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Miombo woodland under threat: Consequences for tree diversity and carbon storage

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ABSTRACT

Agriculture is expanding rapidly in the miombo woodlands of sub-Saharan Africa. Clear felling results in the loss of species and ecosystem services. The remaining woodland is used as a vital support system for the farming communities, and the impact of this utilisation on biodiversity and ecosystem service provision is not clear. Understanding these effects will aid the development of effective, sustainable land management strategies for multiple outcomes, including biodiversity conservation and resource utilisation. This study provides new data on miombo woodland tree species diversity, structure and carbon storage from a 8766 km^2 landscape in south-western Tanzania, which is undergoing rapid conversion to tobacco cultivation.

Human utilisation of the woodland was classified by ground surveys which recorded evidence of use (e.g. cut poles and timber, removal of bark and roots, access routes). Nine sites were surveyed and categorised into three groups: high, medium and low utilisation. To determine the effect of utilisation on the tree community stem density, diameter at breast height, tree species richness and carbon storage were recorded. In the low utilisation sites carbon storage was similar to that found in other miombo woodlands (28 t Ha^{-1}), and the Shannon Wiener diversity score for tree species diversity was 3.44. However, in the high utilisation sites, tree species diversity (2.86) and carbon storage declined (14.6 t Ha^{-1}). In areas of moderate utilisation diversity and carbon storage were maintained, but the structure of the woodland was affected, with a reduction of Class 1 (Diameter at Breast Height (DBH) < 10 cm) stems, demonstrating low recruitment which leads to a reduction in sustainability. Tree species richness and abundance demonstrated an intermediate disturbance effect in relation to utilisation, with highest levels at medium utilisation sites.

Key miombo woodland species from the subfamily Caesalpinioideae in the two genera *Brachystegia* and *Julbernardia* were present in all sites, but the frequency of *Brachystegia* species declined by 60% from low to high utilisation. The IUCN near-threatened timber species *Pterocarpus angolensis*, highly protected in Tanzania, was harvested throughout the study site, and the majority of trees recorded were immature (DBH $\leqslant$ 20 cm), suggesting that it is commercially extinct for the foreseeable future.

These findings illustrate that in miombo woodlands with low to medium utilisation levels key miombo species are retained, and tree species diversity and carbon storage remains optimal. Sustainable land management plans need to regulate utilisation within miombo landscapes and retain areas of woodland. This will ensure their long term viability, and continue to support the 100 million people who are reliant on miombo woodlands for their goods and services.

1. Introduction

The miombo ecoregion covers approximately 3.6 million km^2 in 10 countries of central and southern Africa (Byers, 2001), and has been identified as one of five global wilderness areas that should be prioritised for conservation (Mittermeier et al., 2003). This is due to its large area, high levels of endemicity, and importance as habitat for several threatened species (Conservation

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International, 2012). One such species is the IUCN near-threatened timber species *Pterocarpus angolensis* (World Conservation Monitoring Centre, 1998b). This slow growing tree (Stahle et al., 1999) has very low recruitment levels (Boaler, 1966a) but is heavily sought after for export and domestic use (Caro et al., 2005). Within this ecoregion, miombo woodlands are the most extensive tropical woodlands in Africa, covering 2.4–2.7 million km^2 (Dewees et al., 2010; Frost, 1996; Kutsch et al., 2011). Miombo woodland is characterised by tree species from three genera in the legume subfamily Caesalpinioideae; *Brachystegia*, *Julbernardia* and *Isoberlinia*, although their dominance varies throughout the ecosystem based on rainfall and soil type (Banda et al., 2006). Over 100 million people are directly or indirectly dependent upon miombo woodland for their daily needs (Syampungani et al., 2009). With the population of Sub-Saharan Africa expected to double by 2050 (Eastwood and Lipton, 2011) pressure upon miombo woodland is increasing (Cabral et al., 2011; Dewees et al., 2010). Miombo woodlands are therefore receiving increasing attention as areas where sustainable land management is required (Williams et al., 2008), and have also been highlighted for Reducing Emissions from Deforestation and Degradation (REDD+) projects (Bond et al., 2010; Munishi et al., 2010).

The majority of studies in miombo systems describe species composition and structure within protected areas, yet most miombo woodlands lie outside of protected areas (Timberlake and Chidumayo, 2011), and are affected by human disturbance (Dewees et al., 2011). Most published studies are conducted in areas of dry miombo woodland, and almost none assess miombo in areas where cultivation is currently occurring. Only a few studies are in areas that receive over 900 mm of rainfall a year (Boaler, 1966b; Munishi et al., 2011), and only one has been completed in a high rainfall setting (1200 mm/year (Kalaba et al., 2013)). These are areas where diversity is likely to be higher, with fertile soils providing more attractive arable land which is more profitable to develop, and thus more threatened.

