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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 negative linear associations between tree species richness, relative 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-linear 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

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are associated with ectomycorrhizas, have deep roots and produce 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 *Julbernardia* 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-dominants and their resource acquisition strategy (Tilman 1985). We hypothesize (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 trees, 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). They occupy 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 occur on nutrient-limited soils and at various macro- and micro-climates, and experience high disturbance that influences their 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 ranges 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 geographic 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

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
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

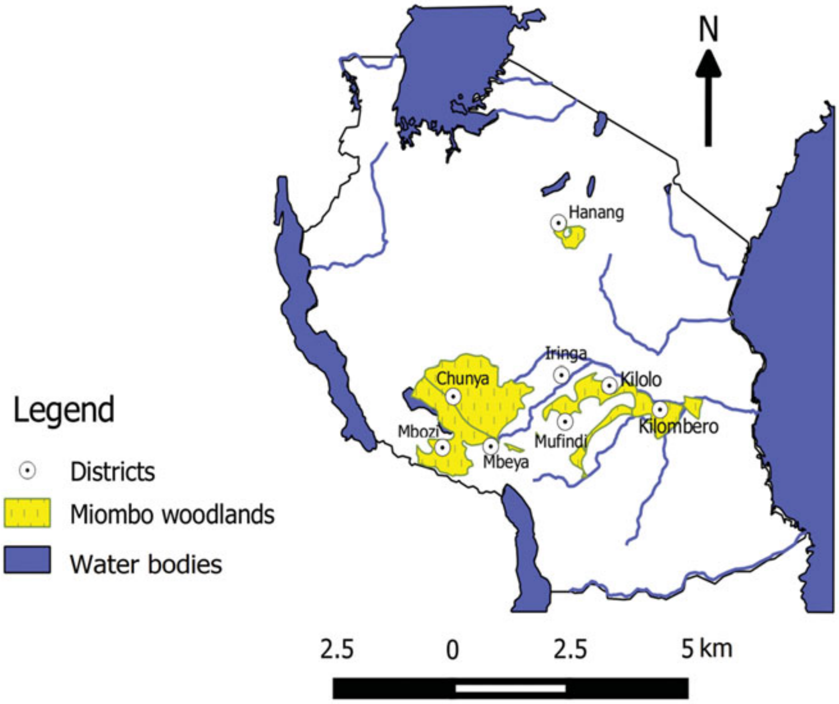

Figure 1. Miombo woodland study locations in Tanzania.

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 *et al.* 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 H_{sp} 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:

$$H_{sp} = -\sum\nolimits_{i=1}^{s} \cdot \sum\nolimits_{j=1}^{B} \begin{cases} p_{ij} \times \ln p_{ij} \text{ if } p_i > 0 \\ \cdot \\ \text{otherwise } 0 \end{cases}$$

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:

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

where H_{sp} = species profile index and $H_{sp\,Max}$ = maximum species profile index, respectively.

We used generalized least square regressions 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 dataset 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 were the most abundant species in 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 with 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 with at low and medium disturbance (Table 3, Figure 6b). The relative species profile index had a negative linear relationship

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
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
Relative 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	–	–

