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Human and natural controls of the variation in aboveground tree biomass in African dry tropical forests

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Abstract. Understanding the anthropogenic and natural controls that affect the patterns, distribution, and dynamics of terrestrial carbon is crucial to meeting climate change mitigation objectives. We assessed the human and natural controls over aboveground tree biomass density in African dry tropical forests, using Zambia's first nationwide forest inventory. We identified predictors that best explain the variation in biomass density, contrasted anthropogenic and natural sites at different spatial scales, and compared sites with different stand structure characteristics and species composition. In addition, we evaluated the effects of different management and conservation practices on biomass density. Variation in biomass density was mostly determined by biotic processes, linked with both species richness and dominance (evenness), and to a lesser extent, by land use, environmental controls, and spatial structure. Biomass density was negatively associated with tree species evenness and positively associated with species richness for both natural and human-modified sites. Human influence variables (including distance to roads, distance to town, fire occurrence, and the population on site) did not explain substantial variation in biomass density in comparison to biodiversity variables. The relationship of human activities to biomass density in managed sites appears to be mediated by effects on species diversity and stand structure characteristics, with lower values in human-modified sites for all metrics tested. Small contrasts in carbon density between human-modified and natural forest sites signal the potential to maintain carbon in the landscape inside but also outside forestlands in this region. Biodiversity is positively related to biomass density in both human and natural sites, demonstrating potential synergies between biodiversity conservation and climate change mitigation. This is the first evidence of positive outcomes of protected areas and participatory forest management on carbon storage at national scale in Zambia. This research shows that understanding controls over biomass density can provide policy relevant inputs for carbon management and on ecological processes affecting carbon storage.

Key words: aboveground biomass; biodiversity and ecosystem function; carbon management and conservation; Miombo woodlands; reducing emissions from deforestation and forest degradation; spatial variability of biomass; variation partitioning.

Introduction

With the Paris Agreement in 2015 (UNFCCC 2015), countries have agreed to put into place ambitious measures to mitigate climate change. One key mitigation approach in the tropics is through conserving and enhancing carbon dioxide sinks and reservoirs via management of terrestrial carbon stocks, especially in forest ecosystems, and by reducing emissions from deforestation and forest degradation in developing countries (REDD+; UNFCCC 2015). Improving our knowledge of the factors affecting the distribution of terrestrial carbon stocks, engendered by both anthropogenic and natural controls, is important to support carbon management and conservation efforts (Lewis et al. 2013, Tyukavina et al. 2015).

Variation in biomass density can be the result of anthropogenic actions through land use and land cover change, including the replacement of forests through deforestation for agriculture or mining as well as through forest degradation for selective logging, shifting cultivation, charcoal production, or fuelwood collection (Lewis et al. 2015, Bustamante et al. 2016). It can also be the result of environmental gradients (Larjavaara and Muller-Landau 2012, Lewis et al. 2013), natural disturbances (fires, droughts, hurricanes; Phillips et al. 2009) or biological processes related to forest structure (Baker et al. 2004, Malhi et al. 2006), species composition, and diversity (Ruiz-Jaen and Potvin 2010, Cavanaugh et al.

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2014, Fauset et al. 2015). Global change also affects forest ecosystem functioning directly and indirectly, contributing to current variations in biomass density (Alencar et al. 2015, Trumbore et al. 2015).

While much work has been done to identify tree biomass correlates and associated spatial patterns for humid tropical forests, knowledge of the human and natural controls over biomass density remains relatively limited for the dry tropical forests of the eastern and southern African region. Although these forests are characterized by lower aboveground biomass (AGB) density than dense humid forests, they play an important role in the global carbon cycle because they cover large areas. They are also essential for biodiversity conservation and for the livelihoods of more than 100 million people (Campbell et al. 2007, Dewees et al. 2011). For instance, the Miombo woodlands that dominate the region are the most extensive tropical seasonal woodland and dry forest formation in Africa, covering around 2.4–3.6 million km^2 (Dewees et al. 2010, Munishi et al. 2010). The Miombo-mopane woodland is also one of the five global ecological zones that have been prioritized for biodiversity conservation and species endemism (Mittermeier et al. 2003). Earlier studies have identified key ecological processes related to biomass accumulation and storage (Frost 1996) and the effect of human activities on carbon stocks in the region (Chidumayo 1993, 2002, 2013), including fire and other disturbances (Ribeiro et al. 2008, Williams et al. 2008, Ryan and Williams 2011). Yet, little is known of the factors that may affect the distribution of biomass at broader geographic scales that are relevant for carbon management and conservation planning for climate change mitigation.

To improve REDD+ planning and implementation, it is essential to develop understanding of the human and natural controls that can explain variations in forest biomass density, some of them being drivers of deforestation and forest degradation, or conversely, appropriate carbon conservation and management approaches (e.g., through reforestation). Effectively, human land use and management can have positive or negative impacts on biomass density or carbon storage. Important factors can then be mitigated or reinforced through appropriate policy approaches and provide useful guidance for conservation and management decision-making.

In this study, we aim to understand the human and natural factors that best explain variation in tree AGB density, using Zambia as a case study. First, we compare variation in AGB density, using a large set of predictor variables, at different spatial scales as well as sites with human land uses (anthropogenic or human-modified sites) and without human land uses (non-anthropogenic sites, hereafter referred to as natural sites). In natural forest sites, we expect biodiversity and environmental variables to contribute the most to explaining variation in tree AGB density, while in human-modified sites, we expect land use and management activities to best explain the observed variation. Second, we compare the diversity, species composition, and stand structure between sites with and without human land uses in order to test the effect of biodiversity on biomass density and obtain insights on potential underlying ecological processes at play. We expect a positive association of diversity to biomass density in both natural and human-modified sites. Third, we evaluate the influence of different management and conservation practices on biomass density to determine if our findings can be used to generate policy recommendation for carbon conservation and management. This study informs carbon management and conservation efforts of the Zambian government by focusing on the causes of variability in biomass density within forest ecosystems, which has been identified as an important knowledge gap (Day et al. 2014).

Methods

The Republic of Zambia, located in the Southern Africa region, is one of 14 pilot countries of the United Nations Collaborative Programme on REDD+ (UN-REDD). The country has been developing its REDD+ national strategy, forest monitoring system and forest reference emission levels with the goal of reducing land-based emissions and increasing carbon storage for climate change mitigation. We used Zambia's Integrated Land Use Assessment (ILUA), the first nation-wide inventory sponsored by the Food and Agriculture Organization (FAO), which covers both human-dominated landscapes and remote areas. A large range of biophysical and socioeconomic variables were collected as part of ILUA. We use these data to explore variation in tree AGB over the country at three spatial scales: the tract level, the plot level, and the land-use level (Fig. 1). At each scale, tree AGB density was calculated based on the Chave et al. (2014) allometric models, and was related to different sets of explanatory variables (see *Explanatory variables*). Further details on ILUA sampling design, biomass calculation, and specific methodologies are provided in Appendix S1.

Explanatory variables

We extracted total annual precipitation, mean minimum temperature, mean maximum temperature, and elevation at the tract and plot levels from global data sets (Appendix S1). Distance to major towns (market) and roads were calculated from GIS layers provided by the Zambia Forestry Department. Household survey data collected during the ILUA project were used to identify the number of inhabitants near the sampling site (in a 5 km radius) and to create a binary variable for presence–absence of population.

