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Butterfly communities in miombo woodland: Biodiversity declines with increasing woodland utilisation

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ABSTRACT

Deforestation and degradation are threatening forests and woodlands globally. The deciduous miombo woodlands of sub-Saharan Africa are no exception, yet little is known about the flora and fauna they contain and the implications of their loss. Butterflies are recognised as indicators of environmental change; however the responses of butterflies in miombo woodlands have received little attention. This paper describes butterfly assemblages and their response to woodland utilisation in an understudied area of miombo woodland in south-west Tanzania. This is an area representative of miombo woodlands throughout sub-Saharan Africa, where woodland is utilised by local communities for a range of products, and is being rapidly converted to agriculture. Baited canopy traps and sweep nets were used to sample frugivorous and nectarivorous butterfly communities at different vertical stratifications in nine different study sites. 104 species were recorded, of which 16 are miombo specialists that have been recorded in Tanzania to the west of the country only. Indicator species were identified for three different levels of utilisation, with species from the sub-family Satyrinae indicating moderate utilisation. Generalised linear mixed effects models showed that butterfly species richness, diversity and abundance all decreased in response to increasing agriculture and anthropogenic utilisation. The loss of miombo woodlands is likely to result in declines in butterfly diversity. However, there was evidence of an intermediate disturbance effect for butterfly species richness, diversity and abundance with one utilisation variable, suggesting that a miombo woodland management plan that allows moderate sustainable utilisation in a heterogeneous landscape of mature miombo woodland and agriculture will simultaneously maintain butterfly communities and enable agricultural production.

1. Introduction

The expansion of agricultural land is recognised as a major driver of global deforestation (Kissinger et al., 2012) resulting in the loss of global and local biodiversity (Green et al., 2005). In order to reduce the negative impacts of this land-use change it is necessary to identify suitable areas for agriculture, and to understand the dynamics of biodiversity within these areas (Scherr and McNeely, 2008). This knowledge can then be incorporated into land management plans that are developed in collaboration with relevant stakeholders (Sayer et al., 2013) to achieve both agricultural productivity and biodiversity conservation and hence support the sustainability of a developing social–ecological system (Berkes et al., 2003).

Very few areas have been identified that are suitable for some form of cultivation, are not under formal protection and have low human population densities (Lambin and Meyfroidt, 2011). Those that have are within the dryland forest belt, including the Cerrado and grasslands of Latin America, and the savannahs and miombo–mopane woodlands of sub-Saharan Africa (Lambin and Meyfroidt, 2011; Laurance et al., 2014). However, the miombo–mopane woodland ecoregion is also one of only five global high biodiversity wilderness areas highlighted for conservation priority (Mittermeier et al., 2003) as a 'proactive' conservation strategy (Brooks et al., 2006). This is because the potential for biodiversity loss is high if large areas of woodland are converted to agriculture, and as such this area has been recognised as an area of high conflict between conservation and agriculture (Shackelford et al., 2015).

Better understanding of the vulnerability of miombo systems is essential to support the design and implementation of conservation and land management strategies. Miombo woodlands form part of the miombo–mopane ecoregion, and cover approximately 2.4 million km^2 of sub-Saharan Africa (Dewees et al., 2011). Virtually no areas of miombo woodland remain uninfluenced by human impacts (Dewees et al., 2011). They are vitally important, supporting over 100 million people for ecosystem services, including fuel, food and medicines (Syampungani et al., 2009). Additionally they provide crucial habitat for threatened species, and contain high levels of plant endemicity (Mittermeier et al., 2003). However, miombo woodlands have received little conservation and research

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attention to date, particularly regarding the response of biodiversity to land-use change, such as conversion to agriculture, and to disturbance caused by human utilisation of remaining woodland.

Butterflies are known to react sensitively to environmental changes (Uehara-Prado et al., 2007). Butterfly species richness has been shown to decrease along a gradient from woodland to agriculture in mixed woodland in Zimbabwe (Tambara et al., 2013) and agroforestry systems in Uganda (Munyuli, 2012). Additionally butterflies have been shown to respond to anthropogenic disturbance, both in tropical (Ghazoul, 2002; Hamer et al., 2003) and temperate areas (Kocher and Williams, 2000). However, there are few published studies of the impact of anthropogenic disturbance on butterflies across sub-Saharan Africa (Munyuli, 2012) and none in miombo woodland.

Butterflies are the best known major group of arthropods in Africa (Larsen, 1995) and the butterfly fauna of East Africa is relatively well studied (Kielland, 1990; Larsen, 1991). Despite this there is little consensus as to which methods are most appropriate for sampling tropical butterflies (Dumbrell and Hill, 2005). Many surveys that use butterflies as indicators focus on fruit-feeding butterflies using bait traps (e.g. Lewis, 2001; Hamer et al., 2003; DeVries et al., 2012), and occasionally supplement with other methods, such as transect walks, observation platforms and sweep-netting. Vertical stratification of fruit-feeding butterflies occurs in tropical forests, and this may be affected by disturbance, a factor often taken into consideration in sampling design (Fermon et al., 2005). Such focus on fruit-feeding butterflies ignores nectar-feeding species, and has contributed to a lack of knowledge surrounding tropical butterflies (Bonebrake et al., 2010). Hence, the response of nectar-feeding insects to environmental changes is not clear.