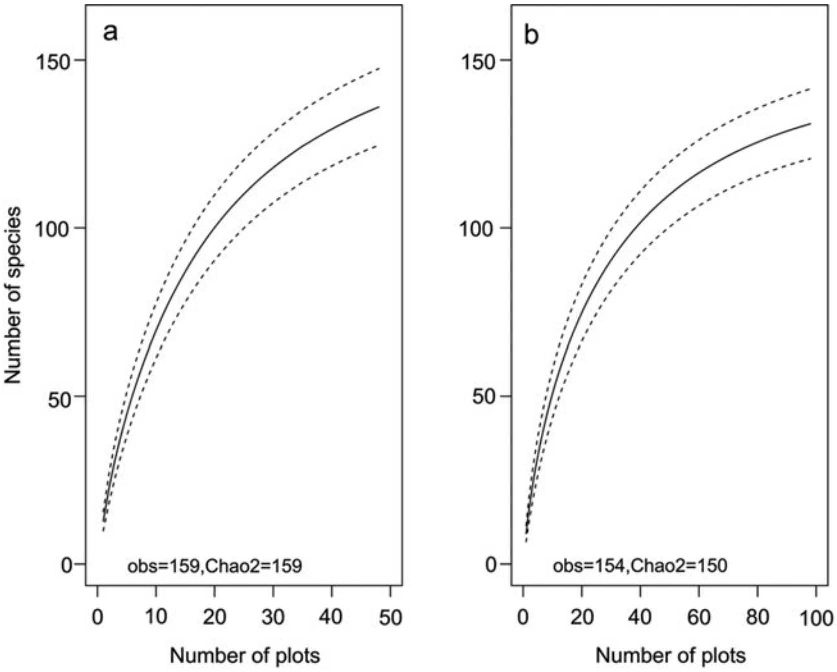

Figure 2. Tree species rarefaction curves (Mao Tau function), indicating sampling efforts in wet (a) and dry (b) miombo woodlands sampled plots in Tanzania. The rarefaction curves in solid lines and 95% confidence intervals in dashed line, obs = number of observed species and Chao2 = the estimated species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

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 relative species profile index and disturbance whereas there were 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

Table 3. The relationships between tree species richness, Shannon diversity, evenness, and relative 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
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
4. Response: Relative 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

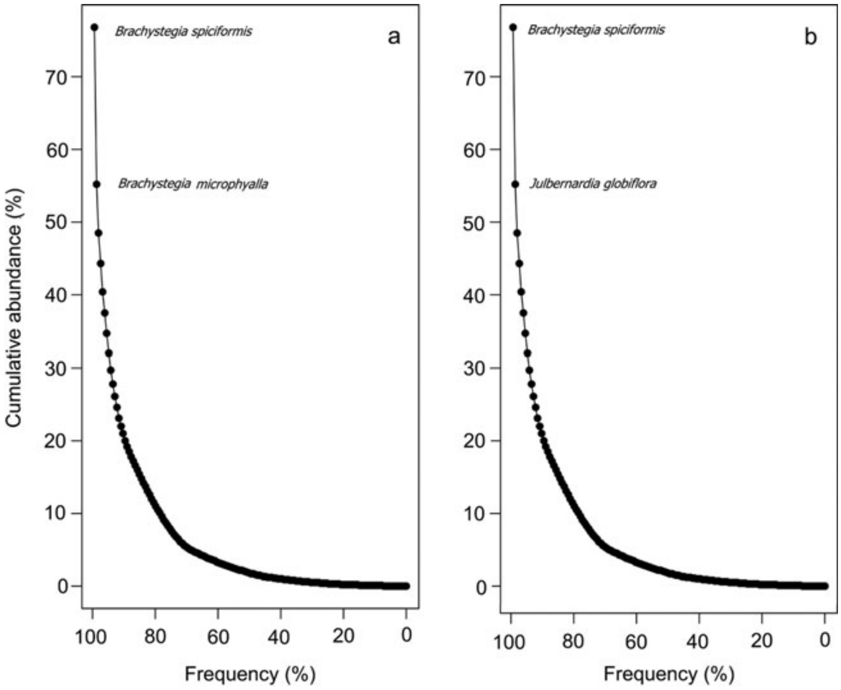

Figure 3. Cumulative abundance as a function of frequency, showing the two most abundant tree species based on their relative basal area for the sampled plots in wet (a) and dry (b) miombo woodlands of Tanzania.