Measurements collected during the ILUA project included aspect and slope as quantitative variables, as well as relief, texture, drainage, and soil organic matter as categorical variables. We calculated the median for quantitative variables and the mode for categorical

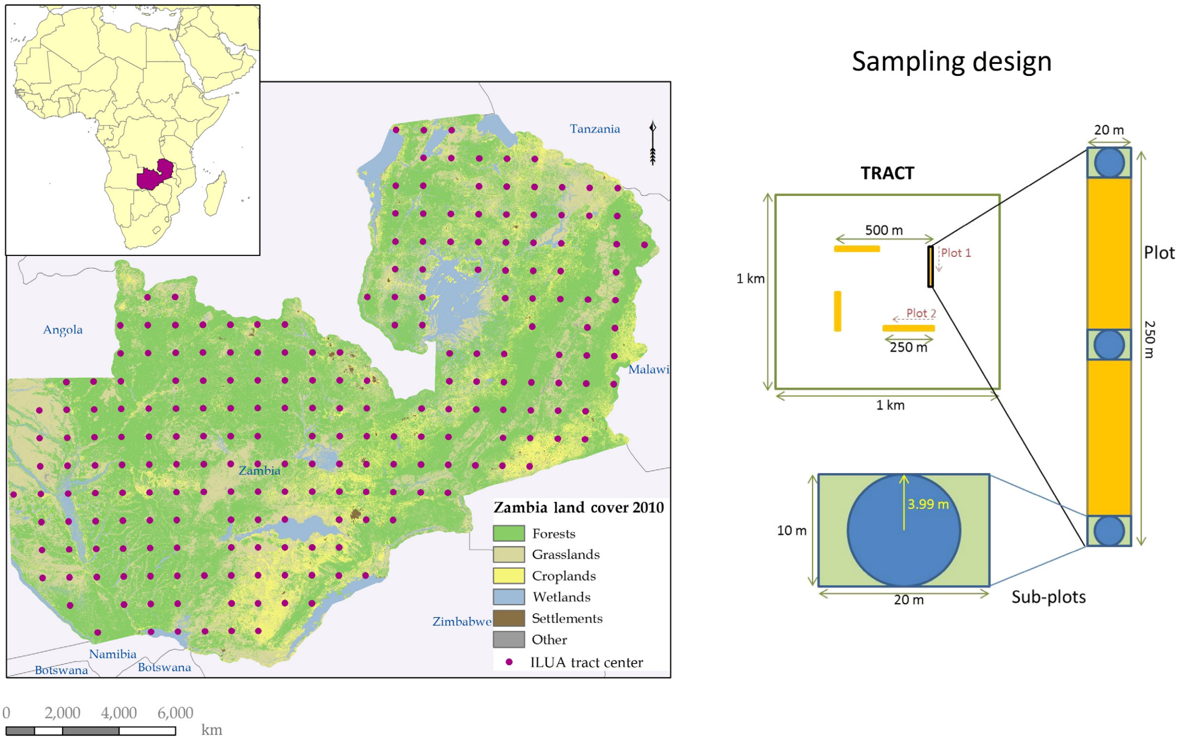

FIG. 1. Distribution of tract center points for the Integrated Land Use Assessment project (ILUA) overlaying the 2010 land cover map of the Republic of Zambia and the schematic of the sampling design for the ILUA inventory. Using a systematic sampling design, the ILUA inventory surveyed vegetation in 221 tracts of 1 × 1 km. In each tract, four plots of 20 m by 250 m (or 5,000 m^2) were surveyed. The sub-plots (three per plot) shown here were used to collect information on aspect, slope, relief, texture, drainage, and soil organic matter and used in this study as descriptors. Data source: ILUA project data set and RCMRD/NASA land-cover map. [Color figure can be viewed at wileyonlinelibrary.com]

variables based on three measurements at the plot level and 12 measurements at the tract level.

We calculated common alpha (α) biodiversity indices (hereafter diversity variables) 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 for each level of analysis. For representing stand structure, we calculated different measures of community structure per level of analysis including species abundance, maximum diameter at breast height (dbh), height, wood specific gravity (WSG), and basal area, as well as stand-level means of dbh, height, and WSG. These indicators of forest structure (stand-level mean, maximum) are indirectly related to biomass density, the sum of all tree biomasses per area, and some relationship is expected since biomass allometric models are based on the height, dbh, and WSG of each individual tree. For this reason, we tested models with and without stand structure characteristics.

We constructed Moran's eigenvector maps (MEM) to model spatial structures at all relevant scales, retaining those positively correlated with tree AGB density (Borcard et al. 2011). MEM are the result of a spectral decomposition of the spatial relationships among the sampling sites, creating variables that correspond to all spatial scales that can be observed in a given data set (Borcard et al. 2004). These spatial variables were used to detect the most meaningful underlying spatial structures by which tree AGB density is organized and integrate this information into our models at the tract and the plot levels.

At the land-use/forest level, management characteristics were tested for their influence on AGB density, including the land designation or protection status, land ownership, fire occurrence, fire area, fire type, and the percent tree canopy coverage. In addition, for forest and other wooded lands, other variables were tested including vegetation stratification (layers), shrub coverage, shrub height, type of management plan, type of management agreement, level of disturbance due to human activities, and timber exploitation. A list of the variables used at the different levels is provided in Appendix S2.

Statistical analysis

We stratified the sampling sites a priori into anthropogenic and natural forest sites in order to identify key controls with and without direct human land use. This stratification was performed to gain insights into how underlying mechanisms that may affect these sites differently. The separation between anthropogenic and natural sites was defined for the three levels of analysis using land use information. At the tract level, natural tracts were selected to be represented by "forest" class only. At the plot level, the entire plot area had to be covered by a forest class. At the land-use level, the natural sites were the sections classified as forest land use. The anthropogenic tracts and plots are characterized by human land uses or a mix of forests and human land uses. Other models were also developed with all the sites and the results are provided in Appendix S1: Fig. S6–S9.

Multiple regression and variation partitioning.—We used multiple regression models to explain variation in tree AGB density between anthropogenic and natural forest sites at three scales (tract level, plot level, and land-use level). For each level, given the large number of explanatory variables, we proceeded by creating separate models by type of descriptors, as these are more likely to be collinear (e.g., environmental data, diversity indices), and by using forward selection to retain only the significant variables at 95% confidence level from each type of descriptor tested. AGB density was normalized using the square-root transformation (tract level) or log-transformation (plot and land-use levels) prior to analysis, as were other quantitative variables if they departed from the normal distribution. Statistically significant explanatory variables were then used to compute a model for each level. We used a forward selection procedure based on Akaike's Information Criterion (AIC) to identify variables that contributed to best explaining the variation in AGB density. We used a variance inflation factor (VIF) to remove any descriptor displaying strong collinearity, that is, all explanatory variables included in the final model had VIF indices lower than 10 (Borcard et al. 2011). When a parsimonious model was obtained, we conducted a variation partitioning analysis to quantify the unique and shared fractions of variation explained by all subsets of the explanatory variables when controlling for the effect of the other subsets (Borcard et al. 2011, Legendre and Legendre 2012). To assess model fit and explained variation, we used the adjusted R^2, which controls for sample size and number of predictors (Peres-Neto et al. 2006). We compared models for anthropogenic and natural sites, and with or without stand structure characteristics. Only sites with no missing values were integrated into the multiple regression models.

Boosted regression trees.—We used boosted regression trees (BRT) to compare to the results obtained using multiple regression models. BRT combines two approaches: regression trees, which are models that associate a response variable to predictor variables using recursive binary partitioning, and boosting, a machine-learning approach used here to combine a large number of simple regression tree models that are fitted similar to individual terms in an additive regression model in a forward and stage-wise fashion to improve the predictive performance (Elith et al. 2008). The advantage of using this approach in our case was that it can accommodate missing values in predictor variables; some of our descriptors could not be tested with multiple regressions without a large decrease in observations, thus in degrees of freedom, due to missing values. BRT also accommodate variables of different types including quantitative, semi-quantitative, and categorical.