Miombo woodlands demonstrate a remarkable capacity to recover after disturbance, due to tree regeneration from the roots and stumps (Shirima et al., 2015a), and they have been shown to do this after agriculture, charcoal production and selective logging (Chidumayo, 2002; Chinuwo et al., 2010; Kalaba et al., 2013; Williams et al., 2008; Schwartz and Caro, 2003). However, it is unlikely that in the future cultivated areas will be left to regenerate for the 20–30 years required to return them to a mature woodland structure (Kalaba et al., 2013) and recover carbon stocks (Williams et al., 2008). Much of the threat to miombo woodland comes from smallholder clear-felling for agriculture (Abdallah and Monela, 2007) and wood extraction for energy (Cabral et al., 2011). Clearance of woodland for agriculture can be detected through remote sensing images (Sedano et al., 2005) and the associated losses in tree species richness, diversity and carbon storage are clear. Disturbance caused by the selective removal of woodland products for subsistence and livelihood purposes are not as easy to detect, and their impacts are more challenging to determine. Throughout this paper the term ‘utilisation’ is used to describe human utilisation of the woodland. Such types of utilisation include the collection of both dead and live wood for cooking (Abbot and Homewood, 1999), the removal of trees for construction, sale, and charcoal production (Kutsch et al., 2011), and the collection of Non-Timber Forest Products (NTFP) for medicines, food and livestock fodder (Dewees et al., 2010). This type of utilisation usually occurs in easily accessible areas, such as around field margins and alongside paths and tracks. Within western Tanzania there is also an additional demand for fuelwood to cure tobacco (Sauer and Abdallah, 2007; Waluye, 1994). The impacts of utilisation on miombo woodlands have received limited attention (see for example Chidumayo, 2002; Banda et al., 2006), as have the effects of selective logging for commercial timber (e.g. Schwartz and Caro, 2003; Schwartz et al., 2002), and require further study.

This study aims to address these knowledge gaps by using a case study site in south-western Tanzania to investigate the impact of differing intensities of woodland utilisation on tree species richness, abundance, diversity, and carbon storage. In this case-study site the miombo woodland is open access with few restrictions on its use; agricultural activities are ongoing; and there are higher levels of rainfall than in many previous studies. This is an area that is in need of effective land management as there is pressure to convert the woodland to tobacco cultivation (Maegga, 2011). It is an appropriate area in which to investigate the effect that utilisation of the woodland has on tree species richness, diversity, composition and structure, and carbon storage, and will enable comparison with previously studied miombo woodland sites. This information can then be used to inform land management strategies and conservation programmes such as those linked to the UN funded REDD+ programme.

2. Materials and methods

2.1. Study area

A remote miombo landscape in Kipembawe Division (8766 km^2) within the Chunya District, Mbeya Region (7°47′29.06″S, 32°57′41.18″E) of south western Tanzania was studied (Fig. 1). Miombo woodland covers 45% of the Tanzanian land surface (Malmer, 2007). The miombo woodland in the Kipembawe Division is an extensive tract of forest bordering the Ruaha National Park to the east and the Zambian border to the far west. Land tenure is governed through Village Councils. Access to woodland is unregulated, apart from three Forest Reserves which are under the jurisdiction of the District Forestry Department, and five Participatory Forest Management (PFM) Reserves, overseen by village-level PFM committees. Hunting and logging permits are issued at District level. However, the reserves are not actively managed, due to a lack of funding and capacity, and very few permits are issued. The population of Chunya is increasing at an average rate of 3.5% annually (National Bureau of Statistics, 2013) and tobacco cultivation is expanding rapidly as the main cash crop in the area (Maegga, 2011).

Average annual precipitation is 933 ± 36 mm (min 602 mm, max 1466 mm, $n = 28$ years). Rainfall occurs from October through to May, with minimal rain falling between June and September. The average temperature is 22.2 ± 2.7 °C. Fieldwork took place March–July 2013, at the end of the wet season and into the beginning of the dry season, where crops and trees are identifiable by their foliage, in a year of average rainfall.

2.2. Site selection

The study landscape has experienced low to moderate agricultural activity over the last 50 years, and this has led to a series of land use types. Land use was broadly categorised using LANDSAT TM satellite images (USGS, 2012) through supervised classification with Erdas Imagine 10 software (ERDAS, 2011). This identified areas that were predominantly agriculture, those that were a mixture of both agriculture and miombo woodland, and those that were predominantly miombo. Ten GPS (Global Positioning System) points were randomly generated within each category, and points were visited prior to commencing the research to verify the classification. Sites were selected based on their representation of the category, and their level of utilisation, obtained through consultation with knowledgeable local people (village chairpersons, game

Fig. 1. Tanzania showing Mbeya Region, Chunya District, Kipembawe Division and the ecological study sites (created from GADM (2015) and Sandvik (2009)).

officers, village elders) who were able to describe the history of the area and its current uses. Utilisation tended to correspond with access – low utilisation areas were further away from roads and villages, whilst high utilisation areas were adjacent to villages. Nine sites were selected to represent a scale from high to low utilisation. All sites were a minimum of 10 km apart, and each site covered 200 ha; the vegetation was sampled in a 4 ha subplot within the site.

2.3. Data collection

In each site, land cover type and the utilisation intensity were surveyed along five 1.5 km transects. Transects were 10 m wide and divided into 20 m sections. The dominant land cover type for each section was recorded, and within each section all live and dead poles and timbers, and cut poles and timbers, were recorded. Poles were defined as having 2 m straight stem and being between 5 and 15 cm Diameter at Breast Height (DBH) which is standardised at 1.3 m. Timbers were >15 cm DBH, with a 3 m straight stem (Blomley et al., 2008; Frontier-Tanzania, 1997). Cut timbers and poles were recorded as old or new. New cuts were identified by the cutting surface being a fresh cream/pink or green colour, with no blackening or other signs of decomposition, indicating that the cut was 0–6 months old (Blomley et al., 2008). Prior to the survey, forest walks were conducted with local people to establish what they would use for poles and timber to assist the researchers with later data collection. All other signs of human utilisation (e.g. beehives, burned trees, tobacco burners, paths) were recorded and categorised into nine variables. All cut stumps of trees DBH > 15 cm within the vegetation plots were also recorded.