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

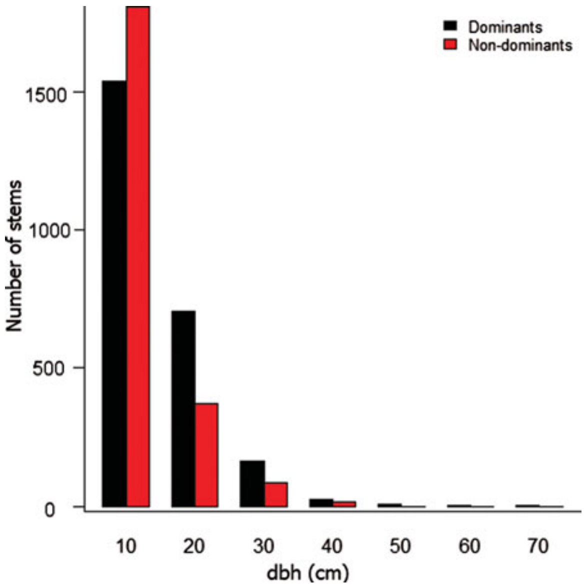

Figure 4. The distribution of tree stems (dbh ≥ 5 cm) in different diameter size classes in miombo woodlands of Tanzania.

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 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 disturbance 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 nutrients, such as extractable phosphorus and water, throughout the soil profile and store considerable quantities of carbohydrates over long

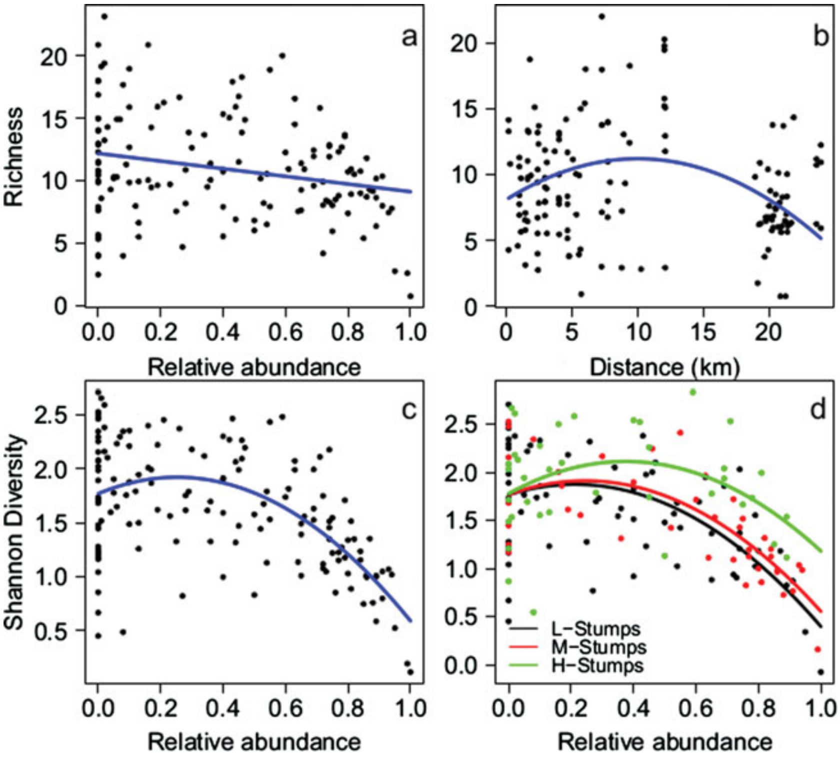

Figure 5. The relationships between non-dominant tree species richness and relative abundance of dominants (a), tree species richness and disturbance (distance from road, (b)), Shannon diversity index and relative abundance of dominants (c), and relative abundance of dominants and the three disturbance 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).