The paucity of knowledge about the biodiversity in miombo systems, coupled with a lack of understanding of how this biodiversity responds to land-use change and human utilisation, severely hampers the production and implementation of land management plans. This paper aims to reduce these gaps by presenting original data on butterfly communities along a gradient of land-cover change and utilisation intensity from extensive miombo woodlands in the Kipembawe Division, a remote area of south-west Tanzania. It assesses the response of butterfly communities to the changes occurring within the woodlands, identifies potential indicator species, and discusses how the loss of butterfly diversity may be avoided through sustainable management of miombo woodland. The following research objectives are addressed:

1. To describe the butterfly species composition of the Kipembawe area, south-west Tanzania;
2. To determine if fruit- and nectar-feeding butterflies have similar or different responses to land-use change and human utilisation;
3. To determine whether and how butterfly species richness, abundance and diversity respond to land cover and utilisation changes within miombo woodland, and to identify appropriate indicator species.

2. Research design and methodology

2.1. Study area and site selection

The Kipembawe Division is in south-west Tanzania, within the Chunya District, Mbeya Region (7°47′29.06″S, 32°57′41.18″E) (Fig. 1). It covers an area of 8766 km^2, with altitudes ranging from 1000–1400 masl. The topography is characterised by flat expanses of miombo woodland, and contains some seasonally inundated floodplains. Average annual precipitation is 933.4 ± 36.5 mm (min 602.8 mm, max 1466.0 mm, n = 28 years). The average annual temperature is 22.16 ± 2.74 °C (min 16.29 °C, max 27.77 °C, n = 13 years), with the highest and lowest temperatures in November and July respectively. This area is a communally used, unprotected area, which is representative of the majority of miombo woodland (Campbell et al., 2007). The population of Chunya is increasing at a rate of 3.5% annually (National Bureau of Statistics, 2013). Tobacco is the main cash crop in the area and responsible for an estimated 1.4% annual deforestation rate (Geist, 1999). Tobacco cultivation in Tanzania increased from 78,930 ha in 2010 to 168,488 ha in 2011, and although it has remained around this level for the last two years (FAO, 2015) it is likely to continue to rise within Kipembawe. The rapid changes in land-use and expanding populations in this area are representative of miombo woodlands elsewhere (Kutsch et al., 2011; Luoga et al., 2000; Malambo and Syampungani, 2008; Syampungani et al., 2009).

The study area was broadly categorised into the three land-use types (agriculture, mixed agriculture and miombo, and miombo woodland) using LANDSAT TM satellite images (USGS, 2012). These were verified on the ground prior to research commencing by visiting the selected sites accompanied by village elders who were able to describe the history of the site. Nine study sites were selected along a gradient of land-use and human utilisation intensity from predominantly miombo woodland (low utilisation) to predominantly agriculture (high utilisation). All sites were a minimum of 10 km apart, and each site covered a block of 200 ha. For full site descriptions see Supplementary Material Table A1.

2.2. Butterfly sampling

Butterflies were sampled in a four month period from April–July 2013, covering the end of the wet season and the beginning of the dry season. This is when the area becomes accessible following the rains, is prior to leaf fall, and is similar in timing to other studies (Nordqvist, 2009). Nine sites were each sampled for a period of five consecutive days. Sampling took place within a 4 ha sub-block which was divided into 25 m^2 quadrats (plots). Butterflies were sampled using sweep netting for nectar feeders (Ricketts et al., 2002) and canopy traps for fruit feeders (Austin and Riley, 1995). Canopy traps were set in pairs (one in the lower canopy/understory and one in the upper canopy (Aduse-Poku et al., 2012). Using two different sampling methods enabled both nectar and fruit feeding communities to be sampled, and setting the canopy traps at different heights captured any potential variations due to vertical stratification. Sweep-netting occurred in ten randomly selected plots using a random number generator in Microsoft Excel, based on xy co-ordinates, covering 0.63 ha in total at each site. Timed one-hour sweep netting took place in the morning and afternoon in different plots, with a total of 10 person-hours of sampling per site. All butterflies were removed from the nets into a polythene bag until the end of the session, when they were identified, photographed and released.

At each site, 10 canopy traps (constructed after Austin and Riley (1995)) were set for five consecutive days, 100 m apart through the centre of the 4 ha sub-block (Ribeiro and Freitas, 2012). Traps were opened between 8–9 am, and closed between 4–5 pm, when the trap was emptied by identifying, photographing and releasing each individual. Traps were baited with bananas which had been left to ferment for 48 h (DeVries and Walla, 2001). At each site 50 trap-days of data were collected, with a total of 450 trap-days across the study site.

Identifications were made using national and regional field guides (Kielland, 1990; Larsen, 1991). When identifications could not be made voucher specimens were taken and sent to a specialist from the African Butterfly Research Institute for identification.

2.3. Land cover, utilisation and environmental variables

To determine what affects the butterfly species composition, richness, diversity and abundance a range of environmental, land cover and utilisation variables were recorded at each site.

2.3.1. Land cover variables

Land cover was measured through ground surveys along 1.5 km transects. Transects were placed 500 m apart and ran from north to south. Each transect was 10 m wide and divided into 20 m sections. The dominant ground cover type for each section was described. These descriptions were categorised into four variables: ‘Agriculture’ (‘Ag’) described some form of agricultural activity (prepared land,

