Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
Department of Ecology
and Natural Resource Management

Philosophiae Doctor (PhD)
Thesis 2015:53

Forests and woodlands of Tanzania: interactions between woody plant structure, diversity, carbon stocks and soil nutrient heterogeneity

Interaksjoner mellom struktur, diversitet, næringsstoffer i jord og karbonlagring i Tanzaniansk skog

Deo Dominick Shirima

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"We might see some changes in abundance and membership, but not a wholesale reconstruction of regional systems and biotas. That is one reason why disparity matters; all else equal the more disparate the biota, the greater its standing morphological-phenotypic variation, the more resilient it will be in the face of change" (Maclaurin and Sterelny 2008)

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TABLE OF CONTENTS

ABSTRACT

In recent years, structural components such as woody species richness, diversity, canopies and non-woody lifeforms in tropical forests and woodlands have experienced increasing rates of degradation and deforestation due to agricultural expansion and other land use changes. The decline in plant species diversity in forests and woodlands has negative effects on ecosystem processes and functions such as atmospheric carbon sequestration and mitigations of global climate changes. However, our knowledge on how varieties of structural components interacts with physiographic conditions and anthropogenic disturbances to influence ecosystem processes are limited. This knowledge gap has consequently undermined our understanding of the potential contributions of structural components in enhancing human wellbeing. This thesis consist of series of studies from a moist forest and miombo woodlands in Tanzania. The main aim was to relate structural components, such as tree species richness, canopy, carbon stocks and their interactions, with physiographic conditions, and anthropogenic disturbances. I explore (1) how do tree species richness relates to vertical heterogeneity, mean and depth specific soil nutrient availability. (2) do dominant tree species influence the richness, diversity, evenness and vertical structure heterogeneity of non-dominant tree species? (3) how do tree canopy characteristics relates to herbaceous biomass and tree species richness? (4) how do the aboveground carbon stocks of trees relate to tree species richness, diversity and evenness along gradients of physiographic conditions and anthropogenic disturbances? Using data from vegetation and soil surveys in a series of regression analyses, I showed that variation in tree species richness were better explained by mean than vertical heterogeneity in soil nutrient availability in moist forest, while in miombo woodlands, vertical heterogeneity explained a large part of the variations in tree species richness than mean soil nutrient availability. Non-dominant tree species richness, Shannon diversity and evenness had negative linear and non-linear relationships with the relative abundance of dominant tree species in wet and dry miombo woodlands. Moreover, tree species structure, physiographic conditions and anthropogenic disturbances explained over 50 % of the variations in leaf area index (LAI) and nearly 20 % of the variations in aboveground herbaceous biomass (AGB_H) in moist forest and miombo woodlands. Furthermore, aboveground carbon stocks of trees were unimodal, positive or negative linearly related to tree species richness, evenness and abiotic factors in the two vegetation types.

The relationships between structural components, physiographic conditions and anthropogenic disturbances has consequences on ecosystem properties such as carbon storage and sequestration, and biodiversity. Understanding of how structural components interact with environmental conditions and anthropogenic disturbances is a step towards establishing the potential contributions of forest and woodlands to local livelihoods. Thus, management of forests and woodlands in Tanzania require strategies that maintains the existing structural complexity.

LIST OF PAPERS

Paper I

Shirima, D. D., Totland, Ø., Moe, S. R. **Tree species richness in tropical forests and woodlands: The relative importance of vertical soil nutrient heterogeneity, mean and depth-specific soil nutrient availability.** *Submitted*

Paper II

Shirima, D. D., Totland, Ø., Munishi, P. K. T., Moe, S. R.(2015) **Does the abundance of dominant trees affect diversity of a widespread tropical woodland ecosystem in Tanzania?** Journal of Tropical Ecology 31, pp 345-359. doi: 10.1017/S0266467415000231.

Paper III

Shirima, D. D., Pfeifer, M., Platts, P. J., Totland, Ø., Moe, S. R. **Interactions between canopy structure and herbaceous biomass along environmental gradients in moist forests and dry woodlands of Tanzania**. *Submitted.*

Paper IV

Shirima, D. D., Totland, Ø., Munishi, P. K. T., Moe, S. R. (2015). **Relationships between tree species richness, evenness and aboveground carbon storage in montane forests and miombo woodlands of Tanzania**. *Journal of Basic and Applied Ecology, 16: 239–249. doi:10.1016/j.baae.2014.11.008*

Synopsis

1.0 INTRODUCTION

The structure of forests and woodlands is characterized by a heterogeneous mixture of patches at different stages of recovery from disturbances and gap replacements (Shugart et al. 2010). According to Zenner (2004) structural components include attributes such as tree species identities, sizes, canopy, dead trees, coarse debris and the interrelations among these attributes, without considering their spatial arrangements in forests. Structural complexity includes structural components, the relationships among their attributes while considering their spatial arrangements in forests (Zenner 2004, McElhinny et al. 2005). Structural components can also be used to express ecosystem processes such as nutrient cycling (Spies 1998, McElhinny et al. 2005). For example, tree canopies, can influence local-climatic conditions in forests, and in turn affect other structural attributes, such as herbaceous plant diversity and their aboveground biomass production (Moore 2009). The distribution of individual structural attributes within and across forest ecosystems is driven by environmental conditions and anthropogenic disturbances (Varga et al. 2005).

The structural components of tropical forests and woodlands are experiencing high rates of degradation due to anthropogenic activities (Bunker et al. 2005, Strassburg et al. 2010), leading to losses of biodiversity (Sala et al. 2000, Barlow et al. 2007) and increase in atmospheric carbon emissions (Gibbs et al. 2007, Ciais et al. 2011). For example, African forest and woodland ecosystems varies from carbon sinks of about 3.2 Pg C yr^{-1} to small sources (i.e. from agriculture and other land use changes) of about 0.44 Pg C yr^{-1} (Ciais et al. 2011). Forest and woodlands in Africa represents more than 30 % of the global forest cover (Malhi et al. 2013), and although woodlands and savannas account for lower carbon storage than forests, they cover an area three times larger than forests (Ciais et al. 2011). Woodlands and savannas in Africa accounts for about 65 % (range: 2.7-3.2 million km^2) of the land-surface (Thomas and Packham 2007). However, over 40% of the growing human population in African countries rely on woodlands and savannas for their livelihoods (Mwampamba 2007, Chidumayo and Gumbo 2010, Bromhead 2012). Charcoal production and agricultural expansion are estimated to contribute about 20-25 % of woodland degradation in Africa (Chidumayo and Gumbo 2010). It is projected that the demand for household fuel-wood in sub-Saharan countries may increase by 20 % from 2010 to 2030 (Bromhead 2012). In Tanzania, about 60-80 % of the energy used by the growing urban population are wood-based, such as charcoal, which are mostly supplied from miombo woodlands (Mwampamba 2007). Electricity covers only 30–40 % of the urban energy supply (Kihwele et al. 2012). Thus, anthropogenic disturbances are the main drivers of changes in ecosystem structure, productivity and carbon balance in Africa (Ciais et al. 2011).

A diverse structure implies an increase in resource heterogeneity and is often associated with high biodiversity in forest and woodland ecosystems (McElhinny et al. 2005). Thus, forests and woodlands with a high plant diversity will use resources more efficiently and thereby may enhance the long-term carbon sequestration and storage, and nutrients cycling (Tilman 1997, Cardinale et al. 2007). Over the last few years, forest management has been geared towards accurate measurements, monitoring, reporting and verification of carbon stocks (DeFries et al. 2006). However, one of the challenges is to unveil the complex links between stand structural components and ecosystem functions (Naeem et al. 2009). This is because structural component assessment at stand scale can be used to inform management actions, such as harvesting or recreations i.e. scenic beauty (McElhinny et al. 2005). There has been a global demand for new sustainable ways to manage and finances ecosystem products and services. Thus, market based initiatives such the clean development mechanisms (CDM), reduced emissions from deforestation and forest degradation plus conservation and carbon stocks enhancement (REDD+), have emerged (Ebeling and Yasue 2008). There are hopes that if well-structured, these initiatives may yield tangible and sustainable benefits to local livelihoods from forest and woodland biodiversity and at same time positively affect global climate (Strassburg et al. 2010). There is also potentials to promote restorations of biological diversity in already degraded terrestrial ecosystems through the REDD+ initiatives if well implemented (Phelps et al. 2012).

One motivation for the REDD+ is to obtain accurate forest carbon stock data at minimum costs, for monitoring and decision making at local scale, to safeguard forest access rights, and to improve the involvement of local people in decision-making (Fry 2011, Skutsch 2012). However, most of the REDD+ readiness programs in developing countries (Danielsen et al. 2011), do not, or have little considerations of the entire structural components and their interactions with environmental conditions and anthropogenic disturbances. For example, REDD+ pilot studies in Tanzania were geared towards generating baselines data. However, in addition to financial and technical constrains (Burgess et al. 2010, Sills et al. 2013), there is a low ability to link carbon measurements to other forest structural components, their environmental conditions and anthropogenic disturbances. This has raised concern that there will be negative environmental consequences if the entire structural components are not well address in the REDD+ process (Dickson and Kapos 2012, Gardner et al. 2012, Phelps et al. 2012). It is crucial that accurate baseline data on structural components, such as species diversity (Gardner et al. 2012) and their interactions with the environment, are part of the baselines for references emission levels, in order for REDD+ to be successful. Failure to account for various forest structural complexities and their interactions with physiographic conditions and anthropogenic disturbances may jeopardize future sustainable flow of goods and services. It also undermines the realization of the potential contributions of biodiversity in enhancing human wellbeing (Naeem et al. 2009).

The aim this study was to explore the existing relationships between tree species diversity, richness and evenness, aboveground carbon stocks and canopy foliage characteristics along gradients of physiographic conditions and anthropogenic disturbances in two vegetation types of Tanzania. The four major question addressed in this study were: (1) how do tree species richness relates to vertical heterogeneity, mean and depth specific soil nutrient availability? (2) do dominant tree species influence the richness, diversity, evenness and vertical structure heterogeneity of non-dominant tree species? (3) how do tree canopy characteristics relates to herbaceous biomass and tree species diversity? (4) how do the aboveground carbon stocks of trees relate to tree species richness, diversity and evenness along gradients of physiographic conditions and anthropogenic disturbances?

The specific objectives of this study were:

1. To explore the relationships between tree species richness and vertical heterogeneity, mean and depth specific soil nutrient availability in moist forest and miombo woodlands of Tanzania (**Paper I**).
2. To explore the relationships between the abundance of dominant tree species and richness, diversity, evenness, and vertical structure heterogeneity of non-dominant tree species in wet and dry miombo woodlands of Tanzania (**Paper II**).
3. To examine the relationships between canopy characteristics, herbaceous biomass, tree species diversity and environmental gradients in moist forest and miombo woodlands of Tanzania (**Paper III**).
4. To examine the relationships between aboveground carbon stocks of trees and tree species richness, diversity and evenness along gradients of physiographic conditions and anthropogenic disturbances in moist forest and miombo woodlands of Tanzania (**Paper IV**).

2.0 MATERIALS AND METHODS

2.1 Study area

This study was carried out in a moist forest and in miombo woodlands, which are the major vegetation types in Tanzania (Figure 1, Plate 1). Permanent vegetation plots were established in the Hanang moist forest in the Hanang district and in miombo woodlands in the Kilombero, Kilolo, Mufindi, Iringa rural, Mbeya rural, Mbozi and Chunya districts of Tanzania. These districts were selected to represent a wide range of climatic and topographic gradients in miombo woodlands.

Forests are land areas (> 0.5 ha), mostly formed by trees (> 5 m height), and with canopy density of at least 10 %, while woodlands occurs in relatively small areas with trees of at most 40 % canopy density (Thomas and Packham 2007, FAO 2015). Miombo woodlands are the most extensive vegetation type, and cover more than 90 % of the forested land in Tanzania (URT 1998). They occur in a wide range of tropical and subtropical local climates, are classified as wet or dry based on a 1000 mm annual rainfall threshold (White 1983, Frost 1996), and are strongly influenced by frequent fires and anthropogenic activities (Campbell et al. 1996, Furley et al. 2008). In the selected districts miombo woodlands spans an elevation range of 25-2000 m, a temperature range of 16-30 °C, and a rainfall range of 650-1400 mm (Frost 1996, Platts et al. 2014). Similar to other parts of East and Southern Africa (Thomas and Packham 2007), they are dominated by the genera *Brachystegia* and *Julbernadia,* and characterized by a low soil nutrient contents, well-drained and highly leached soils (Jeffers and Boaler 1966).

The Hanang moist forest is located in the Hanang district and spans an elevation range of 1860-3418 m, and the vegetation is dominated by species within the genera *Abizia, Cassipourea, Hygenia, Prunus, Cussonia, Olea* and *Vernonia* (Lovett and Pocs 1993). It is characterized by humus-rich loam and volcanic rock soils, and receives a mean annual rainfall range of 750-2000 mm and has a mean annual temperature range of 16-25 °C (Lovett and Pocs 1993, Platts et al. 2014).

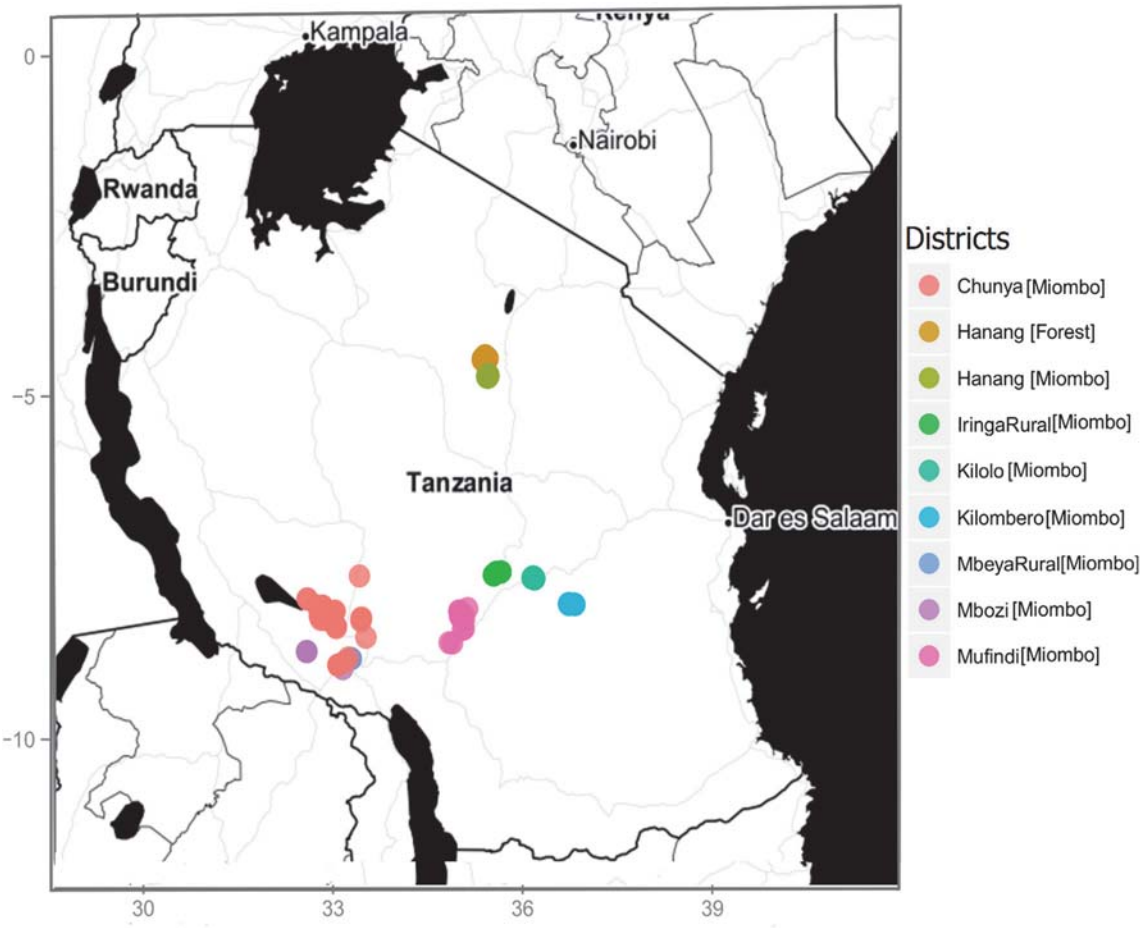

Figure 1. Location of the study areas in Tanzania.

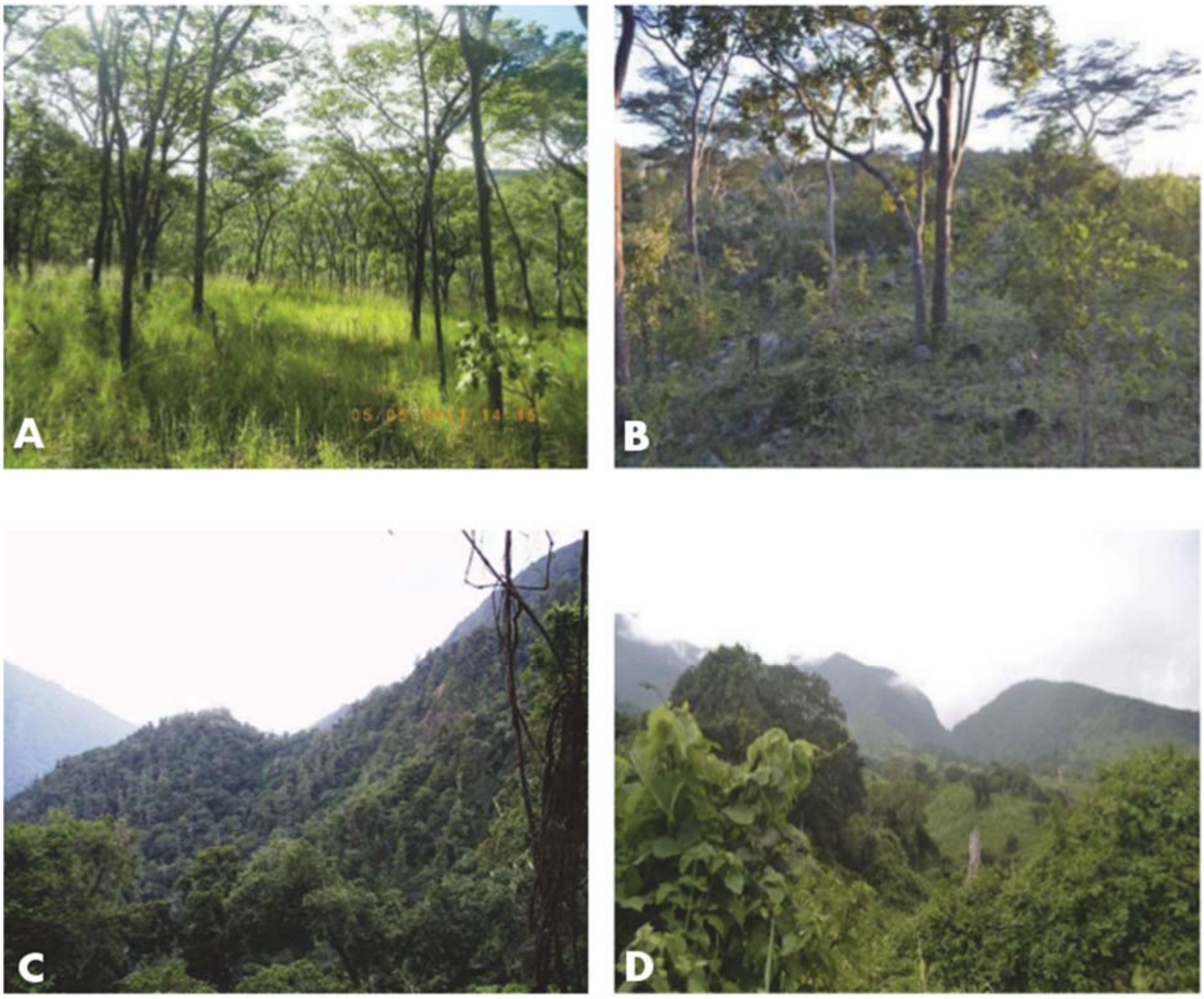

Plate 1. The two main vegetation types in Tanzania: Miombo woodlands with minimum anthropogenic disturbances (A), relatively high anthropogenic disturbances (B), moist forest with minimum anthropogenic disturbances (C), and relatively high anthropogenic disturbances (D). All photos were taken during the wet season. *Photos: Deo Shirima*

2.2 Data collection

2.2.1 Vegetation survey

In the vegetation survey, plots (Figure 2) of 20 m × 40 m were established in miombo woodlands (n=162) and moist forest (n=60). Plots were positioned along elevation (100-3000 m) gradients at a minimum distance of 400 m apart. The first plot was established haphazardly at least 20 m away from any entrance path or forest edge. Subsequent plots were systematically spaced between 0.4 to 1 km apart from the first plot to minimize spatial autocorrelation in floristic composition, biomass and environmental condition. If a plot occurred on a treeless site (e.g. due to agriculture or selective harvesting), a nearby tree-covered site was randomly selected. A hand held GPS (Map76cx) was used to record the geographical location and elevation of each plot.

In each plot, all tree diameter at breast height (dbh ≥5 cm) were recorded. Tree heights were measured using a measuring rod and suunto-hypsometer, otherwise, tree heights for unmeasured trees were obtained by regressing dbh against the previously measured heights (Mugasha et al. 2013). Tree species identities were recorded in the field, otherwise voucher specimens were collected and identified at Tanzania National Herbarium. Tree stumps were recorded and distances (km) from the nearest roads or settlement to each plot were estimated to account for anthropogenic disturbances (Baas et al. 2011). Wood cores used in estimating tree species biomass were collected from dominant tree species using standard procedures (Williamson and Wiemann 2010).

Aboveground herbaceous plant material (clipped at ground level) and litter material were collected from five quadrats (1 × 1 m), and tree seedlings (trees below 1.3 m height) were counted in four quadrats (2 × 2 m), nested at random within eight (10 m × 10 m) alternate subplots (Figure 2). The total fresh weight of herbaceous and litter samples were recorded in the field, subsampled from the total fresh weights, and were later oven-dried in the laboratory to a constant weight at 70 ºC for 48 h to obtain dry mass. Dry mass from each subplot was aggregated into dry mass per plot.

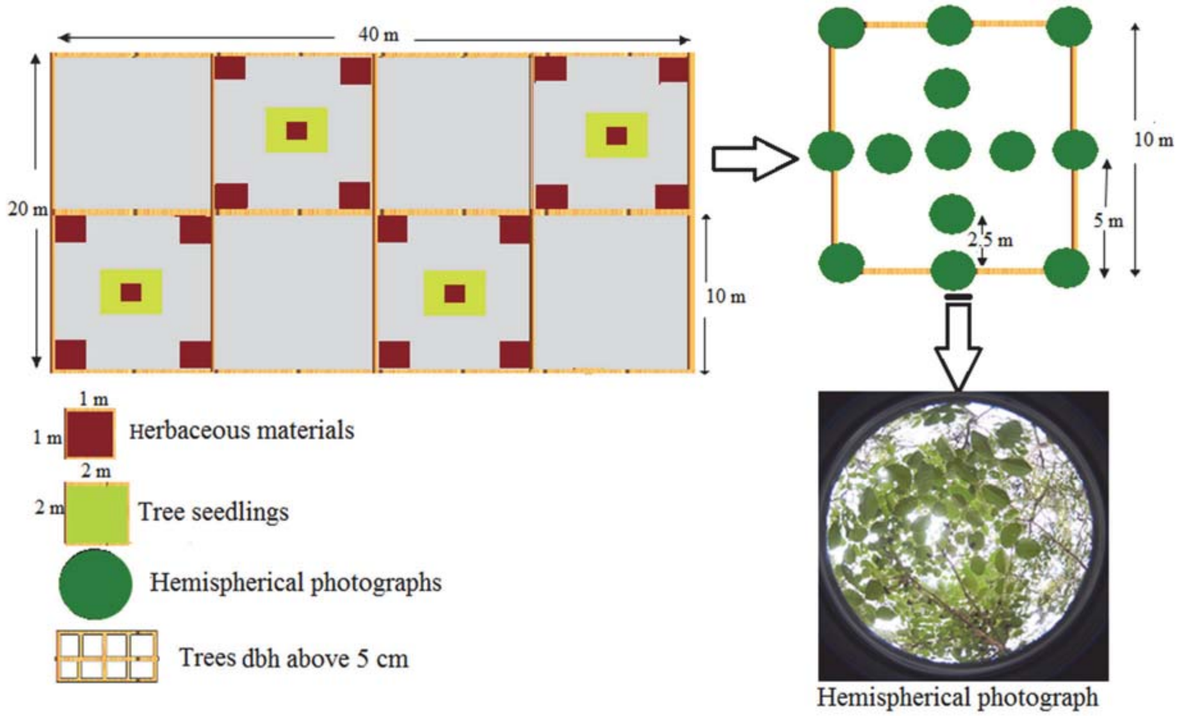

Figure 2. A sketch of a sample plot design used in the moist forest and miombo woodlands of Tanzania.

2.2.2 Soil survey

Soil surveys were carried out between May 2011 and March 2012, at the same time when the vegetation was surveyed. Soil samples were collected at 0–15 cm, 15–30 cm and 30–60 cm depths, from the four corners, at the plot centre, and later aggregated into three depth-specific composite samples. Samples were analysed at Seliani Agricultural Research Institute, Arusha, Tanzania. In the laboratory, all samples were air dried and sieved through a 2 mm wire mesh and subsequently analysed for soil pH (at 1:2.5 soil:H_2O), percentage organic carbon (Walkley-Black method), available phosphorous (Bray II), total nitrogen (Kjeldahl method), potassium, calcium and magnesium (ammonium acetate 1.0 M pH7.0 extraction). Soil particles were classified into clay (< 2 µm), silt (2 to 20 µm), fine sand (20 to 50 µm) and coarse sand (50 µm to 2000 µm), (Brady and Weil 1999, Fullen and Catt 2004).

2.2.3 Hemispherical photography

Hemispherical photographs were taken in all plots during wet season in March 2012 (Figure 2). Tree canopy characteristics were estimated by leaf area index (LAI) using standardized protocols as described in Pfeifer et al. (2012) and Pfeifer and Gonsamo (2014). A total of 13 hemispherical photographs were taken in each of the four systematically selected subplots (10 m × 10 m) using a Nikon D3100 camera with a fish-eye lens, mounted on a 1 m tripod stand (Figure 2). Images were processed using CAN-EYE software version 6.38 (Weiss and Baret 2014), which estimates plant area index (PAI; as opposed to LAI), since stems, branches and twigs are included in the images (Breda 2003). However, because there are high uncertainties in extracting actual LAI from PAI (Hardwick et al. 2015), we used the term LAI to represent PAI as it has been applied and described in previous studies (Pfeifer et al. 2012, Pfeifer and Gonsamo 2014). Values of LAI from the four subplots were averaged into a single mean value per plot for subsequent analysis.

2.3 Derived variables

Tree species richness were defined as the total number of tree species observed in a plot, and stem density as the number of individual tree stems (dbh ≥ 5 cm) in a plot per hectare. Tree species evenness (J) and diversity (H′) were estimated using Pielous's index (Pielou 1969) and Shannon diversity index, respectively (Shannon 1949).

In **Paper I**, the coefficients of variations in soil nutrient availability from three soil depth layers were determined and used as a measure of vertical heterogeneity in soil nutrient availability (Baer et al. 2005, Holl et al. 2013). The mean soil nutrient availability was calculated using the arithmetic mean of soil nutrient availability from the three-soil depth layers in each plot.

In **Paper II,** tree species rarefaction and richness estimates were determined using Mao Tau rarefaction, and Chao 2 estimator in EstimateS 8.2.0 (Colwell et al. 2012) to account for the differences in sampling efforts between wet and dry miombo woodlands, because species richness is sensitive to sample size (Chao et al. 2013). Two hierarchical species groups; named dominants and non-dominants, were obtained by grouping species based on their relative abundance of species basal area (Grime 1998). Tree species were ranked by their relative basal area abundances and their cumulative abundances in ascending order. Then, a tree species was grouped arbitrary as dominant if its relative basal area abundance was greater than 50% and its cumulative relative abundance was over 70%, and all other species as non-dominants (Grime 1998, Mariotte et al. 2013). Vertical structure heterogeneity was estimated from the non-dominants tree species as a measure of how tree species are related to stem heights, using the species profile index (H_{sp}), (Pretzsch 1996, Lei et al. 2009).