We followed the guidance developed by Elith et al. (2008) to identify optimal settings for the learning rate (lr), determining the contribution of each tree to the growing model, and the tree complexity (tc) controlling how interactions are modelled (the number of nodes in a tree). BRT were constructed with all predictors at each level, with or without stand structure characteristics and MEM spatial variables, and separating between anthropogenic and natural sites at the plot and land-use levels. For each model, we evaluated the relative importance of predictor variables and the percentage of the deviance explained by the predictors.

Analysis of variance, species ranking, and correlation test.—We used one-way analysis of variance (ANOVA) with permutation test (Legendre 2007) followed by Tukey HSD post hoc test in order to test for significant differences in biomass density between classes for land designation and ownership at the land-use level, as well as the type of management agreement, the type of management, the level of disturbance and fire occurrence for forest sites.

We used Pearson's product-moment correlation to look at the relationships between biomass density and different measures of the stand structure and diversity characteristics for all tracts, as well as separating the anthropogenic and natural variables at the plot and the tract levels. We used ANOVA with permutation test to compare anthropogenic and natural plots for these characteristics.

Species were ranked based on their contributions to AGB density to assess species dominance and composition between anthropogenic and natural plots. We estimated the mean percent (with confidence intervals) contribution to per plot biomass for each species and the contribution of each species to the total biomass density for anthropogenic plots and for natural plots. For forest sites, the species contributing the most to the total biomass per forest types was calculated. All analyses were performed with R software (R Core Team 2013).

RESULTS

Explaining variation in biomass density

We found that diversity variables are key factors explaining variation in AGB density in Zambia (Fig. 2), when stand structure characteristics are not included in the models. For anthropogenic sites, the variation partitioning results showed that diversity variables are of

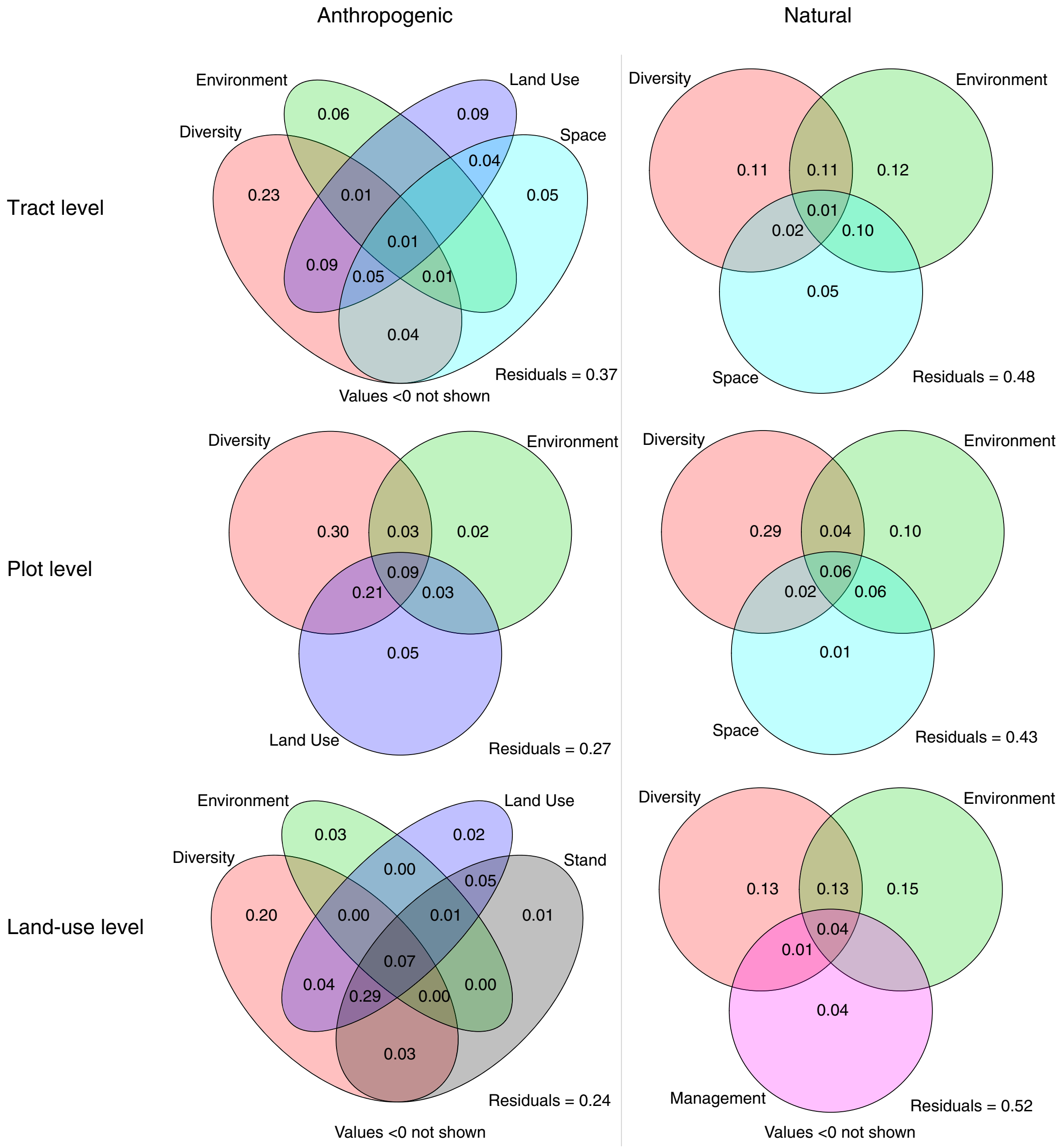

FIG. 2. Venn diagram of the variation partitioning following the forwardly selected multiple regression models explaining variation in biomass density. The left column presents variation partitioning for anthropogenic sampling sites at the tract level, the plot level and the land-use level. The right column shows variation partitioning of natural forest sites at the same scale of analysis. Variables tested in regression models vary between levels and between anthropogenic and natural sites. These models do not include stand structure variables. "Space" refers to the Moran's Eigenvector Maps variables forwardly selected. [Color figure can be viewed at wileyonlinelibrary.com]

foremost importance in predicting biomass density. Land-use variables explain an important share of the variation in biomass density, but mostly in conjunction with diversity variables. These results are similar to what is observed in models combining all the sites, though the variation explained by land-use alone is somewhat higher (13–16%; Appendix S1: Fig. S6, S8). In contrast, for natural sites, diversity or environmental variables alone and in combination explain most of the variation in biomass density. Overall, AGB density was better predicted in anthropogenic sites (from 62.6% to 75.8%) than natural sites (from 48.2% to 56.9%).

Shannon evenness index, which combines the sample sizes of all species present at one site, was selected through the forward selection procedure for all models except for natural sites when stand structure and MEM variables are included, at the tract level (Table 1) and at the plot level (Table 2). Shannon evenness index was negatively associated with biomass density. That is, species evenness was lower in sites with high biomass. In the multiple regression and BRT models, richness, Shannon diversity number and Shannon entropy were positively associated with high biomass values.

Among the environmental variable selected, the province is one categorical predictor most frequently selected in models, which may signal indirect effects of different drivers on biomass acting in different ways in distinct areas of the country. Other environmental variables selected include soil texture, elevation, mean maximum temperature, and distance to roads (Tables 1, 2).

At the land-use level, the percentage of tree canopy coverage, jointly with land use and diversity, explain the greatest share of the variation in AGB density (29%), followed by diversity alone, explaining 20% of the variation. Environmental variables, including elevation and average maximum temperature, explain 11% of the variation alone and with its shared fractions (Fig. 2e).