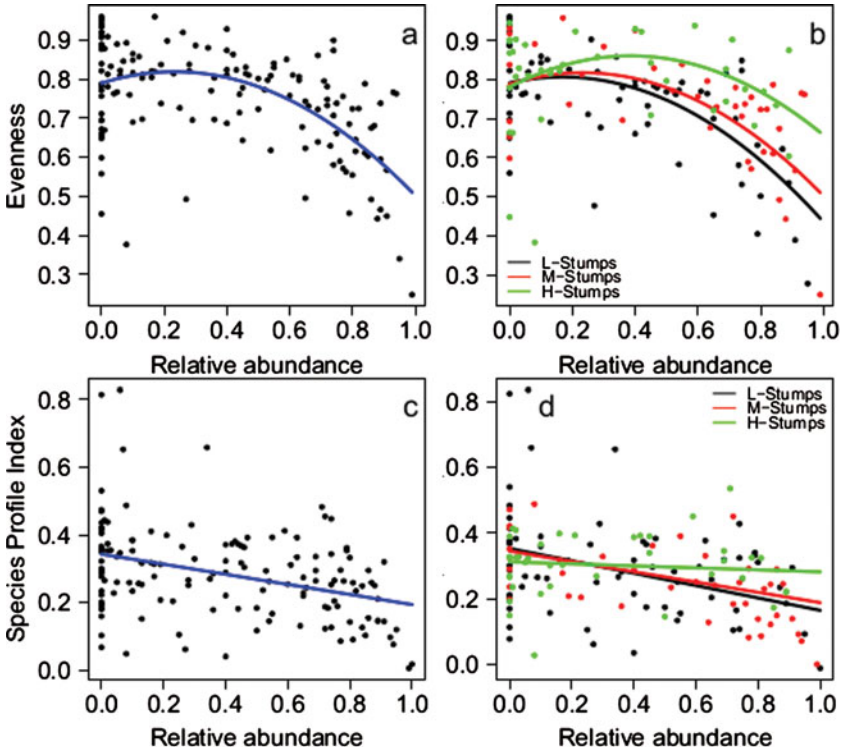

Figure 6. The relationships between non-dominant tree species evenness and tree species relative abundance (a), tree species evenness and relative abundance of the dominants, and the three disturbance levels (b), when all other variables are set to their medians, tree species profile index and tree species relative abundance (c), and relative 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, relative 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).

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.* 2011, 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 with plots that are far from an 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 an 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 play 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 relative 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 relative 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 relative 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 dominant tree species 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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Appendix 1. A list of species encountered in plots (n = 146) surveyed in miombo woodlands of Tanzania.