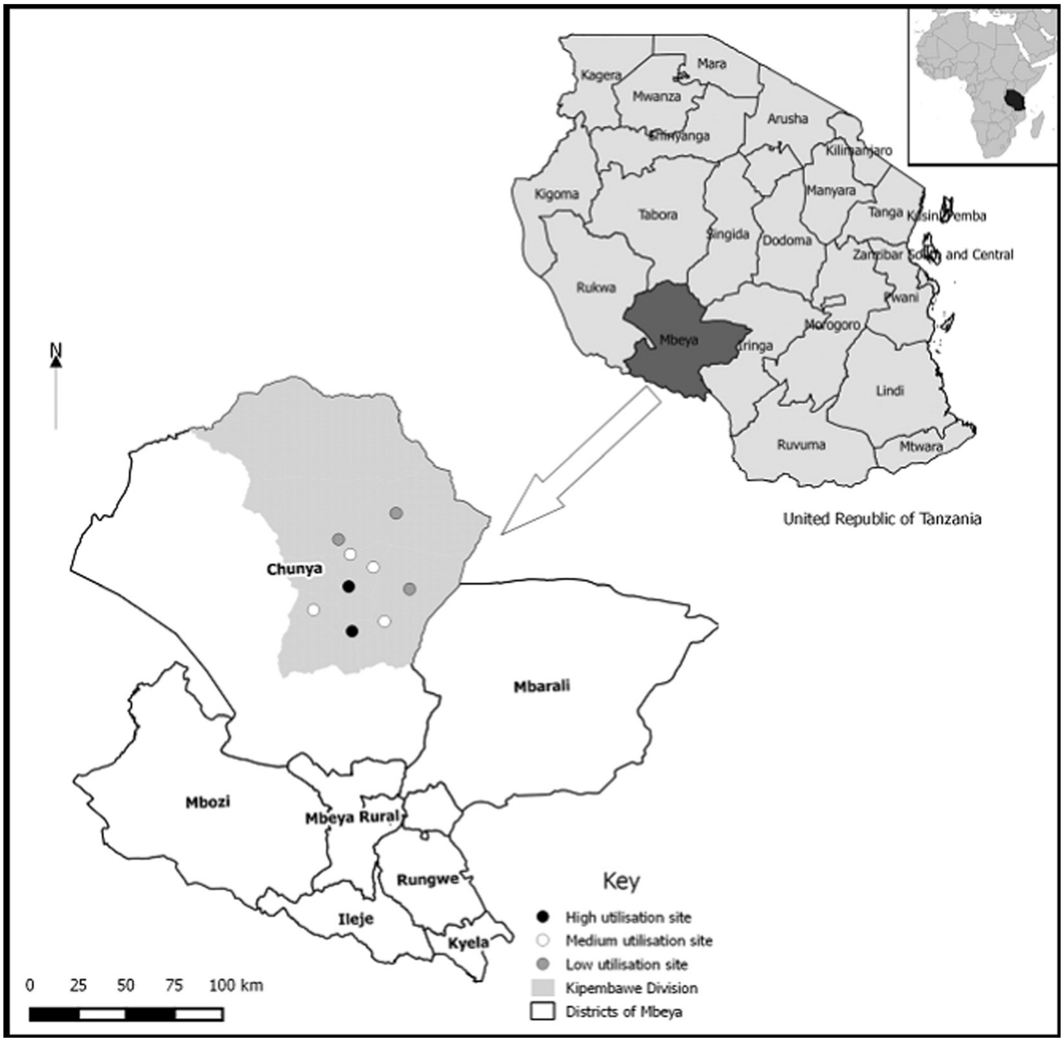

Fig. 1. Biodiversity sites of high, medium and low human utilisation (see Section 2.4) were located in the Kipembawe Division of Chunya District, Mbeya Region. The location of the Mbeya Region within Tanzania is also shown.
Created from GADM (2015); Sandvik (2009).

cultivated land, fallow land); 'regenerating miombo' ('ReMi') described miombo which had regenerated after previous cultivation; 'Open miombo woodland' ('Mio'), included all areas of mature woodland, and 'seasonal floodplain' ('SFP'), represented all areas of habitually flooded grasslands. For each butterfly sweep-net plot and canopy site habitat type was allocated to eight categories. In order to fully describe heterogeneous landscapes a habitat was described as 'adjacent to' if a different habitat was 100 m or less away from the sample plot.

2.3.2. Utilisation variables

Utilisation was used to describe extraction of resources from the woodland. This was quantified along the 1.5 km transects by recording all alive and dead poles, timbers, and cut poles and timbers within each 20 m section. Poles were defined as 5–15 cm diameter at breast height (1.3 m DBH), with a 2 m straight stem. Timbers were >15 cm DBH, with a 3 m straight stem (Blomley et al., 2008; Frontier-Tanzania, 1997). Prior to the survey, forest walks were conducted with local people to establish what stems they would use for poles and timber to assist the researchers with later data collection. Data from this survey is allocated to the variable 'CutTrees'. All other signs of human utilisation (e.g. beehives, burned trees, tobacco burners, paths) were also recorded and categorised into nine variables (Table A1). 'NTFP' represented all woodland utilisation and disturbance for the purpose of collecting Non-Timber Forest Products, such as products for rope, medicine and food. In 10 plots within the 4 ha sub-block all stumps of trees with an estimated diameter at breast height of >15 cm were recorded, and allocated to the variable 'Stumps'. The age of the agriculture at each site was ascertained through local knowledge, and allocated to the variable 'Age'.

2.3.3. Environmental variables

Altitude was recorded at each site, and the maximum and minimum temperature and rainfall were recorded daily at each site for the duration of the research period. Additionally the number of tree species per hectare ('Trees') was calculated using tree species counts from ten randomly placed 25×25 m^2 plots within the 4 ha sub-block.