To measure tree species diversity, composition, structure and carbon storage across the landscape vegetation was surveyed within 25 × 25 m quadrats (from here referred to as plots) (Kati et al., 2004) in each 4 ha subplot. In total 106 plots were sampled, covering a total of 6.63 ha. Within each plot all trees and shrubs with a DBH > 5 cm were measured. Stems forking below 1.3 m were measured and recorded separately (Williams et al., 2008; Kalaba et al., 2013), and where there were deformities or injuries at breast height the stem was measured above or below it, whichever was judged most appropriate (Shirima et al., 2011). Bole and canopy heights were estimated, species were identified and verified using field guides (Dharani, 2011; Smith and Allen, 2004). Where necessary specimens were collected and deposited at the University of Dar es Salaam herbarium for verification.

3. Data analysis

3.1. Land use and utilisation

Data were analysed according to both land cover and utilisation, and were calculated at plot and site level. To identify land cover type the number of sections on each transect that were covered by each land cover type were calculated as a percentage, and then grouped into four main land cover categories. ‘Agriculture’ represented all land cover that was cultivated. This included areas that had been prepared for cultivation, as well as land that was under crop. The main crops are tobacco and maize, and small amounts of other food crops such as sweet potato and beans are also grown. ‘Regenerating miombo’ encompassed all woodland that was regenerating as a result of disturbance. This is identified by the presence of many stems sprouting from stumps or roots that are all of a similar age. The final two categories are ‘Miombo woodland’, which is evident by the presence of mature trees and ‘Seasonal floodplain’ – areas that are seasonally inundated with water, identified by a lack of mature trees and the presence of grasses.

The type of utilisation within this area includes harvesting poles and timber for construction of houses, tobacco burners and stores; the collection of non-timber forest products such as roots and bark for rope and medicine; the construction of beehives; commercial logging; and collecting timber to cure tobacco.

To determine utilisation levels the numbers of harvested timber and poles were calculated as the percentage of poles and timbers that were cut from all available poles and timbers (dead and alive) and allocated to the category ‘CutTrees’. All stumps were summed per vegetation plot, and allocated to the category ‘Stumps’. For other types of utilisation the number of each type was summed across the site. The nine sites were then grouped into three utilisation categories (low, medium and high) based on the results for each type of utilisation. Differences between each variable category were calculated using a one-way ANOVA and the post-hoc test Tukey’s HSD in R (R Core Team, 2014) (Table S1).

3.2. Tree species richness, diversity and composition

Plot data from all sites were pooled. Diversity scores for each plot were calculated using the Shannon Wiener Diversity Index using the ‘Diversity’ function in the package ‘Vegan’ in R (Oksanen et al., 2013). Diversity, richness and abundance were plotted according to utilisation category using the first 10 plots for each site to ensure equal sampling effort.

The effects of utilisation on tree species richness, abundance and diversity were statistically modelled using generalised linear models. The predictor data were centred and scaled prior to analysis. The predictor data were allocated as follows: ‘Site’ as the random effect, ‘CutTrees’, ‘Stumps’, ‘DistSettle’(Distance from site to settlement), and ‘AgeAg’(the length of time the area had been cultivated), Non-Timber Forest Products (NTFP) and the quadratic terms of each variable as fixed effects, allowing for temporal impacts on species richness. The models were simplified to minimal adequate models by backwards selection using likelihood-ratio tests, validated and checked for over-dispersal (Zuur et al., 2009). The effect on species richness was calculated using a generalised linear mixed effects model with Poisson error distribution, the effect on abundance was calculated using a negative binominal generalised linear model; and the effect on diversity used a linear mixed effects model. All models were calculated in R using the packages ‘lme4’, ‘nlme’, ‘rcpp’ and ‘MASS’ (Bates et al., 2014; Pinheiro et al., 2014; Venables and Ripley, 2002; Eddelbuettel and Francois, 2011).

Detrended Correspondence Analysis (DCA (Hill and Gauch, 1980)) was performed to detect any relationship between the species composition and the explanatory site-level land use variables, also using the R package ‘Vegan’, function ‘decorana’. Prior to this, the interrelationships between all variables were tested for correlation using the Pearson’s correlation test. Only variables that were not highly correlated were used ($r < 0.7$) (Loos et al., 2014). A permutation test was used to fit and test the correlation of the land use variables with the ordination.

The species composition was examined in greater detail using the Importance Value Index (IVI). The IVI describes the floristic structure and composition of the woodland, and has been used frequently in miombo systems (e.g. Kalaba et al., 2013; Giliba et al., 2011; Munishi et al., 2011; Mwakalukwa et al., 2014). It demonstrates how often a species occurs at a site, the size of the trees and how abundant they are. It is calculated for each species using the equation:

$$\begin{aligned}\text{IVI} = (&\text{Relative frequency} + \text{relative basal area}\\ &+ \text{relative density})/3(\text{Curtis and McIntosh, 1951})\end{aligned}$$

The IVI was calculated for each utilisation level category. The value that is produced is a score, which is then ranked against the other species within that category – i.e. a rank of 1 demonstrates that the species is the most dominant within that category. The highest 10 ranking species for each utilisation level were identified. Protected species were identified and examined to determine any trends and patterns in their distribution and sizes.