In **Paper III,** tree canopies and the herbaceous layers were characterized using LAI and aboveground herbaceous biomass (AGB_H), respectively. The stand size structures were characterized by the quadratic mean diameter (QMD) and the predominant height (PDH). The quadratic mean diameter (QMD) was estimated in each plot, and was preferred over the arithmetic mean diameter because it is strongly related to stand volume and basal area (Van Laar and Akça 2007). The predominant height (PDH) was estimated as an average height of the 100 tallest trees per hectare, based on a selection of single tallest trees in each subplot in the forest and woodlands (West and West 2009).

In **Paper IV**, aboveground live tree species biomass was estimated using two allometric equations, one for the moist forest and another for the miombo woodlands (Chave et al. 2005). Total aboveground carbon stock (AGC per hectare) at plot level was estimated as 50 % of the total aboveground live tree species biomass aggregates in a plot.

2.4 Statistical analyses

A variety of univariate statistical analyses techniques were used to explore patterns and relationships among tree species richness, evenness, carbon stocks, physiographic conditions and anthropogenic disturbances in the two vegetation types. Where data exploration indicated nonlinear relationships between a response and a predictor, the predictor was fitted using quadratic term (**Paper I-IV**). All predictor variables were checked for correlation and multcolinearity using VIF ≤ 8.0 (Zuur et al. 2010) and Pearson correlation (r ≤ 70 %) as cut-off points for the subsequent regression analysis (**Paper I-IV**, Dormann et al. 2013). Moreover, where data exploratory indicated high heteroscedasticity, all continuous predictor variables were checked for skewness and corrected accordingly to approximately zero skewness (Økland et al. 2001). Continuous predictor variables were scaled where necessary to improve the interpretability of the regression coefficients (**Paper I – IV**, Schielzeth 2010).

Generalized least square regression models (gls) were fitted to explore; (1) the relationships between tree species richness and vertical heterogeneity (VH), mean (M) and depth specific soil nutrient availability in moist forest and miombo woodlands (**Paper I**), (2) the relationships between tree species richness, Shannon diversity, evenness, species profile index, and relative abundance of the dominant tree species and anthropogenic disturbances in miombo woodlands (**Paper II**), (3) the relationships between AGC and tree species richness, evenness, soil nutrient availability, topographic condition and anthropogenic disturbances (**Paper IV**) in moist forest and miombo woodlands. Furthermore, generalized linear models (GLM) with Gaussian distribution error and identity link function (Zuur et al. 2009) were used to explore the relationships between LAI, AGB_H and stand structural attributes such as tree sizes and richness along with soil nutrient availability, topographic conditions and anthropogenic disturbances (**Paper III**) in moist forest and miombo woodlands.

3.0 RESULTS AND DISCUSSIONS

3.1 Thesis overview

This thesis demonstrates the relationships between structural components, physiographic conditions and anthropogenic disturbances in forest and woodlands of Tanzania. The study shows that interactions between stand structural components, physiographic conditions and anthropogenic disturbances play major roles in maintaining key ecosystem processes in forests and woodlands (Chapin et al. 2002). Heterogeneous environmental conditions promotes the structural complexity in forests and woodlands and facilitate plant species coexistence, because of functional differences between coexisting species and increasing efficiency in resource utilization (Cardinale et al. 2007, Diaz et al. 2009). Overall, tree species richness was negatively related to vertical heterogeneity, mean, and depth-specific soil nutrient availability in the moist forest and miombo woodlands (**Paper I**). Furthermore, variation in tree species richness was largely explained by mean soil nutrient availability in the moist forest, and by vertical soil nutrient heterogeneity in miombo woodlands (**Paper I**).

Increased resource availability in plant communities may result in increase in aboveground biomass of dominating species, causing a decline in plant species richness (Pretzsch 1998, Creed et al. 2009). Tree species richness, Shannon diversity, evenness and height profile index of the non-dominants had negative relationships with the relative abundance of the dominant tree species in wet and dry miombo woodlands (**Paper II**). Forest canopy is of great significance because of its ability to influence local-climatic conditions and in turn affecting other structural components, such as herbaceous plant growth (Moore 2009). A high tree species richness increases the use of canopy space, and may optimize the capture of incoming light, which will enhance forest productivity (**Paper III**). The relationships between tree species richness, evenness and tree carbon stocks in forest and woodland stands depends partly on the stem sizes, physiographic conditions and anthropogenic disturbances (Strassburg et al. 2010). Aboveground carbon stocks had a unimodal pattern with tree species richness and diversity in moist forest and miombo woodlands, and a negative association with tree species evenness in miombo woodlands (**Paper IV**).

There were varying and complex patterns in the relationships between structural components, physiographic conditions and anthropogenic disturbances (**Paper I-IV**). It appears that vertical heterogeneity, mean and depth specific soil nutrient availability and tree species abundance can affect tree species richness, while tree species richness may affect forest canopy characteristics, aboveground tree carbon storage and herbaceous biomass. However, anthropogenic disturbances and topographic conditions affect tree species richness, canopy characteristics, aboveground tree carbon storage and herbaceous biomass simultaneously. This suggests that there is high structural complexity in the moist forest and miombo woodlands, which if well understood and properly managed, will provide long-term ecosystem goods and services to local livelihoods. Thus, stand-based assessments of structural components and their links to ecosystem processes and functions is required for successful management of forest and miombo woodlands.

3.2 Tree species richness and soil nutrient availability

Soil nutrient availability vary vertically and horizontally across space in forest landscapes, and this variation may have profound effects on plant species establishment, their biomass productions, and community composition (Huston 1979, Maestre et al. 2006, Lundholm 2009). Moreover, previous studies suggest that plant species richness is governed by the spatial heterogeneity of the most limiting resources, such as soil nutrient availability and light (Tilman and Pacala 1993, Stevens and Carson 2002, Musila et al. 2005, Reynolds et al. 2007). Results from the moist forest support the argument that tree species richness are more related to soil nutrient quantities than soil nutrient heterogeneity (**Paper I**, Table 2 & Figure 2), perhaps due to a prevailing limitations on other resources such as light availability (Lundholm 2009, Holl et al. 2013). Similarly, Huston (1980), observed high tree species richness in plots with low mean potassium and sodium in a moist forest in Costa Rica. In miombo woodlands, on the other hand, vertical heterogeneity in soil nutrient availability explained a large portion of the variation in tree species richness (**Paper I**, Table 2 & Figure 2). The strong interactions between grasses and trees in regularly disturbed miombo woodlands may have contributed to a large vertical heterogeneity in soil nutrient availability, which in turn will have a stronger influence on tree species establishment and subsequent recruitment patterns and diversity at later stages. Elsewhere, in tallgrass prairie ecosystems, small scale vertical soil nutrient heterogeneity has positive effect on plant species richness (Williams and Houseman 2014).

The results also show that soil nutrient availability in the top soil explained a larger part of the variation in tree species richness than nutrient availability in the deeper soil layer in the two vegetation types (**Paper I**, Table 3 & Figure 3). Perhaps because most of the essential soil nutrients for plant growth occur in the top soils (Jobbágy and Jackson 2001). Similar to results in **Paper I**, previous studies have shown that there are more negative than positive relationships between plant species richness and soil nutrient availability in tropical forest (Huston 1980). According to Huston (1994), forest of high species diversity are often found in areas with low soil nutrient availability. Moreover, similar to results in **Paper I**, a positive relationship between tree species richness, and magnesium have been reported in Borneo forest (Ashton 1989). Nevertheless, according to Perroni-Ventura et al. (2006) the nature of the relationships between plant species richness and soil nutrients depends on the amount of available soil nutrient and local environment conditions. Thus, the associations between tree species richness and vertical heterogeneity or mean soil nutrient availability would vary, depending on soil nutrient availability, environmental conditions and ecosystem types.

3.3 Non-abundant and relative abundance of dominants woody species

Dominant plant species can influence the environmental conditions experienced by other species, and stabilize fundamental ecosystems processes, such as carbon cycling, and energy and water flow in the entire ecosystems (Martin and Goebel 2013). Biotic and abiotic interactions shape not only plant species composition, but also their spatial and temporal distribution within ecosystems (Magurran and McGill 2011, Wisz et al. 2013). Results show that tree species richness, Shannon diversity, and evenness of non-dominant species had negative relationships with the relative abundance of dominant tree species in wet and dry miombo woodlands (**Paper II**, Figures 5 & 6). These results suggest that dominant tree species may control a large proportion of the resources available in the ecosystem, and in turn suppress the establishment and abundance of non-dominant species (Creed et al. 2009). Plant species with dominating traits, such as prolonged root systems and mycorrhiza associations may have a strong influence on other species, due their ability to control limiting resources and accumulate a high biomass (Bengtsson et al. 1994). Similarly, a previous study in a temperate forests showed that eastern hemlock had a significant negative effect on plant species richness (Martin and Goebel 2013). There were many stems in the low diameter classes of both non-dominant and dominant tree species (**Paper II**, Figure 4), which may suggest intensive competition for space and soil nutrients between dominant and non-dominants during regeneration stages. Dominant miombo tree species are adapted to disturbances, low nutrient availability and can re-sprout from stems and root suckers, which provide them with a competitive advantage over other tree species (Backéus et al. 2006, Furley et al. 2008, Chidumayo 2013).

The non-linear patterns between Shannon diversity, evenness and the relative abundance of the dominant tree species, and the interactions between relative abundance of the dominant tree species and stump counts (**Paper II**, Figure 6 a & b), shows that anthropogenic disturbances can influence tree species diversity and evenness (Connell 1978, Frost 1996, Dewees et al. 2010). There was a strong negative relationship between the tree species profile index and the relative abundance of the dominant tree species (**Paper II**, Figures 6c & d), which indicates that dominant tree species are occupying the upper canopy stratum (Pretzsch 1998). These results suggest that dominant tree species suppress non-dominant tree species. Furthermore, similar to previous studies from miombo woodlands (Frost 1996, Dewees et al. 2010), the results show that the influence of anthropogenic disturbance on tree species diversity varies across landscapes.

3.4 Tree canopies, species richness, herbaceous biomass and abiotic factors

Tree canopies can influence forest micro-climatic conditions, and may also suppress herbaceous plant growth (Moore 2009). Results show that stand structural attributes, topography and anthropogenic disturbance explained over 50 % of the variation in LAI and nearly 20 % of variation in aboveground herbaceous biomass (AGB_H), in both vegetation types (**Paper III**, Table 3). These results suggest that tree species morphological and physiological adaptations to the environmental conditions in forest and woodlands are important for allowing co-existence among plant species of different life forms (Gilliam and Roberts 2003). Leaf area index increased with tree richness in both vegetation types and with tree stem density in miombo woodlands (**Paper III**, Table 3), suggesting that tree species diversity may promote complementarity in resource use among species (Unger et al. 2013). Similarly, a positive relationship between LAI and tree species diversity has been reported in a tropical montane forest in North Eastern Ecuador (Unger et al. 2013) and in grassland ecosystems of the north-west Switzerland (Spehn et al. 2000). According to Reich (2012), the ability of tree species to intercept light, exchange gasses with the atmosphere, and their leaf photosynthetic chemistry is strongly linked to tree canopy characteristics. Moreover, tree canopies may trap essential nutrients for plant growth from atmospheric dust, smoke particles, and release them into the soils through stem flow in forests and woodlands (Das et al. 2011).

Moreover, the results show that AGB$_H$ in the moist forest decreases with tree species richness, whilst LAI increases with tree richness (**Paper III**, Tables 2 & 3), suggesting that tree richness suppresses AGB$_H$ by increasing canopy density and thereby reducing light availability at the forest floor, which in turn limits herbaceous plant growth. Studies from woodland savanna have found that herbaceous plant cover varies, depending on the density of the tree canopy (Jeltsch et al. 1996, Kahi et al. 2009). However, the influence of forest canopies on herbaceous plant growth varies across landscapes, depending on the intensity of anthropogenic disturbances such as fire and selective harvesting and environmental conditions such as rainfall and soil nutrients (Scholes and Archer 1997, Baudena et al. 2010). Nevertheless, a forest stand with many tree species may optimize light capture due to differences in tree canopies, leading to increased forest aboveground biomass production. Thus, to enhance our understanding of forest and woodlands ecosystem processes, it is important to consider both stand structural attributes and their interactions with environmental conditions and anthropogenic disturbances.

3.5 Aboveground live trees carbon stocks and tree species diversity

Tree carbon stocks plays a major role in the carbon cycle as a key property of ecosystem functioning in forests and woodlands, and has a large influence on ecosystem goods and services (Chapin et al. 2002, Dıaz 2009). Results from this study show that the aboveground live trees carbon stocks (AGC) has a unimodal relationships with tree species richness and evenness, with a strong effect size from tree species evenness in moist forest (**Paper IV**, Figures 3 & 5). These results suggest that in diverse plant communities, individuals optimize resource use through niche partitioning (Cardinale et al. 2009, Diaz et al. 2009). Previous studies have also reported a unimodal patterns between plant species richness and biomass in herbaceous and grassland ecosystems (Gross et al. 2000, Bhattarai et al. 2004, Fraser et al. 2014). AGC decreases with tree species evenness in miombo woodlands (**Paper IV**, Figure 3), suggesting that dominant tree species control the largest proportion of the resources (Cardinale et al. 2009). Studies have shown that the relationships between plant species richness, evenness and aboveground biomass vary from neutral, positive, negative or unimodal in tropical and temperate forest ecosystems (Harrison et al. 2006, Adler et al. 2011, Zhang et al. 2011), raising debate among ecologist about the underlying causes (Adler et al. 2011, Grace et al. 2014). Results from this study (**Paper IV)**, also shows that anthropogenic disturbances and physiographic conditions are important determinants of the AGC-richness relationship (Figure 4). A secondary forest in western Andes of Colombia had a large potential in accumulating carbon stocks and in supporting a high biodiversity after only about 30 years of natural regeneration (Gilroy et al. 2014). Generally, forest biomass-richness relationships are said to be ecosystem specific, scale dependent (morphological sizes, spatial and temporal), and linked to historical disturbances, edaphic factors and local-climatic conditions (Zhang et al. 2011, Marshall et al. 2012).

Hence, there is a potential to enhance carbon and biodiversity co-benefits, which if well utilized could improve local livelihoods through initiatives such as REDD+. I recommend that to enhance ecosystem benefits, management strategies in the moist forest and miombo woodlands in Tanzania should consider both tree species size class, diversity, physiographic conditions and anthropogenic disturbances.

4.0 CONCLUDING REMARKS

Plant species are distributed across space and over time (Begon et al. 2006), in terrestrial ecosystems and depends on environmental conditions such as climate and soil nutrients and disturbances such as selective harvesting. Processes such as regeneration and biomass production are influenced by the complexities in structural attributes in forest and woodlands ecosystems (Zenner 2004, McElhinny et al. 2005). **Paper I-IV** shows that increase in structural complexity in forest and woodlands enhance tree species co-existence through resource use optimization, whilst decrease in structural complexity promotes species dominance due to massive utilization of major available resources by few species. Nevertheless, the associations among different structural attributes are strongly influences by topography, anthropogenic disturbances and available resources such as soil nutrients.

The findings from this study provides useful information on how to link structural components with environmental conditions and anthropogenic disturbances, which is important for forest and woodland conservation. Results may be used to integrate biodiversity and environmental concerns in current REDD+ initiatives. The extensive patterns of relationships between tree species richness, evenness, sizes, and aboveground carbon stocks provide useful information, which can be used in understanding the potential benefits of forest and woodland carbon storage and biodiversity for human wellbeing (Naeem et al. 2009).

Managing forests and woodlands towards diverse structures maintains sustainable flow of benefits to local-livelihoods (Diaz et al. 2009, Alves et al. 2010), and has potential to mitigate global climate changes. Thus, forest and miombo woodland in Tanzania requires management strategies that will maintain or improve the observed complex structural patterns. The high variability in tree species richness, canopy density, herbaceous and tree biomass, and soil nutrients are indications that there are potentials to improve forest and woodland benefits to local livelihoods, which in turn will encourage sound management of the forests and woodlands.

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PAPER I

Tree species richness in tropical forests and woodlands: The relative importance of vertical soil nutrient heterogeneity, mean and depth-specific soil nutrient availability

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ABSTRACT

Heterogeneous environmental conditions promotes plant species richness. However, information on how woody species richness is related to vertical soil nutrient heterogeneity is limited. We compared relationships between tree species richness and 1) vertical soil nutrient heterogeneity, 2) depth-specific soil nutrients availability, and 3) the conventional mean soil nutrient availability. We recorded tree species richness, and measured soil nutrient availability, elevation and anthropogenic disturbance indicators in 186 vegetation plots (20 m x 40 m) in a moist forest (n=60) and miombo woodlands (n=126) in Tanzania. We used generalized least square regressions to examine how tree species richness relates to the three aspects of soil nutrient availability. Vertical soil nutrient heterogeneity alone was the best predictor of tree species richness in miombo woodlands, while mean soil nutrient availability best explained variations in tree species richness in moist forest. Soil nutrient availability in the top (0-15 cm) soil layer explained more of the variations in tree species richness than soil nutrient availability in the middle (15-30 cm) and lower (30-60 cm) soil layers in both vegetation types. Overall, there were more negative than positive relationships between tree species richness and aspects of soil nutrient availability in the two vegetation types. The relationships between tree species richness and vertical heterogeneity, mean, and depth-specific soil nutrient availability are ecosystem specific and varies considerably across topographic conditions and anthropogenic disturbances. Although generally neglected, vertical soil nutrient heterogeneity may be important in explaining variation in woody species richness in forests and woodlands.

Key words Disturbance ▪ Miombo ▪ Moist forest ▪ Plant Diversity ▪ Resources variations

INTRODUCTION

Numerous studies in community ecology have shown that heterogeneous environmental conditions support a high plant species richness (Huston 1979; Lundholm 2009; Stein et al. 2014). The interactions between biotic and abiotic ecosystem components affect the inherent vertical succession of nutrient availability in soil horizons (Lavelle and Spain 2001), which in turn may affect plant growth and species distributions. For example, plant growth responses to soil nutrient heterogeneity are species-specific and varies at spatial and temporal scales in terrestrial ecosystems (Maestre et al. 2006; Wijesinghe et al. 2005) since plant species are specialized in nutrient uptake (Lundholm 2009; Huston 1979).

Soil nutrient availability in forest habitats varies across vertical and horizontal spatial scales, depending on the underlying parent rock material, differences in plant species, topography, climatic conditions and with anthropogenic disturbances (Lavelle and Spain 2001; Aponte et al. 2013). Plant species richness also vary across space, depending on the ability of species to acquire patchily distributed quantities of soil nutrients (Ricklefs 1977; Tilman and Pacala 1993; Wright 2002; Hill and Hill 2001; Questad and Foster 2008). Plant species co-existence in forest and woodland reflects the ability of species to avoid competition for resources, partly because of their differential capacity to exploit available soil nutrients at different scales and at different soil depth layers (Sardans and Peñuelas 2013).

Moreover, the availability of the most essential nutrients for plant growth and microbial activities are higher in the top than in the deep soil layers (Jobbágy and Jackson 2001; Jumpponen et al. 2010). Thus, both vertical and horizontal spatial heterogeneity in soil nutrient are important determinants of presence, abundance and distributions of individual plant species across forest ecosystems (Chapin II et al. 2000). Some studies have reported negative relationships between plant species richness and spatial soil nutrient heterogeneity in forest and grassland ecosystems, although theory predicts positive associations between plant species richness and spatial heterogeneity in soil resources (Sheley and Larson 1994; Perroni-Ventura et al. 2006; Silva et al. 2013; Eilts et al. 2011). This has raised a debate among ecologists on whether environmental heterogeneity actually promotes plant species coexistence (Lundholm 2009).

Previous studies have shown that anthropogenic disturbance may influence how plant species richness relates to soil nutrient availability across spatial scales in forest and grassland ecosystems (Silva et al. 2013; Fraterrigo et al. 2005; Abrams and Hulbert 1987). According to Bartels and Chen (2010), external factors, such as anthropogenic disturbances, that interferes with plant demands for nutrient availability can influence the relationship between plant species richness and the heterogeneity in resources such as soil nutrient availability in forest ecosystems.

Previous studies have focused mainly on how plant species richness varies across horizontal spatial scales and with temporal patterns of soil nutrient heterogeneity (Musila et al. 2005; Perroni-Ventura et al. 2006; Tilman and Pacala 1993; Stevens and Carson 2002; Reynolds et al. 2007). However, some studies have indicated that soil depth (Dornbush and Wilsey 2010) and vertical soil nutrient heterogeneity (Williams and Houseman 2014) may affect plant species richness in grassland ecosystems. Thus, there is limited knowledge on how vertical soil nutrient heterogeneity influence tree species richness, especially in tropical forests and woodlands.

In this study, we explore the relationships between woody species richness and vertical soil nutrient heterogeneity, depth-specific soil nutrient availability as well as mean soil nutrient availability in two vegetation types in Tanzania. We predict; (1) positive relationships between woody species richness and vertical soil nutrient heterogeneity, because theoretical evidences predicts that environmental heterogeneity promotes species coexistence through multiple realized niches (Chesson 2000), and recent experimental studies have shown that vertical soil nutrient heterogeneity and soil depths have positive effects on grass species richness (Dornbush and Wilsey 2010; Williams and Houseman 2014), (2) that tree species richness is negatively related to mean soil nutrient availability across the soil horizons, because previous studies have suggested that an overriding resource limitations causes species diversity to be more associated with the mean in resource availability than the variation in resources (Lundholm 2009; Holl et al. 2013), and finally, (3) we predict that nutrient availability in the upper soil horizon explains more of the variation in tree species richness than soil nutrient availability in lower horizons, because most of the essential nutrients for plant growth, and over 60% of plant root weights occurs in the top soil layers in forest ecosystems (Jobbágy and Jackson 2001; Jacke and Toensmeier 2005; Gregory 2008).

MATERIALS AND METHODS

Study area

We surveyed vegetation and measured soil nutrient availability in a moist forest in Hanang district and in miombo woodlands in Kilombero, Kilolo, Mufindi, Iringa rural, Mbeya rural, Mbozi and Chunya districts of Tanzania. These districts were selected to represent a wide range of topographic gradients and climatic conditions in moist forest and miombo woodlands (Figure 1).

Miombo woodlands covers about 90 % of the forested land in Tanzania (URT 1998). It occurs in a wide range of tropical and subtropical climates, is classified as wet or dry by using a threshold level of 1000 mm annual rainfall (White 1983; Frost 1996). They are strongly influenced by frequent fires, micro-climatic conditions and anthropogenic disturbances (Campbell et al. 1996; Furley et al. 2008). Miombo woodlands in the study sites spans an elevation range of 25-2000 m, a temperature range of 16-30 °C, and a rainfall range of 650 - 1400 mm (Frost 1996; Platts et al. 2014). They are dominated by the genera *Brachystegia* and *Julbernadia* like in other parts of East and Southern Africa (Thomas and Packham 2007). Moreover, miombo woodlands are characterized by low nutrient availability, well drained and highly leached soils (Jeffers and Boaler 1966).

The Hanang moist forest spans an elevation range of 1860-3418 m, and is dominated by species of the genera *Abizia, Cassipourea, Hygenia, Prunus, Cussonia, Olea* and *Vernonia* (Lovett and Pocs 1993). The moist forest is characterized by humus-rich loam and volcanic rock soils, receives a mean annual rainfall ranging between 750-2000 mm and has a mean annual temperature of 16-25 °C (Lovett and Pocs 1993; Platts et al. 2014).

Data collection

We measured and collected data from vegetation plots of 20 m × 40 m in moist forest (n=60) and miombo woodlands (n=126). Plots were positioned along elevation gradients at a minimum distance of 400 m apart. We recorded the geographic location and elevation of plots with a hand held GPS (Map76cx). Trees with dbh $\geq$ 5 cm were recorded and generally identified in the field. For unidentified trees species, voucher specimens were identified at the National Herbarium in Arusha, Tanzania. In order to account for potential effects of disturbance on the relationships between species richness and aspects of soil nutrient availability, we recorded tree stumps in each plot, and also estimated distances (km) from the nearest road and human settlement (Baas et al. 2011).

We sampled soils between May 2011 and March 2012 at the same time with the vegetation survey in the two vegetation types. Soil samples were collected at 0–15 cm, 15–30 cm and 30–60 cm depths, from the four corners and at the centre of each plot. Thereafter, the samples were aggregated into three composites of one sample per soil depth layer in each plot. A total of 378 soil samples were collected, but only 375 samples were analysed since three samples from one plot were lost. Analyses were done at Seliani Agricultural Research Institute, Arusha, Tanzania. In the laboratory, all samples were air dried and sieved through a 2 mm wire mesh and subsequently analysed for soil pH (at 1:2.5 soil:H_2O), percentage organic carbon (Walkley-Black method), available phosphorous (Bray II), total nitrogen (Kjeldahl method), potassium, calcium, and magnesium (ammonium acetate 1.0 M pH 7.0 extraction). Soil particle size were classified into clay (< 2 µm), silt (2 to 20 µm), fine sand (20 to 50 µm) and coarse sand (50 µm to 2000 µm) (Brady and Weil 1999; Fullen and Catt 2004).

Statistical analysis

Derived variables

Tree species richness is the total number of tree species occurring in each plot. To estimate vertical soil nutrient heterogeneity (VH) we calculated coefficient of variation in soil nutrients from the three soil depth layers in each plot (Baer et al. 2005; Holl et al. 2013). We calculated mean soil nutrient availability (M) as the arithmetic mean of soil nutrients from the three soil depth layers in each plot. Hence, the explanatory variables were: CV-Phosphorous (CV-P), CV-Nitrogen (CV-N), CV-Potassium (CV-Na), CV-Silt, CV-Fine sand, CV-Coarse sand, CV-pH and CV-Organic carbon (CV-OC), mean P, mean N, mean K, mean Silt, mean Fine sand, mean Coarse sand, mean pH and mean OC, and actual soil nutrient values in each specific soil depth layer. In addition, we included the number of tree stumps (stump-cuts), distance from the nearest settlement to each plot (settlement), distances from nearest access road to each plot (road) and elevation as explanatory variables (Table 1). Data exploration indicated high heteroscedasticity and therefore all continuous explanatory variables were checked for skewness and corrected accordingly to approximately zero skewness (Økland et al. 2001) and scaled to improve the interpretability of regression coefficients (Schielzeth 2010).

Model prediction and validation

We used generalized least square models (gls) to explore the relationships between tree species richness and vertical soil nutrient heterogeneity (VH), mean soil nutrients (M), and depth-specific (DS) soil nutrient availability in moist forest and miombo woodlands. We fitted three separate models, first using solely vertical soil nutrient heterogeneity (VH) or mean soil nutrients (M), and second by combining vertical soil nutrient heterogeneity and mean soil nutrient availability (VH+ M) in one model for each vegetation type. Third, we fitted three (Top, Mid and Lower) subsequent models using soil nutrient availability in each soil depth for each vegetation types. In addition, each of these models included stump-cuts, distance from settlements (settlement), distance from access roads (road), elevation and their first term interactions with all soil nutrient explanatory variables, in order to account for their potential effects on the relationships between species richness and aspects of soil nutrient availability. Data exploration indicated a nonlinear relationship between tree richness and elevation in miombo woodlands, and consequently this relationship was fitted using a quadratic term. We checked for correlations within groups of explanatory variables, to ensure that all explanatory variables included in the regression models had VIF ≤ 8.0 (Zuur et al. 2010) and Pearson correlation (r) ≤ 70% (Dormann et al. 2013). Generalized least square models were preferred to account for the high heteroscedasticity in the data (Zuur et al. 2009; Zuur et al. 2013).

We used a stepwise backward elimination procedure and the Akaike Information Criterion (AIC) in final models selection (Zuur et al. 2009). Models with the lowest AIC and variables of significant contributions ($p < 0.05$) were selected as the most parsimonious models (Zuur et al. 2009). We assessed the goodness of the model fits, validated the final models by observing the spread of residual patterns and compared models using the likelihood ratio test (Zuur et al. 2010; Zuur et al. 2009).

