GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 16 (2015) 239–249
Basic and Applied Ecology
www.elsevier.com/locate/baae

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

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Received 3 February 2014; accepted 30 November 2014
Available online 5 December 2014

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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http://dx.doi.org/10.1016/j.baae.2014.11.008

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

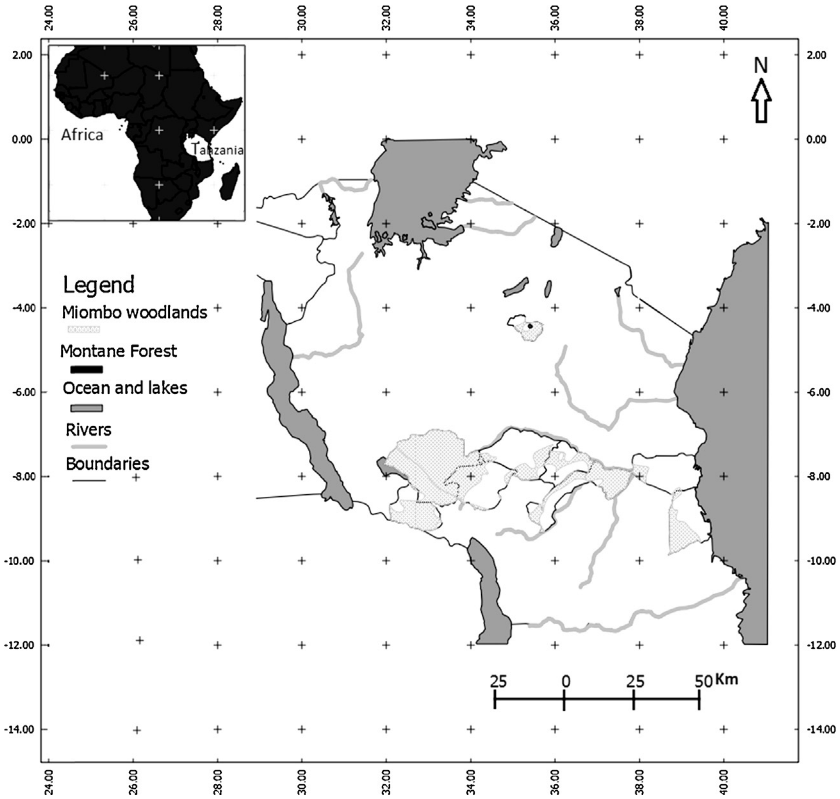

Fig. 1. Location map of forest and miombo woodlands study sites in Tanzania.

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 ≥ 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 ($VIF \leq 3$) 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