3.3. Woodland stand structure and carbon storage

Site-level stand structure was determined based on the size classes of the trees. All trees were classified according to their DBH, into six classes: (1) DBH < 10 cm; (2) DBH 11–20 cm; (3) DBH 21–30 cm; (4) DBH 31–40 cm; (5) DBH 41–50 cm; (6) DBH 50+ cm (Mwakalukwa et al., 2014). The abundance of trees in each class was used to record the age and structure of the woodland.

Stem biomass was calculated using four allometric equations from similar ecosystems with DBH and height data (Table 1); using multiple approaches to estimate biomass allows realistic uncertainties to be generated (Williams et al., 2008). The mean of these equations was then used to produce a final estimate of biomass (Williams et al., 2008; Shirima et al., 2011; Kalaba et al., 2013). Wood biomass was assumed to be composed of 50% carbon (IPCC/OECD/IEA, 1997). Data from each plot were then summed to utilisation level and calculated per hectare.

Differences between carbon storage at each utilisation level were calculated with plot-level data using a one-way ANOVA and the post-hoc test Tukey’s HSD in R (R Core Team, 2014). Subsequently these data were introduced to a linear mixed effects model with the fixed effects ‘CutTrees’, ‘Stumps’, ‘AgeAg’ and ‘DistSettle’, with random effect ‘Site’. These fixed effects allowed for a temporal effect on stand structure. All response variables were centred, scaled and run using the ‘Maximum Likelihood’ estimation in the

Table 1
Allometric equations used to estimate biomass.

Author	Equation	Source country	Total above ground biomass
Brown et al. (1989)	$B = 34.4703 - 8.0671(D) + 0.6589(D^2)$	Dry tropical, not miombo specific	For all trees
Malimbwi et al. (1994)	$B = 0.06 * D^{2.012} * H^{0.71}$	Dry miombo, Tanzania	For trees $\geqslant$ 5 cm DBH
Chidumayo (1997)	$B = 3.02D - 7.48$	Wet miombo, Zambia	For trees $\leqslant$ 10 cm DBH
	$B = 20.02D - 203.37$		For trees $\geqslant$ 11 cm DBH
Chamshama et al. (2004)	$B = 0.0625 \times D^{2.553}$	Tanzania	For trees $\geqslant$ 5 cm DBH

B = Biomass (kg); D = Diameter at breast height (cm); H = crown height (m).

'nlme' package in R (Pinheiro et al., 2014), then selected using backward selection.

4. Results

4.1. Species richness, diversity and composition

Across the nine sites 3252 stems were recorded, representing 122 species from 86 genera in 46 families (Table S3). The dominant family is Fabaceae, the legume family, with 21 species. Fabaceae contains the subfamily Caesalpinioideae, which is dominant within miombo systems. From this sub-family the genus *Brachystegia* was represented by six species. Only the five species *Brachystegia boehmii*, *Julbernardia globiflora*, *Lannea schimperi*, *Pseudolachnostylis maprouneifolia* and *P. angolensis* were present at all nine sites. Within the high utilisation sites (which included the highest amounts of regenerating miombo) species from the defining miombo genera (*Julbernardia*, *Brachystegia* and *Isoberlina*) were either absent or present in low densities. The presence of *Brachystegia* species declined by 60% from low to high utilisation levels.

Species richness and abundance were not significantly different across the three utilisation levels (Fig. 2) (richness: ANOVA: $df = 2$, $F = 0.854$, $p = 0.431$; abundance: ANOVA: $df = 2$, $F = 1.109$, $p = 0.336$). Species diversity showed a significant difference between high and low utilisation levels (ANOVA: $df = 2$, $F = 4.094$, $p = 0.0214$, Tukey's HSD: $p = 0.0162$ (Table S2)).

There was a significant relationship between the number of stumps and all three metrics. The relationship with diversity was linear, but the relationships with abundance and richness were significantly non-linear and were modelled with quadratic regressions (Table 2). These humped relationships (Fig. 3) are perhaps best described as "an intermediate disturbance effect" (Connell, 1978) – moderate levels of utilisation can be associated with increased richness and abundance as it allows recruitment of new species, but higher levels of utilisation result in decreased richness and abundance. Tree species richness also demonstrated a significant linear relationship with the length of time the area had been cultivated (AgeAg) and a quadratic relationship with the numbers of cut poles and timbers (CutTrees) (Table 2). All other utilisation variables were not significantly associated with the three metrics.

Changes in land use and utilisation do influence species composition. The variables that have a significant effect on species composition are distance from settlement, regenerating miombo, the collection of NTFP and harvesting of poles and timbers (Fig. 4). This shows that as the distance from settlements increases and miombo regenerates there is a positive effect on species composition, whereas the collection of NTFPs, poles and timbers has a negative effect. Disturbance also influenced the species composition of the woodland. The first axis on the DCA estimates that 43% of the changes in species composition are associated with a gradient from extractive utilisation (cutting timber and poles, and extracting NTFPs and honey) to regenerating miombo. The second axis demonstrates that a further 25% of changes in species composition is associated with the distance to settlements.