For natural forested sites, diversity and environment (including drainage and aspect) alone explain 13% and 15% of the variation, respectively, as well as a shared fraction of 13% (Fig. 2f). Management, including land designation, fire area, and levels of human disturbance, explains at best 9% of the variation in biomass density.

When stand structure characteristics are included in the models (including abundance, stand-level mean and maximum height, dbh and WSG), those variables explain most of the variation in biomass density alone and/or shared with diversity (Fig. 3). For anthropogenic tracts and plots, as well as natural plots, about half of the variation in biomass density is explained by stand structure and half is shared by diversity measures and stand structure (Fig. 3a, c, d). For natural forest tracts, 71% of the variation is explained by stand structure variables, with only a small fraction explained jointly by diversity and stand structure, and jointly by spatial structure (MEM) and stand structure (Fig. 3b). When stand structure variables are included as explanatory variables, models for natural forest sites performed as well as those for anthropogenic sites, both at the tract (Table 1) and at the plot level (Table 2).

In general, there is a high level of concordance between the results obtained with multiple regression and BRT models. Other predictive variables were identified with BRT models including the human population near the sites, distance to market and total annual precipitation. We looked more closely at human intervention-related variables between anthropogenic and natural sites, including distance to road, distance to nearest town (market), and the population near sites using separate linear regressions (Fig. 4a, b, c). Significant relationships were identified, except for the distance to town (market) that was not significant for natural forest plots and the number of inhabitants near sites was not significant for anthropogenic plots.

Management and conservation

Important differences relevant to biomass management and conservation emerged using ANOVA with permutation tests and Tukey's HDS post-hoc comparisons. For land designation or protection status, we found that natural/wildlife reserves, national parks, and other protected and multipurpose areas have significantly higher AGB density than production, undefined, or other areas, with the highest biomass density measured in protected areas managed for conservation (Fig. 5a). Land ownership status revealed that other private ownership (defined as land owned by private co-operatives, corporations, religious and educational institutions, pension or investment funds, NGOs, nature conservation societies and other private institutions) and state-owned land have significantly higher biomass than customary lands (land tenure and management based on traditional common rule or practice and determined at the local level, rather than by law or contract, often based on oral agreements), which in turn has significantly higher biomass than land with unknown ownership or owned by individuals (Fig. 5b).

Biomass density was found to be significantly higher in forest sites for which the management has been devolved (i.e., transferred) to communities, and was significantly different than other types of ownership or management agreement, except in the case where a joint forest management (JFM) with the private sector was established (Fig. 5c). Compared to JFM, the devolution of forest management to communities can be defined as the transfer of power and assets to non-state bodies (e.g., citizens, forest user organizations) not created or controlled by the state (Charnley and Poe 2007). There is also a significant difference between the types of forest management plan, that is, any existing forest or woodland management plan applied in forest lands. Forests under a formal management plan both formulated and implemented showed significantly higher biomass density than those under traditional management where no formal management plan is formulated or where a formal management plan is formulated but not implemented (Fig. 5d).

Fire area was negatively correlated to AGB density but we found no significant difference between groups using ANOVA for fire occurrence between forest sites without evidence of fire, with fire in the current year or fire in previous years. The vast majority of fires (n = 770) were surface fires, that is fire spreading through the ground cover where it consumes litter and ground vegetation without reaching the tree canopies. We found a significant difference in AGB density between the levels of human disturbances in forest sites (Fig. 4d).

Table 1. Multiple regression models for anthropogenic and natural sites and boosted regression tree models at the tract level, with or without stand structure and Moran eigenvectors maps (MEM) spatial variables.

	Multiple regression models								Relative contribution to boosted regression tree models (%)		
	All + MEM				All + MEM + SS						
	Anthropogenic		Natural		Anthropogenic		Natural				
Parameter	β	*P*	β	*P*	β	*P*	β	*P*	All	All + SS	All + SS + MEM
Intercept	4.15×10^{0}	5.5×10^{-6}	8.02×10^{0}	1.66×10^{-12}	-6.06×10^{0}	6.80×10^{-6}	-5.67×10^{0}	1.35×10^{-7}			
Richness	7.93×10^{-2}	4.05×10^{-6}	3.96×10^{-2}	4.46×10^{-2}					12.9		
Shannon evenness	-3.66×10^{0}	1.32×10^{-4}	-4.13×10^{0}	2.95×10^{-3}	-1.69×10^{0}	7.25×10^{-3}			15.2	2.3	1.6
Shannon entropy					7.91×10^{-1}	1.58×10^{-6}					
Simpson evenness									11.1	0.8	
Simpson index									4.8		
Elevation			-5.37×10^{-1}	2.63×10^{-2}					2.6		
Province: Lusaka			-2.44×10^{0}	1.92×10^{-2}					15.0†	4.2†	2.7†
Province: Southern			-2.25×10^{0}	4.16×10^{-3}							
Soil texture: Loam	-1.60×10^{0}	3.33×10^{-2}							2.0‡	0.7‡	
Distance to road	5.32×10^{-1}	4.00×10^{-3}			1.77×10^{-1}	6.64×10^{-2}			2.2		
Semi-evergreen forest	9.63×10^{-5}	5.33×10^{-5}					2.29×10^{-5}	2.14×10^{-2}	14.3	1.3	1.1
Deciduous forest	6.52×10^{-5}	3.36×10^{-2}							2.7		
Other natural forest	1.20×10^{-3}	3.62×10^{-2}									
Abundance					1.90×10^{-2}	1.71×10^{-6}	2.88×10^{-2}	$<2.00 \times 10^{-16}$		41.1	37.4
Mean dbh					6.35×10^{-2}	5.67×10^{-5}	3.59×10^{-2}	7.10×10^{-2}		5.2	4
Mean Height					2.86×10^{-1}	$<2.00 \times 10^{-16}$	2.10×10^{-1}	1.63×10^{-9}		30.3	27.7
Mean WSG							6.44×10^{0}	1.45×10^{-5}		2.9	1.5
Dominant dbh					1.44×10^{-2}	5.88×10^{-3}	2.09×10^{-2}	1.44×10^{-4}		5.2	4.3
Spatial structure 1			-1.65×10^{-2}	4.35×10^{-2}			-1.04×10^{-2}	3.07×10^{-3}			
Spatial structure 2	-1.32×10^{-2}	6.84×10^{-3}			-5.39×10^{-3}	4.18×10^{-2}					
Spatial structure 3											1.4
Spatial structure 4					-4.22×10^{-3}	3.93×10^{-2}					
Spatial structure 5	7.68×10^{-3}	2.65×10^{-2}									
Adjusted R^2	0.63		0.52		0.89		0.90		56.0§	82.8§	82.4§

Notes: dbh, diameter at breast height; WSG, wood specific gravity.
† Factor of province.
‡ Factor of texture.
§ Deviance explained.

TABLE 2. Multiple regression and boosted regression tree models for anthropogenic and natural sites at the plot level including Moran eigenvectors maps (MEM) spatial variables, with or without stand structure.