RESULTS

In miombo woodlands, the most parsimonious model, explaining tree species richness included only vertical soil nutrient heterogeneity (VH: AIC=694, R^2=42 %), although it was not significant different from models with mean soil nutrients only (M: AIC=698, R^2=38 %) or the combination of mean soil nutrient availability and vertical soil nutrient heterogeneity (VH+M: R^2=42 %, AIC=702, Table 2, Appendix 1 & 2). In moist forest model with mean soil nutrient availability only (M: AIC=316, R^2=59 %, Likelihood ratio test ($LRT_{21.9}$): P=0.001) explained significantly larger variations in tree species richness compared to models with vertical soil nutrient heterogeneity alone (VH: AIC=326, R^2=53 %) or the combination of mean soil nutrient availability and vertical soil nutrient heterogeneity (VH+M: AIC=318, R^2=36 %, $LRT_{13.71}$: P=0.003; Table 2, Appendix 1 & 2). Generally, there were more negative than positive relationships between tree species richness and the mean soil nutrient availability or vertical soil nutrient heterogeneity in the two vegetation types (Figure 2). Tree species richness had a strong positive association with vertical soil nutrient heterogeneity (CV-pH; Table 2) in miombo woodlands. However, vertical soil nutrient heterogeneity interacted with settlements (i.e. proxy for disturbance) and elevation in that the relationships were negative when the interactions were included (Figure 2). Tree species richness had significant positive association with mean soil nutrient availability (mean silt), but the relationship shifted from positive to negative upon interaction between mean silt and anthropogenic disturbance (distance from road) in moist forest (Table 2, Figure 2). CV-P, mean K, mean silt, stump-cuts, and elevation had nearly similar effect sizes on tree species richness in the two vegetation types (Figure 2).

The relationship between species richness and soil nutrient availability differed substantially among the three soil depth layers (Table 3, Figure 3, and Appendix 3). The variation in tree species richness was best explained by soil nutrient availability in the top soil layer in the two vegetation types (forest: AIC= 308; R^2=66 %, $LRT_{25.0}$: P<0.001; miombo: AIC=679; R^2=49 %, $LRT2_{8.45}$: P<0.001), followed by soil nutrient availability in the middle (forest: AIC=323; R^2=49%, $LRT_{3.35}$: P=0.06; miombo: AIC=690, R^2=35 %, $LRT_{6.35}$, P=0.011) and by soil nutrient availability in the lower (forest: AIC=325; R^2=46 %, miombo: AIC=694, R^2=32 %,) soil depth layers (Table 3, Figure 3, and Appendix 3).

In general, there were more negative relationships between tree species richness and soil nutrient availability in moist forest than in miombo woodlands in all the three soil depth layers (Figure 3). However, the relationships between tree species richness and soil nutrients also showed complex patterns. In moist forest, tree species richness had a strong positive relationship with Mg in the top soil layer but the relationship was negative in the lower soil layer (Table 3, Appendix 3). In miombo woodlands, tree species richness had a strong positive relationship with Ca in the top soil layer, while it was negative in the middle soil layer (Table 3, Appendix 3).

Finally, tree species richness had positive associations with coarse sand and Mg in the top soil layer in moist forest, but this relationship turned negative upon interactions between coarse sand and anthropogenic disturbance (settlement), coarse sand and elevation, and Mg and elevation (Table 3, Figure 3). Moreover, tree species richness decreased with fine sand in the top soil layer in moist forest, but turned significantly positive upon interactions between anthropogenic disturbance (settlement) and elevation (Table 3, Figure 3). In miombo woodlands, tree species richness increased with Ca, OC, and pH, although these relationships strongly decreased upon the interactions between Ca and stump-cuts, OC and road, and pH and settlement in the top soil layer (Table 3, Figure 3). Furthermore, tree species richness decreased with coarse sand and silt, but this relationship changed to positive on the interactions between coarse sand and elevation, and silt and road in the top soil depth layer (Table 3, Figure 3).

DISCUSSION

We have showed that vertical soil nutrient heterogeneity may be an important predictor of tree species richness. Vertical soil nutrient heterogeneity (VH) explained larger variations in tree species richness than mean soil nutrient availability in miombo woodlands. In moist forest, on the other hand, mean soil nutrient availability (M), rather than vertical soil nutrient heterogeneity (VH), explained the variations in tree species richness. We found more negative relationships between tree species richness and soil nutrients. Generally, theory suggests that heterogeneity in resources such as soil nutrients explain much variations in plant species richness, and hence is the major cause of high plant diversity in tropical forests (Stein et al. 2014). However, previous studies have shown that relationships between plant richness and soil nutrient heterogeneity and mean soil nutrient availability in tropical forests are often hump-shaped or positive, but occasionally negative or no relationships (Huston 1994; Lundholm 2009; Stein et al. 2014; Pausas and Austin 2001). Our results indicate that vertical soil nutrient heterogeneity and depth specific soil nutrient availability affects tree species richness in forests and woodlands. Thus the relationships between tree species richness and environmental conditions such as soil nutrient availability are ecosystem specific and are influenced by disturbance factors, topographic conditions and biotic interactions (Pausas and Austin 2001).

In miombo woodlands the variations in tree species richness was better explained by vertical soil nutrient heterogeneity, although miombo woodlands are known to be limited in soil nutrient availability, particularly the essential nutrients for tree growth, such as P and K (Frost 1996). Possibly the high grass-tree ratio and frequent fires in miombo may create a large vertical heterogeneity in soil nutrient availability. Studies have reported that an increase in the grass to woody plant ratio results into increased spatial heterogeneity in soil nutrient availability in tropical Savannas (Pärtel and Wilson 2002; Schlesinger et al. 1996), which can also apply to vertical soil nutrient heterogeneity. The dynamics of grass to tree ratio in miombo woodlands is, among other things, determined by fire, herbivory, soil nutrients and water (February et al. 2013; Frost 1986), which can to a great extent influence the vertical variations in essential soil nutrients for grass and tree growth . Trees, especially species of the legume family, have a long and horizontally wide root system, enabling them to extract soil nutrients at lower soil horizon and balance the effect of leaching, as well as distributing soil nutrients to a wide range in the top soil horizon (Frost 1986 ; Frost 1996). This favors herbaceous plants such as grasses whose fibrous root systems can extract available soil nutrients more intensively at the top soil horizon (Pärtel and Wilson 2002; Frost 1986).

In moist forest tree species richness seems to be more related to soil nutrient availability than soil nutrient heterogeneity, probably due to strongly limited resources (Lundholm 2009; Holl et al. 2013). Resource limitations are likely to occur in ecosystems such as tropical moist forest, which has limited light availability caused by relatively dense canopy (Bartels and Chen 2010). Trees species with high biomass production and large canopy sizes dominate access to soil nutrients and light availability, making soil nutrient availability more of a limiting factor for species coexistence than soil nutrient heterogeneity (Stevens and Carson 2002).

We found more negative than positive relationships between tree species richness and vertical soil nutrient heterogeneity and mean soil nutrient availability in the two vegetation types. These results support the hypothesis that tree species richness in tropical forests decrease with increasing soil fertility (Huston 1980; Huston 1994) because of intensified competition as plants increase in sizes (Perroni-Ventura et al. 2006; Toledo et al. 2011). Tree species richness had negative relationships with the most essential nutrients for tree growth, such as P (i.e. CV-P) and K (i.e. mean K), and nearly similar effect sizes in the two vegetation types. In terrestrial ecosystems, increase in soil nutrient supply rates may promote above-ground biomass production which limit resources (e.g. light) to smaller trees and thus leading to a decrease in tree species richness (Stevens and Carson 2002). Therefore, the directions of the relationships between richness and soil nutrient availability is determined not only by niche differentiation among plant species, but also by their size (Tilman and Pacala 1993; Eilts et al. 2011).

Soil nutrient availability in the top soil layer explained larger variations in tree species richness than in the middle and lower soil layers in the two vegetation types, perhaps because most essential soil nutrients for plant growth are concentrated in the top soil (Jobbágy and Jackson 2001). However, there were complex patterns in the relationships between tree species richness and soil nutrient availability in the three soil depth layers in moist forest and miombo woodlands. For example, tree species richness had positive relationship with Mg in the top, and a negative relationship with Mg in the lower soil depth layers in moist forest. While tree species richness had a positive relationship with Ca in the top, and a negative relationship in the middle soil depth soil layers in miombo woodlands. These results suggests that soil nutrient availability at different soil layers may have contrasting effects on growth of different plant species. This is partly because the vertical distributions of soil nutrients in the soil profiles is determined by plant species nutrient cycling characteristics such as biomass cycling rates, root distribution and rooting depths as opposed to leaching and chemical weathering (Jobbágy and Jackson 2001). Thus, it is not only the soil depth that influence plant species richness (Dornbush and Wilsey 2010), but also the variations in soil nutrient availability at different soil depths. The wide range of positive and negative relationships between tree species richness and soil nutrient availability in the three soil layers in each vegetation type suggest complex tree richness-soil nutrient patterns and further studies are needed to disentangle the underlying mechanisms.

Tree species richness had significant positive or negative associations with vertical soil nutrient heterogeneity, depth-specific soil nutrients and mean soil nutrient availability. These relationships were highly modified upon interactions with anthropogenic disturbances (settlement, road and stump–cuts) and elevation in moist forest and miombo woodlands. Disturbances such as frequent recurring fires in miombo woodlands are critical for the development of soil nutrient availability (Frost 1996; Williams et al. 2008), which in turn has a potential influence on plant species growth, richness and composition (Shelukindo et al. 2014). Tree species richness strongly increased with vertical soil nutrient heterogeneity (CV-pH) in miombo woodlands. However, the relationship decreased significantly upon interactions between vertical soil nutrient heterogeneity (CV-pH) and settlement, and elevation. Furthermore, tree species richness increased with Ca, OC, and pH, although these relationships strongly decreased upon the interactions between Ca and stump-cuts, OC and road, and pH and settlement in the top soil layer. This suggest that, relationships between tree species richness and vertical soil nutrient heterogeneity, depth-specific and mean soil nutrient availability may be influenced by topography and anthropogenic disturbances. Although not tested in this study random stochasticity, species dispersal and local climatic conditions may also affect the relationships between tree species richness and soil nutrient availability (Salas-Morales and Meave 2012; Sarr et al. 2005; Connell 1978).

In conclusion, understanding of how plant species richness relate to vertical soil nutrient heterogeneity, depth-specific and mean soil nutrient availability may be useful in maintaining plant species structure and diversity in forest and woodland ecosystems. Our findings suggest that there are strong relationships between tree species coexistence and the vertical heterogeneity in essential soil nutrients for plant species growth. Vertical soil nutrient heterogeneity and depth-specific soil nutrient availability are important determinants of plant species richness, worth considering when determining relationships between plant species diversity and resources heterogeneity in forests and woodlands.

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TABLES

Table 1. Stand variables, mean (arithmetic mean soil nutrients for all measured plots), mean CV (arithmetic mean of the coefficients of variations) and range (minimum and maximum values) in moist forest (*n*=60) and miombo woodland (*n*=125) of Tanzania.

Variables	**Vegetation type**							
	Moist Forest				**Miombo Woodlands**			
	Mean	**Range**	**Mean CV**	**Range**	**Mean**	**Range**	**Mean CV**	**Range**
Richness	8.9	1-18	-	-	9.8	1-24	-	-
Clay (%)	38.2	24.4-57.6	0.2	0.02-0.6	53.6	14.9-87.4	0.1	0.0-0.4
Silt (%)	5.5	4.1-6.9	0.6	0.0-0.2	3.6	1.8-5.1	0.1	0.01-0.3
Fine Sand (%)	14.2	7.3-23.1	0.9	0.0-0.3	5.3	2.0-10.7	0.1	0.01-0.3
Coarse Sand (%)	38.3	16.1-68.7	0.4	0.04-1.0	24.5	10.2-67.3	0.2	0.01-0.7
Soil pH	6.0	5.8-6.3	0.03	0.0-0.05	5.9	4.8-7.1	0.01	0.0-0.08
Soil Nitrogen (%)	0.2	0.06-0.6	0.3	0.03-0.9	0.03	0.01-0.1	0.2	0.01-0.6
Soil Organic Carbon (%)	1.9	0.8-4.9	0.3	0.02-0.7	1.0	0.1-2.6	0.2	0.01-1.0
Soil Phosphorous (mg kg^{-1})	3.5	1.9-6.07	0.2	0.02-0.7	4.8	1.6-9.5	0.1	0.0-0.4
Soil Potassium (cmol kg^{-1})	1.1	0.5-2.1	0.2	0.02-0.6	0.3	0.03-1.2	0.2	0.01-0.9
Soil Calcium (cmol kg^{-1})	15.0	2.7-37.4	0.5	0.07-1.0	1.6	0.1-18.0	0.4	0.01-1.0
Soil Magnesium(cmol kg^{-1})	0.4	0.1-0.9	0.2	0.02-0.7	0.2	0.01-1.3	0.2	0-1.0
Soil Sodium (cmol kg^{-1})	0.1	0.05-0.4	0.2	0.02-0.7	0.07	0.01-0.6	0.1	0.0-1.0
Elevation (m)	2187	1900-2622	-		1221	25-2012	-	
Stumps-Cuts	5.1	0-18	-		5.0	0-24	-	
Road distances (Km)	5.0	1.8-7.8	-		11.3	0.1-24.8	-	
Settlement distances (Km)	6.7	3.1-11.5	-		19.3	0.2-51.9	-	

Table 2. The relationships between tree species richness and vertical heterogeneity (VH), mean (M) soil nutrients availability, distances (road, settlement and stump-cuts) and elevation in moist forest (*n*=60) and miombo woodland (*n*=125) of Tanzania. Results are from generalized least square (gls) models (VH + MH, VH and MH) showing the coefficients (Standard error (SE)) of the significant ($\alpha \leq 0.05$) model covariates, CV is the coefficient of variations, see Table 1 for more details on the variables used.

Variables	**VH + M**	**VH**	**M**
	Coefficients (SE)	Coefficients (SE)	Coefficients (SE)
Moist Forest: (Intercept)	6.74(1.83)	8.21 (1.25)	12.67(4.39)
CV-P	-8.67(1.94)	-6.40 (1.86)	-
CV-N	4.58(1.67)	-	-
Stump-Cuts	9.12(1.85)	8.51 (1.94)	8.48(1.84)
Mean K	-7.08(1.91)	-	-5.30(2.29)
Mean Silt	7.91(2.56)	-	29.82(5.99)
Mean Na	-	-	-8.84(3.65)
Mean Fine Sand	-	-	-4.6(2.18)
Road	-	-	11.36(3.81)
Elevation	-	-	-16.42(5.67)
Mean Silt: Road	-	-	-30.77(8.25)
Miombo woodlands: (Intercept)	13.15(2.03)	24.18(3.26)	11.75(3.72)
CV-P	-5.59(1.67)	-	-
CV-OC	-	-4.87(1.96)	-
CV-pH	-10.03(3.38)	-22.33(5.52)	-
Mean Silt	5.01(2.21)	-	-
Mean P	-	-	-
Mean K	-6.47(2.54)	-	-8.074(3.35)
CV-Coarse Sand	11.18(4.27)	-	-
Mean pH	-	-	13.28(4.70)
Mean Coarse Sand	-	-	-26.71(7.67)
Settlement	-	-13.07(4.14)	17.79(6.17)
Elevation	20.99(5.40)	17.20(5.70)	19.61(6.02)
Elevation^2	-28.95(5.59)	-36.34(5.44)	-42.67(6.29)
CV-Coarse Sand: Settlement	-23.18(7.74)	-	-
CV-pH: Settlement	18.71(6.65)	21.90(8.19)	-
CV-pH: Elevation	-	19.57(5.48)	-
Mean pH: Settlement	-	-	-33.62(10.62)
Mean Coarse Sand: Elevation	-	-	36.62(10.37)

Table 3. The relationships between tree species richness, soil nutrient availability, disturbances (stump-cuts, road and settlement) and elevation in moist forest (n=60) and miombo woodland (n=125) of Tanzania. Results are from generalized least square (gls) models and show the coefficients (Standard error (SE)) of the significant ($\alpha \leq 0.05$) model covariates from the three soil depth layers (top, mid and lower), CV is the coefficient of variations, see Table 1 for more details on the variables used.

Variables	**Top (0-15 cm)**	**Mid (15-30 cm)**	**Lower (30-60 cm)**
Forest: (Intercept)	-2.29(12.30)	21.59(5.07)	29.67(9.05)
Coarse Sand	49.97(14.71)	-	-
Elevation	9.45(17.14)	-17.92(6.48)	-33.92(13.84)
Fine Sand	-61.06(17.00)	-9.84(4.17)	-37.77(15.51)
Mg	41.31(16.16)	-	-6.56(2.53)
OC	-	6.55(2.60)	7.61(2.90)
K	-11.82(2.86)	-8.14(1.96)	-
Settlement	-2.50(4.64)	-8.61(3.91)	-
Stump-cuts	8.44(1.73)	9.66(1.98)	9.29(2.07)
Coarse Sand:Settlement	-26.43(6.49)	-	-
Coarse Sand: Elevation	-42.80(21.65)	-	-
Fine Sand: Settlement	29.44(8.54)	20.53(7.87)	-
Fine Sand: Elevation	63.54(23.70)	-	47.39(22.13)
Mg :Elevation	-46.20(21.56)	-	-
Miombo woodlands:(Intercept)	1.37(4.98)	15.14(3.76)	-13.70(10.92)
Ca	4.59(4.35)	-28.68(10.14)	-
Coarse Sand	-11.09(5.83)	-	-
Elevation	21.15(7.01)	14.83(8.78)	25.81(5.78)
Elevation2	-39.61(6.45)	-28.49(6.29)	-33.21(5.98)
OC	12.08(5.18)	-	-
K	-	21.26(8.94)	26.72(12.72)
pH	16.89(5.81)	-	-
Silt	-8.07(3.79)	-	-
Roads	0.07 (6.25)	-	-
Settlement	13.11(6.29)	-	54.33(24.01)
Stump-cuts	16.18(5.23)	-	-
Ca: Elevation	-	49.88(17.63)	-
Ca: Stump-cuts	-28.41(9.25)	-	-
Coarse Sand: Elevation	20.10(9.30)	-	-
OC: Road	-20.43(8.66)	-	-
K: Elevation	-	-41.63(14.19)	-
pH: Settlement	-32.45(12.75)		-64.23(28.04)
Silt :Road	24.61(7.26)	-	

FIGURES

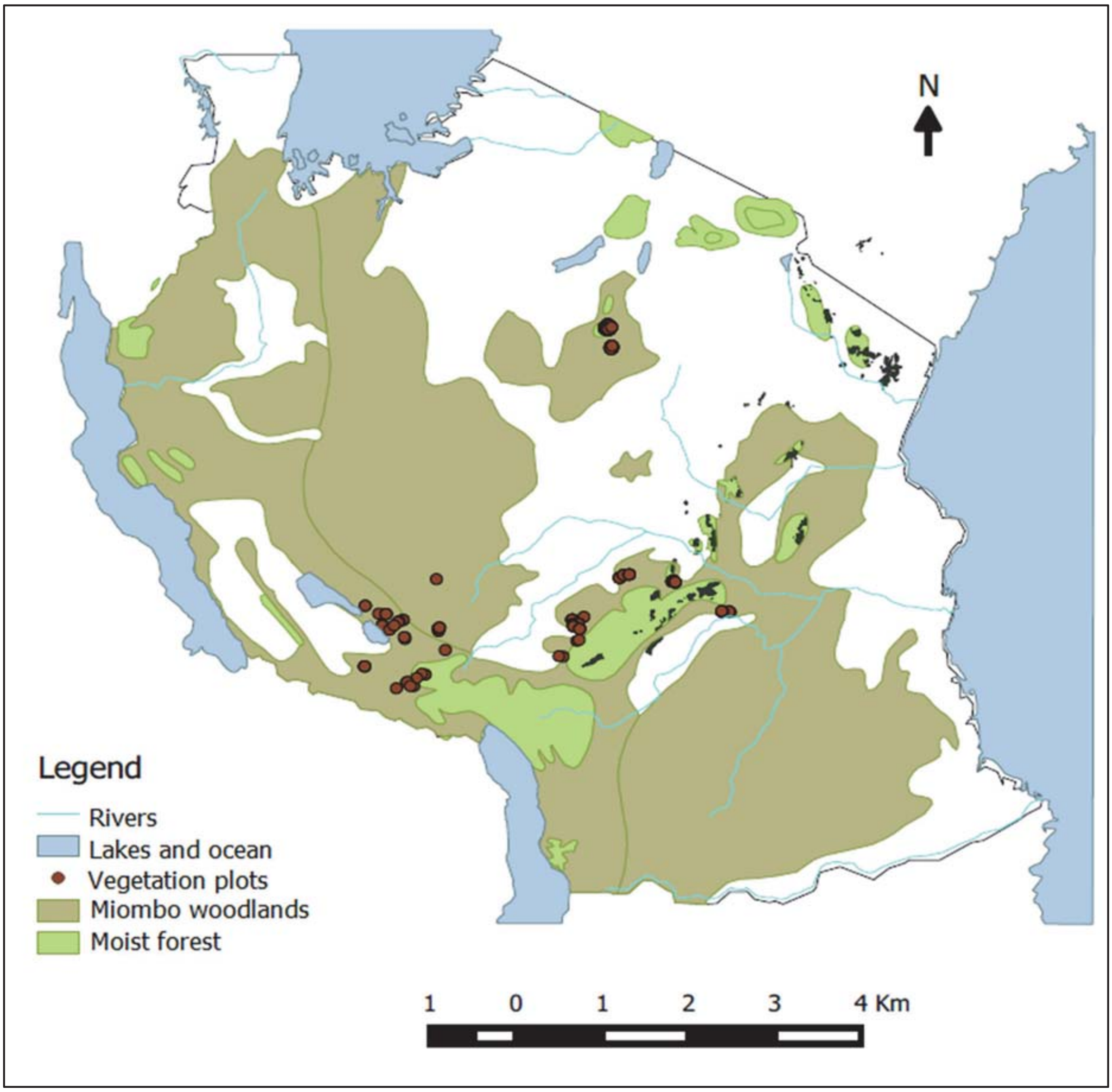

Figure1: A map showing the study area

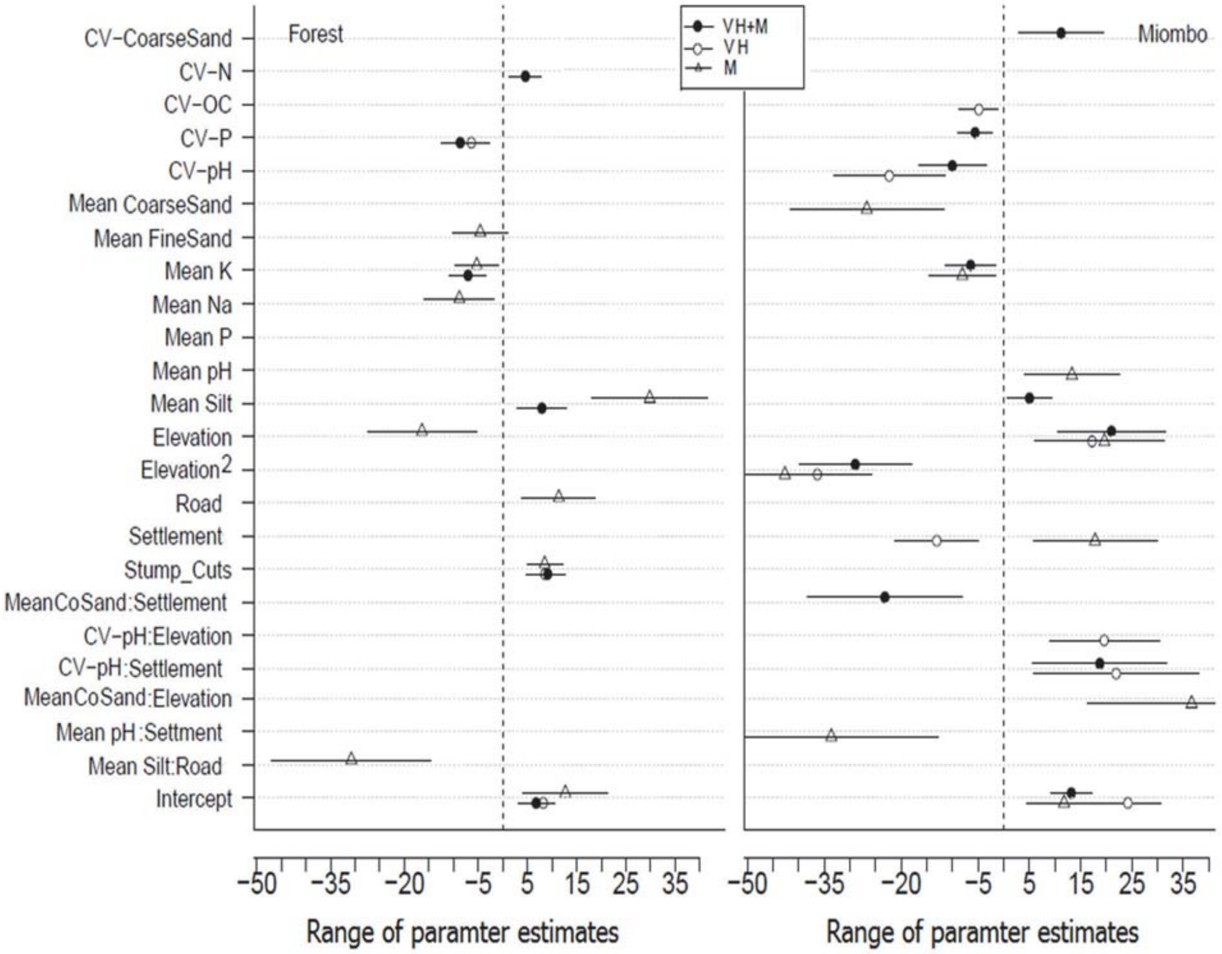

Figure 2. The relationships between tree species richness and vertical heterogeneity (VH), mean (M) soil nutrient availability distances (road, settlement and stump-cuts) and elevation in moist forest (n = 60) and miombo woodland (n = 125) of Tanzania. A graphical representation of results from three generalized least square (gls) models (VH + M, VH and M; see Table 2; Appendix 1 & 2) showing point plots with error bars: black circles for combined model (VH + M), white circles for VH and triangle for M, respectively. Points represent the model estimates and the horizontal lines are 95% confidence intervals, while range of covariate estimates displayed on x-axis and their labels on the y-axis. CV is coefficient of variations, see Table 1 and method section for more detail on the variables used.