A change in species composition in response to utilisation is further evidenced by the changes in species dominance according to the Importance Value Index (IVI). In lightly to moderately utilised areas, the key miombo species from the genera *Julbernardia*, *Brachystegia* and *Isoberlina* were dominant. However, in sites of high utilisation they were replaced by other species. Table 3 illustrates the reducing dominance of *Brachystegia* species and *P. angolensis* with increasing utilisation, which are both absent from the top 10 highest ranking species in the high utilisation site. There is also a reduction in species that are utilised for medicines, alternative food sources, and fibres, such as *L. schimperi*, *Uapaca kirkiana* and *Oldfieldia dactylophylla* (Smith and Allen, 2004).

4.2. Vegetation structure

Woodland stand structure varied in relation to the utilisation of the sites, with the woodland classified as low utilisation demonstrating a typical reverse J-shaped curve (Hörnberg et al., 1995), with the highest numbers of stems in Class 1. The numbers of stems in Class 1 in the high utilisation site are due to regenerating trees of a similar age (5–10 years). There are relatively few class 1 stems in the medium utilisation site. There are also no stems in classes 5 and 6 in the high utilisation site (Fig. 5).

4.3. Carbon storage

At high utilisation sites average carbon storage was 14.6 t Ha^{-1}; at medium utilisation sites 33.1 t Ha^{-1}; and at low utilisation 28.5 t Ha^{-1}. There were significant differences in carbon storage between high utilisation sites and low utilisation sites (ANOVA, $df = 2$, $F = 12.38$, $p < 0.0001$, Tukey's HSD: $p = 0.004$), and between high and medium utilisation sites (Tukey's HSD: $p < 0.0001$), but not between low and medium sites (Tukey's HSD: $p = 0.13$). The linear mixed model demonstrated that as the number of stumps (cut stumps of trees DBH > 15 cm) increased, the amount of carbon stored decreased (lme, $F = 14.15$, $p < 0.0001$), which is expected, and is consistent with the results for carbon storage at utilisation level.

5. Discussion

Miombo woodlands are affected by both deforestation through the clearance for agriculture and degradation through the utilisation of woodland products. Agriculture provides both income and food for local people, and the utilisation of woodland products is equally vital to their livelihoods, as their use can prevent households falling into poverty by providing alternative food sources, medicines and fuelwood (Campbell et al., 2007). This paper discusses the impact that this use has on the tree community, and provides insights that can be used to inform the future management of miombo in Africa.

5.1. Species richness, diversity and composition

There were 122 species recorded across the study area. Shannon Weiner diversity scores ranged from 2.86–3.44. These are similar

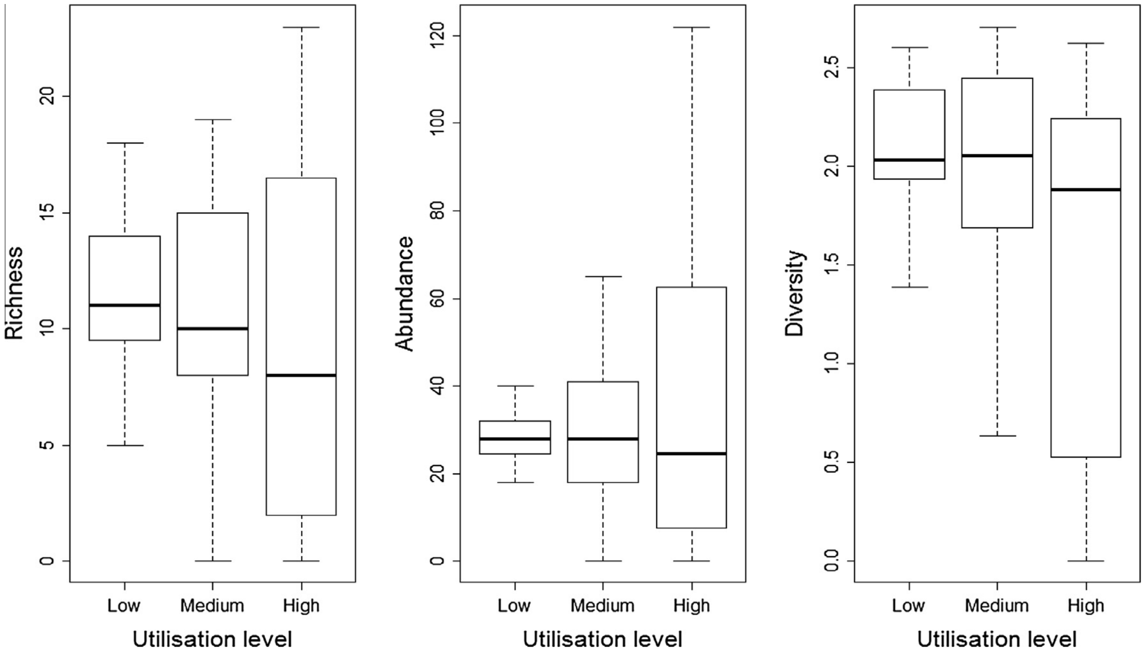

Fig. 2. Tree species richness, abundance and diversity at different utilisation levels.