2.4. Analysis

Each butterfly species was assessed according to descriptions in Kielland (1990) to determine habitat preferences and ranges. All data analysis was conducted using R version 3.1.0 (2014-04-10) (R Core Team, 2014). Utilisation variables for each site were grouped into three levels of utilisation — "Low" (n = 3), "Medium" (n = 4) and "High" (n = 2) according to the values of each utilisation variable (Fig. 1 and Table A1). The average of each group was calculated to demonstrate the differences between the levels, differences between the utilisation levels for each variable were calculated using one-way

Analysis of Variance (ANOVA) and the post-hoc Tukey's Honest Significant Difference test (HSD) (R Core Team, 2014).

Changes in the composition of nectar- and fruit-feeding butterfly communities (sampled through sweep netting and canopy trapping respectively) in response to land cover, utilisation and environmental variables were analysed using Detrended Correspondence Analysis (DCA) with a down-weighing of rare species using the function 'decorana' in the package 'vegan' (Oksanen et al., 2013). DCA was chosen because this ordination technique is able to deal with many zeros in the data set, and because it removes possible arch effects by splitting up the axis into segments and detrending the scores in each segment (Zuur et al., 2007). The environmental, land cover and disturbance variables were then superimposed using the function 'envfit', also in 'vegan' in order to find significant influences on the ordination. ANOVA and the post-hoc test Tukey HSD was performed to examine the differences in species richness, abundance and diversity across the eight habitat categories (pooled across all the sites) and the three utilisation levels (using the first two sites from each level to ensure equal sampling size), which were then displayed using boxplots.

Total species richness across the entire study site was estimated using the Chao estimator in the package SPECIES (Wang, 2011), which is suitable for non-parametric data containing single- and doubletons, and uses abundance data (Chao, 1984). Species richness was analysed using non-rarefied data to avoid the loss of power associated with singletons; the results are qualitatively similar to the use of rarefied data. Species richness, species abundance and species diversity (calculated as the Shannon–Wiener index) were further examined using a model approach. Species richness was modelled in a generalised linear mixed effects model with Poisson error distribution in the 'lme4' package of R (Bates et al., 2014). Abundance data were over-dispersed, and therefore a negative binominal generalised linear model was fitted using the 'MASS' package of R (Venables and Ripley, 2002). A linear mixed effects model with Gaussian distribution was used to examine species diversity with the 'nlme' package of R (Pinheiro et al., 2014). 'Site' was included in mixed models as a random effect, because the plots are nested within the sites. Data were pooled across all the sites ($n = 177$) by trap. These data did not demonstrate temporal autocorrelation. The full models contained the following variables as fixed effects: 'CutTrees' (linear and quadratic term), 'Stumps' (linear and quadratic term), and 'NTFP' (linear and quadratic term). None of these variables correlated with any other utilisation or land cover category. The model was simplified to minimal adequate models using backwards selection (Zuur et al., 2009). The models were validated and checked for over-dispersion using the package 'blmeco' of R (Korner-Nievergelt et al., 2015).

Indicator species were identified using the Indicator Value (Indval, Dufrêne and Legendre, 1997) with the multipatt function in the package 'indicspecies' of R (De Caceres and Legendre, 2009) and assessed according to utilisation level. This method assesses the frequency of a species within a habitat and the strength of its association with that habitat (Cleary, 2004). Significance was based on a randomisation procedure of sites, with 1000 iterations. Only species with Indicator Values ≥0.25 and $P < 0.01$ were considered to remove species with weak indicating capacities (González et al., 2013).

3. Results

3.1. Butterfly assemblages in Kipembawe

In total, 45 days of sampling throughout a four month period with canopy traps and sweep netting caught 4608 individuals, representing 104 species in 5 families and 51 genera (Table C1). The total minimum species richness across the study site is estimated at 144, using the Chao estimator (Chao, 1984). Miombo specialists were represented by 22 species, of which 16 species are only found in Tanzania to the west of the country (Tables 1 and C1).

3.2. Effects of environmental and land-use variables on the composition of fruit- and nectar-feeding butterfly communities

A Detrended Correspondence Analysis (Fig. 2) with superimposed environmental variables illustrates the effects of land-use and environmental variables on the composition of both fruit and nectar-feeding communities, and demonstrates the lack of overlap between communities sampled by different methods. Canopy traps sampled fruit-feeding butterflies, while the sweep nets sampled nectar feeders. Rainfall appeared to influence species composition along the first axis, and on the second axis utilisation had the most impact, on a gradient from agriculture to miombo woodland.

Separate analyses of the frugivore community sampled by the canopy traps and the nectarivore community sampled by the sweep nets demonstrate that they have different associations with the land cover, utilisation and environmental variables. Species composition of frugivores showed correlations with various environmental variables, with a gradient from the number of tree species to the age of the agricultural land along the first axis and a gradient from the amount of natural habitat (miombo) to variables representing disturbance of the natural habitat along the second axis. Species composition of the nectarivores was influenced by fewer variables than the frugivores, with the most important influence along the first axis being a gradient of high temperatures and extraction of NTFP to a greater amount of regenerating miombo woodland, and the only influential variable along the second axis being the age of the agricultural land (Fig. 3). DCA analysis was performed on the upper and lower canopy traps, which did not demonstrate any significant differences in species assemblages (Fig. B1).

3.3. Differences in species richness, diversity and abundance with habitat and utilisation levels

Species abundance (ANOVA, $df = 2$, $F = 33.34$, $P < 0.0001$), richness (ANOVA, $df = 2$, $F = 19.32$, $P < 0.001$), and diversity (ANOVA, $df = 2$, $F = 26.61$, $P < 0.0001$) varied significantly between all three levels of utilisation (Fig. 4B, Table A2). Butterfly species abundance, richness and diversity were lower in modified habitat (agriculture and regenerating miombo) than in miombo woodland. However, values from disturbed miombo habitat were similar to those in miombo woodland (Fig. 4A, Tables A3, A4).