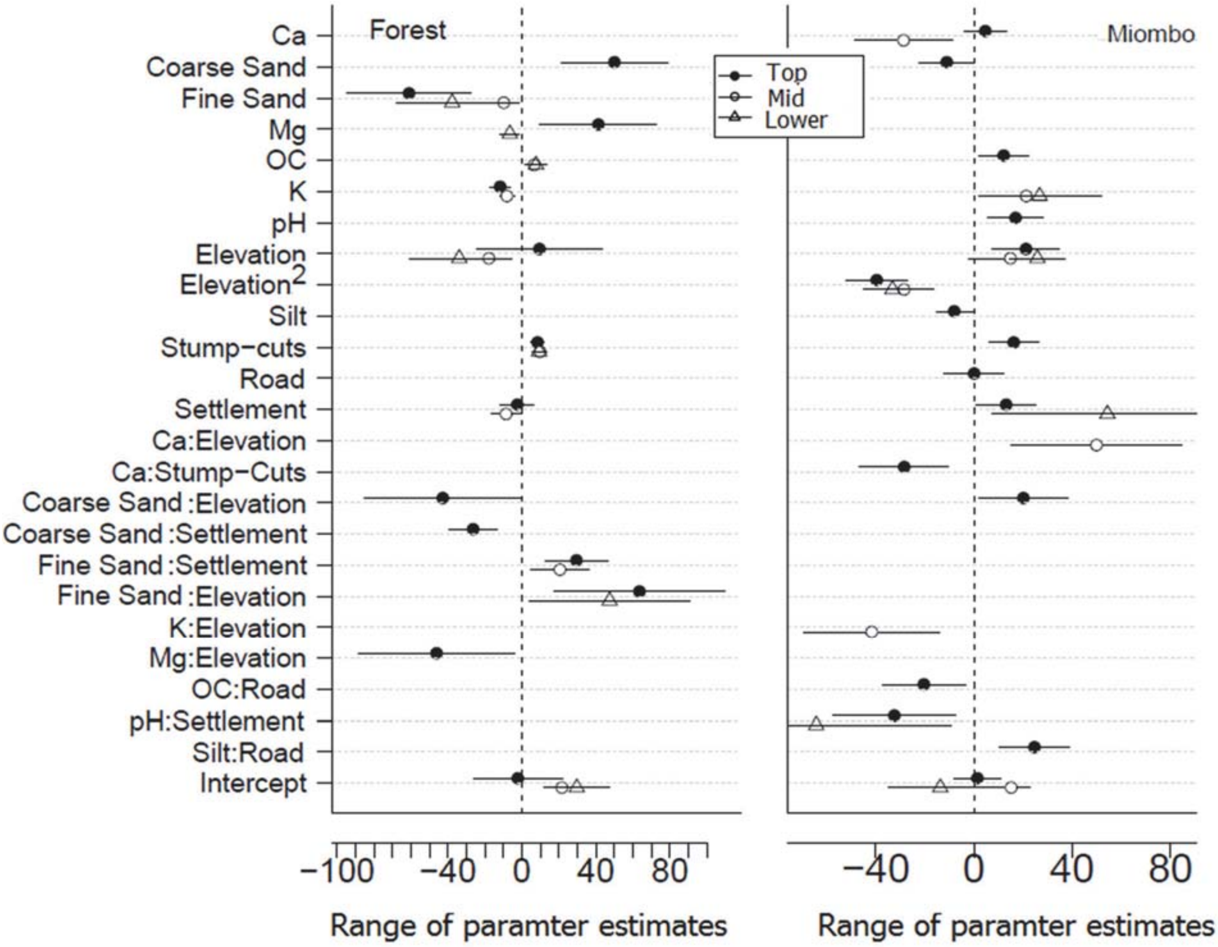

Figure 3. The relationships between tree species richness, soil nutrient availability, stump-cuts, distances (road and settlement) and elevation in moist forest (n = 60) and miombo woodland (n = 125) of Tanzania. A graphical representation of results from three generalized least square (gls) models at each soil depth (Top: 0-15 cm, Mid: 15-30 cm and Lower: 30- 60 cm; see Table 3; Appendix 3) showing point plots with error bars: black circles for Top, white circles for Mid and triangle for Lower depths, respectively. Points represent the model estimates and the horizontal lines are 95% confidence intervals, while range of covariate estimates displayed on x-axis and their labels on the y-axis. CV is coefficient of variations, see Table 1 and method section for more detail on the variables used**.**

APPENDICES

Appendix 1. The relationships between tree species richness and vertical soil nutrient heterogeneity (VH), mean soil nutrient (M), distances (road, settlement and stump-cuts), and elevation in moist forest (n=60) of Tanzania. Results are from generalized least square (gls) models (VH + M, VH and M) showing only significant ($\alpha \leq 0.05$) model covariates, CV is the coefficient of variations, see Table 1 for more details on the variables used.

Variables	**VH+M**				**VH**				**M**			
	Estimates	SE	t-value	p-value	Estimates	SE	t-value	p-value	Estimates	SE	t-value	p-value
(Intercept)	6.74	1.83	3.69	0.001	8.21	1.52	5.39	0.000	12.67	4.39	2.89	0.006
CV-P	-8.66	1.94	-4.47	0.000	-6.40	1.86	-3.44	0.001	-	-	-	-
CV-N	4.57	1.66	2.76	0.008	-	-	-	-	-	-	-	-
CV-Clay	-	-	-	-	-	-	-	-	-	-	-	-
CV-Coarse Sand	-	-	-	-	-	-	-	-	-	-	-	-
Stump-Cuts	9.12	1.85	4.92	0.000	8.51	1.94	4.40	0.000	8.48	1.84	4.61	0.000
Mean K	-7.08	1.91	-3.70	0.001	-	-	-	-	-5.30	2.29	-2.31	0.025
Mean Silt	7.91	2.55	3.10	0.003	-	-	-	-	29.82	5.99	4.98	0.000
Mean Na	-	-	-	-	-	-	-	-	-8.84	3.65	-2.42	0.019
Mean Fine Sand	-	-	-	-	-	-	-	-	-4.60	2.18	-2.11	0.040
Roads	-	-	-	-	-	-	-	-	11.36	3.81	2.98	0.004
Elevation	-	-	-	-	-	-	-	-	-16.42	5.67	-2.89	0.006
Mean Silt: Road	-	-	-	-	-	-	-	-	-30.77	8.25	-3.73	0.001

Appendix 2. The relationships between tree species richness and vertical heterogeneity (VH) and mean (M) soil nutrient availability, distances (road, settlement and stump-cuts) and elevation in miombo woodlands (n=125) of Tanzania. Results are from generalized least square (gls) models (VH + M, VH and M) showing only significant ($\alpha = 0.05$) model covariates, CV is the coefficient of variations, see Table 1 for more details on the variables used.

Variables	**VH+M**				**VH**				**M**			
	Estimates	**SE**	**t-value**	**p-value**	**Estimates**	**SE**	**t-value**	**p-value**	**Estimates**	**SE**	**t-value**	**p-value**
(Intercept)	13.15	2.03	6.46	0.000	24.18	3.26	7.41	0.000	11.75	3.72	3.16	0.002
CV-P	-5.59	1.66	-3.36	0.001	-	-	-	-	-	-	-	-
CV-OC	-	-	-	-	-4.87	1.96	-2.48	0.015	-	-	-	-
CV-pH	-10.03	3.38	-2.97	0.004	-22.33	5.52	-4.05	0.000	-	-	-	-
CV-Coarse Sand	11.18	4.27	2.62	0.010	-	-	-	-	-	-	-	-
Mean K	-6.47	2.54	-2.55	0.012	-	-	-	-	-	-	-	-
Mean Silt	5.00	2.21	2.27	0.025	-	-	-	-	-	-	-	-
Mean Coarse Sand	-	-	-	-	-	-	-	-	-26.71	7.66	-3.49	0.001
Mean pH	-	-	-	-	-	-	-	-	13.28	4.70	2.83	0.006
Settlement	-	-	-	-	-13.07	4.14	-3.16	0.002	17.79	6.17	2.89	0.005
Elevation	20.99	5.40	3.89	0.000	17.20	5.70	3.02	0.003	19.61	6.02	3.26	0.002
Elevation^2	-28.95	5.59	-5.18	0.000	-36.34	5.44	-6.68	0.000	-42.67	6.29	-6.78	0.000
CV-Coarse Sand: Settlement	-23.18	7.74	-2.99	0.003	-	-	-	-	-	-	-	-
CV-pH: Settlement	18.71	6.65	2.82	0.006	21.90	8.19	2.67	0.009	-	-	-	-
CV-pH: Elevation	-	-	-	-	19.57	5.48	3.57	0.001	-	-	-	-
Mean pH: Settlement	-	-	-	-	-		-	-	-33.62	10.62	-3.17	0.002
Mean Coarse Sand: Elevation	-	-	-	-	-			-	36.62	10.37	3.53	0.001

Appendix 3. The relationships between tree species richness, soil nutrient availability, disturbances (stumps counts, road and, settlement) and elevation in moist forest (n=60) and miombo woodland (n=126) of Tanzania. Results are from generalized least square (gls) models showing significant ($\alpha = 0.05$) model covariates from the three soil depth layers (Top, mid and Lower), CV is the coefficient of variations, for more details on the variables used see Table 1

	Top (0-15 cm)				**Mid (15-30 cm)**				**Lower (30- 60 cm)**			
Variables	Estimates	SE	t-value	p-value	Estimates	SE	t-value	p-value	Estimates	SE	t-value	p-value
Forest: (Intercept)	-2.28	12.30	-0.19	0.854	21.59	5.07	4.26	0.000	29.67	9.05	3.28	0.002
Coarse Sand	49.97	14.71	3.40	0.001	-	-	-	-	-	-	-	-
Elevation	9.45	17.14	0.55	0.584	-17.92	6.48	-2.77	0.008	-33.92	13.84	-2.45	0.018
Fine Sand	-61.06	17.00	-3.59	0.001	-9.84	4.17	-2.36	0.022	-37.77	15.51	-2.44	0.018
Mg	41.31	16.16	2.56	0.014	-	-	-	-	-6.56	2.53	-2.59	0.012
OC	-	-	-	-	6.55	2.60	2.52	0.015	7.61	2.90	2.62	0.012
K	-11.82	2.86	-4.14	0.000	-8.14	1.96	-4.16	0.000	-	-	-	-
Settlement	-2.49	4.64	-0.54	0.594	-8.60	3.91	-2.20	0.032	-	-	-	-
Stump-cuts	8.44	1.73	4.86	0.000	9.66	1.98	4.88	0.000	9.29	2.07	4.49	0.000
Coarse Sand : Settlement	-26.43	6.49	-4.07	0.000	-	-	-	-	-	-	-	-
Coarse Sand: Elevation	-42.80	21.65	-1.98	0.054	-	-	-	-	-	-	-	-
Fine Sand : Settlement	29.44	8.54	3.45	0.001	20.53	7.87	2.61	0.012	-	-	-	-
Fine Sand: Elevation	63.54	23.70	2.68	0.010	-	-	-	-	47.39	22.13	2.14	0.037
Mg :Elevation	-46.20	21.56	-2.14	0.037	-	-	-	-	-	-	-	-
Miombo woodlands: (Intercept)	1.37	4.98	0.28	0.783	15.14	3.76	4.03	0.000	-13.70	10.92	-1.25	0.212
Ca	4.59	4.35	1.05	0.294	-28.68	10.14	-2.83	0.006	-	-	-	-
Coarse Sand	-11.09	5.83	-1.90	0.060	-	-	-	-	-	-	-	-
Elevation	21.15	7.01	3.02	0.003	14.83	8.78	1.69	0.094	25.81	5.77	4.47	0.000
Elevation^2	-39.61	6.45	-6.14	0.000	-28.49	6.28	-4.53	0.000	-33.21	5.98	-5.55	0.000

OC	12.08	5.18	2.33	0.022	-	-	-	-	-	-	-	-
K					21.26	8.94	2.38	0.019	26.72	12.72	2.10	0.038
pH	16.89	5.81	2.91	0.005	-		-	-	-	-	-	-
Silt	-8.07	3.79	-2.13	0.036	-		-	-	-	-	-	-
Road	0.07	6.25	0.01	0.991	-		-	-	-	-	-	-
Settlement	13.11	6.29	2.09	0.040	-		-	-	54.33	24.01	2.26	0.026
Stump-cuts	16.18	5.23	3.09	0.003	-		-	-	-	-	-	-
Ca: Elevation					49.88	17.63	2.83	0.006	-	-	-	-
Ca: Stump-cuts	-28.41	9.25	-3.07	0.003	-	-	-	-	-	-	-	-
Coarse Sand: Elevation	20.09	9.30	2.16	0.033	-	-	-	-	-	-	-	-
OC: Road	-20.43	8.66	-2.36	0.020	-	-	-	-	-	-	-	-
K: Elevation	-	-	-	-	-41.63	14.19	-2.93	0.004	-	-	-	-
pH: Settlement	-32.45	12.75	-2.55	0.012	-	-	-	-	-64.23	28.04	-2.29	0.024
Silt :Road	24.61	7.26	3.39	0.001	-	-	-	-	-	-	-	-

PAPER II

Does the abundance of dominant trees affect diversity of a widespread tropical woodland ecosystem in Tanzania?

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ABSTRACT

Dominant woody species can determine the structure and composition of a plant community by affecting environmental conditions experienced by other species. We explored how dominant tree species affect the tree species richness, diversity, evenness and vertical structural heterogeneity of non-dominant species in wet and dry miombo woodlands of Tanzania. We sampled 146 plots from eight districts with miombo woodlands, covering a wide range of topographic and climatic conditions. We recorded 217 woody plant species belonging to 48 families and 122 genera. Regression analysis showed significant decreasing linear associations between tree species richness, species profile index of the non-dominant and the relative abundance of the dominant tree species (*Brachystegia spiciformis* and *Brachystegia microphylla* in wet, and *Brachystegia spiciformis* and *Julbernardia globiflora* in dry miombo woodlands). Shannon diversity and evenness had strong non-liner negative relationships with relative abundance of dominant tree species. A large number of small individual stems from dominant and non-dominant tree species suggesting good regeneration conditions, and intensive competition affecting survival. We suggest that dominant miombo tree species are suppressing the non-dominant miombo tree species, especially in areas with high recruitments, perhaps because of their important adaptive features (extensive root systems and ectomycorrhizal associations), which enhance their ability to access limited nutrients.

Key words: Coexistence ▪ Heterogeneity ▪ Richness ▪ Structure ▪ Tree species

INTRODUCTION

Dominant plant species may regulate surrounding environment to influence other plant species diversity and composition (Angelini *et al*. 2011, Peh *et al*. 2011). According to Grime (1998), ecosystem properties, such as biomass production and diversity, are determined by the traits of the dominant species. Dominant plant species are termed foundation species if they determine the structure and composition of communities at local and regional scales (Caro 2010, Dayton 1972, Ellison *et al*. 2005). However, increasing abundance of the dominant plant species may have contrasting effects on co-occurring species (Dickson & Gross 2013). For example, a *Gilbertiodendron dewevrei*-dominated forest at Ituri reserve in the Democratic Republic of Congo had a comparable tree species richness (dbh ≥ 10 cm) with adjacent mixed forest (Djuikouo *et al.* 2014, Makana *et al.* 2004), while tree species richness (dbh ≥ 10 cm) was lower in *G. dewevrei*-dominated forest in Dja Faunal reserve of Cameroon compared with adjacent mixed forests (Peh *et al.* 2014). Removal of dominant plant species may have a significant impact on the remaining species (Dayton 1972), because dominant species can create and maintain habitats that support other taxa of a community (Martin & Goebel 2013, Smee 2012).

Miombo woodlands, dominated by the genera *Brachystegia* and *Julbernardia*, are the most extensive (range: 2.7–3.2 million km^2) deciduous woodland type in south-central and East Africa (Campbell *et al.* 1996). However, plant species structure and composition in miombo woodlands has recently changed rapidly due to anthropogenic activities, such agricultural expansions, and local-climatic variability in the region (Frost 1996, Spinage 2012). These changes may cause decline in species richness or abundance and consequently influence species recruitment patterns and succession (Backéus *et al*. 2006). For example, intensive removal of species of *Brachystegia* and *Julbernardia* , which are associated with ectomycorrhizas, have deep roots, and produces slowly decomposing litter (Frost 1996), may affect other species recruitment and subsequent succession. Moreover, dominant woody species in miombo woodland often have high basal area and above-ground biomass, which are important in carbon cycling and other regulatory functions of the woodland (Munishi *et al.* 2010, Ryan & Williams 2010). Yet there is limited information on how these dominant species interact with non-dominant woody species and affect community properties.

In this study we explored the relationships between the abundance of dominant miombo tree species richness, evenness, diversity and vertical structural heterogeneity of non-dominant tree species in wet and dry miombo woodlands. Although resprouting from surviving stems and root stocks is the main form of regeneration in miombo woodlands (Chidumayo 2013), the dominant tree species from the genera *Brachystegia* and J*ulbernardia* are known to have low recovery rates after major disturbances because of their low dispersal ability and short-lived seeds (Frost 1996). A previous study suggests that a change in the abundance of dominant plant species may cause changes in the growth patterns of non-dominant and their resource acquisition strategy (Tilman 1985). We hypothesise (1) that there will be a negative relationship between the relative abundance of dominant species (dbh ≥ 5 cm) and the species richness, diversity, evenness and vertical structural heterogeneity of non-dominant tree, because dominant miombo tree species can suppress other tree species after escaping the 'fire trap' (at 3-6 m height, Frost 1996), (2) anthropogenic disturbances will reduce the negative effects of species dominance on Shannon diversity, evenness and vertical structure heterogeneity because frequent disturbance tends to promote plant species diversity in tropical forests (Connell 1978).

MATERIALS AND METHODS

Study area

Miombo woodlands occupies about 90% of forested land from the north-west to the central, and along the eastern coast to regions further south in Tanzania (White 1983). It occupies a wide range of altitude (10–2000 m asl) and climate (mean annual rainfall: 500–1400 mm, mean annual temperature: 15°C–30°C; Frost 1996). Similar ecosystems occur in North-Central and West Africa (Sudanian or Guinea savanna woodlands), but unlike miombo woodlands they lack the dominance of the genera *Brachystegia* and *Julbernardia*. Instead they are dominated by *Isoberlinia* among others, mainly from Caesalpiniaceae (Ernst 1988, Frost 1996).

Miombo woodlands occurs on nutrient-limited soils and at various macro-and micro-climate, and experiences high disturbance that influences its vegetation structure and compositions (Campbell *et al.* 1996). They are categorized as wet miombo woodlands in areas with above 1000 mm or dry in areas with less than 1000 mm mean annual rainfall (Frost 1996, Munishi *et al.* 2011, White 1983). Tree canopy cover varies from closed to open, with closed canopy in wet and open canopy in dry miombo woodlands (Frost 1996). The maximum height of mature tree canopies range between 18–27 m (Frost 1996, Malimbwi *et al.* 1994).We used AFRICLIM, which is a high-resolution climate projections dataset for Africa (Platts *et al.* 2014) to categorize miombo woodlands into wet and dry miombo woodlands (Table 1).

We surveyed miombo woodlands located in Chunya, Hanang, Iringa Rural, Kilolo, Kilombero, Mufindi, Mbeya Rural and Mbozi districts (Figure 1). The districts were selected to represent a wide range of climatic conditions in miombo woodlands, and within each district, miombo woodlands were selected to capture a wide range of topographic gradients (Table 1). We surveyed randomly positioned plots along altitudinal gradients in each district between May 2011 and March 2012, and a total of 48 and 98 plots were measured in wet and dry miombo woodlands, respectively.

Data collection

We used rectangular plots of 20 × 40 m for the vegetation survey in wet and dry miombo woodlands (Shirima *et al.* 2014). Rectangular plots were preferred over circular because they are widely used in vegetation surveys and suitable for capturing variations in heterogeneous environments (Goslee 2006, Scott 1998, Stohlgren *et al.* 1995). Plots were laid systematically along altitudinal gradients, at 400-m inter-plot distance to avoid within-site spatial autocorrelation. Inter-plot distances of 100 m to 1 km have previous been used for vegetation surveys in miombo woodlands (Banda *et al.* 2006, Munishi *et al.* 2011). We used a hand-held Garmin Map76cx GPS to record the geographical location and altitude of each plot.

We measured tree stem diameter at breast height (dbh), tree height, and recorded species identity in each of the 146 plots (total 11.68 ha). Multi-stemmed individuals branching below 1.3 m were treated as separate individual stems. Tree heights were measured using a calibrated wooden rod and a Suunto hypsometer. We counted the number of stumps after tree felling in each plot and estimated the distance (km) from the nearest access road as indicators of disturbance from human activities. We identified tree species in the field where possible; otherwise, voucher specimens were collected and later identified at the Tanzania National Herbarium in Arusha.

Statistical analysis

We estimated the relative abundance of each species from individual species basal area divided by the total basal area of all species. We used an abundance distribution curve to identify the two most abundant species in wet and dry miombo woodlands, and derived two species groups (dominants and non-dominants) according to their relative abundance (Grime 1998).

Tree species were ranked by their relative abundance in ascending order and cumulative abundances for each species, where 100% frequency means that the species is present in all plots and 100% cumulative abundance corresponds to the most abundant species (Mariotte *et al.* 2013). In each woodland type, two tree species were grouped arbitrarily as dominant (combined frequency greater than 90% and highest cumulative abundance), and the remaining tree species as non-dominants (Grime 1998, Mariotte *et al.* 2013). Tree species richness were estimated as the total number of tree species, tree species diversity using Shannon's diversity index (Shannon 1948), and evenness using Pielou's index (Pielou 1969), in the non-dominant group in each plot. Since species richness is highly sensitive to sample size (Chao *et al.* 2014), we calculated species rarefactions (using the Mao Tau rarefaction) to compare the two woodland types and estimated species richness of the non-dominants using Chao 2 estimator in EstimateS 8.2.0 (Colwell 2012).

We estimated the vertical structural heterogeneity of the non-dominant tree species, using the species profile index (H_{sp}: Lei *et al.* 2009, Pretzsch 1996). This index is derived from the Shannon diversity index (*H*), and is based on grouping tree species into different height classes in a stand. These classes were defined relative to the height of the tallest tree in a stand (Class 1: within 81%-100% of the tallest tree, Class 2: 50%–80% of the tallest tree, Class 3: <50% of the tallest tree, Pretzsch 1998). Individual tree heights were allocated to their appropriate classes, and *Hsp* is the proportion of each individual species occurring in the three classes, relative to the total number of trees species in the plot, as follows:

$$H_{sp} = -\sum_{i=1}^{S} \cdot \sum_{j=1}^{B} \begin{cases} p_{ij} \times lnp_{ij} \quad if\ p_i > 0 \\ \qquad\qquad . \\ \qquad otherwise\ 0 \end{cases}$$

Where H_{sp} = species profile index, *S* = tree species richness, *B* = number of height classes (3), p_{ij} = proportion of species *i* in $class_j$.

The species profile index varies with the number of tree species and classes. To compare plot values therefore, we calculated a relative measure of the species-profile index (RH_{sp}) in each plot:

$$RH_{sp} = \frac{H_{sp}}{H_{spMax}} \text{ where } H_{spMax} = \ln(S \times B)$$

Where H_{sp} = species profile index and H_{spMax} = maximum species profile index, respectively.

We used generalized least square regression to fit separate models of tree species richness, Shannon diversity, evenness and the relative species profile index as response variables against the relative abundance of the dominant tree species, disturbance (distance from nearest access road and number of stumps) and interactions between disturbance and relative abundance of the dominant tree species as predictor variables. Exploratory analysis indicated non-linear relationships between tree richness, Shannon diversity, evenness and disturbance (distance from nearest access road) and the relative abundance of dominant tree species were therefore fitted using quadratic terms. Generalized least square models were preferred over multiple linear regressions to account for high heterogeneity among predictors in the data set caused by large variation among different areas sampled (Zuur *et al.* 2009). Each model was fitted by including one nominal weight (miombo woodland type) as a variance-covariate structure using restricted maximum likelihood (RML), because RML estimates stable variance components (Zuur *et al.* 2009). We validated the final models and assessed their goodness–of-fit by observing the residual patterns (Zuur *et al.* 2010). All statistical analyses were done with the R software, version 3.1.0.

RESULTS

A total of 217 woody plant species (dbh ≥ 5 cm) from 48 families and 122 genera were recorded in 146 plots, amounting to a sampled area of 11.68 ha (Table 1, Appendix 1). The richness and the Shannon diversity of the non-dominant tree species were significantly higher in wet than in dry miombo woodlands (Table 1, 2). However, species rarefaction curves showed a similar pattern in species richness between wet and dry miombo woodlands, with slightly higher estimated tree richness in wet than in dry miombo woodland (Chao2 estimator, Figure 2a, b). Moreover, stem density and basal area of the non-dominant tree species were significantly higher in wet than in dry miombo woodlands (Table 2). The two most abundant species in wet miombo woodland were *Brachystegia spiciformis* Benth. and *Brachystegia microphylla* Harms, while *Brachystegia spiciformis* and *Julbernardia globiflora* (Benth.) Troupin dominated the dry miombo woodland, all from Caesalpiniaceae (Appendix 1, Figure 3a, b). Dominant tree species represented 37% and 45% of all tree stems in wet and dry miombo woodland, respectively (Table 2). In general, there was a relatively high dominance of small trees of both dominant and non-dominant tree species in the woodlands. Moreover, there were few large individual trees with dbh >50 cm of the dominant tree species and none of non-dominant tree species (Figure 4).

Tree species richness was negative and linearly related to the relative abundance of the dominant tree species (P = 0.03, Table 3, Figure 5a), and had a hump-shape relationship with disturbance (distance to nearest access roads; P = 0.001, Table 3, Figure 5b). Tree species Shannon diversity had a negative non-linear relationship with relative abundance of the dominant tree species (P = 0.001, Table 3, Figure 5c). However, a significant interaction between relative abundance and disturbance shows that disturbance to some extent modified this relationship (P = 0.005, Table 3, Figure 5d): at high disturbance the relationship became significantly less negative compared to at low and medium disturbance. Tree species evenness had a non-linear negative relationship with the relative abundance (Table 3, Figure 6a). However, a significant interaction between relative abundance and disturbance shows that disturbance to some extent modified this relationship (P = 0.001, Table 3, Figure 6b): as was the case with diversity, at high disturbance the relationship became significantly less negative compared to at low and medium disturbance (Table 3, Figure 6b). Tree species profile index had a negative linear relationship with the relative abundance of the dominant tree species (P = 0.001, Table 3, Figure 6c). There was a significant interaction between the relative abundance of the dominant tree species and disturbance (P = 0.034, Table 3, Figure 6d): at high disturbance, there was no relationship between species profile index and disturbance whereas there was significant negative relationships at low and medium disturbances.

DISCUSSION

We found negative relationships between tree species richness, Shannon diversity and evenness, and the relative abundance of dominant tree species in both wet and dry miombo woodlands. In habitats with intermediate resource levels, competition among dominant plant species tends to outweigh their facilitation effects on other plant species (Angelini *et al.* 2011, Bertness & Callaway 1994, Huston 1979). Also high rates of biomass production by the dominant tree species can constrain space and nutrient availability to other plant species (Grime 1998). Previous studies have shown that re-sprouting from stems and root suckers are the main forms of tree species regeneration in miombo woodlands (Backéus *et al*. 2006, Chidumayo 2013). Our results indicate that the mean stem basal area of dominant tree species was slightly lower than that of non-dominant tree species in the two woodland types. Both non-dominants and dominants had a high number of stems in the low diameter size classes, which may indicate a good regeneration but also intensive competition between dominants and non-dominants in miombo (Backéus *et al*. 2006). In addition, there were more large stems of dominant than non-dominant species, perhaps due to selective harvesting. The increase in canopy size and biomass of the large-stemmed dominants may suppress non-dominant species (Munishi *et al*. 2010). Dominant miombo tree species can exploit limited soil nutrients more effectively than non-dominants because they have an extensive ectomycorrhizal root systems (Frost 1996), which enhances their biomass production (Bâ *et al.* 2012, Diédhiou *et al.* 2005, Frost 1996). Nevertheless, our results suggest a good recovery, particularly after selective harvesting, which is the main anthropogenic disturbances factor in miombo woodlands (Backéus *et al*. 2006, Chidumayo 2013).

We found a hump-shaped pattern between Shannon diversity and the relative abundance of the dominant tree species, and the interactions between relative abundance of the dominant tree species and disturbance (number of stumps). This may imply that the influence of disturbance on biotic interactions is determined by disturbance intensity (Connell 1978). However, the dominant tree species can assimilate nutrient, such as extractable phosphorus and water, throughout the soil profile and store considerable quantities of carbohydrates over long periods, thereby buffering the system against losses through fire, herbivory and year-to-year fluctuations in climate (Bâ *et al*. 2012, Chidumayo & Gumbo 2010, Munyanziza 1994). Although, it is well established that plant species diversity in miombo woodlands is shaped by historical disturbances (Dewees *et al.* 20011, Frost 1996, Runyan *et al.* 2012), we did not have adequate estimates of disturbances, especially those that are more linked to dominant tree species. Thus, further studies are required to disentangle the underlying mechanism for the observed hump-shaped pattern.

We found a non-linear relationship between tree species richness and disturbance (distance to access road), which suggests that vegetation in plots near the road are recovering faster after disturbance compared to plots that are far from access road. A previous study has documented that there is intensive harvesting of trees along roads, targeting tree species suitable for charcoal and timber production (Ahrends *et al*. 2010, Schwartz & Caro 2003). We found a negative non-linear relationship between Shannon diversity, evenness and relative abundance of the dominant tree species at low disturbance (low number of stumps), suggesting that disturbance can also reduce tree species diversity (Connell 1978). Apart from selective harvesting, other forms of disturbance such as frequent fires have impact on plant diversity in miombo woodlands (Frost 1996). For example, previous results from fire experiments in miombo woodlands of Zambia have shown that disturbances from fire plays a crucial role in maintaining species diversity and composition in the woodland ecosystem (Trapnell 1959). Moreover, regular fire occurrences promote rapid pulsing of nutrient release from otherwise slowly decomposing litter and herbaceous biomass (Chamshama & Vyamana 2010). Miombo woodlands in Tanzania, like in other parts of Africa, have experienced climatic and anthropogenic disturbances for decades (Campbell *et al.* 1996), which has varying impacts on the species diversity in the woodland ecosystem (Frost 1996, Spinage 2012). Furthermore, our results show that observed tree species richness differ significantly between wet and dry miombo woodland, but the estimated richness (Chao 2) and rarefaction pattern suggested that the wet and dry miombo woodlands may have little difference in tree richness if sampled adequately. The actual observed tree species richness and diversity, was from a wide range of families and genera, similar to previous studies (Banda *et al*. 2006, Munishi *et al*. 2011).