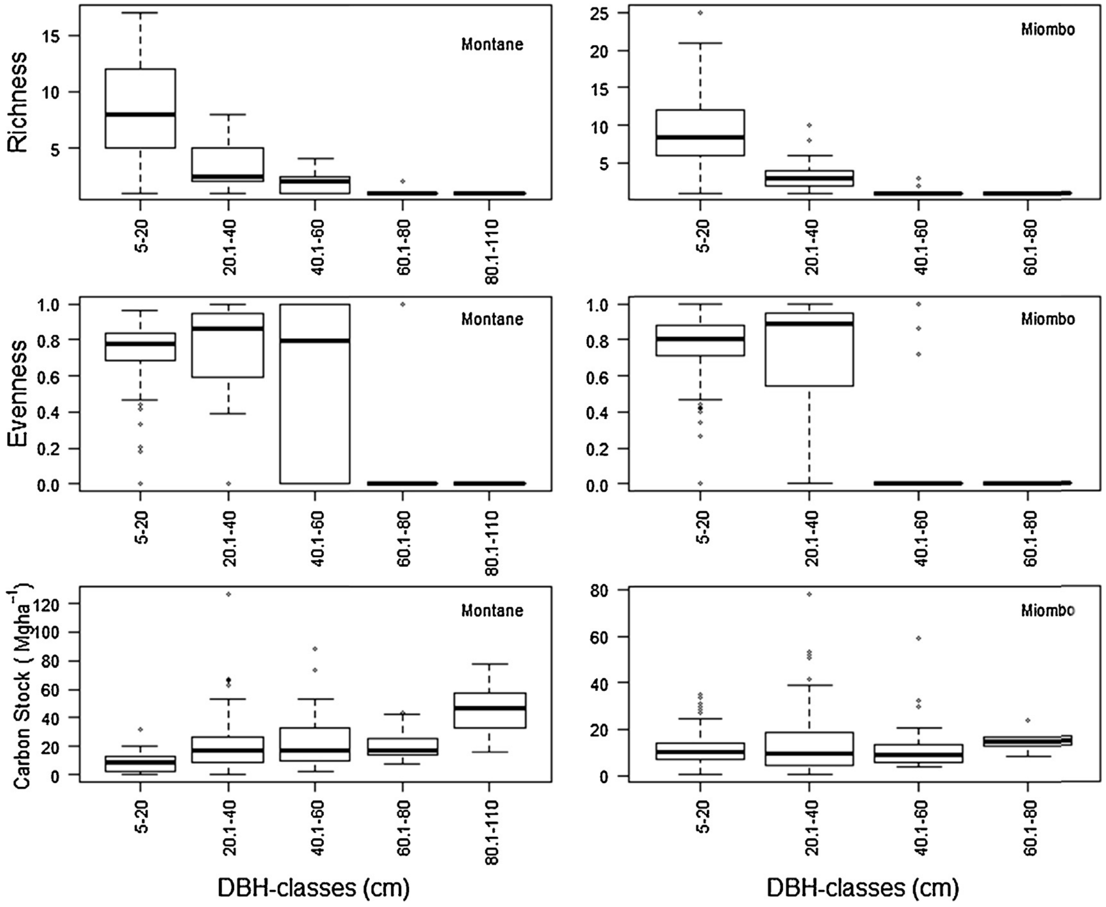

Fig. 2. Tree species richness, evenness and aboveground live tree carbon stocks (AGC) in diameter size classes for montane forest and miombo woodlands in Tanzania. The bottom and the top of each box represent 25th and 75th percentiles, the thick band in the box represents the median, the whiskers show 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

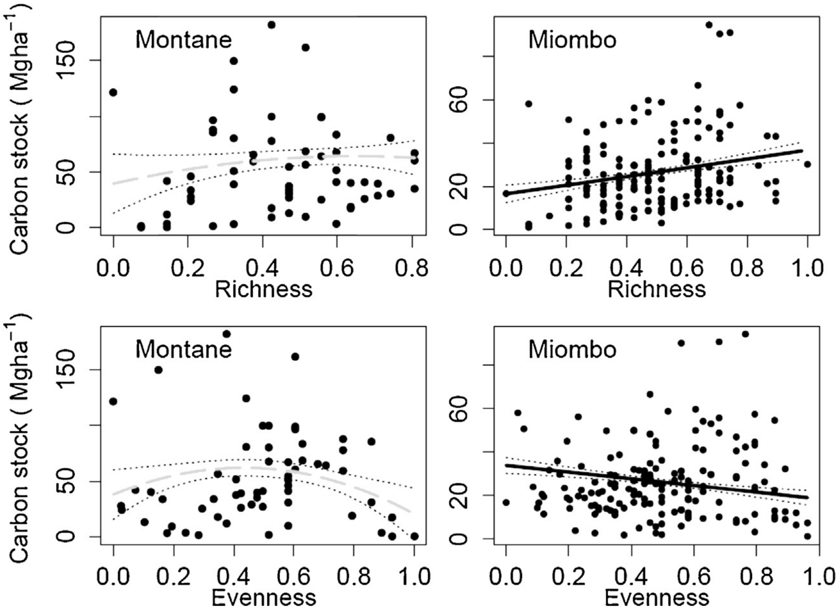

Fig. 3. Associations between aboveground live tree carbon stocks (AGC) and tree species richness and evenness in montane forest and miombo woodlands in Tanzania. The dots are raw data, lines (±SE) are predictions from the optimal averaged Gaussian generalized linear model (including the significant (solid 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.