	Multiple regression models								Relative contribution to boosted regression tree models (%)					
	All + MEM				All + MEM + SS				Anthropogenic			Natural		
	Anthropogenic		Natural		Anthropogenic		Natural							
Parameter	β	*P*	β	*P*	β	*P*	β	*P*	All	All + SS	All + SS + MEM	All	All + SS	All + SS + MEM
(Intercept)	9.3×10^{0}	3.3×10^{-4}			-2.5×10^{-1}	3.4×10^{-1}	$4.63.4 \times 10^{-1}$	2.0×10^{-2}						
Richness	1.4×10^{-1}	$<2 \times 10^{-16}$			3.2×10^{-2}	1.5×10^{-4}			19.7	1.9	1.6	9.3		
Shannon evenness	6.6×10^{-1}	3.8×10^{-7}	-2.7×10^{0}	$<2 \times 10^{-16}$	-9.5×10^{-1}	6.2×10^{-6}			4.5	1.1	0.6	9.5		
Simpson evenness							-8.5×10^{-1}	$<2 \times 10^{-16}$	4.5	1.2	0.6	4.0		
Shannon number			9.2×10^{-2}	$<2 \times 10^{-16}$			2.9×10^{-2}	9.9×10^{-10}						
Shannon index									4.3	0.9	0.7			
Elevation	-2.8×10^{-3}	2.2×10^{-6}	-1.2×10^{-3}	7.1×10^{-11}			-2.6×10^{-4}	3.4×10^{-4}	3.4			9.1		
Province: Copperbelt			6.6×10^{-1}	2.4×10^{-4}					10.1	2.2	0.5	21.0	0.9	0.5
Province: Eastern	-7.4×10^{-1}	6.0×10^{-5}												
Province: Nortwestern			3.3×10^{-1}	3.2×10^{-4}										
Province: Southern			-3.5×10^{-1}	1.8×10^{-3}										
Soil texture: Clay			5.8×10^{-1}	8.7×10^{-4}			2.1×10^{-1}	9.5×10^{-3}	3.2			7.1	0.5	
Soil texture: Rock			-5.1×10^{-1}	7.3×10^{-4}			-1.5×10^{-1}	3.1×10^{-2}						
Mean maximum temperature	-2.1×10^{-1}	3.4×10^{-3}												
Exposition									3.5	0.8		4.5	0.2	
Slope												5.3	0.6	0.1
Distance to road									3.5			3.4		
Distance to market									2.6			3.5		
Population near site												5.0	0.1	
Semi-evergreen forest	2.2×10^{-4}	1.2×10^{-12}			1.1×10^{-4}	4.8×10^{-12}			19.1	6.1	5.6			
Deciduous forest	1.7×10^{-4}	1.3×10^{-5}			5.0×10^{-5}	1.7×10^{-2}								
Evergreen	3.6×10^{-4}	2.4×10^{-3}												

(*Continued*)

TABLE 2. (Continued)

	Multiple regression models								Relative contribution to boosted regression tree models (%)					
	All + MEM				All + MEM + SS				Anthropogenic			Natural		
	Anthropogenic		Natural		Anthropogenic		Natural							
Parameter	β	*P*	β	*P*	β	*P*	β	*P*	All	All + SS	All + SS + MEM	All	All + SS	All + SS + MEM
Stem density					7.5×10^{-3}	3.8×10^{-8}	8.2×10^{-3}	$<2 \times 10^{-16}$		19.8	21.6		25.8	26.9
Mean height					8.1×10^{-2}	3.7×10^{-12}	7.4×10^{-2}	$<2 \times 10^{-16}$		25.5	26.2		24.0	22.7
Mean dbh					1.9×10^{-2}	3.7×10^{-5}				5.0	2.8		19.2	16.8
Mean WSG							1.6×10^{0}	2.2×10^{-15}						8.7
Dominant dbh					1.4×10^{-2}	1.3×10^{-12}	1.3×10^{-2}	$<2 \times 10^{-16}$		7.8	6.8		13.2	14.2
Dominant height					2.4×10^{-2}	2.9×10^{-4}	1.4×10^{-2}	7.1×10^{-4}		21.2	19.6		3.5	3.3
Dominant WSG					4.6×10^{-1}	1.5×10^{-2}							1.7	1.7
Spatial structure 1			-4.1×10^{-3}	1.3×10^{-2}			-2.2×10^{-3}	8.9×10^{-3}						
Spatial structure 2			3.6×10^{-3}	1.2×10^{-2}										
Spatial structure 3			3.4×10^{-3}	1.3×10^{-2}										
Adjusted R^2 or Deviance explained	0.73		0.57		0.88		0.89		64.7†	82.2†	79.8†	61.8†	86.8†	85.6†

† Deviance explained.

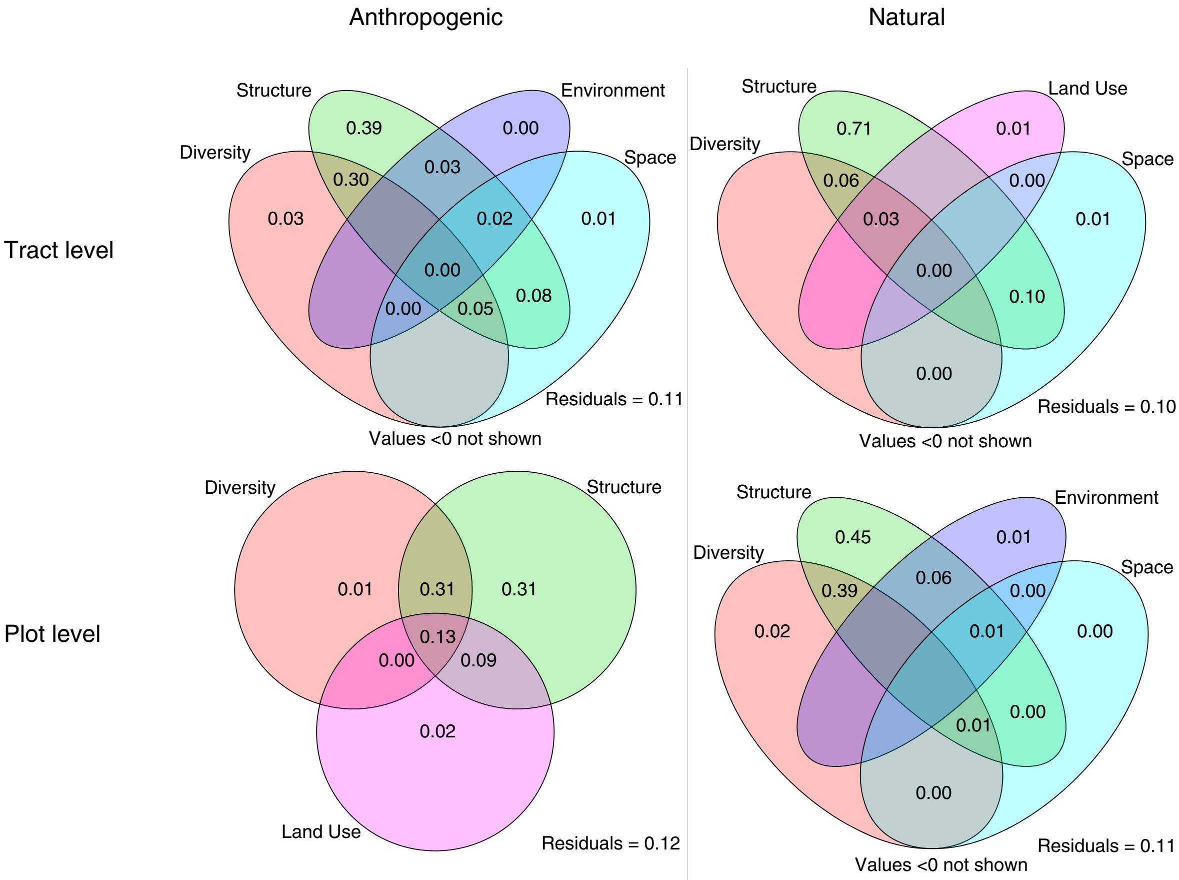

Fig. 3. Venn diagram of the variation partitioning following the forwardly selected multiple regression models explaining the variation in biomass density including stand structure characteristics as explanatory variables, including abundance, dominant height, diameter at breast height (dbh), and wood specific gravity (WSG) and stand-level mean height, dbh, and WSG. The left column presents variation partitioning for anthropogenic sampling sites at the tract level and the plot level. The right column shows variation partitioning of natural forest sites at the tract and the plot level. Variables tested in regression models vary between levels and between anthropogenic and natural sites. [Color figure can be viewed at wileyonlinelibrary.com]

Relation of diversity, stand-level characteristics and species ranking with biomass density

We found a significant difference between anthropogenic and natural forest sites for all diversity and stand structure variables tested, with natural forest plots having higher mean values for all stand characteristics, including richness, abundance, dominant tree dbh, height, WSG, and basal area, and stand-level mean dbh, height, and WSG (Table 3).