We observed a significant negative relationship between the tree species profile index and the relative abundance of the dominant miombo tree species. This suggests that dominant miombo tree species are supressing the non-dominant tree species and hence dominate the higher canopy stratum (Pretzsch 1998). Moreover, the tree species profile index decreased with increasing relative abundance of dominant tree species at low disturbance (low number of stumps), which further suggest that dominant tree species are supressing the non-dominant tree species. The vertical structure of miombo woodlands is characterized by a uniform canopy of the dominant tree species within single sites, with large areas ranging from a discontinuous shrub layer (Frost 1996) to a homogeneous overstorey canopy. Strong interspecific competition for space between the most dominant tree species and other tree species at different growth stages may result in niche partitioning among tree species (Peterson *et al.* 2013), which could promote vertical size differentiation among trees if exposing the understorey species to more space and light resources.

We found a negative association between tree species richness, Shannon diversity, evenness and profile index of the non-dominant and relative abundance of the dominant tree species. It is possible that dominant miombo tree species out-compete other tree species due to their extensive root systems with ectomycorrhizal associations (Bâ *et al.* 2012, Frost 1996), which enhance their ability to access limited nutrients. This competition effect may be enhanced because these dominants may not be the main targeted in selective logging because of their relatively low preference in charcoal and timber uses (Ahrends *et al.* 2010, Schwartz & Caro 2003). Moreover, dominant miombo tree species are known to have a high recovery rate after mild disturbance or after escaping the ‘fire trap’, because of their ability to coppice from surviving stems or root suckers (Frost 1996). It will likely require further efforts to understand how dominant miombo tree species influence trees species diversity under contrasting local physiographic and anthropogenic disturbance factors.

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TABLES

Table 1. A list of main variables estimated (mean ± SE) from the surveyed wet and dry miombo woodlands in Tanzania. A comparison of the main variables using Mann-Whitney-Wilcox test (U-test) between plots from dry and wet miombo woodlands.

Attributes	**Wet**	**Dry**	**U-test (W)**	**P-value**
Number of plots	48	98	-	-
Temperature ranges (°C)	17.0-24.9	16.4-21.3	-	-
Rainfall ranges (mm yr^{-1})	1012-1855	651-996	-	-
Elevation range (m)	280-1932	1030-2012	-	-
Disturbance (Distance to road (km))	0.1-24.0	0.1-21.7	-	-
Disturbance (Number of stumps)	0-24	0-28	-	-
Basal area (m^2 ha^{-1}; Mean ± SE)	12.3±0.39	9.5±0.73	3109	0.001

Table 2. Structural attributes of non-dominants and dominant tree species of wet and dry miombo woodlands from eight districts (Figure 1) in Tanzania. A comparison of estimates, tree species structural characteristics using Mann-Whitney-Wilcox test (U-test (W)) between plots from dry and wet miombo woodlands.

Attributes	**Wet**	**Dry**	**U-test (W)**	**P-value**
Non-dominants				
Tree species richness	159	154	2943	0.01
Shannon diversity index (Mean ±SE)	1.8±0.1	1.59±0.1	2828	0.05
Tree species profile index (Mean ± SE)	0.3±0.02	0.27±0.01	2717	0.13
Stem density (Stems ha^{-1}; Mean ± SE)	593.7±46.5	388.0±26.1	1465	0.001
Basal area (m^2 ha^{-1}; Mean ± SE)	7.7±0.7	5.2±0.4	3089	0.002
Tree maximum height (m)	13.2±0.8	12.6±0.5	2439	0.64
Species relative proportion (%)				
Julbernardia globiflora	12.1	-	-	-
Uapaca kirkiana	-	6.8	-	-
Dominants				
Stem density (Stems ha^{-1}; Mean ± SE)	228.7±38.8	273.0±25.5	1747	0.15
Basal area (m^2 ha^{-1}; Mean ± SE)	4.5±0.7	4.2±0.4	2320	0.89
Tree maximum height (m)	12.9±0.7	12.3±0.5	1706	0.23
Species relative proportion (%)				
Brachystegia spiciformis	22.7	23.2	-	-
Julbernardia globiflora	-	21.6	-	-

Table 3. The relationships between tree species richness, Shannon diversity, evenness, and species profile index of the non-dominants and relative abundance of the dominant tree species in miombo woodlands of Tanzania. Generalized least squares models, showing significant variables ($\alpha \leq 0.05$) only.

Parameters	Estimates	SE	t-value	P-value
1. Response: Richness (Intercept: 9.36)				
Dominants	-3.06	1.03	-2.99	0.003
Disturbance (Distance to road (km))	0.62	0.23	2.73	0.007
Disturbance (Distance to road (km))^2	-0.03	0.01	-3.27	0.001
Wet Vs Dry miombo woodlands	1.83	0.85	2.16	0.033
2. Response: Shannon Index (Intercept: 1.76)				
Dominants	1.01	0.45	2.26	0.025
Dominants^2	-2.38	0.49	-4.87	0.001
Disturbance (Number of stumps)	0.001	0.01	0.06	0.949
Dominants vs Disturbance (Number of stumps)	0.08	0.03	2.85	0.005
3. Response: Evenness (Intercept: 0.79)				
Dominants	0.18	0.11	1.61	0.109
Dominants^2	-0.54	0.13	-4.28	0.001
Disturbance (Number of stumps)	-0.001	0.002	-0.41	0.688
Dominants vs Disturbance (Number of stumps)	0.02	0.007	3.47	0.001
3. Response: Species Profile Index (Intercept: 0.35)				
Dominants	-0.19	0.04	-4.21	0.001
Disturbance (Number of stumps)	-0.004	0.003	-1.43	0.156
Dominants vs Disturbance (Number of stumps)	0.02	0.01	2.14	0.034

FIGURES

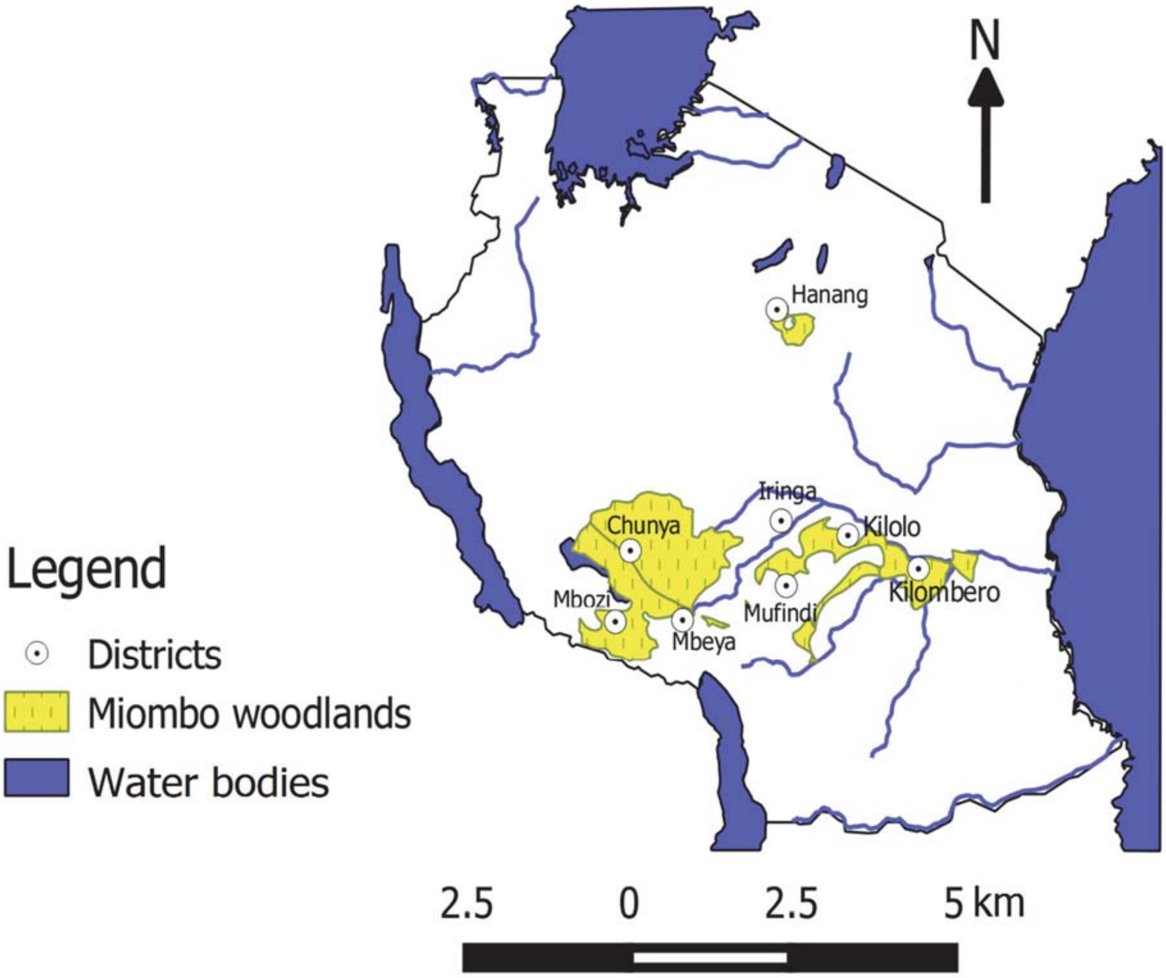

Figure 1. Miombo woodland study locations in Tanzania.

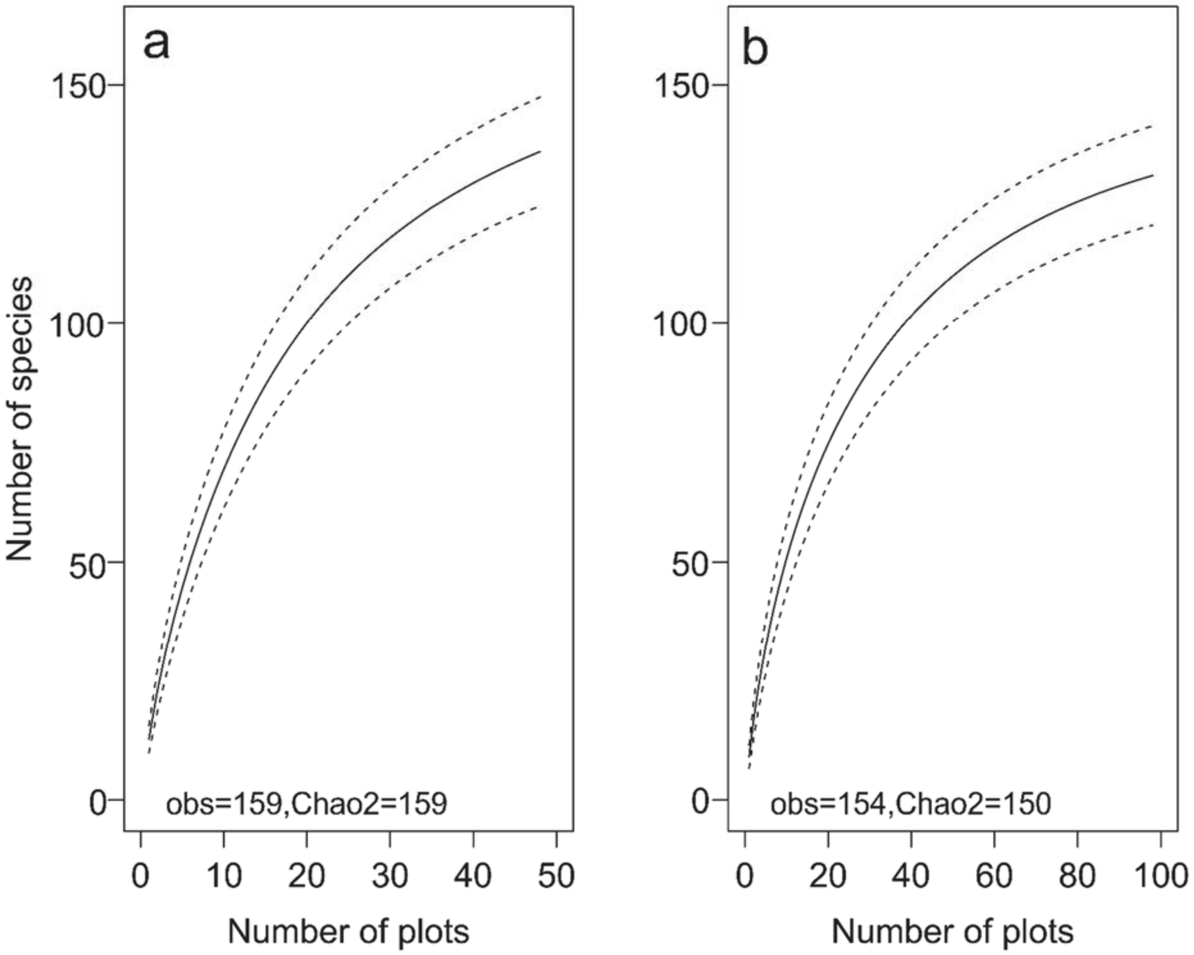

Figure 2**.** Tree species rarefaction curves (Mao Tau function), indicating sampling efforts in wet (a) and dry (b) miombo woodlands sampled plots in Tanzania. The rarefaction curves in solid lines and 95% confidence intervals in dashed line, obs = number of observed species and Chao2 = the estimated species richness from 48 plots in wet and 98 plots in dry miombo woodlands.

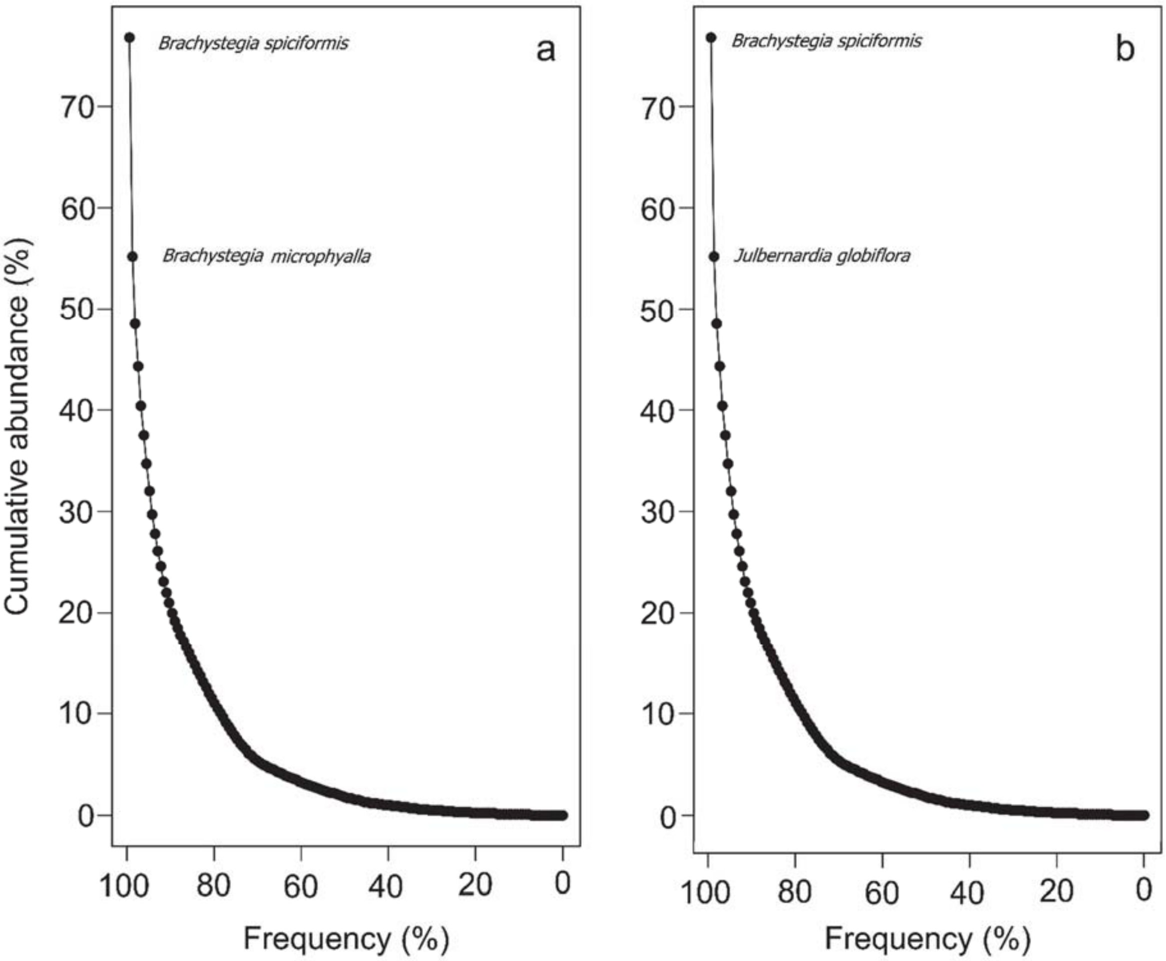

Figure 3. Cumulative abundance as a function of frequency, showing the two most abundant tree species based on their relative basal area for the sampled plots in wet (a) and dry (b) miombo woodlands of Tanzania.

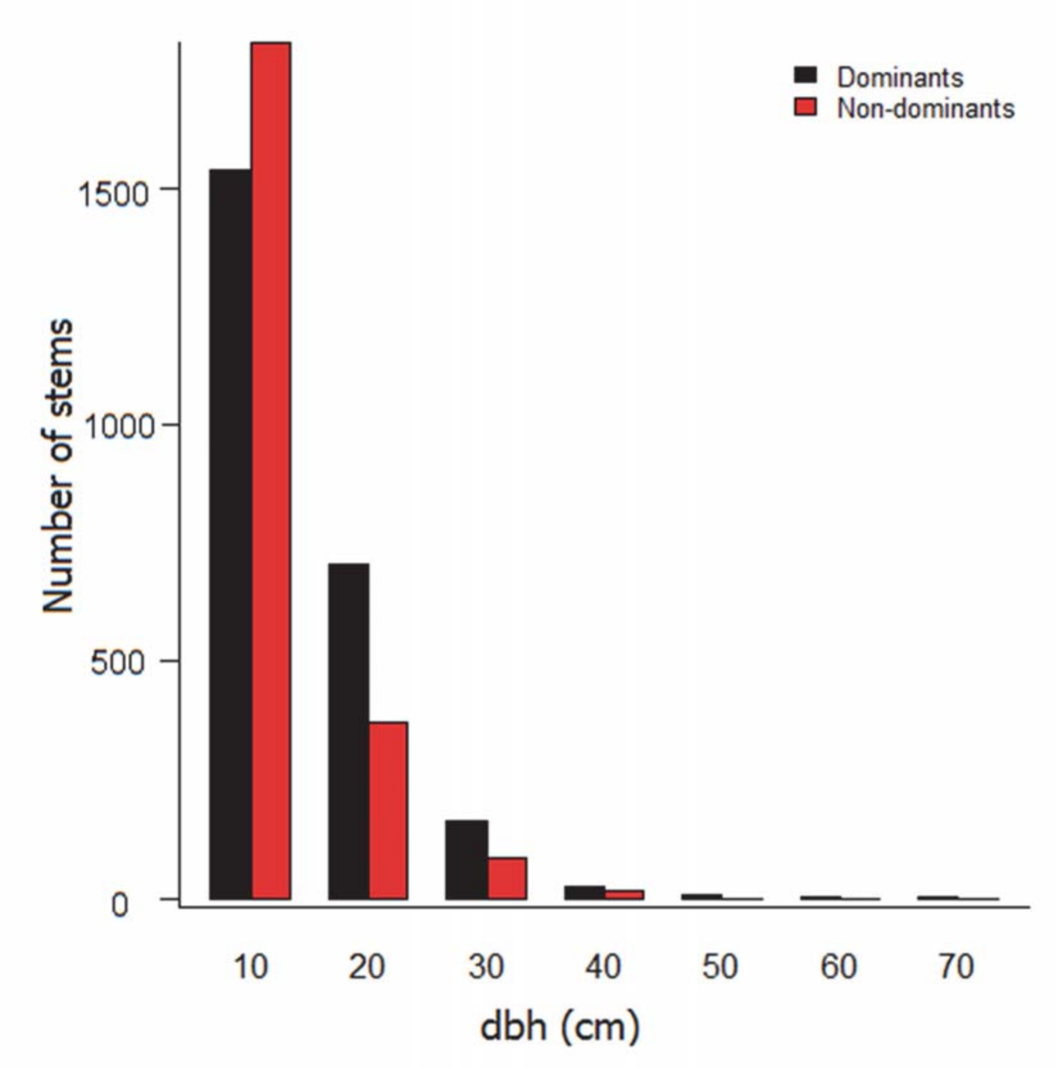

Figure 4. The distribution of tree stems (dbh ≥ 5 cm) in different diameter size classes in miombo woodlands of Tanzania.

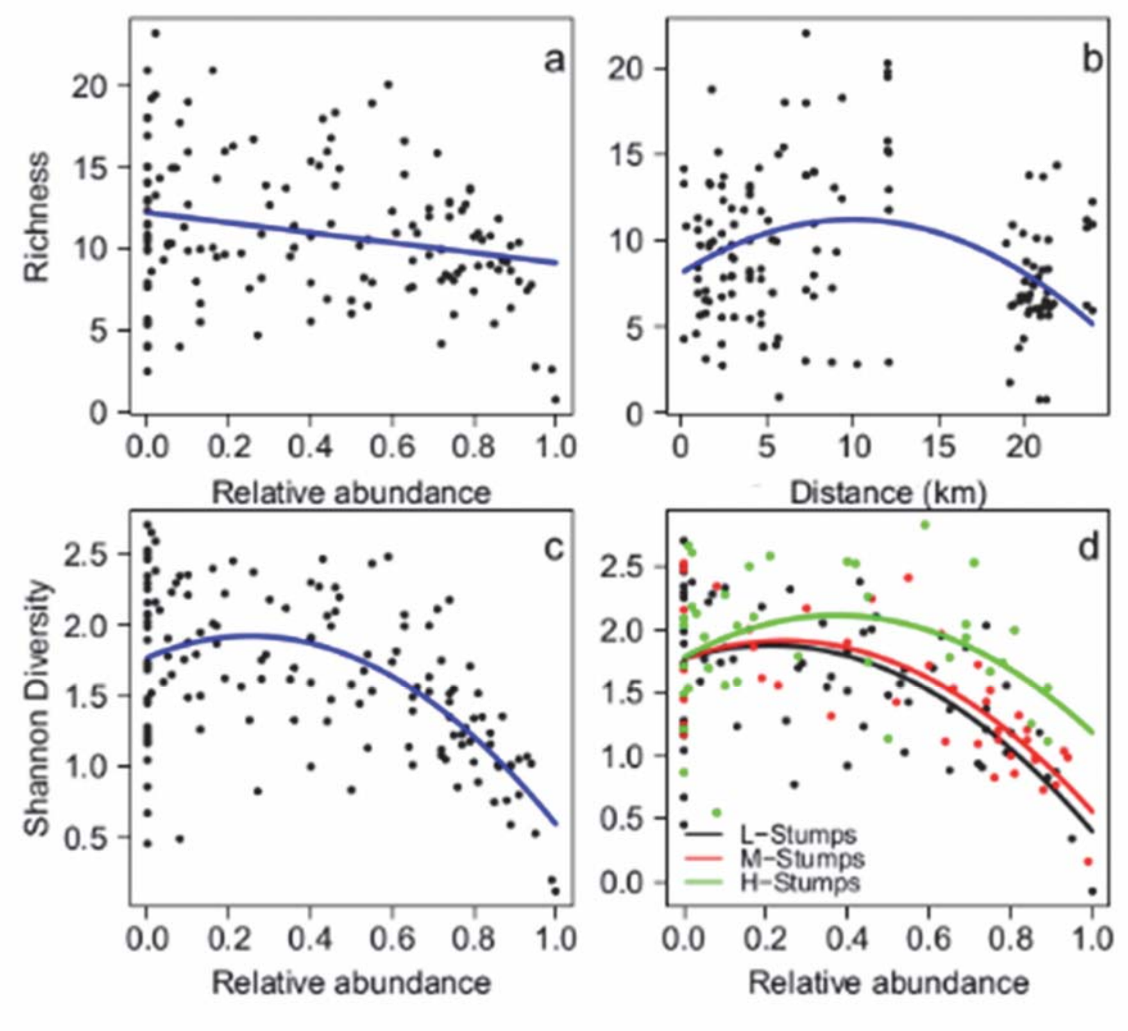

Figure 5. The relationships between non-dominant tree species richness and relative abundance of dominants (a), tree species richness and disturbance (distance from road, (b)), Shannon diversity index and relative abundance of dominants (c), and relative abundance of dominants and the three disturbance levels (d), when all other variables are set to their medians in miombo woodlands of Tanzania. Plots show partial regression lines from generalized least square regression models of the relationships between tree species richness, Shannon diversity and the labelled variables (L-Stumps, M-Stumps and H-Stumps are Low, Medium and High number of stumps, respectively and represent disturbance levels).

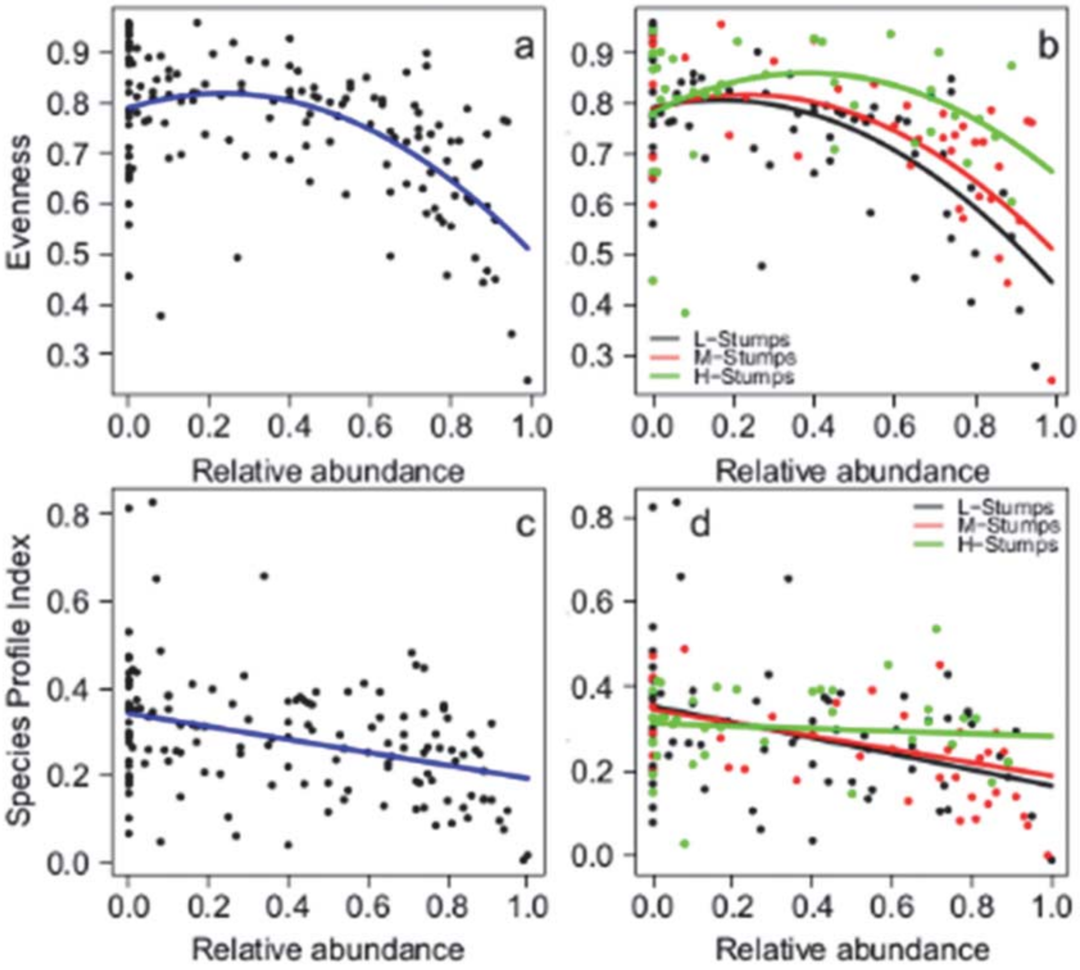

Figure 6. The relationships between non-dominant tree species evenness and tree species relative abundance (a), tree species evenness and relative abundance of the dominants, and the three disturbance levels (b), when all other variables are set to their medians, tree species profile index and tree species relative abundance (c), and tree species profile index and relative abundance of the dominants, and the three disturbance levels (d), when all other variables are set to their medians in miombo woodlands of Tanzania. The plots show partial regression lines from generalized least square regression models of the relationships between tree species evenness, tree species profile index and the labelled variables (L-Stumps, M-Stumps and H-Stumps are Low, Medium and High number of stumps, respectively and represent disturbance levels).