Table 2
Relationships between species abundance (negative binominal generalised linear model); species richness (generalised linear mixed effects model); and species diversity (linear mixed effects model) and agricultural utilisation and timber use (assessed by density of stumps) with significance levels indicated by: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Response variable *model*	Predictor variable		Estimate	*SE*	*Z*	*Pr* > |*z*|
Abundance *Negative binominal glm*	Intercept		3.38156	0.07555	44.761	<2e−16***
	Stumps		−0.12274	0.10814	−1.135	0.256
	Quadratic term of stumps		−0.15815	0.05548	−2.850	0.004**
Richness *glmer*	Intercept		2.61473	0.08484	30.819	<2e−16***
	CutTrees		0.10968	0.4301	2.550	0.011*
	Quadratic term of CutTrees		−0.22299	0.06806	−3.277	0.001**
	Stumps		−0.07637	0.07477	−1.021	0.307
	Quadratic term of stumps		−0.14087	0.04248	−3.316	<0.001***
	AgeAg		−0.12599	0.05575	−2.260	0.024*
		Value	*SE*	*df*	*t*-Value	*p*-Value
Diversity *lme*	Intercept	1.8598682	0.08398535	90	22.145151	0***
	Stumps	−0.3529426	0.05604944	90	−6.296987	0***

to scores found in Zambia by Kalaba et al. (2013) (2.8, average rainfall 1200 mm/yr), but much higher than those of Shirima et al. (2011) (1.05–1.25, average rainfall 720 mm/yr) in the Udzungwa Mountains in Tanzania. Differences in richness and diversity throughout miombo habitats are likely to be due to differing rainfall regimes, because many of the differences in woodland composition are dependent upon the amount of rainfall that is received, leading to the ‘dry’ (<1000 mm/yr) and ‘wet’ (>1000 mm/yr) miombo classifications (Frost et al., 2003). Tree species richness, diversity and abundance all declined with increasing disturbance in the study landscape. However, in areas of moderate utilisation these values were retained, and species richness and abundance initially increased with disturbance. Similar responses to disturbance such as selective and reduced impact logging have been observed elsewhere (Imai et al., 2012; Putz et al., 2012), and indicate that management strategies can accommodate low to moderate levels of utilisation whilst maintaining tree species richness, diversity and abundance.

Regional changes in miombo woodland species composition are well documented, and can be due to various environmental factors such as altitude, rainfall, soils and underlying geology (Banda et al., 2006; Giliba et al., 2011). However, the landscape changes reported here, when geology, soil type and altitude are relatively uniform, are more likely to be due to land use changes. Replacement of *Brachystegia* in particular may be due to the genera being preferred for drying tobacco and it is therefore overharvested in highly utilised areas. Additionally, *Brachystegia spiciformis* was absent in regenerating areas; probably because previously farmed areas have usually been burned frequently, and this species is fire-sensitive (Cauldwell and Zieger, 2000). The loss of defining miombo species such as this from regenerating areas has been found elsewhere (Williams et al., 2008). In high utilisation sites *Combretum zeyheri* became dominant. *Combretum* spp. are fast growing, and dominate in early stage succession (Backéus et al., 2006). This is likely to occur in these high utilisation areas, when short fallow periods occur, and typical miombo species are unable to become established.

There were two species of vulnerable trees in the study site, *P. angolensis*, listed as near-threatened on the IUCN Redlist of Threatened Species (World Conservation Monitoring Centre, 1998b), and *Prunus africana*, listed as vulnerable (World Conservation Monitoring Centre, 1998a). *P. africana* was recorded once at a

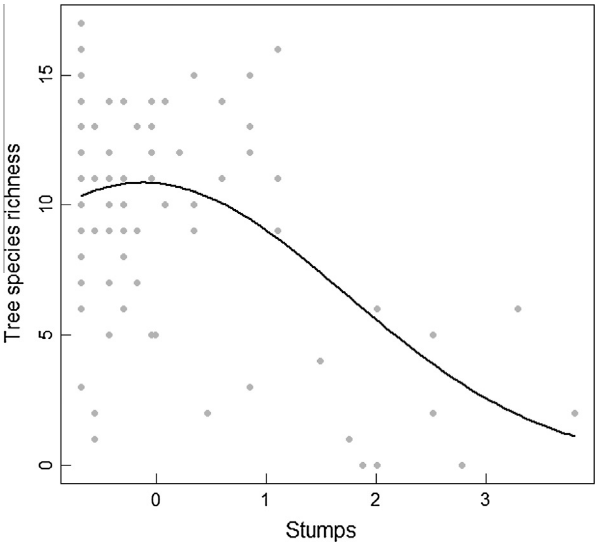

Fig. 3. The quadratic relationship between tree species richness and the number of stumps (glmer, −0.14087, *SE* = 0.042, $p < 0.001$). Stumps data are centred and scaled. This demonstrates an intermediate disturbance effect where richness initially increases with the number of stumps before decreasing.