Stand characteristics were positively correlated with the biomass density at the plot level, while evenness indices showed significant negative correlations (Table 3). Species abundance appears to be more strongly correlated with biomass in natural plots (0.74 vs. 0.64), while richness was more correlated to biomass in anthropogenic plots than in forest plots (0.59 vs. 0.43). Height was more highly correlated to AGB density than any other tree measurements in plots with or without human land use. Stand-level mean WSG was not correlated in anthropogenic plots. Similar results were obtained at the tract level (Appendix S1: Fig. S3).

We found little overlap when comparing the first 20 species ranked based on the average percentage of biomass by species in each plot with and without human land use (Appendix S1: Fig. S4a, b), with only one species in common. In anthropogenic plots, dominant species obtained from this ranking were characterized by unique value (no error) or large error bars, characteristic of limited sample size. This indicates that a few plots were dominated by uncommon species that might reflect disturbed sites and other land use types than forestland.

When comparing the percent of the total biomass for the 20 species contributing the most to total AGB density, anthropogenic and natural forest plots shared 15 species in common (Appendix S1: Fig. S4c, d). For natural plots, *Colophospermum mopane* ranks first in both rankings, showing its overall dominant contribution to biomass, followed by *Julbernardia paniculata* and *Brachystegia spiciformis.*

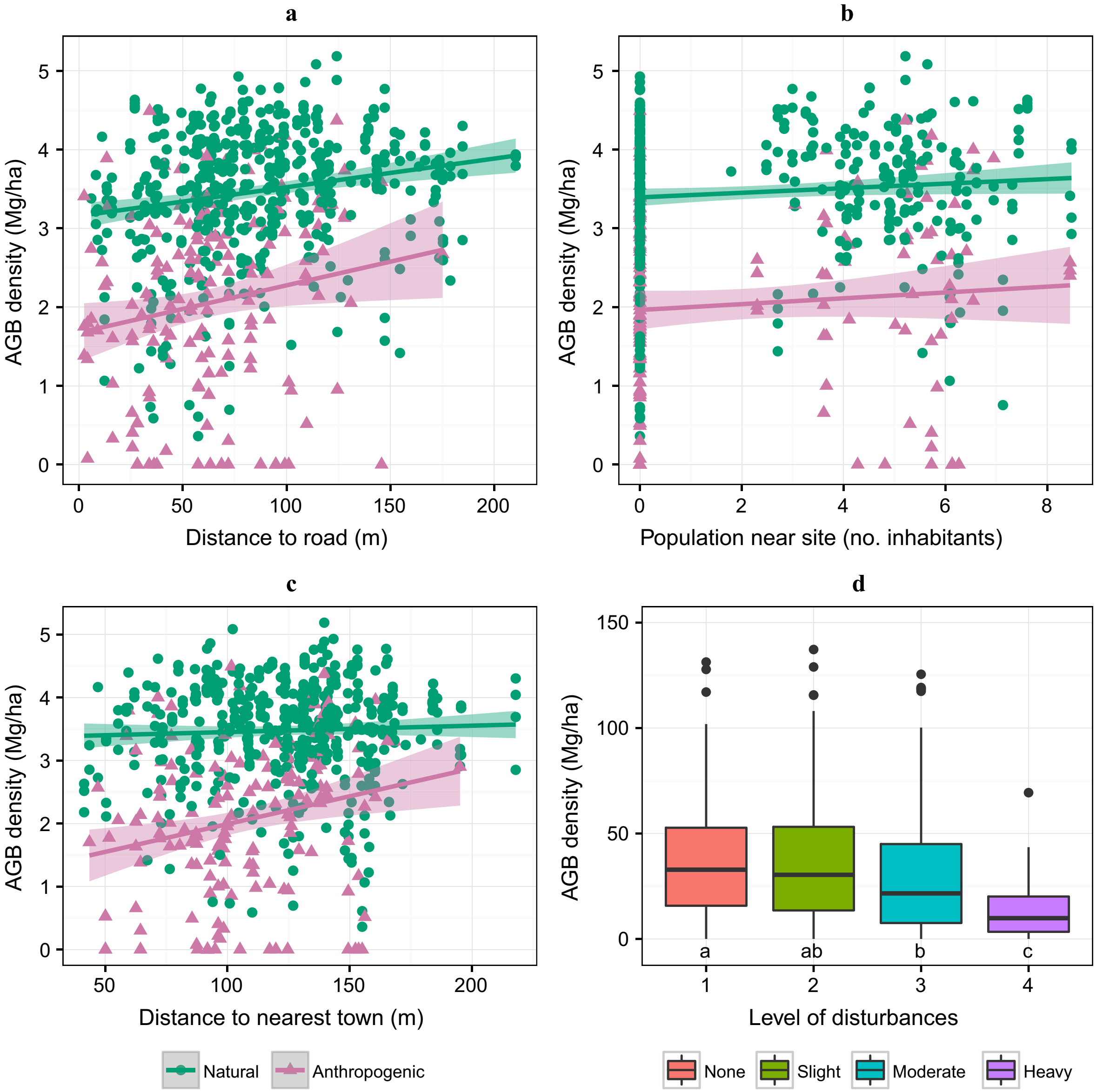

FIG. 4. Human effects on aboveground biomass (AGB) density. (a–c) Scatterplots of AGB square-root or log-transformed data with transformed distance to road, population near site, and distance to nearest town (market) descriptors, respectively, with trend lines and 95% confidence intervals. Green dots show natural sites and pink triangles display anthropogenic sites at the plot level. For panel a, we obtained a significant positive relation between biomass density and distance to road for both natural (R^2 adjusted = 0.0138, P = 0.005) and anthropogenic sites (R^2 adjusted = 0.0247, P = 0.024). For panel b, for population near sites, the relation is slightly significant for natural sites (R^2 adjusted = 0.0241, P = 0.012), but not for anthropogenic sites. When all sites are combined, there is no significant relation between population near sites and AGB density. For panel c with distance to nearest town, there is a significant positive relation for anthropogenic sites (R^2 adjusted = 0.0450, P = 0.003), but not for natural sites. These three variables do not explain well the variation in biomass density. (d) A box plot of AGB density and the level of human disturbances, showing the median, the lower and upper hinges corresponding to the first and third quartiles, the upper and lower whiskers corresponding to 1.5 * interquartile range, and the outlying points. We found a significant difference between groups using ANOVA with permutation test ($F_{3,\ 688}$ = 10.38, P = 0.001), indicating a significant decrease in AGB density with increase in disturbance level. The difference between groups obtained with Tukey HSD pairwise comparison is shown by lowercase letter. [Color figure can be viewed at wileyonlinelibrary.com]