Species	Familly
Acacia amythethophylla Steud. ex A. Rich.	Mimosaceae
Acacia nigrescens Oliv.	Mimosaceae
Acacia seyal Del.	Mimosaceae
Acacia sp.	Mimosaceae
Acacia tortilis (Forssk.)Hayne	Mimosaceae
Acacia hockii De Wild.	Mimosaceae
Acacia senegal (L.) Willd.	Mimosaceae
Acalypha sp.	Euphorbiaceae
Aeschynomene sp.	Papilionaceae
Afzelia quanzensis Welw.	Caesalpiniaceae
Albizia amara (Roxb.) B.Boivin	Mimosaceae
Albizia antunesiana Harms	Mimosaceae
Albizia harveyi E. Fourn	Mimosaceae
Albizia schimperiana Oliv.	Mimosaceae
Albizia sp.	Mimosaceae
Allophyllus sp.	Sapindaceae
Allophylus rubifolius (Hochst. ex A.Rich.) Engl.	Sapindaceae
Annona senegalensis Pers.	Annonaceae
Antidesma venosum E. Mey. ex Tul.	Euphorbiaceae
Apodytes dimidiata E. Mey. ex Arn	Icacinaceae
Azanza garckeana (F. Hoffm.) Exell & Hillc	Malvaceae
Baphia sp.	Papilionaceae
Bauhinia petersiana Bolle	Caesalpiniaceae
Bauhinia thonningii Schumach.	Caesalpiniaceae
Bobgunnia madagascariensis (Desv.) J.H. Kirkbr. & Wiersama	Papilionaceae
Boscia angustifolia A. Rich.	Capparaceae
Boscia mossambicensis Klotzsch	Capparaceae
Boscia salicifolia Oliver	Capparaceae
Boscia sp.	Capparaceae
Brachystegia boehmii Taub.	Caesalpiniaceae
Brachystegia bussei Harms	Caesalpiniaceae
Brachystegia longifolia Benth	Caesalpiniaceae
Brachystegia manga De Wild.	Caesalpiniaceae
Brachystegia sp.	Caesalpiniaceae
Brachystegia spiciformis Benth	Caesalpiniaceae
Brachystegia utilis Burtt Davy & Hutch	Caesalpiniaceae
Brachystegia microphylla Harms	Caesalpiniaceae
Brachystegia tamarindoides Benth	Caesalpiniaceae
Bridelia cathartica G.Bertol	Phyllanthaceae
Bridelia duvigneaudii J. Léonard	Phyllanthaceae
Bridelia micrantha (Hochst.) Baill.	Phyllanthaceae
Bridelia scleroneura Mull.Arg.	Phyllanthaceae
Burkea africana Hook	Caesalpiniaceae
Byrsocarpus orientalis (Baill.) Baker	Connaraceae
Canthium burttii Bullock	Rubiaceae
Canthium sp.	Rubiaceae
Cassia abbreviata Oliv.	Caesalpiniaceae
Cassia sp.	Caesalpiniaceae
Cassipourea malosana (Baker) Alston	Rhizophoraceae
Cassipourea mollis (R.E. Fr.) Alston	Rhizophoraceae
Cassipourea sp.	Rhizophoraceae
Catunaregam spinosa (Thunb.) Tirveng.	Rubiaceae
Combretum apiculatum Sond.	Combretaceae
Combretum collinum Fresen.	Combretaceae
Combretum molle R. Br. ex G. Don	Combretaceae
Combretum sp.	Combretaceae
Combretum zehyeri Sound	Combretaceae
Commiphora africana (A. Rich.) Engl.	Burseraceae
Commiphora mossambicensis (Oliv.) Engl.	Burseraceae
Commiphora schimperi (O. Berg) Engl.	Burseraceae
Commiphora sp.	Burseraceae
Commiphora campestris Engl.	Burseraceae