PAPER III

Interactions between canopy structure and herbaceous biomass along environmental gradients in moist forests and dry woodlands of Tanzania.

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ABSTRACT

Diverse forest and woodlands have wide ranges of trees sizes, shapes and canopies that interacts with each other and the environment to facilitate coexistence and biomass production. But, few studies have quantified the interrelations between canopy foliage, herbaceous biomass and environmental gradients. We measured forest structure, herbaceous biomass, physiographic and anthropogenic disturbance in 100 permanent vegetation plots (0.08 ha) in 2012, with the aim of understanding how leaf area index (LAI) and herbaceous biomass (AGB_H) vary along structural and environmental gradients in two important vegetation types in Tanzania. Regression models revealed that structural attributes, environmental and disturbances factors explained about 50% and 20% of variations in LAI and AGB_H in the two vegetation types. Tree richness, tree predominant height in moist forest and miombo woodland, and tree stem density in miombo woodlands had positive relationships with LAI perhaps due to high optimizations of light capture among species of different sizes. Herbaceous biomass was higher under less dense vegetation canopies in miombo woodlands but lower in more species-rich moist forest stands, which in turn tends to have denser canopies. LAI had positive relationship with soil nitrogen in moist forest and negative relationship with soil pH in miombo woodland at high disturbance. Diverse forest have high canopy leaf area, highly productive, and have negative impact on herbaceous biomass. Yet, we have observed complex interactions between LAI, AGB_H, tree sizes, soil nutrients and elevation. Thus, to enhance our understanding of forest and woodlands ecosystem processes, it is important consider both stand structural characteristics, and their interactions with environment and anthropogenic factors.

Key words: Leaf area index ▪ Diversity ▪ Ecosystem functions ▪ Miombo ▪ Anthropogenic-disturbances

INTRODUCTION

Tree species vary in their capacity to use abiotic resources, promoting coexistence among life forms at different growth stages (Kohyama 1993, Ishii et al. 2013). Morphological differences among tree crowns, for example, should enhance the forest community's capacity to exploit light resources (Ashton et al. 2010, Sapijanskas et al. 2014). As forests with high tree diversity are more likely to have individuals with different foliage sizes and shapes, this should facilitate a greater niche partitioning in canopy space (Lowman and Rinker 2004, Ishii et al. 2013, Unger et al. 2013). This in turn should increase the canopy's capacity to harvest light and fix carbon (Reich 2012) regulating stand-scale forest biomass production. However, few studies have explore interrelationships between canopy structure, biomass and tree diversity, especially in the Afrotropics.

Light extinction through multi-layered vegetation canopies creates a strong vertical light gradient and reduces light availability at the forest floor (Gilliam and Roberts 2003). Canopy leaf area is the main regulator of radiation absorption and can block over 95% of visible light from reaching the forest floor underneath dense canopies (Turner 2001). Canopy leaf area shapes microclimate within the forest, with warmer and drier conditions underneath more open canopies(Hardwick et al. 2015). Microclimate, light availability, soil moisture and soil fertility interact to regulate plant growth in sub-canopy layers, including the herbaceous layer (Sagar et al. 2012). But, little is known to what extent canopy structure can affect herbaceous plant growth in tropical forests of Africa and to what extent this potential relationship varies along environmental gradients, including climate, land use and soil nutrients.

Forest and woodland ecosystems in Eastern Africa have been under severe stress, owing to high human population pressure often associated with frequent fires, logging, charcoal production and increased grazing affecting their structure and regenerations (Murphy and Lugo 1986, Campbell et al. 1996, Shirima et al. 2011). Land use and climate change interact to modify natural variability in tree canopy structure. Canopy leaf area declines in response to forest degradation and increases non-linearly with water availability across East Arica's woody ecosystems (Pfeifer et al. 2014). A lack of data limits our understanding of how these two environmental change drivers interact at local scale to shape canopies and hence productivity of woody biomes along soil gradients and how this feeds through to processes at the forest floor.

Here, we analyse how canopy structure and herbaceous biomass vary along biotic and environmental gradients across two dominant forest types in Tanzania. We focus our analyses on tropical dry woodland (Campbell et al. 1996) and moist forests. Miombo woodlands are characteristic for Southern and Eastern Africa (Thomas and Packham 2007), cover extensive areas , featuring deciduous tree assemblages with open canopies. Miombo soils have low nutrient content, are well drained, highly leached, acidic and contain less organic matter (Frost 1996). Moist forests are predominantly evergreen, forming dense canopies and have lower herbaceous cover than miombo woodlands. They occupy wetter climates and more nutrient-rich soils (Thomas and Packham 2007), which in Eastern and Southern Africa often occurs in mountainous and coastal regions (Pfeifer et al. 2012a). We ask, 1) whether forest stand attributes such as tree diversity and size distribution are related to leaf area index (LAI), 2) whether aboveground herbaceous biomass (AGB_H) responds to canopy LAI, and if relationships exist, 3) whether they are modified by environmental conditions and anthropogenic disturbances.

MATERIALS AND METHODS

Study Region

We conducted our study in Hanang and Dirma forest reserves in Tanzania (Figure 1). Hanang forest reserve (forest extent: 58.71 km^2, Figure 1), a central government catchment reserve, spans an elevation range of 1860 - 3418 m (Lat: -4.44º, Long: 35. 40 º). The reserve receives a mean annual rainfall around 750 - 1500 mm at lower elevations and > 2000 mm at higher elevations; mean annual temperature varies between 20 and 25 ºC (Lovett and Pocs 1993). Grasses and thickets dominate the highest elevations and steepest slopes; moist forests with canopy species such as *Albizia gummifera* and *Cassipourea malosana* dominate at mid to high elevations, interspaced irregularly by moorland patches. The forest is characterized by volcanic soils ranging from sandy to humus rich loams in the upland moorlands and upper montane areas (Lovett and Pocs 1993).

Dirma village forest reserve (miombo extent: 63.5 km^2, Figure 1) spans an elevation range of 1800 – 2500 m (Lat: -4.70º, Long: 35. 44 º). Miombo woodland assemblages, characterized by *Brachystegia spiciformis* and *Julbernadia globiflora*, dominate Dirma reserve. The reserve receives approximately 100 - 700 mm rainfall annually, and has mean monthly temperatures of 15 - 30°C (Platts et al. 2014a). Soil nutrients are low and vegetation cover is highly influenced by frequent fires and anthropogenic disturbances, similar to miombo woodland elsewhere in Eastern Africa (Campbell et al. 1996, Scholes et al. 1996). Miombo woodland cover much larger areas than moist forests in Southern and Eastern Africa (2.7 vs. 0.064 million km^2 (Campbell et al. 1996, FAO 2015)). However, miombo woodlands have received less attention in the scientific literature, perhaps because they have low carbon content and biodiversity per unit area (Dewees et al. 2010, Munishi et al. 2010, Shirima et al. 2011).

Vegetation and soil surveys

We surveyed 100 vegetation plots of 20 m × 40 m (60 plots in moist forest and 40 plots in miombo woodland), separated by a minimum distance of 400 m. In each plot, we recorded all individual trees with diameter at breast height (dbh) ≥ 5 cm, and identified each of these trees to species-level. Where species identification was impossible in the field, voucher specimens were collected and identified at Arusha national herbarium in Tanzania. We recorded geographical location and elevation using a handheld GPS (Map76cx). We measured tree height in the field whenever conditions allowed, using a Suunto-hypsometer; the remaining tree heights were estimated using biome-specific height-dbh regression equations, based on our own field data. We recorded the number of tree stumps in each plot as an indicator of anthropogenic disturbance (Baas et al. 2011) (hereafter referred to as DISTURBANCE).

To estimate herbaceous biomass (AGB_H), litter biomass and tree seedling density, each plot was subdivided into eight (10 m × 10 m) subplots. Aboveground herbaceous plant materials (clipped at ground level) and litter materials were collected from 1 m × 1 m quadrats, and tree seedlings (trees below dbh) were counted in 2 m × 2 m quadrats, placed at random within alternate subplots. We recorded the total fresh weight of herbaceous and litter samples in the field, collected a subsamples from the total fresh weights, which were oven dried in the laboratory to a constant weight at 70 ºC for 48 h to obtain dry mass. Dry mass from laboratory samples were then equated to the total fresh weights to obtain the total dry mass per plot.

Soil samples were collected at three different soil depths (0–15 cm, 15–30 cm and 30–60 cm), from the four corners and from the center of the main plot in March 2012. Samples for each depth were aggregated into composites for subsequent analyses. The 300 soil samples were air-dried and sieved through a 2 mm wire mesh and analysed for soil pH (at 1:2.5 soil : H_2O), organic carbon (Walkley-Black method), available phosphorous (Bray II), total nitrogen (Kjeldahl method), potassium and sodium (ammonium acetate 1.0 M pH7.0 extraction) by the laboratory at Seliani Agricultural Research Institute, Arusha, Tanzania. We used the average across the three soil layers for subsequent modelling.

Canopy structure data acquisition

Canopy leaf area index (LAI) was estimated following standard protocols as described in Pfeifer et al. (2012b, 2014) and Pfeifer and Gonsamo (2014). We took 13 hemispherical photographs in each of four subplots (10 m × 10 m) using a Nikon D3100 camera with fish-eye lens, mounted on a 1 m tripod stand. All photographs were taken during the wet season in March 2012. Images were processed using CAN-EYE software version 6.38 (Pfeifer et al. 2012b, Weiss and Baret 2014), which estimates plant area index (as opposed to LAI) since stems, branches and twigs are included in the images (Breda 2003). Tropical dry deciduous and moist evergreen forest are comprised of leaf area as opposed to branches and twigs (Pfeifer et al. 2012b). Furthermore, it is not possible to recognize leaves on the branches, stems and trunk, masking these parts of plant and attempts to correct for invisible leaves aiming for LAI may lead to underestimation of actual LAI (Hardwick et al. 2015). Values of LAI from the four subplots were averaged into a single mean value per plot for subsequent analysis.

Forest stand parameters

Tree richness was estimated as the total number of tree species per plot; stem density was estimated as the number of individual tree stems (dbh ≥ 5cm) in a plot per ha. We used Pielous's index (J) as an estimate for tree species evenness (Pielou 1969) and Shannon diversity index (H′) for tree species diversity (Shannon 1949). We estimated the quadratic mean diameter (QMD) for all trees with DBH > 5 cm as $QDM = \sqrt{\left(\overline{d}^2 + S^2\right)}$, where $\overline{d}^2$ is the square root of arithmetic mean diameters and S^2 is the variance of tree diameters in a plot. QMD has a strong correlation to stand volume and basal area, and is a preferred measure of stand structure over the arithmetic mean diameter (Van Laar and Akça 2007). We estimated predominant height (PDH) of the forest and woodland stands as the average height of the 100 tallest trees per hectare, a selection of single tallest trees in each subplot (West and West 2009).

Predictors were categorised into stand structural variables (Tree seedling density, richness, evenness, Shannon diversity, stem density, predominant height (PDH), quadratic mean diameter (QMD)) and environmental attributes (Soil organic carbon, phosphorous, nitrogen, potassium, sodium, pH and elevation) for subsequent modelling. All predictor variables used in the analysis and their units of measurement are shown in Table 1.

Modelling vegetation structure and links to environmental drivers

We used generalized linear models (GLM) with Gaussian distribution error and identity (Crawley 2009, Zuur et al. 2009) to explore the relationships between stand structural attributes and LAI, environmental gradients and LAI, stand structural attributes including LAI and

AGB_H, environmental gradients and AGB_H (see Table S1). We developed these models for moist forest and miombo woodlands, separately.

In a first step, we fitted two subset models focussing on: (1) solely using structural variables as predictors of either LAI or AGB_H and (2) solely using environmental variables as predictors of either LAI or AGB_H. Each of these models included DISTURBANCE as additional predictor and first term interactions between all predictors. In a second step, (3) we combined both structural and environmental predictors, DISTURBANCE and first term interactions between predictors into one single model. Data exploration indicated nonlinear relationships between LAI, tree richness and predominant height, and so these predictors were fitted using quadratic terms (Table S1).

We used Pearson correlation (r) and variance inflation factor (VIF) to assess collinearity among structural and among environmental predictor variables (Dormann et al. 2013). In cases of high collinearity between two predictor variables ($|r| > 0.5$ and $VIF > 3.0$), we retained only those predictors showing a stronger univariate relationship with the response variable (Zuur et al. 2010). Final global models are detailed in Table S1.

We used backward-forward stepwise model selection based on the Akaike Information Criterion to identify optimal models from the global models (Murtaugh 2009, Zuur et al. 2009). The relative contributions of predictor variables were determined by the reduction in explained deviance (D^2 in %) for both within model predictors and optimal models (Crawley 2009). We used likelihood ratio tests to compare the reduced subset models with unreduced models (Zuur et al. 2009). We validated residual spread and estimated the predictive error using leave-one-out cross-validation (James et al. 2013), implemented using the *"cv.glm"* function in R (Canty and Ripley 2014), in conjunction with the mean squared error of prediction (Quinn and Keough 2002). Moreover, we used paired Mann-Whitney-Wilcox tests between observed and predicted LAI and AGB_H to assess the significance of mean squared error of prediction as a measure of model bias (Quinn and Keough 2002).

RESULTS

Stand structural attributes

We identified 97 tree species from 46 families and 62 species from 29 families in moist forest and miombo woodlands, respectively. Both Shannon diversity (Table 1, $U = 1500$, $P < 0.03$, $R^2 = 0.21$) and tree richness (Table 1, $U = 1567$, $P < 0.001$, $R^2 = 0.26$) differed significantly between both forest types. Both forest types differed significantly in LAI, AGB_H, soil pH, soil phosphorus, soil nitrogen, soil potassium and soil sodium (Table 1, U: $P < 0.001$ and $R^2 > 0.30$ in all cases).

Structural and environmental influences on LAI

The combined model explained 76% of variations in LAI of moist forests outperforming all other models. LAI of miombo woodland was best predicted (66% of variation explained) by the model relying on structural attributes (Table 2). Although the combined model explained 82% of variations in LAI in miombo woodland, the amount of deviance explained by the full (unreduced) model was higher and significant ($P = 0.01$) than the reduced model (Table 2), therefore was not considered as an optimal model.

Canopy leaf area increased nonlinearly with predominant height in both forest types (Table 2, Figure 2). Additionally, the LAI of moist forest increased strongly with tree richness and weakly with DISTURBANCE but decreased with soil nitrogen. LAI increased with soil nitrogen and decreased with soil pH under high DISTURBANCE (Table 2, Figure 2). The LAI of miombo woodland increased with stem density (Table 2).

Structural and environmental influences on AGB_H

The combined model explained around 25% of variations in AGB_H of moist forest, while model relaying on environmental attributes explained 27% of variation in miombo woodlands (Table 3). AGB_H in moist forests decreased linearly with tree richness, followed an inverted hump-shape curve in response to LAI (Table 3, Figure 3), and decreased with LAI at lower elevations whilst increasing with LAI at higher elevations (Figure 3). Aboveground herbaceous biomass in miombo woodland increased linearly with soil nitrogen, decreased linearly with both soil pH and DISTURBANCE (Table 3), and showed a monotonic increase with soil pH under high DISTURBANCE (Figure 3).

DISCUSSION

Structural and environmental influences on LAI

Plant growth and biomass production in forests are influenced by tree foliage density, tree sizes and their ability to intercept light and atmospheric nutrients (Reich 2012). We found substantial differences in structural attributes and environmental factors between moist forest and miombo woodlands of Tanzania, and demonstrate that they affect forests differently.

Stand structural attributes and environmental factors explained over 50% variation in LAI and nearly 20% of variations in AGB_H, in both vegetation types, which suggests that forests and woodlands respond to the environment based on morphological and physiological adaptations (Gilliam and Roberts 2003). We show that LAI increases with tree richness in both vegetation types and with tree stem density in miombo woodland, similar to findings in tropical lowland and montane forests in Ecuador. This finding lends support to the hypothesis of resource use complementary and higher productivity in more diverse forests (2013).

We also show that while LAI increases with tree height, this relationship is not linear and LAI saturates or decreases for forest stands featuring larger trees, a pattern we find for both, moist forests and miombo woodland (Table 2 and Fig. 2). Similar findings were reported for Acadia forest in the US (2010), where the gradual decline in leaf area index with tree height was attributed to severe branch abrasion and loss of new foliage as trees grow taller [39]. Yet, our finding contradicts findings from a global meta-analysis, which report positive, non-saturating relationships between remotely sensed LAI and field-measured tree height across broadleaf forests and savanna (2013). The difference in findings may partly arise from the different spatial scales and resolutions used in Yuan et al.'s study, and the additional uncertainty introduced by different instruments used to estimate LAI at different sites. However, it should also be noted that LAI estimated from hemispherical images will saturate in high-biomass biomes due to methodological constraints (Jonckheere et al. 2004).

Our data also showed an interaction effect of DISTURBANCE with soil attributes on LAI of moist forests. LAI increased with soil nitrogen and decreased with soil pH under higher DISTURBANCE suggesting that anthropogenic disturbances can influence forest canopy at different levels of soil nutrient availability. However, more detailed experimental studies would be required to disentangle anthropogenic effects such as logging from those of soil and other stand attributes on the forest canopy and its productivity (Das et al. 2011).

Structural and environmental influences on AGB_H

As the herbaceous layer is likely to affect soil, surface fluxes, and ground-dwelling organisms, understanding how canopy structure interacts with this layer can aid in understanding the response of sub-canopy biodiversity and ecosystem processes to climate and land uses (Pfeifer et al. 2012b, Unger et al. 2013).

Previous studies suggested that trees can benefit herbaceous vegetation through amelioration of harsh environmental conditions and increase in nutrient availability (Scholes and Archer 1997). However, trees have also been reported to suppress herbaceous biomass by altering light availability and soil fertility on the forest floors (Gilliam 2007).

AGB_H in the moist forest decreased with tree species richness, whilst LAI increased with tree richness. We interpret this as tree richness suppressing AGB_H by increasing canopy density thereby reducing light availability at the forest floor limiting herbaceous plant growth. Patterns are complex, though, as indicated by the U-shaped association between AGB_H and LAI. The slight increase in AGB_H with LAI at high elevations suggests a decline in the impact of light limitation due to declines in tree growth at higher altitudes (Coomes and Allen 2007).

In miombo woodland, herbaceous biomass was higher under denser vegetation canopies suggesting an amelioration of harsher environments characterized by either drought or frequent fires. Miombo features open canopies, and sub-canopy plant growth is likely to be soil nutrient and water-limited rather than restricted by light availability. Unsurprisingly, disturbance, which further opens up miombo canopies and prevents canopy closure, interacts with soil nutrients and LAI to regulate biomass in the herbaceous layer. Again, patterns are complex and require further studies and experiments. Soil nutrient from decaying tree stump or ring-backed roots and deposits from biomass burning have been associated with increased herbaceous biomass in miombo woodland (Frost 1996, Runyan et al. 2012). Meanwhile, human activities may affect AGB_H depending on disturbance type (i.e. grazing and fire).

CONCLUSIONS

Tree diversity and tree size affect canopy structure in both, moist forests and miombo woodland of Tanzania. Our findings provide support for the hypothesis of niche complementarity, with higher tree diversity enabling a better use of canopy space optimizing light capture of forest canopies. As canopy leaf area is a good indicator of photosynthetic capacity, diverse forests are more productive. Denser forest canopies, on the other hand, should have negative impact on herbaceous biomass (Scholes and Archer 1997). Our data provide little support for this assumption, but rather suggest complex interrelationships between environmental and structural parameters to be at work. Anthropogenic disturbance modifies both canopy structure as well as herbaceous biomass, but interacts with environmental gradients, like soil nutrient in our study, complicating analyses. Thus, to enhance our understanding of forest and woodlands ecosystem processes, it is important consider both stand structural characteristics and their interactions with environment and anthropogenic factors. To reveal the particular contributions of soil, climate, light and disturbance drivers probably requires multi-factorial experiments in the field.

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TABLES

Table 1 Comparison of stand structure attributes and environmental variables (Mean ± SE) measured and their corresponding Mann-Whitney-Wilcox test showing the differences between moist forests (N = 60 plots) and miombo woodlands (N = 40 plots) of Hanang district in Tanzania.

Variable	**Forest types**		**Mann-Whitney-Wilcox**		
	Forest	Miombo	Estimate	*P*	*R*^{2}
Structural attributes					
Leaf Area Index (LAI)	1.39 ± 0.1	0.93 ± 0.07	2299	0.001	0.77
Herbaceous Biomass (Mg ha^{-1})	1.27 ± 0.1	0.91 ± 0.10	1675	0.001	0.33
Litter Biomass (Mg ha^{-1})	2.54 ± 0.1	1.82 ± 0.2	1675	0.001	0.33
Seedling density ha^{-1}	3758.3± 382.1	3850± 222.31	1055	0.309	0.10
Shannon diversity Index	1.54 ± 0.1	1.35 ± 0.1	1500	0.034	0.21
Richness	8.85 ± 0.6	6.65 ± 0.4	1567	0.001	0.26
Evenness	0.73 ± 0.0	0.74 ± 0.0	1313.5	0.426	0.08
Stem density (trees ha^{-1})	722.08 ± 55.6	471.88 ± 30.4	1608.5	0.004	0.29
Predominant-Height (PDH; m)	13.66 ± 0.1	9.269 ± 0.5	1789	0.001	0.41
Quadratic mean diameter (QMD;	19.54 ± 1.3	14.97 ± 0.7	1497	0.036	0.21
Environmental attributes					
Elevation (m)	2186.92 ± 21	1630.33 ± 3.1	2400	0.001	0.84
Soil pH	5.05 ± 0.0	4.64 ± 0.0	2388	0.001	0.84
Soil Organic carbon (%)	1.87 ± 0.1	1.39 ± 0.1	1825	0.001	0.44
Soil Phosphorous (mg/Kg)	3.46 ± 0.1	6.40 ±0.2	45	0.001	0.81
Soil Nitrogen (%)	0.19 ± 0.0	0.03 ± 0.0	2398	0.001	0.84
Soil Potassium (meq/100g)	1.12 ± 0.3	0.05 ± 0.0	2383	0.001	0.83
Soil Sodium (meq/100g)	0.11 ± 0.0	0.06 ± 0.0	2090	0.001	0.63
DISTURBANCE	4.26 ± 0.5	3.60±0.4	1271	0.614	0.61

Table 2 Results of generalized linear models predicting LAI as function of stand structural attributes (1), and environmental factors (2), and their combination (3) in moist forests and miombo woodlands of Hanang district in Tanzania. Final models terms (their comparable full models using likelihood ratio test (LRT) at α = 0.05), percent deviance explained (D^2; in *italics* for each predictor term and bolded for the entire reduced model), probability deviation from a slope of zero (*p[t]*), mean square error of prediction (MSEP), Akaike Information Criterion (AIC), and Mann-Whitney-Wilcox test (U-test) prediction bias test. See Table S1 for details on global models.

Model subsets	**Reduced model**	**Estimates**	**D^2 (%)**	**AIC**	**Df**	**LRT**	***P***	**MSEP**	**U-test**
Moist forest									
1.Structure:	Slope: (*p [t]*= 0.001)	0.04	**64**	74.83	1	11.49	0.12	0.2	0.87
	Richness	0.17	*18*				0.003		
	(Richness)^2	-0.01	*11*				0.015		
	Predominant-Height	0.19	*42*				<0.001		
	(Predominant-Height)^2	-0.004	*14*				0.004		
2.Environment:	Slope: (*p [t]*= 0.001)	-16.58	**30**	116.29	1	9.67	0.07	0.39	0.74
	DISTURBANCE	3.49	*0.5*				0.013		
	Soil Nitrogen	-2.14	*0.3*				0.11		
	Soil pH	3.86	*3*				0.003		
	DISTURBANCE: Soil Nitrogen	0.65	*18*				0.03		
	DISTURBANCE: Soil pH	-0.71	*11*				0.01		
3. Combined:	Slope: (*p [t]*= 0.001)	-5.88	**76**	58.601	1	3.60	0.37	0.16	0.98
	Richness	0.05	*0*				<0.001		
	Predominant-Height	0.18	*3*				<0.001		
	(Predominant-Height)^2	0	*0*				0.002		
	DISTURBANCE	2.32	*19*				0.008		
	Soil Nitrogen	-2.42	*42*				0.006		
	Soil pH	1.37	*17*				0.09		
	DISTURBANCE : Soil Nitrogen	0.51	*25*				0.005		
	DISTURBANCE: Soil pH	-0.48	*14*				0.005		
Miombo									
1.Structure:	Slope: (*p [t]*= 0.001)	-1.01	**66**	22.32	1	6.01	0.40	0.1	0.97
	Density	0.13	*31*				0.03		
	Predominant-Height	0.34	*44*				0.01		
	(Predominant-Height)^2	-0.01	*11*				0.04		
2.Environment:	Slope: (*p [t]*= 0.04)	-16.58	**19**	58.72	1	2.32	0.47	0.26	0.89
	DISTURBANCE	3.49	*2.8*				0.17		
	Soil potassium	-2.14	*1.1*				0.05		
	Soil Nitrogen	3.86	*0.7*				0.12		
	Soil pH	0.65	*15.0*				0.02		
3.Combined:	Slope: (*p [t]*= 0.001)	-0.68	**82**	16.8	1	17.0	0.014	0.09	0.71
	Richness	0.26	*2*				0.067		

	Evenness	-6.14	*25*	0.014
	Density	-16.04	*18*	0.024
	Predominant-Height	1.77	*50*	0.082
	Soil Phosphorous	1.23	*1*	0.022
	Soil potassium	-1.14	*0*	0.011
	Soil Nitrogen	0.19	*4*	0.006
	Soil pH	-0.01	*1*	0.756
	Phosphorous : Richness	-0.06	*5*	0.012
	Potassium : Richness	0.59	*4*	0.018
	Potassium : Predominant-Height	0.37	*14*	0.013
	Soil pH :Richness	-0.23	*15*	0.039

Table 3 Results of generalized linear models predicting aboveground herbaceous biomass (AGB_H) as function of stand structure attributes (1), and environmental factors (2), and their combination (3) in moist forests, and miombo woodlands of Hanang district in Tanzania. Final models terms (their comparable full models using likelihood ratio test (LRT) at α = 0.05), percent deviance explained (D2; in italics for each predictor term and bolded for the entire reduced model), probability deviation from a slope of zero (p[t]), mean square error of prediction (MSEP), Akaike Information Criterion (AIC), and Mann-Whitney-Wilcox test (U-test) prediction bias test. See Table S1 for details on global models.