low utilisation site, demonstrating that it is rare within this area. It is an evergreen tree which usually occurs in riparian woodlands (Dharani, 2011), and the rarity of this habitat type within this area of miombo woodland may explain its low abundance here. *P. angolensis* was recorded at all sites, with the highest abundance in moderate utilisation sites, most likely due to the identified intermediate disturbance effect. Due to this species' threatened status, the Tanzanian Government stipulates that only trees over 60 DBH may be harvested (Caro et al., 2005). The average time for *P. angolensis* to reach a DBH of 35 cm is 88–137 years when rainfall is 600–700 mm/year, although this can vary considerably, particularly with higher rainfall (Stahle et al., 1999). At this DBH trees are able to produce a larger number of seedlings to enable a greater change of regenerative success, although only 2% of fruits produced germinate in the field (Boaler, 1966a) demonstrating its very low recruitment rate. This was evident within this study site, where only five *P. angolensis* seedlings were detected within the regeneration quadrats. Of the 88 individual *P. angolensis* that were observed in this study there were no trees over 60 cm DBH, and only two were over 35 cm DBH, with the majority (71) being in the lowest two DBH classes (DBH ⩽ 20 cm). It was noted that *P. angolensis* was harvested, regardless of the size of the tree. However, in areas where trees have been selectively logged there has been no reported increase in the recruitment of trees, where compensatory recruitment would be expected to occur due to the increase in light (Schwartz and Caro, 2003). The long-term viability of this species within this area is in doubt, as it is in other areas (Caro et al., 2005; Schwartz et al., 2002; Stahle et al., 1999).

5.2. Vegetation structure

The reverse J-shaped curve of woodland structure is an indicator of a steady and expanding population, which has more trees in the smaller classes (Peters, 1994), indicating continuous recruitment in a sustainable system (Hörnberg et al., 1995). Other studies in miombo woodland in protected areas demonstrate this structure (Giliba et al., 2011; Mwakalukwa et al., 2014; Shirima et al., 2011), as do the sites within this study with low utilisation. However, harvesting of trees significantly affects the structure of the woodland (Luoga et al., 2004). In the moderately disturbed sites there are low numbers of trees in Class 1 due to overharvesting of this class, which suggests that utilisation is not sustainable. In the high utilisation sites, there are an unusually high number of trees in Class

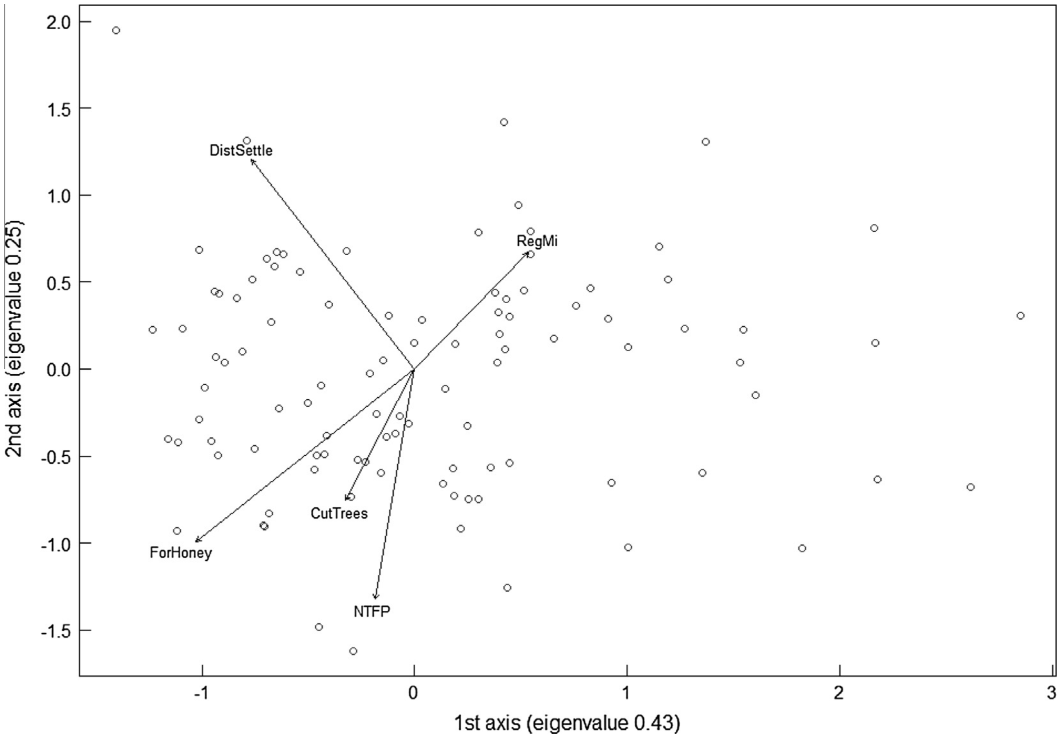

Fig. 4. DCA of tree species community. Variables which had a significant association ($p < 0.05$) with community composition are represented by arrows: 'DistSettle' – distance from settlement; 'RegMi' – regenerating miombo woodland; 'ForHoney' – extraction of resources for the purpose of collecting honey; 'NTFP' – collection of Non-Timber Forest Products; 'CutTrees' – harvest of timbers and poles.

Table 3
Importance Value Index.

IVI rank	Utilisation level		
	Low	Medium	High
1	*Brachystegia boehmii*	*Julbernardia globiflora*	*Combretum zeyheri*
2	*Julbernardia globiflora*	*Brachystegia spiciformis*	*Pseudolachnostylis maprouneifolia*
3	*Pseudolachnostylis maprouneifolia*	*Pseudolachnostylis maprouneifolia*	*Isoberlinia angolensis*
4	*Lannea schimperi*	*Brachystegia boehmii*	*Julbernardia globiflora*
5	*Brachystegia spiciformis*	*Burkea africana*	*Pericopsis angolensis*
6	*Pericopsis angolensis*	*Pterocarpus angolensis*	*Clerodendrum* sp.
7	*Parinari curatellifolia*	*Diplorhynchus condylocarpon*	*Terminalia sericea*
8	*Uapaca kirkiana*	*Pericopsis angolensis*	*Diplorhynchus condylocarpon*
9	*Pterocarpus angolensis*	*Lannea schimperi*	*Piliostigma thonningii*
10	*Oldfieldia dactylophylla*	*Anisophyllea boehmii*	*Mangifera indica*

1; this is due to the stems regenerating at the same time, approximately 10–15 years ago. The lack of large trees in these sites also indicates that they are overharvested. Sustainable management of these areas would require restricting utilisation of younger trees.