Analysis of the relationship between species abundance, richness and diversity with the predictor variables demonstrated that there

Table 1
Species that are miombo specialists and have only been described in Tanzania in the west of the country. Their frequency of occurrence per site for each utilisation level is shown.

Species	Frequency per utilisation site		
	High	Medium	Low
Acraea caldarena	0.5	0.75	0.00
Acraea utengulensis	1	0.5	2.00
Belenois calypso[b]	0	0.25	0.00
Bicyclus cooksoni[b]	0	0.25	2.33
Charaxes castor[a]	0	0	0.33
Colotis regina	0.5	0.5	1.00
Crenidomimas concordia	0	5	16.00
Hemiolaus caeculus dolores	0.5	0	0.00
Junonia artaxia	0.5	1	6.33
Junonia touhilimasa	0.5	0.25	0.00
Meza larea[a]	0	0	0.33
Precis actia[b]	0	3.75	5.00
Precis ceryne	0.5	0.25	1.00
Precis pelarga	0.5	4.25	1.33
Pseudacraea poggei f carpenteri[a]	0	0	0.33
Teracolus subfasciatus ducissa	0.5	1	0.67

[a] Highly likely to become extinct in Tanzania if miombo habitat within Western Tanzania is utilised — did not occur in high or medium utilisation sites.
[b] Highly likely to become extinct in Tanzania if miombo habitat in Western Tanzania is highly utilised — did not occur in high utilisation sites.

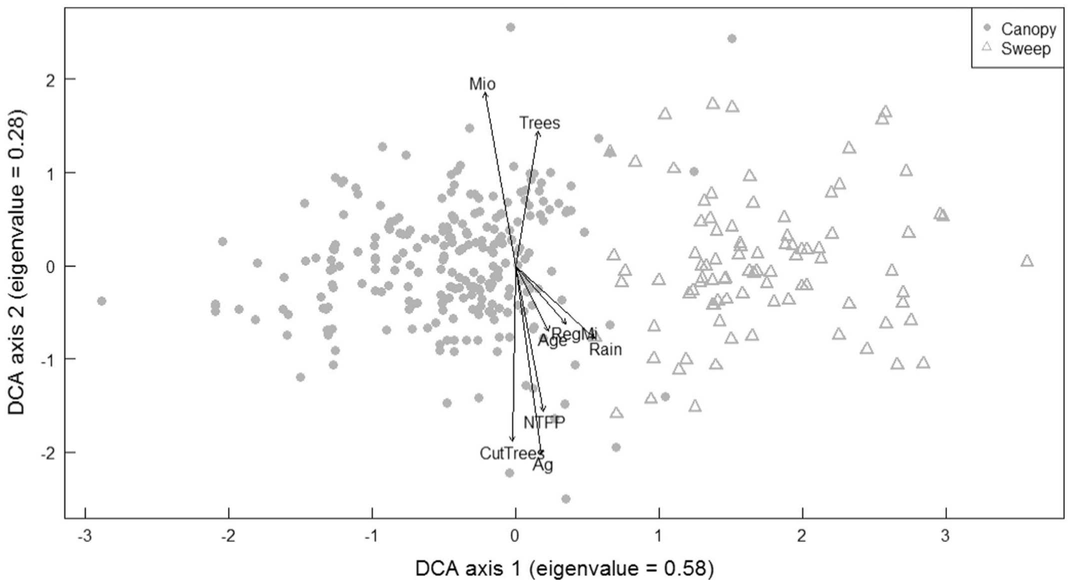

Fig. 2. DCA ordination plot of the butterfly community sampled by sweep netting and canopy traps. Variables which had a significant association ($P < 0.05$) with community composition are represented by arrows. Environmental variables — rainfall ('Rain'); tree species richness per hectare ('Trees'): land cover variables — Agriculture ('Ag'); open miombo woodland ('Mio'); regenerating miombo woodland ('ReMi'): utilisation variables — cut timbers and poles ('CutTrees'); Non-Timber Forest Products ('NTFP') and the age of the agricultural land ('Age').

was a significant negative relationship between stumps and all three metrics, and that the collection of Non-Timber Forest Products also negatively correlated with abundance and richness (Table 2). The quadratic term of stumps was also significant for all three metrics, showing that as the number of stumps increased butterfly species abundance, richness and diversity increased, until a point where they declined with increasing numbers of stumps, producing a hump-shaped relationship (Fig. 5).

3.4. Indicator species

Indicator species were identified for all three utilisation levels (Table 3). Fewer species were significantly associated with high utilisation sites than medium and low utilisation sites.

4. Discussion

4.1. The butterfly assemblages of Kipembawe

This study provides original data regarding butterfly communities within Tanzania, and adds to the understanding of butterflies within miombo woodlands. Sixteen species were recorded that are both miombo specialists and are only found in Tanzania to the west of the country, and are therefore at high risk of extinction within Tanzania should the miombo woodlands in this area become heavily utilised. Two of these are subspecies (*Teracolus subfasciatus ducissa* and *Hemiolaus caeculus dolores*) that are endemic to Western Tanzania. Additionally *Acraea utengulensis* has been found occasionally in other areas of Tanzania, and may be present in North-East Zambia, but the main global population of