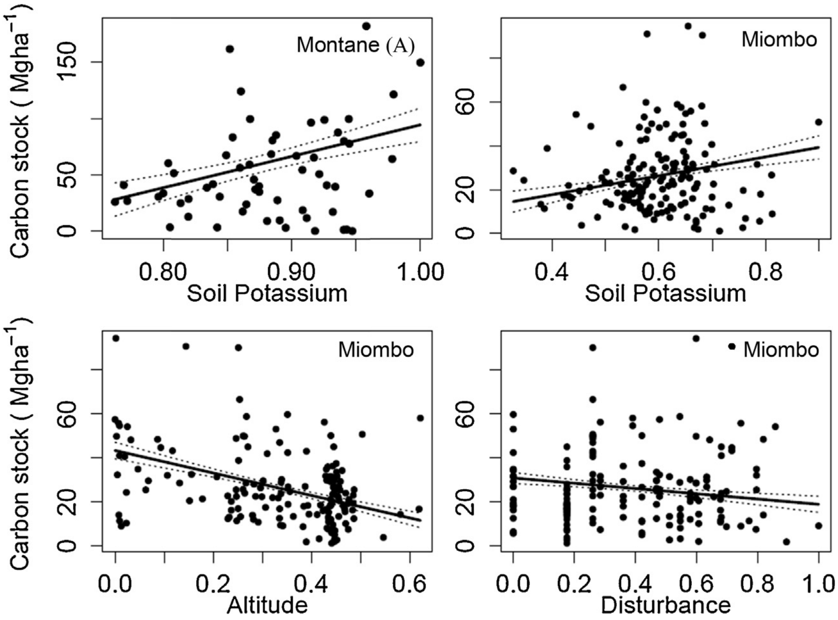

Fig. 4. Associations between aboveground live tree carbon stocks (AGC), soil potassium, disturbance and altitude in montane forest and miombo woodlands in Tanzania. Solid points represent raw data and solid lines (±SE) are predictions from the optimal Gaussian generalized linear model when other predictors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

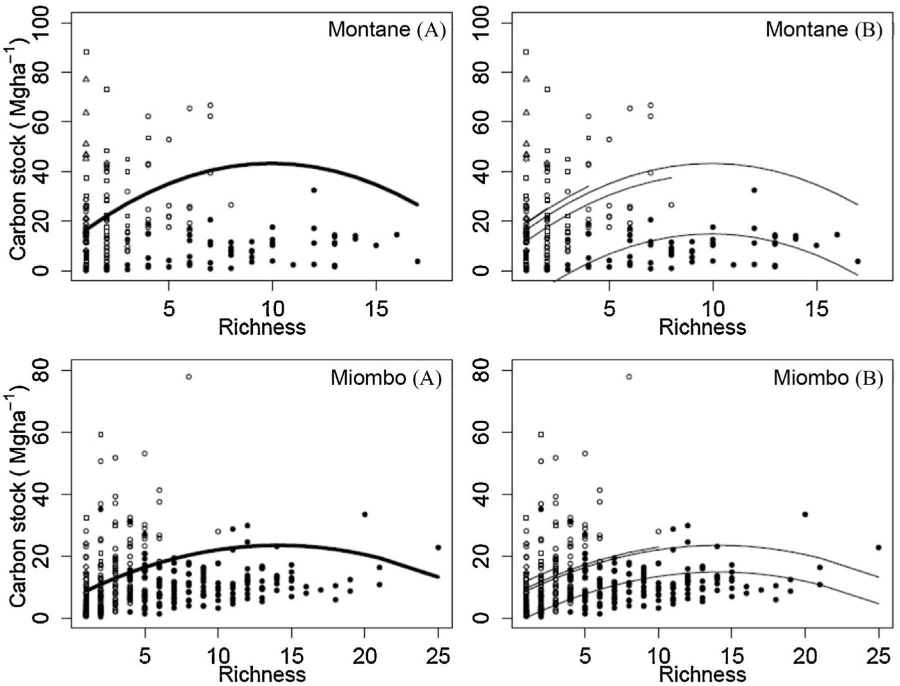

Fig. 5. Associations between aboveground live tree carbon stocks (AGC) and tree species richness for different tree diameter size classes in montane forest and miombo woodlands in Tanzania, using a mixed effect model. A scatter plot of AGC versus richness, row points (Solid circles = 5–20 cm, filled 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.

Acknowledgements

We thank the Norwegian Government through the Climate Change Impacts, Adaptation and Mitigation programme (CCIAM) and the Norwegian State Education Loan Fund for funding this study. Hamidu Seki, Rashi Khasim, John Herbet, George Bulenga, Osca Bakombezi, Godgift Swai, Godbless Lema and Hussein Shelukindo assisted during fieldwork. Yahaya Abeid, Moses Mwangoka and Canicius Kayombo, helped in plant identification. The managing editor and three anonymous referees improved a previous draft of the manuscript.

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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