	Reduced model	**Estimates**	**D^2 (%)**	**AIC**	**Df**	**LRT**	***P***	**MSEP**	**U-test**
Moist forest									
1.Structure	Slope: (*p [t]*= 0.052)	4.55	**19**	129.05	1	8.34	0.4	0.48	0.001
	Litter biomass	-0.35	*3*				0.06		
	LAI	-2.51	*0*				0.001		
	$(LAI)^2$	0.53	*17*				0.001		
2.Environment	Slope: (*p [t]*= 0.61)	1.46	**5.5**	138.2	1	5.63	0.34	0.61	0.001
	Elevation	-0.18	*0*				0.24		
	DISTURBANCE	-0.02	*1*				0.54		
	Elevation : DISTURBANCE	0.05	*5*				0.01		
3.Combined	Slope: (*p [t]*= 0.052)	-6.52	**25**	128.47	1	51.5	0.15	0.47	0.001
	Elevation	0.26	*0*				0.05		
	Richness	-6.14	*5*				0.02		
	LAI	-16.04	*3*				0.005		
	$(LAI)^2$	1.77	*12*				0.02		
	Elevation : LAI	1.23	*7*				0.05		
Miombo									
1.Structure	Slope: (*p [t]*= 0.022)	0.66	**26**	54.14	1	18.6	0.08	0.21	0.97
	DISTURBANCE	0.17	*0*				0.001		
	LAI	0.25	*8*				0.29		
	DISTURBANCE : LAI	-0.16	*19*				0.001		
2.Environment	Slope: (*p [t]*= 0.021)	2.33	**27**	55.6	1	4.95	0.21	0.26	0.87
	Nitrogen	27.59	*13*				0.001		
	Soil pH	-0.49	*7*				0.56		
	DISTURBANCE	-1.95	*0*				0.07		
	Soil pH : DISTURBANCE	0.42	*9*				0.07		
3.Combined	Slope: (*p [t]*= 0.001)	-4.4	**45**	46.2	1	69.38	0.001	0.17	0.81
	Soil Nitrogen	26.77	*13*				0.001		
	Soil pH	0.87	*7*				0.05		
	DISTURBANCE	0.19	*0*				0.001		
	LAI	0.41	*5*				0.07		
	DISTURBANCE : LAI	-0.18	*28*				0.001		

FIGURES

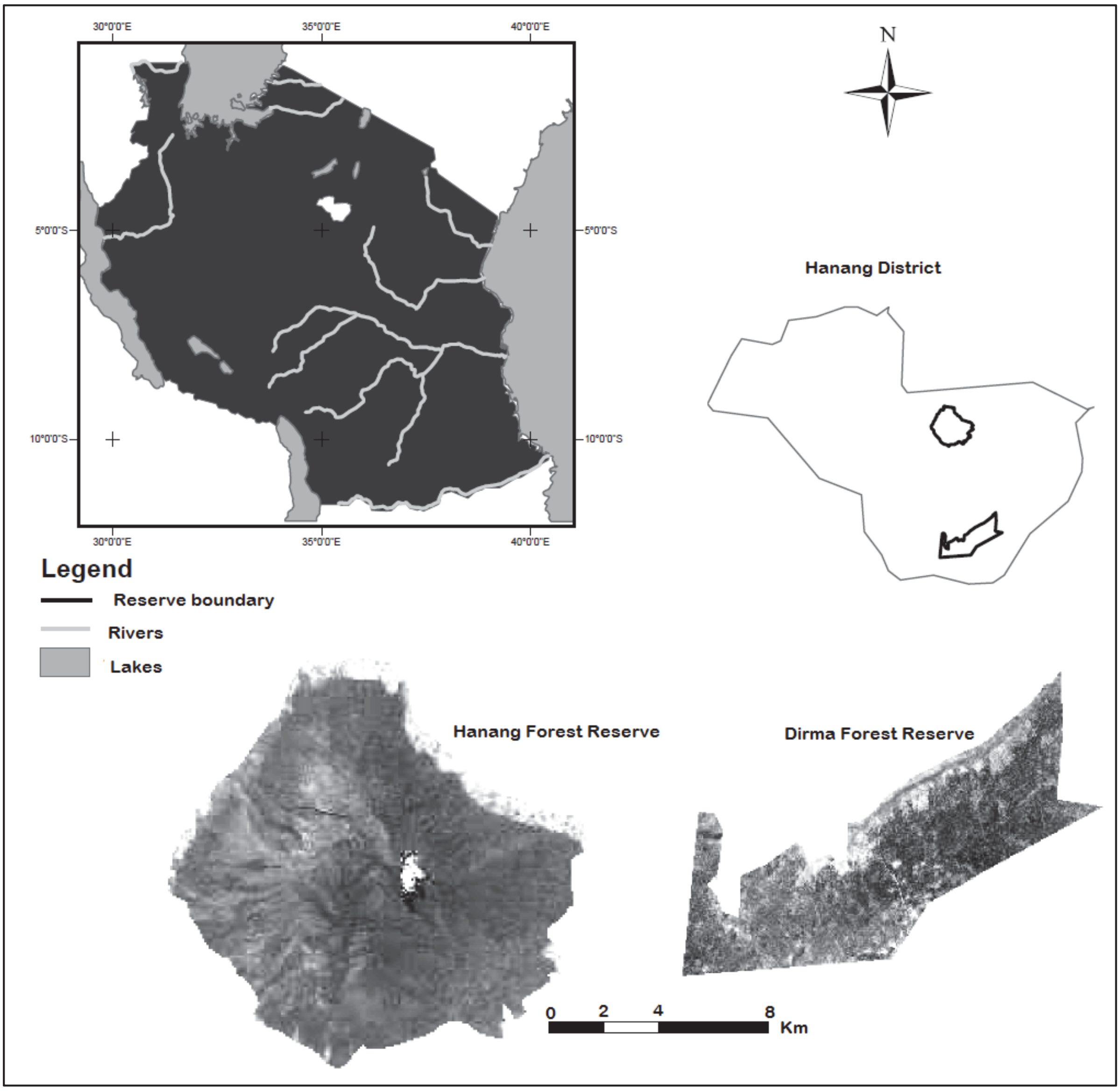

Figure 1. A map showing location of the study area in Tanzania

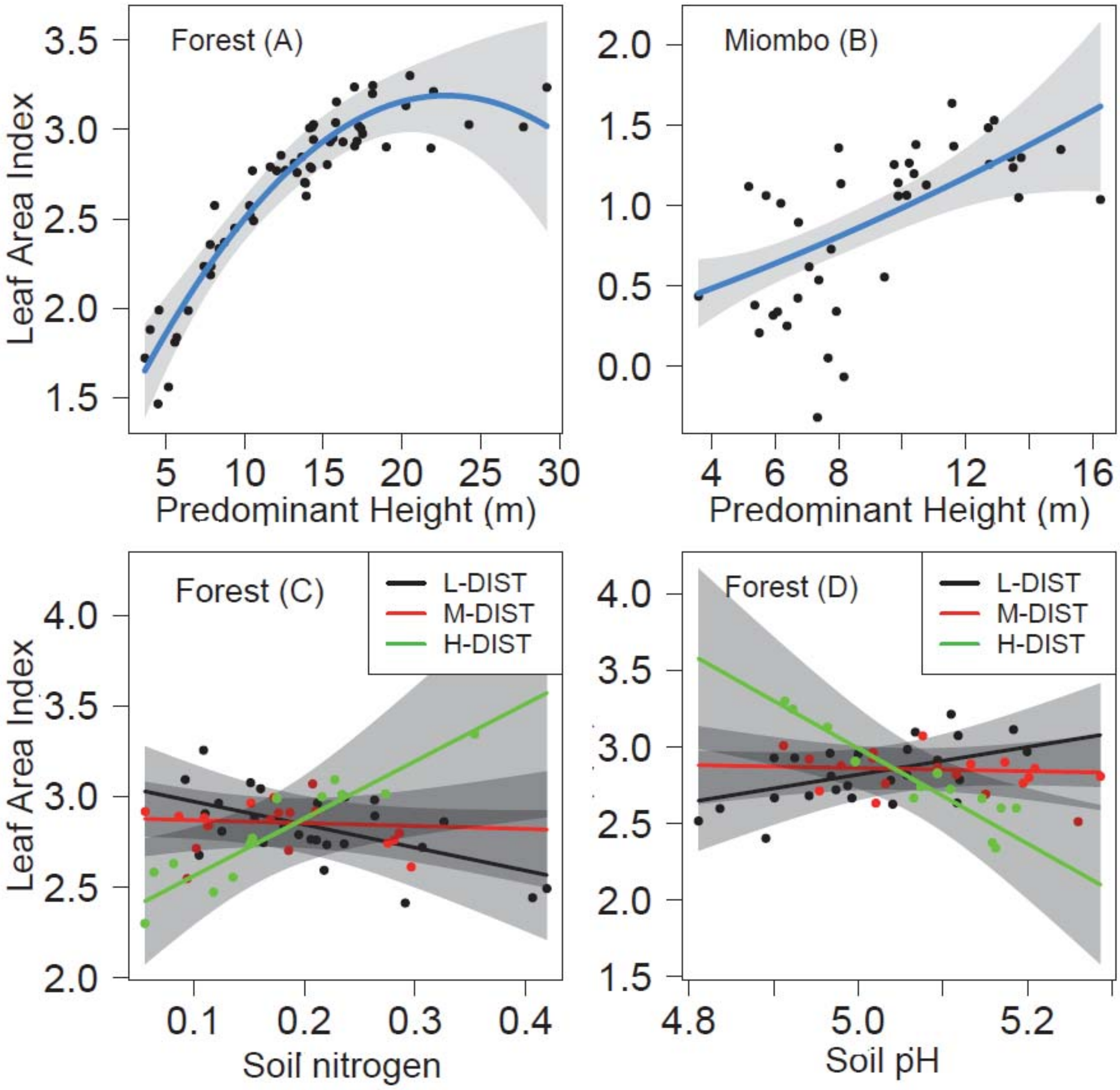

Fig. 2 Relationships between LAI and stand structural, edaphic and anthropogenic factors in moist forest and miombo woodland of Hanang district in Tanzania. Figures show results from generalized linear model:- (A) and (B) the relationship between LAI and tree predominant height in moist forest and miombo woodlands, (C) and (D) the interactions effects between soil nitrogen , soil pH and stump counts on LAI. The solid lines indicate are the fitted lines at 10th (L-DIST: Low DISTURBANCE), 50th (M-DIST: mean DISTURBANCE) and 90th (H-DIST: High DISTURBANCE) percentiles, with shaded 95% confidence band.

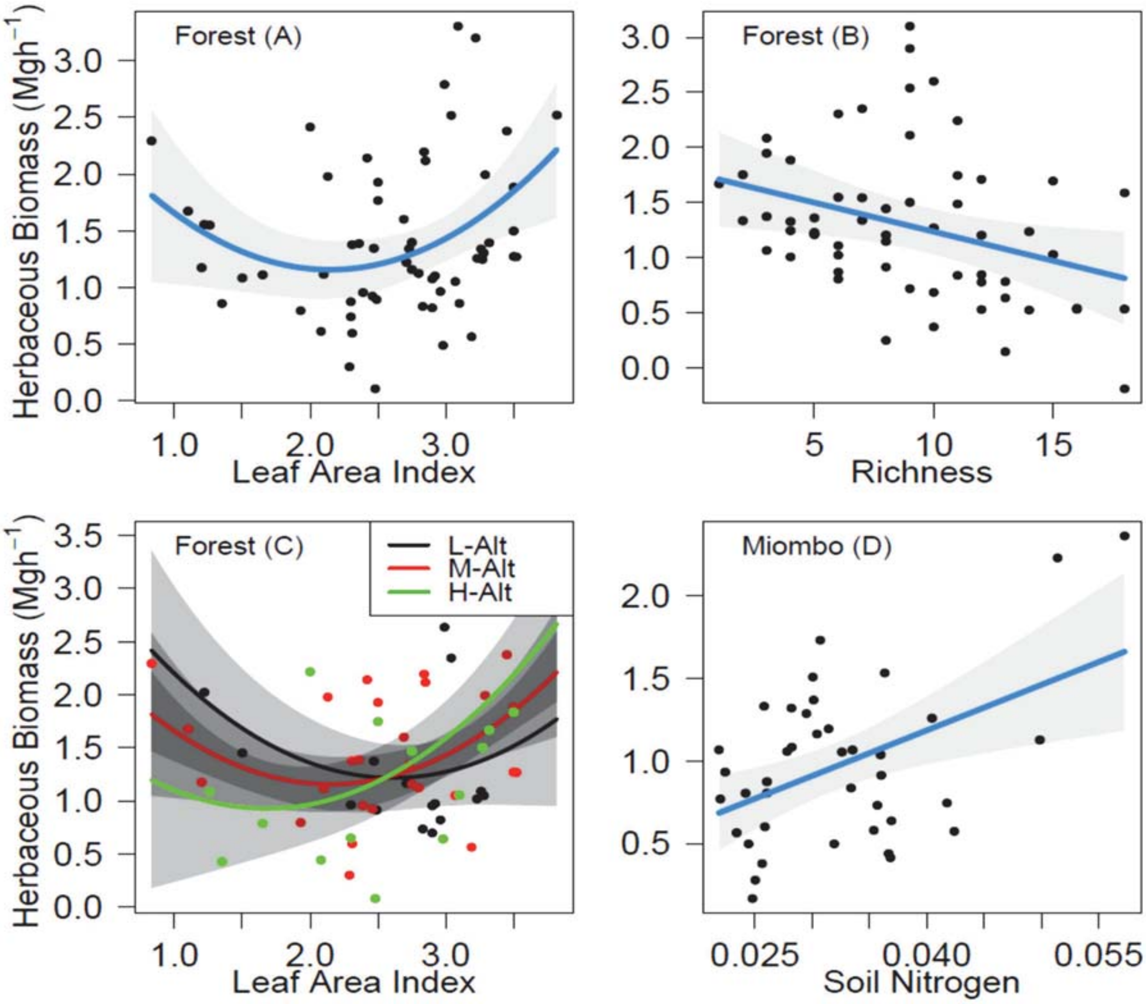

Fig. 3 Relationships between aboveground herbaceous biomass and stand structural, edaphic and anthropogenic factor in moist forest and miombo woodlands of Hanang district in Tanzania. Figures show results from generalized linear model: - the relationships between aboveground herbaceous biomass and (A) tree predominant height, (B) tree richness in moist forest, (C) the interaction effects between LAI and elevation, (D) interaction effects between soil pH and stump counts on herbaceous biomass in moist forest and miombo woodlands. The solid lines indicate are the fitted lines at 10th (L-Alt: Low Elevation), 50th (M-Alt: mean Elevation) and 90th (H-Alt: High Elevation) percentiles, with shaded 95% confidence band.

APPENDICES

Table S1 Model forms used in predicting leaf area index (LAI) and aboveground herbaceous biomass (AGB_H) as function of stand structural attributes (1), and environmental factors (2), and their combination (3) of moist forests and miombo woodlands of Hanang district in Tanzania. Note: Only predicator variables with variance inflation factor (VIF) ≤ 3 and Pearson correlation coefficient (r) ≤ 50% are included in model.

Model	Model parameters	Descriptions
1	LAI = Richness+ $Richness^2$ + Evenness + Stem density + Predominant height+ predominant $height^2$ + DISTURBANCE	The relationships between stand structural attributes and LAI with DISRTUBNCE
2	LAI = Phosphorus + Potassium + Nitrogen + pH + Elevation + DISTURBANCE	The relationships between environmental gradients and LAI, with DISRTUBNCE
3	LAI = Richness + $Richness^2$ + Evenness + Stem density + Predominant height + predominant $height^2$ + Phosphorus + Potassium + Nitrogen + pH + Elevation + DISTURBANCE	The relationships between both structural and environmental predictors combined and LAI with DISTURBANCE
1	AGB_H = Richness + Evenness + Stem density + Quadratic mean diameter + predominant height + LAI + LAI^2 + Seedlings + Litter biomass + DISTURBANCE	The relationships between stand structural attributes including LAI and $AGB_{H,}$ DISTURBANCE
2	AGB_H =Phosphorus + Potassium + Nitrogen + pH + Elevation + DISTURBANCE	The relationships between environmental gradients and AGB_H with DISTURBANCE
3	AGB_H = Richness + Evenness+ Stem density + Quadratic mean diameter + Predominant height + LAI + LAI^2 + Seedlings + Litter biomass + Phosphorus + Potassium + Nitrogen + pH + Elevation + DISTURBANCE	The relationships between both structural and environmental predictors combined and AGB_H with DISTURBANCE

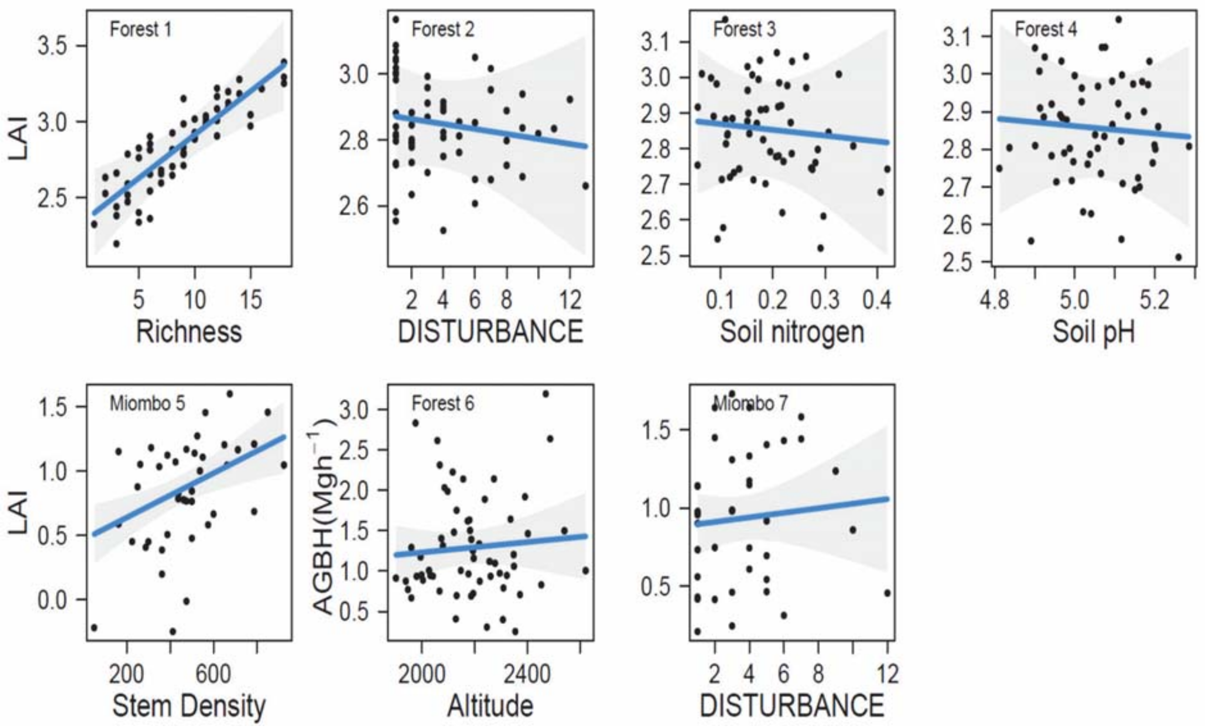

Figure S4: The relationship between LAI (Figures 1-5), aboveground herbaceous biomass (Figures 6 - 7) and stand structural attributes (1) and environmental factors (2) and their combination (3) of moist forests and miombo woodlands of Hanang district in Tanzania. Figures show results from generalized linear model: - the relationships between LAI and (1) tree richness, (2) DISTURBANCE, (3) soil nitrogen (4) and soil pH in moist forest and (5) stem density in miombo woodlands; and relationships between aboveground herbaceous biomass and (6) elevation and (7) DISTURBANCE in moist forest and miombo woodlands. The solid lines are the fitted lines with shaded 95% confidence band.

PAPER IV

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Relationships between tree species richness, evenness and aboveground carbon storage in montane forests and miombo woodlands of Tanzania

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Abstract

Understanding how carbon storage and tree diversity are related in forests and woodlands is crucial for a sustainable flow of ecosystem goods and services. The goal of this study was to determine how tree species richness, evenness and environmental factors influence aboveground live tree carbon stocks (AGC) in two tropical vegetation types in Tanzania. We surveyed trees and sampled soil from 222 vegetation plots (20 m × 40 m) in montane forests ($n = 60$) and miombo woodlands ($n = 162$). We used a multimodel inference approach to determine how AGC related to tree species richness, evenness and environmental factors, and linear mixed effect models to test the role of tree sizes on the AGC-richness and evenness associations. AGC were related unimodally to tree species richness and evenness in the montane forest. Likewise, AGC in the miombo woodlands was positively related to tree species richness. AGC from small trees were related unimodally to tree species richness in both vegetation types. Apparently the AGC had both monotonically increasing and decreasing associations with all abiotic environmental factors in both vegetation types. We emphasize that both tree size, number of multi-stemed trees and environmental factors have an important role in determining how AGC are related to richness and evenness. Finally, management of montane forests and miombo woodlands of Tanzania to enhance ecosystem benefit, such as AGC, will require strategies that consider tree sizes, tree species richness, evenness and underlying environmental and disturbance factors.

Zusammenfassung

Zu verstehen, in welcher Beziehung Kohlenstoffspeicherung und Baumdiversität in Wäldern und Gehölzen zueinander stehen, ist entscheidend für einen nachhaltigen Fluss von Ökosystemprodukten und -dienstleistungen. Das Ziel dieser Untersuchung war zu bestimmen, wie Baumdiversität und -evenness sowie Umweltfaktoren die oberirdischen Kohlenstoffvorräte in lebenden Bäumen (AGC) in zwei tropischen Vegetationstypen in Tansania beeinflussen. Wir untersuchten Bäume und nahmen Bodenproben auf 222 Probeflächen (20 m × 40 m) in Bergwäldern ($n = 60$) und in Miombo-Baumsavannen ($n = 162$). Wir wählten einen Mehr-Modell-Analyse-Ansatz um zu bestimmen, wie der AGC mit der Baumdiversität und -evenness sowie Umweltfaktoren verknüpft ist, und lineare gemischte-Effekte-Modelle, um den Einfluss der Baumgröße auf die Beziehung zwischen

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AGC und Artenreichtum bzw. AGC und Evenness zu testen. Der AGC war im Bergwald unimodal mit Baumartenreichtum und -evenness verknüpft. Ebenso war der AGC in der Miombo-Baumsavanne positiv mit dem Baumartenreichtum verbunden. Der AGC von kleinen Bäumen war in beiden Vegetationstypen unimodal mit dem Artenreichtum der Bäume verknüpft. Offenbar hatte der AGC in beiden Vegetationstypen sowohl monoton ansteigende als auch abfallende Beziehungen mit allen abiotischen Umweltfaktoren. Wir betonen, dass sowohl Baumgröße, Anzahl der mehrstämmigen Bäume und Umweltfaktoren eine wichtige Rolle für die Beziehung zwischen AGC und Artenreichtum bzw. Evenness spielen. Um den Ökosystemnutzen, z.B. AGC, zu steigern, wird das Management der Bergwälder und Miombo-Baumsavannen in Tansania Strategien erfordern, die Baumgröße, Artenreichtum, Evenness und zugrundeliegende Umwelt- und Störungsfaktoren berücksichtigen.

Keywords: Biodiversity; Species dominance; Ecosystem services; Biomass production; Soil-nutrients

Introduction

Trees play major roles in carbon storage and forest ecosystem functioning (Lopez-Toledo et al. 2012). Forest plant diversity has the potential to modify the rate of carbon fluxes and to mitigate effects of climate change (Dıaz, Hector, & Wardle, 2009). At a landscape scale, tree species diversity interacts with water, soil nutrients, litter quality and quantity, and light availability to govern carbon input into the ecosystem (Chapin, Matson, & Mooney 2002). However, current rates of forest degradation, deforestation and a general decline in tree species diversity have influenced forest ecosystem processes, such as carbon cycling (Butchart et al. 2010). Species richness may be strongly associated with carbon storage (Strassburg et al. 2010) and richness and biomass may relate positively, negatively or unimodally (Ruiz-Jaen & Potvin, 2011; Grace, Adler, Harpole, Borer, & Seabloom 2014). However, few studies have determined how carbon storage changes with plant species evenness (Collet, Ningre, Barbeito, Arnaud, & Piboule 2014; Orwin, Ostle, Wilby, & Bardgett 2014). Primarily two hypothetical mechanisms (complementarity effect and selection effect hypotheses) underline how plant species diversity and biomass production are related (Tilman et al. 1997; Cardinale, Hillebrand, Harpole, Gross, & Ptacnik 2009). In diverse plant communities, individuals optimize resource use through niche partitioning, unlike communities dominated by few plant species, where resource allocation will largely depend on the dominant species (Cardinale et al. 2009; Dıaz et al., 2009). According to Gross and Cardinale (2007), resource supply can affect species richness and in turn can affect biomass production. However, the causality in the richness-biomass production association, especially in natural vegetation at local and regional scales, is still unclear (Oksanen 1996; Grace et al. 2014).

Contrasting results on the association between plant biomass and plant species richness indicate the complexity underlying mechanisms and a need for further studies (Willig 2011). Although Strassburg et al. (2010) found that carbon stocks are related to plant diversity on a global scale, attempts to generalize this pattern has been challenging and consequently raised a debate among ecologists (Grace et al. 2014). Lack of consistent pattern on how biomass production and richness are related could be due to spatial and temporal interacting factors, such as physiographic, edaphic, climatic and disturbance conditions (Chisholm et al. 2013). The use of multiple measures, such as richness, evenness, diversity and environmental factors, may enhance our understanding of how carbon storage and plant species richness are related in various ecosystems (Willig 2011). Moreover, although tree size has a large influence on aboveground carbon storage (Sist, Mazzei, Blanc, & Rutishauser 2014), to our knowledge no study has focused on how tree size can influence the way aboveground carbon stocks are related to richness and evenness.

This study examines how tree Shannon diversity, richness and evenness are related to aboveground live tree carbon stocks (AGC) under different abiotic environmental conditions in montane forests and miombo woodlands in Tanzania. Based on the biodiversity-ecosystem function theory (Cardinale et al. 2009), we used AGC as a response variable with measures of tree species richness, evenness and abiotic environmental factors (edaphic and disturbance) as explanatory variables. We ask the following questions: (1) Do AGC relate to tree species richness and evenness in the two vegetation types? (2) Do environmental factors affect how richness and evenness are related to AGC in the two vegetation types? (3) Does tree size determine how AGC are related to richness and evenness in the two vegetation types?

Materials and methods

Study area

We studied a montane forest on the northern rift zone in the Hanang district and miombo woodlands in the Kilombero, Kilolo, Mufindi, Iringa, Mbeya, Rufiji, Kilwa and Chunya districts in Tanzania (Fig. 1). The Hanang forest occurs at an altitude rage of 1980 to 3300 m with a wide range of forest types, from montane to upper montane and dry montane forests (Lovett & Pocs 1993). The dominant

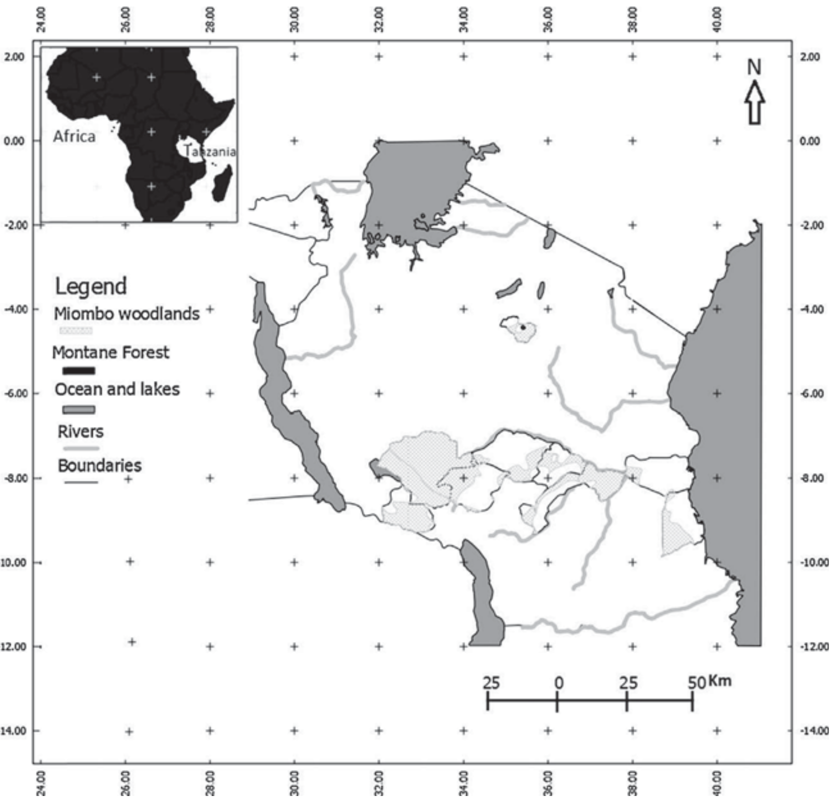

Fig. 1. Location map of forest and miombo woodlands study sites in Tanzania.

vegetation in the Hanang forest includes *Abizia*, *Cassipourea*, *Hygenia*, *Prunus* and *Mystroxylon* (Lovett & Pocs 1993). The forest is characterized by humus-rich loam and volcanic rock soils, with the exception of less fertile shallow soils and rocky areas on the western side. The annual rainfall ranges between 750 and 2000 mm and the mean annual temperature is 22.5 °C.