5.3. Carbon storage

Although miombo woodlands store up to 10 times less carbon per hectare than tropical forests, they cover a much greater area and are therefore an important carbon store (Munishi and Shear, 2004; Shirima et al., 2011, 2015b). Carbon storage in this study is similar to that in other studies, demonstrating that miombo generally holds similar carbon stocks, regardless of the rainfall regime (Shirima et al., 2011; Williams et al., 2008). Increasing utilisation resulted in the decline of carbon stored across the study area. However, in areas of moderate utilisation carbon storage was similar to that in low utilisation areas, suggesting that in areas where utilisation is managed carbon stocks will be retained.

6. Conclusion

Miombo woodland in sub-Saharan Africa will continue to be converted to agriculture and utilised for the needs of local people. If left without regulation and landscape management planning, it is likely that such utilisation will not be sustainable, with the loss of biodiversity and ecosystem services provision. Therefore it is vital that sustainable land use management plans are developed that incorporate biological concerns and also take into consideration the needs of the local communities. This research has demonstrated that areas of high utilisation, which have little remaining mature miombo and large areas converted into agriculture, result in decreases in species richness, abundance and diversity, carbon storage, and a loss of large trees and key miombo species. In these areas fallow periods are not long enough to return to a woodland habitat similar to miombo, and instead a shift to a more fire-resistant shrubland thicket may occur (Stromgaard, 1986). It is also apparent that in areas where mature woodland is maintained within a mosaic of agriculture, and utilisation levels are moderate, these metrics are maintained at similar levels to low utilisation sites. However, over-exploitation at a moderate level of utilisation can severely damage the stand structure of the woodland, and therefore careful monitoring of the woodland is required.

Land management options should aim to create a mosaic of woodland and agriculture, and avoid total clearance. A comprehensive monitoring programme is necessary to monitor the levels of utilisation and impacts on the woodland. Enforcement of current restrictions of harvesting is required, as demonstrated by the overharvesting of *P. angolensis*. However, the practical application of such management strategies remains challenging given the lack of capacity in forest governance. To achieve more sustainable woodland management strengthening of capacity in forest and

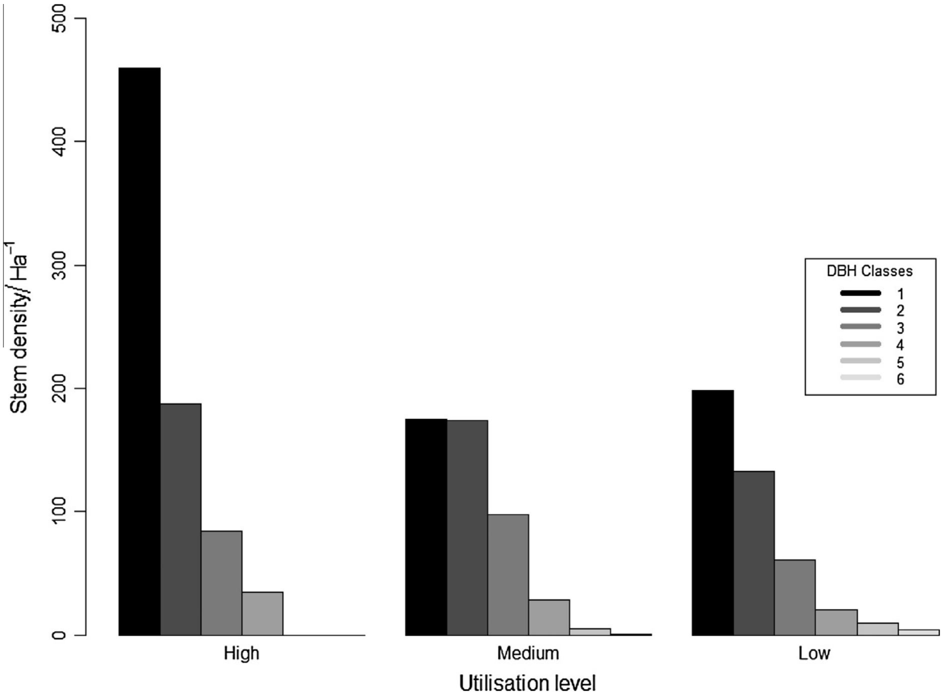

Fig. 5. Stand structure according to DBH classes at sites representing different utilisation levels. Class (1) DBH < 10 cm; (2) DBH 11–20 cm; (3) DBH 21–30 cm; (4) DBH 31–40 cm; (5) DBH 41–50 cm; (6) DBH 50+ cm.

natural resource governance is required to enable the regulation of utilisation and maintenance of mature woodland; this will ensure the long term viability of miombo woodlands, and their continued support of local and wider communities.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.11.011.

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