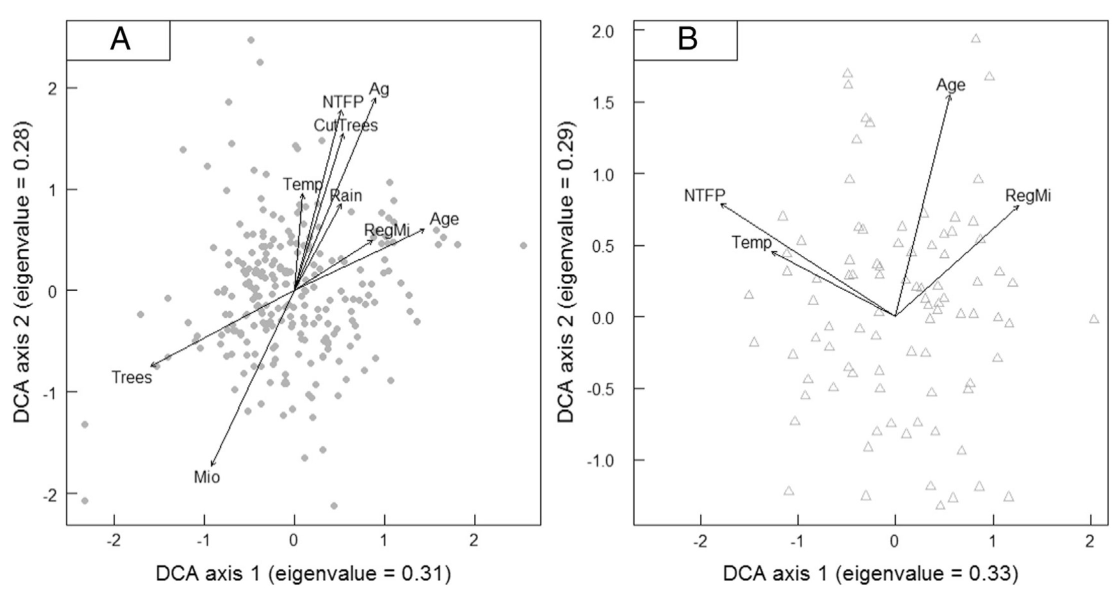

Fig. 3. DCA ordination plots of butterfly communities sampled by different methods (A. canopy traps; B. sweep netting). Variables which had a significant association ($P < 0.05$) with community composition are represented by arrows. Environmental variables — rainfall ('Rain'); temperature ('Temp'); tree species richness per hectare ('Trees'): land cover variables — agriculture ('Ag'); open miombo woodland ('Mio'); regenerating miombo woodland ('ReMi'): utilisation variables — cut timbers and poles ('CutTrees'); Non-Timber Forest Products ('NTFP') and the age of the agricultural land ('Age').

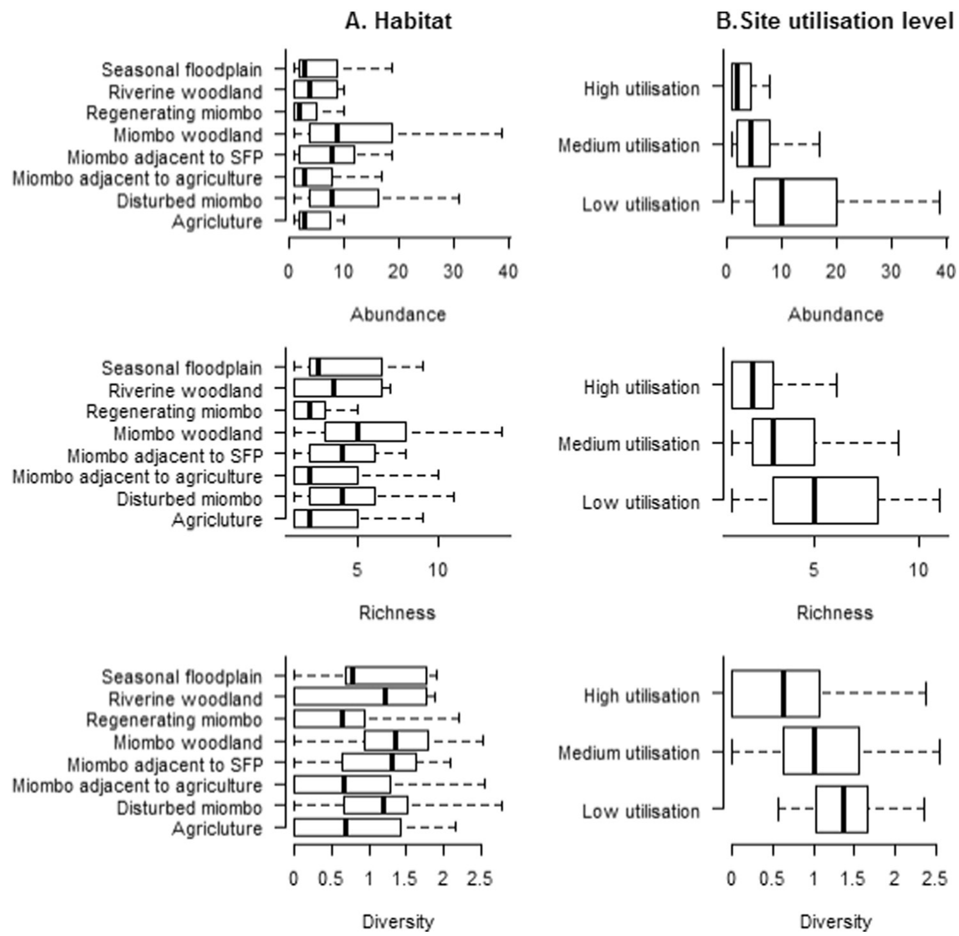

Fig. 4. Species abundance, richness and diversity in response to A) habitat type and B) utilisation levels.

this species is in Western Tanzania (Kielland, 1990). Therefore these species are at risk of global extinction should the area become heavily utilised. They have not been assessed on the IUCN Red List of Threatened Species (IUCN, 2015). This demonstrates the value of the miombo woodland in the Kipembawe Division, indicating that conservation efforts are required to maintain viable woodland in this area.