We also looked at the five species contributing the most to total biomass per forest type in the natural plots inventoried (Appendix S1: Fig. S5) and we found *C. mopane* contributed to more than 35% of the biomass in deciduous forests whereas *Pterocarpus angolensis* contributed to more than 25% of the biomass in the evergreen forests (although sample size was small for the latter). *Brachystegia boehmii* and *B. spiciformis* contributed a substantial fraction of the biomass in all three forest types, while *B. spiciformis* and *J. paniculata* both

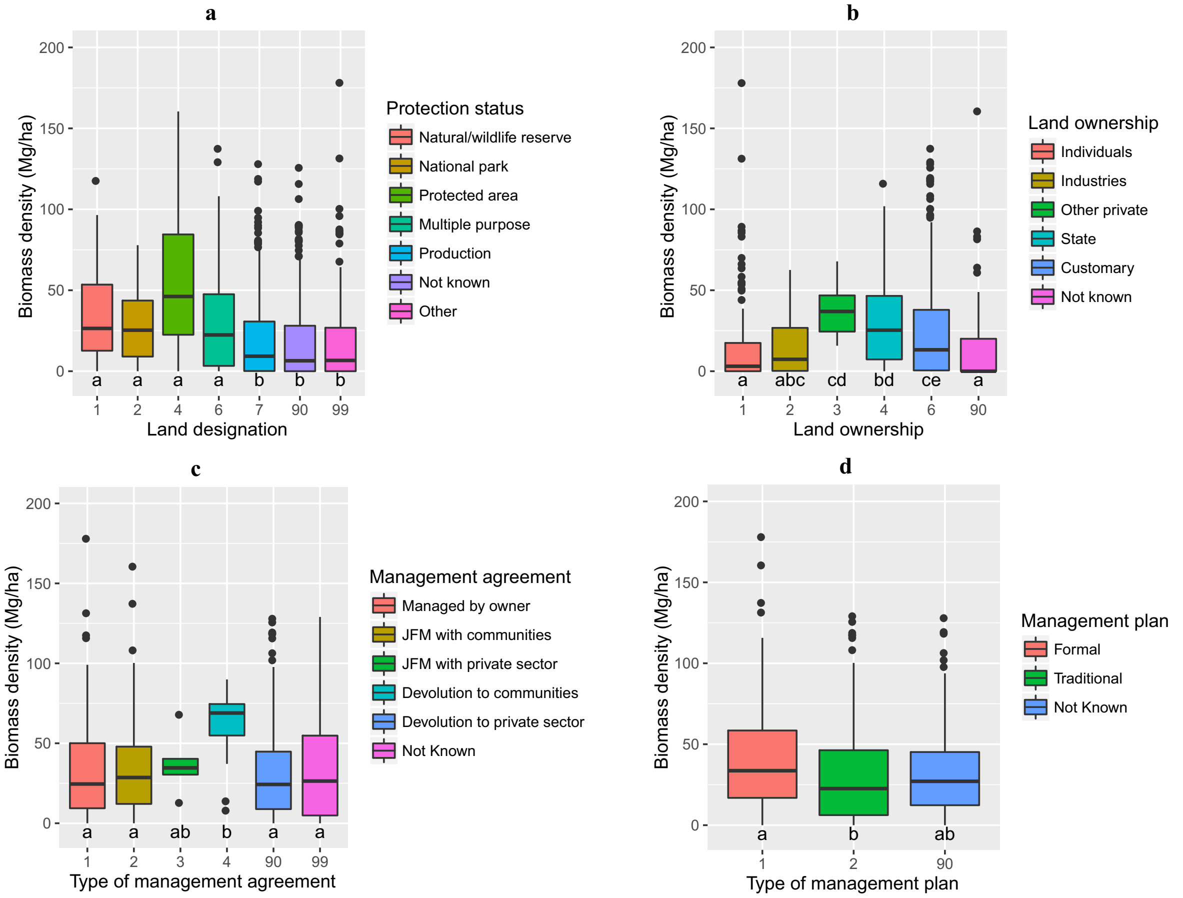

FIG. 5. Box plots of the log-transformed biomass density with (a) land designation ($F_{7,\ 1105} = 10.75$, $P = 0.001$) and (b) land ownership ($F_{6,\ 1111} = 13.69$, $P = 0.001$) for all land use sections as well as with (c) the types of management agreement ($F_{5,\ 715} = 2.36$, $P = 0.048$) and (d) the type of management plan ($F_{2,\ 715} = 5.90$, $P = 0.004$) for forest and other wooded lands. Significant differences in biomass density were found between groups for these four variables using ANOVA with permutation test. The Tukey HSD pairwise comparison results are illustrated below each group. JFM, joint forest management. [Color figure can be viewed at wileyonlinelibrary.com]

represented more than 10% of the total biomass in semi-evergreen Miombo forests.

DISCUSSION

By comparing human and natural forest sites in Zambia across spatial scales, this study brings some fundamental insights into the factors controlling variability in AGB density in this ecoregion, which is representative of eastern and southern Africa tropical dry forest ecosystems. One of our key findings is that variation in tree biomass density is mostly explained by biotic processes related to tree diversity and composition, including stand structure, in both anthropogenic and natural sites. Tree diversity and structure variables explained more of the variation than environment, spatial structure modelled with MEM or even land use variables. The positive association of diversity to biomass density in both human and natural sites demonstrates synergies between biodiversity conservation and climate change mitigation.

The relationship between diversity and ecosystem function has received a great deal of attention as an underlying mechanisms determining tropical forest carbon storage (Balvanera et al. 2005, Poorter et al. 2015). This relationship has been shown to vary between forest biomes (Paquette and Messier 2011), and has not yet been directly explored in the dry tropical forests of Africa at a large scale. We found AGB density was positively correlated with species richness, but negatively with evenness (dominance structure), emphasizing not only the complementarity of these two diversity metrics but also the underlying differences in mechanisms that determine the influence of diversity on biomass density. Two underlying mechanisms have been proposed to generate positive effect of biodiversity on ecosystem functioning, including on biomass density (or carbon storage): the complementarity effect, i.e., through (1) niche partitioning and facilitation and (2) the

Table 3. Correlations of aboveground tree biomass per plot with different stand characteristics for anthropogenic plots and natural forest plots and comparison of the stand-level characteristics between anthropogenic and natural plots using ANOVA with permutation test, with significant difference obtained for all characteristics.

	Correlation of tree biomass per plot with stand characteristics		ANOVA with permutation test between anthropogenic and natural plots		
Characteristic	Anthropogenic plots, $n = 256$	Natural plots, $n = 478$	F	df	P
Richness	0.594	0.434	37.38	1, 732	0.001
Abundance	0.642	0.744	125.45		0.001
Shannon evenness	−0.486	−0.499	90.07		0.001
Simpson evenness	−0.515	−0.484	84.02		0.001
Stand-level mean dbh	0.410	0.286	38.52		0.001
Stand-level mean height	0.658	0.579	127.59		0.001
Stand-level mean wood specific gravity	−0.032*	0.136	6.58		0.006
Dominant tree dbh	0.606	0.504	38.60		0.001
Dominant tree height	0.719	0.575	80.59		0.001
Dominant tree wood specific gravity	0.236	0.314	13.35		0.001
Dominant tree basal area	0.606	0.504	25.56		0.001

Note: The asterisks (*) indicate that the Pearson's product-moment correlations is not significant.

sampling effects, by favoring the selection of certain functional traits (Loreau 1998, Turnbull et al. 2016). Most of the variation in AGB density was explained by stand structure trait-based variables, jointly with diversity measures, highlighting the role of tree species dominance and species composition in determining patterns of tree biomass density. Dominance (or evenness) can directly affect carbon storage via species identity (dominant trait) and evenness (the frequency distribution of those traits), but also indirectly through its effect on species richness (e.g., competition), which, in turn, influences ecosystem processes (Hillebrand et al. 2008). These results are consistent with findings from hyper-diverse humid tropical forest sites, where both richness and dominance are important in explaining variation in tree biomass density (Ruiz-Jaen and Potvin 2010, Cavanaugh et al. 2014).