Appendix 1. Continued

Species	Familly
Crossopteryx febrifuga (G. Don.) Benth.	Rubiaceae
Croton sp.	Euphorbiaceae
Cussonia arborea Hochst. ex A. Rich	Araliaceae
Cussonia holstii Engl.	Araliaceae
Cussonia sp.	Araliaceae
Cussonia spicata Thunb.	Araliaceae
Cussonia zimmermannii Harms	Araliaceae
Dalbergia boehmii Taub	Papilionaceae
Dalbergia lacteal Vatke	Papilionaceae
Dalbergia melanoxylon Gill. & Perr.	Papilionaceae
Dalbergia nitidula Welw. ex Baker	Papilionaceae
Dichrostachys cinerea (L.) Wight & Arn.	Mimosaceae
Diospyros sp.	Ebenaceae
Diospyros usambarensis F. White	Ebenaceae
Diplorhynchus condylocarpon (Müll. Arg.) Pichon	Apocynaceae
Dissotis melleri Hook.f.	Melastomataceae
Dodonaea viscosa (L.) Jacq.	Sapindaceae
*Dombeya rotundifoli*a (Hochst.) Planch	Sterculiaceae
Dombeya sp.	Sterculiaceae
Ekebergia benguelensis C.DC.	Meliaceae
Erica arborea L.	Ericaceae
Erica sp.	Ericaceae
Erythrina abyssinica Lam. ex DC.	Papilionaceae
Euphorbia candelabrum Welw	Euphorbiaceae
Euphorbia cuneata Vahl	Euphorbiaceae
Euphorbia matabelensis Pax.	Euphorbiaceae
Euphorbia sp.	Euphorbiaceae
Excoecaria bussei (Pax)Pax	Euphorbiaceae
Faidherbia albida (Delile) A. Chev.	Mimosaceae
Faurea rochetiana (A. Rich.) Pic.Serm.	Proteaceae
Faurea saligna Harv.	Proteaceae
Faurea sp.	Proteaceae
Ficus glumosa Delile	Moraceae
Ficus thonningii Blume	Moraceae
Flacourtia indica (Burm. f.) Merr.	Salicaceae
Garcinia sp.	Cluciaceae
Garcinia buchananii Baker	Cluciaceae
Gardenis ternifolia Schum. & Thonn.	Rubiaceae
Gaya parviflora (Phil.) Krapov.	Mimosaceae
Grewia bicolor Juss.	Tiliaceae
Grewia sp.	Tiliaceae
Grewia conocarpa K.Schum.	Tiliaceae
Hexalobus monopetalus (A.Rich.) Engl. & Diels	Annonaceae
Holarrhena pubescens Wall. ex G. Don	Apocynaceae
Hymenocardia acida Tul	Phyllanthaceae
Hymenodictyon floribundum (Hochst. & Steud.) B. L. Rob.	Rubiaceae
Indigofera tinctoria L.	Papilionaceae
Isoberlinia angolensis (Welw. ex Benth.) Hoyle & Brenan	Caesalpiniaceae
Julbernardia globiflora (Benth.) Troupin	Caesalpiniaceae
Kigelia africana (Lam.) Benth.	Bignoniaceae
Lannea humilis (Oliv.) Engl.	Anacardiaceae
Lannea schimperi (A.Rich.) Engl.	Anacardiaceae
Lannea schweinfurthii (Engl.) Engl.	Anacardiaceae
Lannea sp.	Anacardiaceae
Lonchocarpus bussei Harms	Papilionaceae
Lonchocarpus capassa Rolfe.	Papilionaceae
Lonchocarpus constrictus Pittier.	Papilionaceae
Lonchocarpus sp.	Papilionaceae
Maerua angolensis DC.	Capparaceae
Maerua sp.	Capparaceae
Manilkara sansibarensis (Engl.) Dubard	Sapotaceae
Margaritaria discoidea (Baill.) Webster	Euphorbiaceae
Markhamia zanzibarica (Bojer ex DC.) K. Schum.	Bignoniaceae