Developing indicators of disturbance within forests and woodlands can assist in developing rapid, cost effective measures of land use change, and butterflies are recognised as suitable indicators (Bhardwaj et al., 2012). This study identified *Bicyclus* species from the sub-family Satyrinae as indicative of medium utilisation. Satyrinae are shade-loving, but the larvae food preference is grasses (Kielland, 1990), which are most likely to occur in woodland gaps, therefore making moderately disturbed habitats preferable. This supports research elsewhere that suggests that Satyrinae are suitable indicators of disturbance (Bossart et al., 2006).

Table 2
Results for the three different linear models: species abundance (negative binominal generalised linear model); species richness (generalised linear mixed effects model); and species diversity (linear mixed effects model). P values (Pr(>Chisq)) for the glmer determined using the 'car' package in R (Fox and Weisberg, 2011). Significance levels indicated by: *P < 0.05; **P < 0.01; ***P < 0.001.

Response variable model	Predictor variable	DF	Deviance	AIC	LRT	Pr(>Chi)
Abundance	Stumps	1	197.09	1461.2	7.8911	0.004968**
Negative binominal glm	Quadratic term of stumps	1	211.01	1475.1	21.8102	3.010E − 06***
	NTFP	1	208.22	1472.3	19.0221	1.292E − 05***
		Estimate	SE	Z	Pr > |z|)	Pr(>Chisq)
Richness	Intercept	2.2594	0.04566	49.48	<2E − 16***	
glmer	Stumps	− 0.06411	0.03269	− 1.96	0.04987*	9.101E − 05***
	Quadratic term of stumps	− 0.23745	0.0413	− 5.75	8.95E − 09***	1.669E − 07***
	NTFP	− 0.08108	0.02932	− 2.77	0.00568**	0.06304
		Value	SE	DF	t-Value	P-value
Diversity	Intercept	1.8431	0.06548	166	28.14706	0***
lme	Stumps	− 0.08970	0.0434	166	− 2.06667	0.0403*
	Quadratic term of stumps	− 0.18727	0.05375	166	− 3.48418	0.0006***

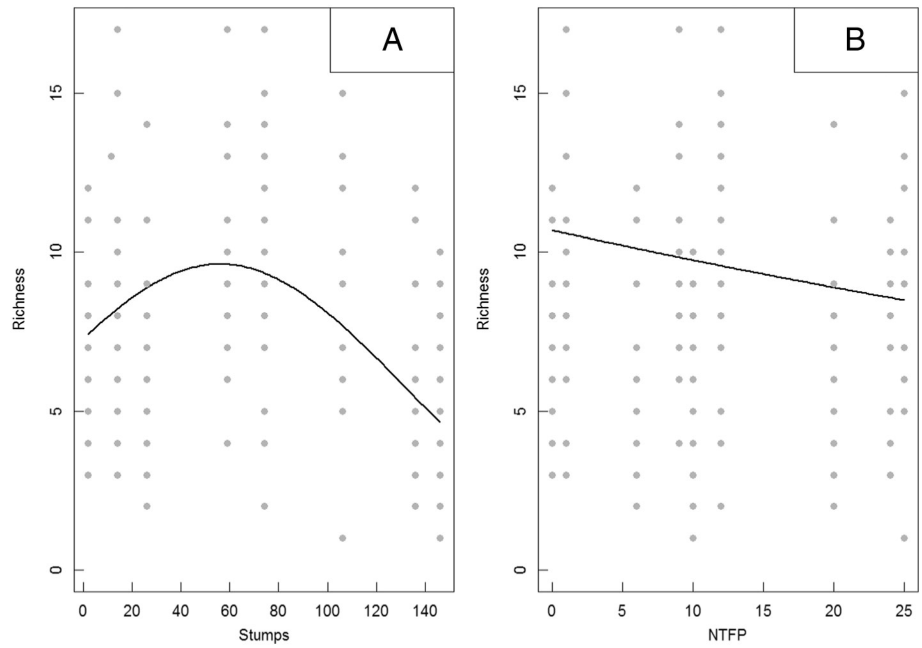

Fig. 5. The relationship between butterfly species richness and A) Stumps, with a negative unimodal response (glmer, −0.23745, SE = 0.04, P < 0.0001), and B) Non-Timber Forest Products (NTFP), demonstrating a negative linear response (glmer, −0.06411, SE = 0.03, P < 0.0001).

4.2. Response of butterfly communities to land cover and utilisation changes disturbance

When considering the entire butterfly community it is evident that there are responses to land cover and utilisation changes, altering species composition and decreasing species richness, abundance and diversity as the landscape becomes more utilised, as has been found with intensive logging and cultivation in tropical forests (Dumbrell and Hill, 2005; Lewis, 2001; Ribeiro and Freitas, 2012), in dry savannah forests (Fitzherbert et al., 2006; Tambara et al., 2013; Akite, 2008) and in coffee–banana agroforests (Munyuli, 2012).