Miombo woodlands are the most extensive vegetation type in Tanzania and are commonly classified into dry and wet miombo. They are characterized by a distinct grass-dominated field layer and an open to closed tree canopy layer. Miombo are dominated by the genera *Brachystegia* and *Julbernadia* with *Brachystegia spiciformis* and *Julbernadia globiflora* as the most common tree species (Frost 1996). Miombo have a low soil nutrient content, are well drained, highly leached, acidic and low in organic matter. They occur from the coast to about 2500 m altitude in areas which receives mean annual rainfall ranges between 500 and 1400 mm and have annual mean temperature ranges between 15 and 30 °C (Frost 1996).

Data collection

We surveyed 20 m × 40 m plots in wet and dry miombo woodlands ($n = 162$) and montane forests ($n = 60$) (Table 1; Fig. 1). Plots were positioned along slopes at an elevation range of 100–3000 m a.s.l., and captured a wide range of environmental gradients. The first plot was established haphazardly at least 20 m away from path or forest edge inside the forest and in the woodlands. Subsequent plots were separated by a minimum distance ranges between 400 m and 1 Km to avoid spatial autocorrelation in floristic composition, biomass and environmental factors. All plots were laid along an axis perpendicular to the direction of the slope. In case there were no trees in a plot, especially in the woodlands, we randomly shifted the plot location into a nearby tree-covered area. We used a hand held GPS (Map76cx) to record geographical location and altitude for each plot. In each plot we recorded tree species and diameter at breast height (DBH) for all trees with DBH $\geq$ 5 cm. We measured 98% of tree heights directly with a measuring rod and Suunto-hypsometer, while the remaining 2% were estimated by regressing DBH against the previously measured heights (Mugasha, Bollandsås, & Eid, 2013). If plants could not be identified in the field, voucher specimens were identified in Tanzania National Herbarium. We counted the number of stumps in each plot as an indicator of ongoing human activities (Baas, Keßler, Slik, ter Steege, & Raes 2011). Wood cores were collected from dominant tree species based on standard procedures (Williamson & Wiemann 2010) and later used to estimate biomass.

Soil samples were collected from three layers (0–15 cm, 15–30 cm, 30–60 cm) from the main plot corners and at the center, and then aggregated into three samples representing the three layers of soil depths. The 666 soil samples (only

Table 1. Stand structure characteristics (±SE) of montane forest and miombo woodlands in Tanzania.

Vegetation types	No. plots	Stem density (ha^{-1})	AGC ($Mg\,ha^{-1}$)*	Richness (*S*)	Evenness (*J*)	Shannon-diversity (*H*)
Montane forest	60	722.08 ± 55.62	54.30 ± 5.84	8.85 ± 0.56	0.67 ± 0.03	1.54 ± 0.08
Miombo woodlands	162	636.50 ± 23.47	26.00 ± 1.34	9.83 ± 0.36	0.71 ± 0.01	1.68 ± 0.04

* 1 Mg = 1 Metric ton.

665 samples were used in the analysis because of a labeling error) were taken to Seliani Agricultural Research Institute in Arusha, Tanzania, for analysis. In the laboratory, all samples were air-dried and sieved through a 2 mm mesh and subsequently analyzed for soil pH (at 1:2.5 soil/H_2O), organic carbon (Walkley–Black method in %), available phosphorous (Bray II; in mg/kg), total nitrogen (Kjeldahl method in %), and potassium and sodium (Ammonium acetate 1.0 M pH7.0 extraction; in cmo/kg). Soil samples and tree inventory data were collected from May to July 2011 and in March 2012.

Data analysis

We estimated aboveground biomass using two allometric equations; the moist forest equation for montane vegetation and the dry forest equation for miombo (Chave et al. 2005). We used wood basic density (g/cm^3 at 12% moisture content) values from our field estimates and values from the literature for the same species or mean values for the genera or family in case of missing data from the field estimates (Carsan et al. 2012). Biomass values were aggregated into total carbon density (AGC per hectare) at plot level, where 50% of the biomass was assumed to be carbon.

We summed species from each plot as species richness (*S*). The Shannon index (Shannon 1948) was used to describe tree diversity and Pielou's evenness (J') index (Pielou 1969) was used to describe tree species evenness. When assessing associations between richness, evenness and tree carbon storage under different environmental factors, the soil data from the three layers were averaged to single plot values. Plot disturbance was estimated as the number of stumps recorded in a plot, in relation to the sum of all stumps in all plots from a particular vegetation type. All predictors were standardized to zero-skewness and unit variance before the analyses because they had different measurement scale, and checked for collinearity using variance inflation factor (VIF ≤ 3) as an indicator (Zuur, Ieno, Walker, Saveliev, & Smith 2009). Tree Shannon diversity had high collinearity with other predictors in both vegetation types, whereas soil nitrogen and soil organic carbon had high collinearity with other predictors in montane forest only. Therefore tree Shannon diversity was removed from the analysis in both vegetation types, while soil nitrogen and soil organic carbon were removed from the analysis in montane forest only. Before statistical analysis we checked for the effects of tree stem density on AGC and no significant association was found (see Appendix A: Fig. A1) which shows that, AGC was not simply a result of tree densities.

We used a multimodal inference procedure where the final parsimonious model was determined by a model averaging technique (Grueber, Nakagawa, Laws, & Jamieson 2011). We used a generalized least square (gls)-global regression model with AGC as response and tree species richness, evenness and their first-order quadratic term, soil nitrogen, soil potassium, soil organic carbon, soil pH, soil sodium, soil phosphorous, disturbance and altitude as predictors (Appendix A: Table A1). We use AGC as a response to tree richness, evenness based on the biodiversity ecosystem function hypothesis that species diversity drives biomass production (Gross & Cardinale 2007; Cardinale et al. 2009; Gamfeldt et al. 2013). In order to account for heterogeneity in our data set in each vegetation type, the global models were fitted with a maximum likelihood distribution error structure and without interactions terms to avoid model complexity and over-fitting (Anderson 2008).

We used the function dredge, implemented in the package MuMIn in R (Barton & Barton 2013), to generate a set of sub-models from the global model. We obtained the top subset models based on Δ2AIC cut-off (Burnham & Anderson 2002), using the function *get.models* and model average using the function *model.avg* in MuMIn package (Barton & Barton 2013). The estimated evidence ratio (ED) between the best fitted model and the subsequent models in the top best sub-sets and information theory (I–T) model probabilities were used to set criteria for identifying the most parsimonious models (Burnham & Anderson 2002; see Appendix A: Table A1).

To determine how tree size affects the association between AGC and tree species richness and evenness, we grouped trees in each plot into DBH-classes (5–20 cm, 20.1–40 cm, 40.1–60 cm, 60.1–80 cm, 80.1–100 cm and 100.1–110 cm). We determined AGC, tree species richness and evenness in each DBH-class for each plot. Using a regression model, we fitted a random intercept mixed model with AGC as response variable and tree species richness, evenness and their first order quadratic terms as predictors with DBH-class as a random factor (Zuur et al. 2009). The analyses were done with the R-Software 3.0.1 (RCoreTeam, 2013).

Results

Montane forest had higher mean AGC and lower mean tree species richness and evenness than miombo (Table 1; Fig. 2) However, mean tree species richness (t_{216}; $p = 0.15$), evenness (t_{216}; $p = 0.84$) and Shannon diversity (t_{216}; $p = 0.15$) were not significantly different between the two vegetation types. The two most abundant tree species contributed up to

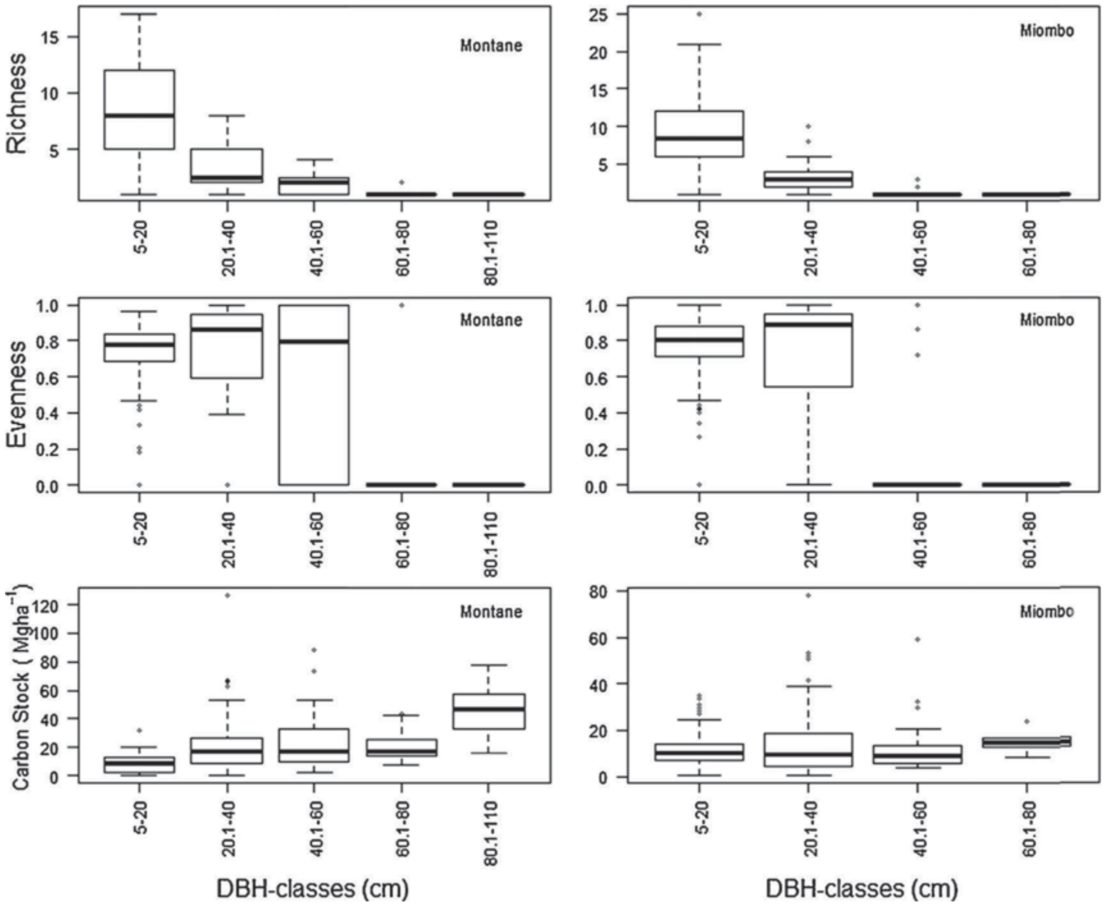

Fig. 2. Tree species richness, evenness and aboveground live tree carbon stocks (AGC) in diameter size classes for montane forest and miombo woodlands in Tanzania. The bottom and the top of each box represent 25th and 75th percentiles, the thick band in the box represents the median, the whiskers show the lowest and the highest values within 1.5 times the inter-quartile range and the dots are values outside the range.

about 50% of all trees and less than 50% of the total AGC in montane forest and about 60% of all trees and total AGC in miombo woodlands (See Appendix A; Fig. A2). In both vegetation types, there was higher tree species richness in the low DBH-class than in the high DBH-class (Fig. 2). Tree species richness decreased with DBH-class whereas tree species evenness and AGC increased with DBH-class (Fig. 2).

In montane forest, tree species richness and evenness were unimodally related to AGC, with the highest effect size for tree species evenness (Table 2; Fig. 3). In miombo, AGC decreased monotonically with tree species evenness and increased monotonically with tree richness (Table 2; Fig. 3), was strongly and negatively related to altitude (Table 2; Fig. 4) and with disturbance (Table 2; Fig. 4). In both vegetation types, AGC was strongly and positively related to soil potassium (Table 2; Fig. 4). In addition, AGC was weakly and negatively correlated to soil pH (Table 2).

The unimodal relationships between AGC and tree species richness occurred mainly in the lower diameter size class in both montane forest and miombo woodlands (Fig. 5B). In both vegetation types, AGC was unimodally related to tree species richness (Table 3; Fig. 5A). Moreover, there was a weak unimodal pattern between AGC and tree species evenness in montane forest (Table 3).

Discussion

Similar to other studies from montane forests and miombo woodlands in Tanzania (Shirima et al. 2011; Marshall et al. 2012), AGC in montane forest was higher than in miombo (Table 1), and trees were larger in montane forest than in miombo. Mean tree species richness, evenness and Shannon diversity were not significantly different between the vegetation types, probably due to higher sampling effort in miombo than in montane forest, which in general has a higher diversity than miombo woodlands (Sharma 1994). Although about 50% of all trees in montane forest were from the two most abundant tree species, they contributed less than 50% to the total AGC, suggesting that trees from the two abundant species were of relatively small size, unlike in miombo

Table 2. The associations between aboveground live tree carbon stocks (AGC), tree species richness and evenness along environmental gradients in montane forest and miombo woodlands in Tanzania. A summary of averaged model estimates using the multimodal inference technique, with variables significantly related to AGC presented in bold and marginally significant variables presented italics (see Appendix A; Table A1).

Variables	Montane forest					Miombo woodlands		
	Estimates	SE	*Z*-value	*p*-Value	Estimates	SE	*Z*-value	*p*-Value
(Intercept)	−248.29	98.98	2.45	0.01	31.46	12.26	2.55	0.01
Evenness	112.47	92.25	1.20	0.23	*−15.30*	*8.61*	*1.76*	*0.08*
Evenness^2	*−151.09*	*80.09*	*1.84*	*0.07*	−4.82	22.46	0.21	0.83
Richness	75.35	101.06	0.74	0.46	**19.60**	**9.87**	**1.97**	**0.05**
Richness^2	−148.13	117.83	1.23	0.22	9.23	25.73	0.36	0.72
Altitude	10.51	62.57	0.16	0.87	**−51.15**	**10.72**	**4.74**	**<0.001**
Disturbance	−3.67	25.60	0.14	0.89	**−11.99**	**5.64**	**2.11**	**0.04**
Soil potassium	**279.03**	**108.84**	**2.51**	**0.01**	**43.11**	**17.01**	**2.52**	**0.01**
Soil sodium	104.21	83.11	1.23	0.22	−13.55	13.16	1.02	0.31
Soil phosphorous	24.32	63.32	0.38	0.71	12.14	11.45	1.05	0.29
Soil pH	22.21	147.96	0.15	0.88	*−20.63*	*12.18*	*1.68*	*0.09*
Soil organic carbon	–	–	–	–	−18.49	12.25	1.50	0.13
Soil nitrogen	–	–	–	–	−8.96	17.46	0.51	0.61

woodlands (see Appendix A; Fig. A2). In both vegetation types, there was low stem density and tree species richness in larger DBH-class, as expected in natural forests and woodlands (Shirima et al. 2011).

Aboveground live tree carbon stocks and tree species richness were related unimodally in montane forest, with a decreasing trend from around 60 Mg ha^{-1} (Table 2; Fig. 3), which is similar to a previous study from a subtropical forest in Puerto Rico (Vance-Chalcraft, Willig, Cox, Lugo, Scatena 2010). Our results also show that in both vegetation types, the unimodal pattern occurred mainly at low DBH-class (Fig. 5B), suggesting that tree size is an important determinant of the AGC-richness relationship. Apparently, small-sized trees contribute considerably to the overall unimodal AGC-richness association observed in the final model (Fig. 3). A high plant diversity may result in more effective resource utilization, and hence in an increase in forest biomass, as suggested in previous experimental studies from grassland communities (Tilman et al. 1997). We also suggest that forests with a high number of multi-stemmed individuals

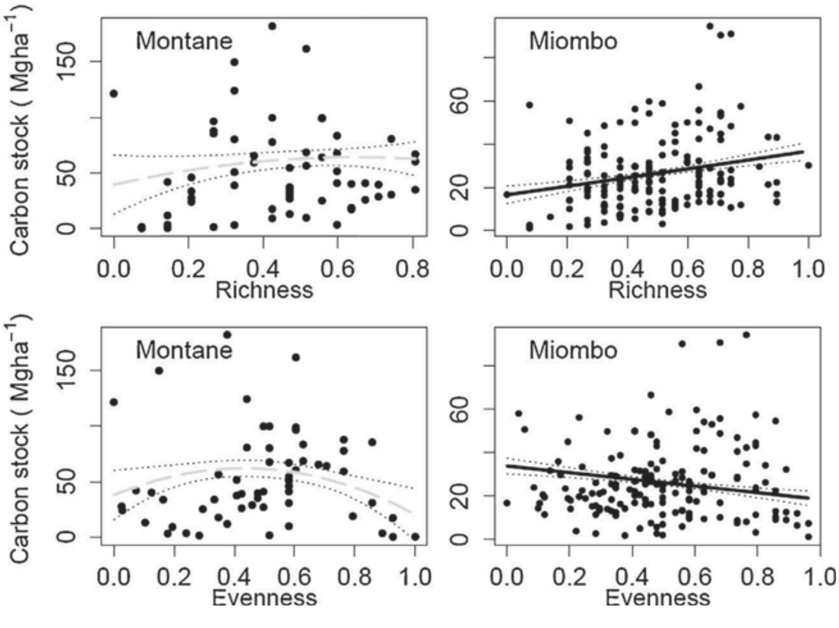

Fig. 3. Associations between aboveground live tree carbon stocks (AGC) and tree species richness and evenness in montane forest and miombo woodlands in Tanzania. The dots are raw data, lines (±SE) are predictions from the optimal averaged Gaussian generalized linear model (including the significant (solid lines) and non-significant (dotted lines) quadratic curves) when other predictors are kept constant. *Note: x*-axes represent standardized predictor variables per plot and *y*-axes represent the total plot AGC density.

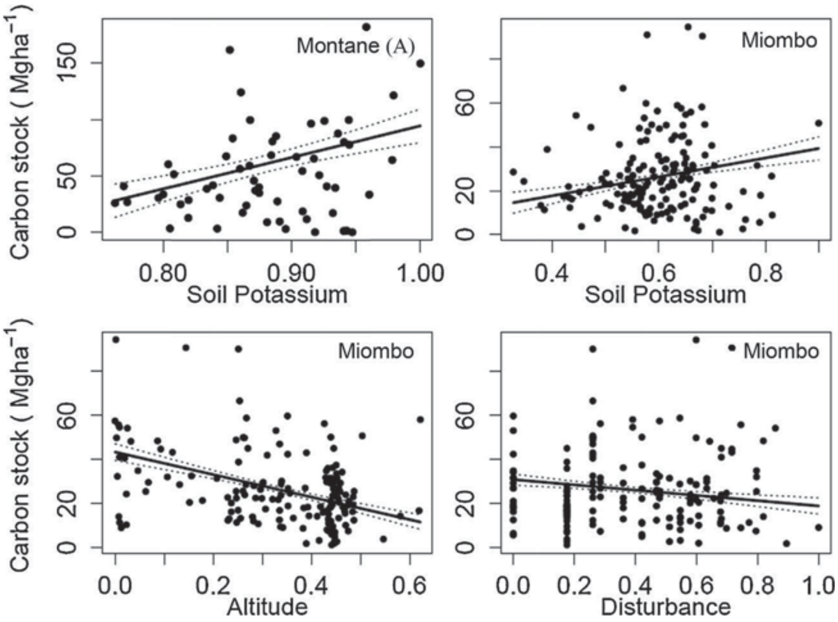

Fig. 4. Associations between aboveground live tree carbon stocks (AGC), soil potassium, disturbance and altitude in montane forest and miombo woodlands in Tanzania. Solid points represent raw data and solid lines (±SE) are predictions from the optimal Gaussian generalized linear model when other predictors are kept constant. *Note: x*-axes represent standardized predictor variables per plot and *y*-axes represent the total plot AGC density.

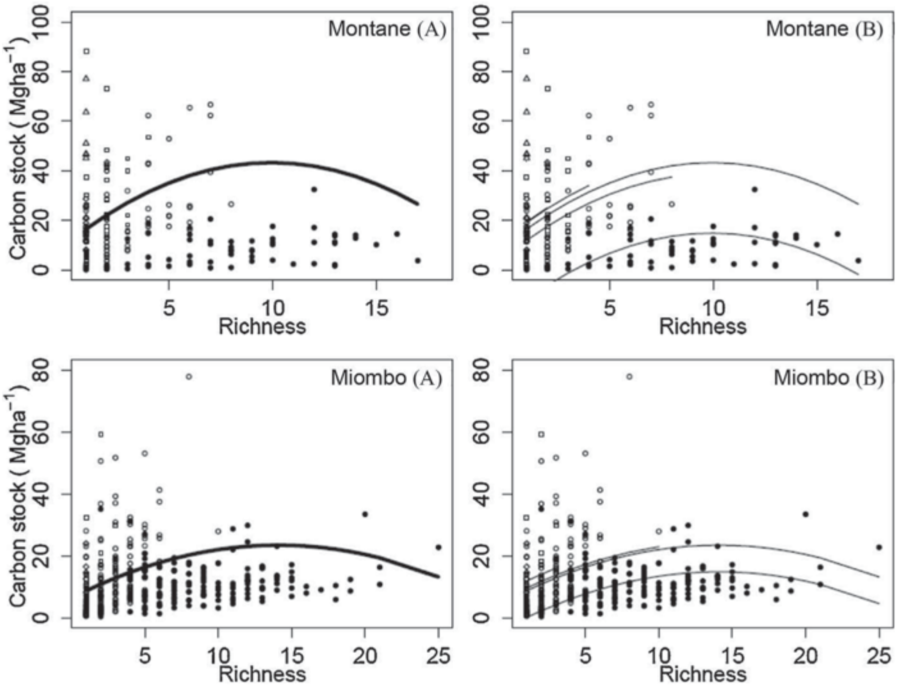

Fig. 5. Associations between aboveground live tree carbon stocks (AGC) and tree species richness for different tree diameter size classes in montane forest and miombo woodlands in Tanzania, using a mixed effect model. A scatter plot of AGC versus richness, row points (Solid circles = 5–20 cm, filled circles = 20.1–40 cm, filled square = 40.1–60 cm and filled diamond = 60.1–80 cm). The thick lines (A) represent the fit of the fixed part (richness) of the mixed model, and the thin lines (B) are the fits for individual diameter size classes obtained by adding the random intercept to the fixed part of the model (i.e. thin lines (B) are the contributions from each diameter size class to the fixed part of the curve, see Table 3).

Table 3. The associations between aboveground live tree carbon stocks (AGC) and tree species richness and evenness in montane forest and miombo woodlands in Tanzania. The table shows a summary of statistical estimates from a random intercept mixed model fit between AGC and the quadratic terms of richness and evenness with tree size diameter class as random factors, with variables significantly related to AGC presented in bold and marginally significant variables presented italics (See Fig. 5).

Vegetation types	Parameter	Value	SE	*t*-Value	*p*-Value
Montane forest	(Intercept)	10.15	9.58	1.06	0.29
	Richness	**6.66**	**1.34**	**4.98**	**<0.001**
	Richness^2	**−0.34**	**0.08**	**−4.03**	**<0.001**
	(Intercept)	21.77	18.09	1.20	0.23
	Evenness	61.58	48.68	1.27	0.21
	Evenness^2	*−63.57*	*35.59*	*−1.79*	*0.08*
Miombo woodlands	(Intercept)	6.33	3.52	1.80	0.07
	Richness	**2.43**	**0.45**	**5.35**	**<0.001**
	Richness^2	**−0.09**	**0.02**	**−4.02**	**<0.001**
	(Intercept)	26.08	10.71	2.44	0.02
	Evenness	11.04	26.38	0.42	0.68
	Evenness^2	−24.59	18.30	−1.34	0.18

may contribute to the unimodal pattern in the AGC-richness relationship, because multi-stem dominated plots comprise less biomass than plots dominated by large single-stem trees and low tree species richness.

The unimodal associations between AGC and tree species evenness in montane forests and for small tree sizes in miombo woodlands (Table 2; Fig. 3), is different from previous studies from sub-tropical forests in Puerto Rico (Vance-Chalcraft et al. 2010) and in the Terai area of Nepal (Mandal, Dutta, Jha, & Karmacharya 2013). This discrepancy could be due to differences in forest tree structure response to growth limiting factors, such as light availability (Cai, Poorter, Han, & Bongers 2008). In addition, none of these studies tested the importance of tree sizes on the AGC-evenness relationship. Selective logging of large-size trees may promote tree species richness at early stages but may also reduce trees species evenness at later stages (Mulder et al. 2004). Reduction in the density of large-sized abundant tree species by selective logging has likely resulted in an increase in stem density and richness in small-sized tree species (Gutiérrez-Granados, Pérez-Salicrup, & Dirzo 2011), thereby reducing the influence of large-size dominant tree species on AGC.

The positive correlation between AGC and tree species richness in miombo (Fig. 3), is similar to Chisholm et al. (2013) findings that there is a general positive association between species richness and aboveground woody dry biomass in temperate and tropical forests at small plot sizes (<1 ha). However, Chisholm et al. (2013) did not test for the effect of trees sizes on the AGC-richness relationship. Gamfeldt et al. (2013) also found AGC to increase with species richness in boreal forest. Although a general positive trend between tree species richness and biomass at small plot size (<1 ha) has previously been reported (Chisholm et al. 2013), Guo and Berry (1998) found a negative association between herbaceous species richness and biomass in a shrub-land habitat in Arizona. Apparently, the AGC-richness association differs among ecosystems and functional groups, and plant species richness does not necessarily enhance AGC because of influences from other external factor, such as disturbance (Fox 2003).

Aboveground live tree carbon stocks were marginally and negatively related to tree species evenness in miombo woodlands (Fig. 3), because there were few large trees with large contribution to the AGC (Fig. 2). Furthermore, the association between AGC and tree species evenness was negative for large trees in both vegetation types. According to Bengtsson, Fagerström, and Rydin (1994), plant competition for nutrients and light in forest ecosystems is more related to size differences among individual trees than to their species identity. However, both tree size and species identity may act concurrently to influence tree resource acquisition through dominance of the most productive species (selection effect hypothesis) and niche partitioning (complementarity hypothesis) in space or time (Cardinale et al. 2009).

Aboveground live tree carbon was negatively related to disturbance in miombo (Table 2; Fig. 4), suggesting that degradation is an important driver of AGC. A previous study from miombo in Tanzania, based on tree stump counts, has reported AGC removals of more than 33.1 Mg ha^{-1} yr^{-1} (Luoga, Witkowski, & Balkwill 2002). The decrease in AGC with altitude in miombo woodlands (Table 2; Fig. 4) could be explained by local tree species adaptation to differences in edaphic and climatic conditions (Woollen, Ryan, & Williams 2012). At high altitude, trees tend to be small and short, and less variable in diameter sizes, due to limited soil nutrient availability, shallow soil depths and harsh climate conditions (Moser et al. 2011).

Early seasonal burning tends to boost a rapid increase in soil minerals such as nitrogen, phosphorous and potassium in miombo woodlands (Strømgaard 1992). A positive association between AGC and soil potassium in both vegetation types suggests that soil potassium is an important factor limiting tree growth (Laurance et al. 1999). Similar effects of soil nutrient availability on AGC were reported by Epron et al. (2012) from experimental manipulations in *Eucalyptus* woodland of Australia. Our results show that AGC was negatively, but marginally related to soil pH in miombo, probably because soil pH can regulate several macro and micronutrient processes important for plant growth (Schaffers 2002). According to Chidumayo (1999), most of miombo woodlands occur in areas with low soil fertility and on acidic soils (pH 4–6). High soil alkalinity ($pH > 7$) may reduce essential nutrients for plant growth (e.g. soil phosphorous), which may impair biomass production (Jensen, Michelsen, & Gashaw 2001) while high acidity in soil ($pH < 5$) may be directly harmful to plant growth (Schaffers 2002).

Conclusions

We observed a unimodal association between AGC and tree species richness and evenness in montane forest. There was an increasing and decreasing monotonic association between AGC and tree species richness and evenness in miombo woodlands. Given the limitation that our study was not experimental, we cannot verify any causal relationships of the observed patterns. The humped-shaped patterns in the AGC-richness and evenness association was maintained in the small trees of the montane forest which suggests that within the smaller trees, species optimize resources through niche partitioning (complementarity effect hypothesis), but as trees become larger the dominant tree species control the largest proportion of the resources (selection effect hypothesis). Although not tested in this study, we also suggest that a situation where a woodland or forest has a high number of multi-stem trees, a hump-shaped pattern might occur. We also emphasis that factors such as anthropogenic disturbances and physiographic conditions are important when determining the associations between AGC-richness and evenness. Therefore, management strategies that consider both tree species size class, diversity and underlying edaphic, physiographic and disturbance factors will be required to enhance ecosystem benefits in montane forest and miombo woodlands in south-eastern Africa.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2014.11.008.

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