Appendix 1. Continued

Species	Familly
Markhamia obtusifolia (Baker) Sprague	Bignoniaceae
Maytenus senegalensis (Lam.)	Celastraceae
Memecylon flavovirens Buker	Melastomataceae
Monotes elegans Gilg	Dipterocarpaceae
Monotes sp.	Dipterocarpaceae
Monotes africana A.DC.	Dipterocarpaceae
Morella sp.	Myricaceae
Multidentia crassa (Hiern) Bridson & Verdc.	Rubiaceae
Mundulea sericea (Willd.) A. Chev.	Papilionaceae
Myrica salicifolia Hochst. ex A.Rich.	Myricaceae
Ochna afzelii R Br.	Ochnaceae
Ochna holstii Engl.	Ochnaceae
Ochna sp.	Ochnaceae
Ochna mossambicensis Klotzsch	Ochnaceae
Oldfieldia dactylophylla (Welw. ex Oliv.) J.Léonard	Picrodendraceae
Opilia amentacea Roxb.	Opiliaceae
Ormocarpum kirkii S. Moore	Papilionaceae
Ormocarpum trichocarpum (Taub.) Engl.	Papilionaceae
*Osyris lanceolat*a Hochst. & Steud.	Santalaceae
Ozoroa insignis (Baker f.) J.B.Gillett	Anacardiaceae
Ozoroa obovata (Oliv.) R.Fern. & A.Fern.	Anacardiaceae
Pappea capensis Eckl. & Zeyh.	Sapindaceae
Parinari curatellifolia Planch. ex Benth.	Chrysobalanaceae
Parinari excelsa Sabine	Chrysobalanaceae
Pericopsis angolensis (Baker) Meeuwen	Papilionaceae
Philenoptera bussei (Harms) Schrire	Papilionaceae
Philenoptera violacea (Klotzsch) Schrire	Papilionaceae
Phyllanthus reticulatus Poir.	Euphorbiaceae
Pleurostylia Africana Loes	Celastraceae
Polysphaeria multiflora Hiern	Rubiaceae
*Pristimera graciliflor*a (Welw. ex Oliv.) N.Hallé	Celastraceae
Protea gaguedi J.F.Gmel.	Proteaceae
Protea madiens Oliv.	Proteaceae
Protea sp.	Proteaceae
Pseudolachnostylis maproneifolia Pax.	Euphorbiaceae
Psorospermum febrifugum Spach	Cluciaceae
Psychotria eminiana (Kuntze)Petit	Rubiaceae
Psydrax sp.	Rubiaceae
Pterocarpus angolensis DC.	Papilionaceae
Pterocarpus rotundifolia (Sond.) Druce	Papilionaceae
Pterocarpus tinctorius Welw.	Papilionaceae
Rhoicissus revoilii Planch.	Vitaceae
Rhus natalensis Bernh. ex Krauss	Anacardiaceae
Rhus sp.	Anacardiaceae
Rothmannia engleriana (K. Schum.) Keay	Rubiaceae
Rothmannia sp	Rubiaceae
Rourea orientalis Baill.	Connaraceae
Rytigynia sp.	Rubiaceae
Schrebera trichoclada Welw.	Olacaceae
Sclerocarya birrea var. birrea (A.Rich.)Hochst.	Anacardiaceae
Sclerocarya birrea var. *multifoliolata* (Engl.) Kokwaro	Anacardiaceae
Securidaca longipedunculata Fresen.	Polygalaceae
Senna singueana (Delile) Lock	Caesalpiniaceae
Solanum incanum Scheff.	Solanaceae
Sorindeia madagascariensis Thouars ex DC.	Anacardiaceae
Steganotaenia araliacea Hochst.	Apiaceae
Sterculia quinqueloba (Garcke) K. Schum.	Sterculiaceae
Strychnos innocua Del.	Loganiaceae
Strychnos lucens Baker	Loganiaceae
Strychnos madagascariensis Poir.	Loganiaceae
Strychnos potatorum L.F	Loganiaceae
Strychnos sp.	Loganiaceae
Strychnos spinosa Lam.	Loganiaceae

Appendix 1. Continued

Species	Familly
Syzygium guineense (Willd.) DC.	Myrtaceae
Tamarindus indica L.	Caesalpiniaceae
Tapiphyllum cinerascens (Welw. ex Hiern) Robyns	Rubiaceae
Tarenna supra-axillaris (Hemsl.) Bremek.	Rubiaceae
Terminalia brownii Fresen.	Combretaceae
Terminalia sericea Burch. ex DC.	Combretaceae
Terminalia sp.	Combretaceae
Terminalia mollis M.A.Lawson	Combretaceae
Turraea sp.	Meliaceae
Turraea robusta Gürke	Meliaceae
Uapaca kirkiana Müll.Arg.	Phyllanthaceae
Uapaca nitida Müll.Arg.	Phyllanthaceae
Uvaria sp.	Annonaceae
Uvaria lucida Bojer ex Benth.	Annonaceae
Vangueria infausta Burch.	Rubiaceae
Vangueria sp.	Rubiaceae
Vernonia sp.	Compositae
Vernonia myriantha Hook.f.	Compositae
Vitex doniana Sweet	Lamiaceae
Vitex payos (Lour.) Merr.	Lamiaceae
Vitex sp.	Lamiaceae
Xeroderris stuhlmannii (Taub.) Mendonca & Sousa	Papilionaceae
Ximenia americana L.	Olacaceae
Ximenia caffra Sond.	Olacaceae
Zanha africana (Radlk.) Exell	Sapindaceae
Zanthoxylum chalybeum Engl.	Rutaceae
Zanthoxylum sp.	Rutaceae
Ziziphus abyssinica Hochst. ex A. Rich	Rhamnaceae
Ziziphus mucronata Willd.	Rhamnaceae