There was little overlap in species composition between the fruit-feeding butterfly community sampled by canopy traps, and the nectar-feeding community sampled by sweep netting. The need for multi-dimensional sampling techniques has been highlighted previously (DeVries et al., 1997) although much of the focus surrounding sampling techniques has addressed vertical variation in fruit feeding species assemblages within tropical rainforests (e.g. Aduse-Poku et al., 2012; Dumbrell and Hill, 2005; Fermon et al., 2005; Molleman et al., 2006). Miombo woodlands have canopies of 8–25 m (Frost et al., 2003), and lack a significant understorey layer. Therefore, although canopy traps were positioned in the lower and upper canopies for this study, there was not a significant difference in species composition, and it is recommended that traps should be set in the lower canopy where wind has less impact on capture rates.

The majority of fruit-feeding butterflies caught in the canopy were from the family Nymphalidae, which are often the focus of indicator species research (Bobo et al., 2006; Bossart et al., 2006; Dumbrell and Hill, 2005; Hamer et al., 2003; Lewis, 2001) because they are easy to sample simultaneously in several locations, and have correlated with total butterfly and bird diversity elsewhere (Ribeiro and Freitas, 2012). Within this study the fruit-feeding communities showed significant responses to a range of different land-use, utilisation, and environmental variables, whereas the nectar-feeding butterflies showed responses to fewer variables. However, given the lack of overlap between the two communities comprehensive species inventories require sampling from both guilds.

The decline in abundance, richness and diversity in areas of high agriculture and utilisation may be due to the loss of food sources, increased amounts of pesticides and herbicides (Tambara et al., 2013), and the distance between habitat patches (Loos et al., 2014). Diversity is unlikely to remain in homogenous agriculture (Benton et al., 2003), yet utilised or degraded forests may retain significant diversity (Larsen, 1995). This was evident in this study, where abundance, richness and diversity were maintained in habitats with some disturbance (Fig. 4A). Additionally, a significant quadratic relationship was detected between the three metrics and ‘Stumps’, showing that highest levels of species richness, abundance and diversity were predicted at medium utilisation levels. This supports the intermediate disturbance hypothesis (Connell, 1978) which suggests that at intermediate levels of disturbance diversity is highest because species are present which are both colonising the area and regenerating within it, and inter-specific competition is low. This is aided by the increase in heterogeneity in the landscape (Bennett et al., 2006) which leads to a greater range of ecological

Table 3
Indicator species for high, medium and low utilisation levels (Indval = Indicator Value, significance levels indicated by: **P < 0.01; ***P < 0.001).

High utilisation			Medium utilisation			Low utilisation		
Species	Indval	P-value	Species	Indval	P-value	Species	Indval	P-value
Eurema hecabe solifera	0.279	0.001***	*Belenois thysa thysa*	0.294	0.002**	*Byblia ilithyia*	0.718	0.001***
Eurema regularis regularis	0.326	0.006**	*Bicyclus anynana*	0.383	0.003**	*Catacroptera cloanthe cloanthe*	0.261	0.002**
Ypthima sp.	0.259	0.008**	*Bicyclus campina*	0.354	0.001***	*Crenidomimas concordia*	0.392	0.001***
			Bicyclus ena	0.357	0.005**	*Henotesia simonsii*	0.625	0.001***
			Charaxes guderiana rabiensis	0.543	0.002**	*Neptis morosa*	0.474	0.001***
			Sevinia rosa	0.493	0.002**			

niches (Bazzaz, 1975). A peak in butterfly species richness and diversity has been seen at intermediate disturbance levels in a range of habitats (e.g. Nyafwono et al., 2014; Hamer and Hill, 2000; Blair, 1999). However, this finding should be approached with caution, as the intermediate effect was only demonstrated with one utilisation variable, and it is not evident in Fig. 4B. Nevertheless, this is of particular importance for conservation, as it demonstrates the need for conservation of areas that are utilised, as they are still of value (Gardner et al., 2007), and also demonstrates that it is possible to retain communities in areas which are utilised, meaning that the implementation of land-use strategies to achieve dual goals of biodiversity conservation and woodland utilisation can be successful.

4.3. Management of miombo woodland

High levels of human utilisation and conversion of woodland to farmland alters butterfly community compositions and reduces species richness, diversity and abundance in miombo woodlands, however, with one utilisation variable they were predicted to increase at moderate levels of utilisation. Despite a lack of information on the consequences of different management regimes for lesser known taxa (Gardner et al., 2007), the likelihood that there will be further pressure to expand agriculture into miombo woodland suggests that effective land-use management plans are required now to prevent substantial biodiversity loss in the future. Such land management plans will need to regulate utilisation to moderate levels, and create a heterogeneous landscape which will enable effective conservation outcomes and also accommodate sustainable agricultural production (Bennett et al., 2006). In order to develop such plans the full participation of all relevant stakeholders is essential to enable understanding of the interactions between people and miombo, and the future needs of local communities which can then be incorporated into land management plans. Long term biodiversity monitoring would be required to identify any impacts of the land use plan, and ongoing stakeholder participation would be needed to ensure that their needs continue to be met.

5. Conclusion

Butterfly communities within miombo woodland systems respond to a changing woodland landscape by decreasing in species richness, diversity and abundance with increasing utilisation and agricultural land cover. However, there is evidence of an intermediate disturbance effect, with the highest values for all three metrics predicted at medium utilisation levels for one utilisation variable. Species were recorded here which are not found in other parts of Tanzania, indicating the conservation value of these woodlands. Miombo woodlands are under threat from agriculture and excessive utilisation, and as such require effective, sustainable land management. Empirical data such as those presented in this paper will contribute to the development of such land-use management plans, in conjunction with the full participation of local communities and land-users. Evidence of an intermediate disturbance effect suggests that it may be possible to create sustainable land-use management plans that allow moderate woodland utilisation, thereby enabling biodiversity conservation and agricultural production goals to be achieved.

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Appendix A. Supplementary data

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