility and degree of forest use, must be taken into account to provide a comprehensive picture of the potential of forest and woodland restoration.

More generally, while integrating plot data and spatial data remains a challenge, we have demonstrated how combining these data sources improves analysis of forest recovery and forest-related climate change mitigation activities. This offers new pathways to integrate forest information in national assessments and planning for climate change mitigation actions. In this respect, large-scale ecological questions which merge environmental and human contexts can be answered through the combination of national field endeavours, satellite time series and spatial datasets.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

Acknowledgments

This research is part of CIFOR's Global Comparative Study on REDD+ (www.cifor.org/gcs). The funding partners that have supported this research include the Norwegian Agency for Development Cooperation (Norad), the International Climate Initiative (IKI) of the German Federal Ministry for the Environment, Nature Conservation, Building and Nuclear Safety (BMUB) and the CGIAR Research Program on Forests, Trees and Agroforestry (CRP-FTA) with financial support from the CGIAR Fund Donors.

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