Many forest ecosystem functions are dominated by a few species (Balvanera et al. 2005). In the Amazonian forest, this phenomenon has been described as hyper-dominance in forest function, including in carbon storage (Fauset et al. 2015). In the case of Zambia's dry forests, different species contributed disproportionately to carbon storage, with *Colophospermum mopane* contributing the most to biomass density in deciduous forests, and *Julbernardia paniculata* and *Brachystegia spiciformis* in semi-evergreen Miombo forests. These defining Miombo tree species have important adaptive features, including extensive root systems with ectomycorrhizal associations that enhance their ability to access limited soil nutrients, as well as high recovery rates following moderate disturbance from early dry season fires (Chidumayo 1993, Frost 1996, Ryan and Williams 2011). A recent study suggests that, because of these characteristics, dominant miombo trees may be suppressing non-dominant species (Shirima et al. 2015). The "selection effect," by which species with these particular traits are favored in comparison with other species without those traits, may therefore be an important mechanism at play in enhancing biomass density in these ecosystems (Hillebrand et al. 2008).

Land use and management were not the driving influences determining the variation in AGB density. This result was surprising since we expected land use to explain a larger share of the variation in biomass density. We identified three factors that may explain these findings. First, the dominant drivers of deforestation and forest degradation reducing AGB density are the slow expansion of subsistence agriculture, and the extraction of wood fuel, timber, and charcoal production (Fisher 2010, Hosonuma et al. 2012). These drivers are likely to leave more residual trees on sites, and so biomass, than mechanized agriculture would. There would therefore be more carbon distributed in the landscape generally, regardless of the land use. Second, AGB density is generally much lower in tropical dry forests than in humid tropical forests, so the differences in AGB density between the sites with or without human intervention is necessarily smaller than in the humid tropical forests. Third, there is evidence that Miombo forests are resilient to some intermediate level of disturbances (Chidumayo 2013, Jew et al. 2016). For example, Miombo woodlands in Tanzania having medium utilization levels retain key Miombo species, and maintain tree species diversity and carbon storage compared to low utilization sites (Jew et al. (2016). In terms of carbon conservation and management, the limited contrast in biomass density between human-modified and natural sites highlights the potential for maintaining carbon in the landscape outside forestland, and for forests to be managed to fulfill multiple purposes.

The impact of land use on biomass density in sites with human land uses appear to be mediated by its influence on tree diversity and stand structure, since a large fraction of the explained variation is shared between diversity and land use variables. Human activities have detectable impacts by reducing biomass density, richness, abundance, and other stand structure characteristics. We also detected a significant difference in biomass density in response to different levels of human disturbances. Our results from species ranking of total percent biomass show similar species composition in anthropogenic sites and natural forest sites, but the contribution to biomass, or biomass dominance, differs between those same species. This similarity in species composition provides insights into the ecological processes acting after anthropogenic disturbance where sites retain the same species instead of switching to a different successional stage. In effect, all tree species of the Miombo have the capacity to resprout by coppicing or by root suckering after logging or fire (Chidumayo 1997, Syampungani et al. 2016). Despite the apparent resiliency of Miombo to different perturbations, species composition does not always recover and may be replaced by secondary species (Williams et al. 2008, Ribeiro et al. 2015) as we also detected when ranking species by the mean percentage contribution to biomass. This change in species composition may or may not affect carbon storage over time.

The disturbance history, including the effect of land use, fire and elephants, is known to affect tree species diversity and carbon storage. Time since disturbance was shown to be an important factor promoting forests structure complexity and diversity in Tanzania (Mwampamba and Schwartz 2011), as well as biomass recovery within two to three decades following farm land abandonment in the tropical dry forests of Mozambique (Williams et al. 2008). Fire control has been identified as crucial to maintaining woody biomass in dry forests and woodlands in a previous study in Zambia (Chidumayo 2013), though we found no significant difference of tree biomass, possibly due to the overwhelming presence of surface fires. More information on site disturbance history, including disturbance frequency and intensity, would be needed to obtain more in-depth understanding of its effects on carbon storage over time.

Overall, environmental controls were more important in natural forests and appear to play a limited role in explaining the AGB density variation at sites where land use and management controls dominate. At natural forest sites, AGB is explained by both diversity factors and environmental drivers including elevation and soil texture. These results are similar to the findings from case studies looking at environmental covariates of tree AGB in the Miombo woodlands in Mozambique (Ryan et al. 2011, Woollen et al. 2012). However, as it has been reported in other studies of African savanna ecosystems (Colgan and Asner 2014) as well as in humid tropical forests (Cavanaugh et al. 2014), environmental controls played a relatively minor role compared to biotic processes (e.g., resulting from competition).

From a management perspective, our results indicate that protected areas in Zambia have higher biomass density than lands that are not under conservation status (Fig. 5a). Similarly, our results indicate that the devolution of forest management directly to communities shows forests with significantly higher biomass density than other types of forest management agreements, followed by JFM agreements with the private sector (Fig. 5c). Consultative processes for REDD+ in Zambia have already identified protected areas and collaborative forest management through JFM as promising avenues for REDD+, though no national study has yet provided clear evidence for success of these approaches in conserving carbon stocks (Kokwe 2012). Our results lend support to these policies as effective means to conserve forest carbon stocks and avoid emissions from deforestation and forest degradation.

In terms of land ownership, our results show that areas of group ownership have higher biomass density than individual or undefined ownership. Undefined ownership is generally undesirable for maintaining forests, but state-owned lands may show similar outcomes when rules for forest access and use are not enforced (Chomitz et al. 2007). Individual ownership can lead to both increases and decreases of carbon stocks depending on the incentives in place. Defining ownership and providing forest conservation incentives to individual landowners can be an important component for maintaining forest carbon stocks, but supporting the creation of cooperatives and other private entities to manage forests appears to also generate positive outcomes.

Our results provide some of the first evidence of the positive relationship of land management and conservation on carbon stocks in Zambia, but spatially explicit evaluation of forest cover change and forest inventory over time with higher sampling intensity for each type of management approach would be needed to establish a firmer basis for policy recommendations. The impacts of ownership and management of carbon stocks need to be considered for a range of different approaches and over time, since conservation areas and collaborative management may have been established in higher AGB density sites. Next-generation nationwide forest inventories will contribute to further evaluation of our results and assessing the success of various policy options.

In conclusion, understanding human and natural controls on variations in AGB density is crucial for orienting and formulating carbon management and conservation policies. Our study explored variations in AGB density for a region of significance in the global carbon cycle, as well as a valuable source of ecosystem services to humanity. We found the variation in AGB density is determined largely by biotic processes, linked to both species richness and dominance, and to a lesser extent, by environmental controls, land use, and underlying spatial structure. The impacts of human activities on AGB density of disturbed or managed sites is not as severe as expected, probably due to trees remaining in the landscape after disturbance, generally lower biomass density in tropical dry forests, and the apparent resilience of these forest ecosystems to some level of utilization. The consequence of human activities on AGB density is largely mediated through its effects on diversity and stand structure characteristics. Additional research on the role of tree functional diversity, as well as disturbance history is needed in these African dry tropical forest ecosystems. More information about the specific human activities that lead to biomass change is also needed to inform forest management policies. Our results highlight the potential for positive outcomes from policies that emphasize forest management for multiple purposes including participatory management and conservation in Africa's dry forest ecosystems, supporting climate change mitigation, ecosystem functions and human livelihoods.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1550/full