Influence of large termitaria on species composition and tree height structure in a modified *Brachystegia/Julbernardia* miombo woodland in Chizarira National Park, Zimbabwe.

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Summary

1. Large *Macrotermes* mounds in the miombo woodlands in Zimbabwe support dense vegetation patches in a nutrient poor ecosystem. It has been proposed that these large termitaria enhance woody species composition, richness and tree height structure in these woodlands. To test this hypothesis, species composition and vegetation tree height structure were sampled (n = 86) on termitaria and in the adjacent woodland matrix in Chizarira National Park.

2. Woody plant species composition on termitaria differs from the surrounding miombo woodland matrix. There was a 66.5 % difference in species composition between mounds and the woodland matrix.

3. Termite mounds had 90 woody plant species and the woodland matrix 86 species of which 18 species were restricted to termite mounds, 13 species to the matrix and 67 species were shared.

4. Mounds and the woodland matrix have distinct species assemblages among different catenal positions in the landscape. Catenal position strongly influences woody plant species distribution and richness in Chizarira National Park.

6. Termitaria harbor a higher species richness of tall trees (i.e. > 6 m and between 3 – 6 m) than the matrix. Tall trees are characteristic of termitaria, whereas the woodland matrix is dominated by coppiced and resprouting *Brachystegia* shrubs and *Combretum* species.

7. Termitaria form refugia for the growth of tall trees in this study site, where elephant and fire are major disturbance factors. The results of the study show clearly that termitaria are patches of different species composition and protect tall trees from elephants and fire in the miombo woodlands than the woodland matrix areas of Chizarira National Park.

8. *Synthesis:* The presence of large *Macrotermes* mounds in the miombo woodlands of Zimbabwe support a different plant species composition, vegetation height structure and biodiversity in Chizarira National Park.

Key words: plant composition, woodland matrix, vegetation classification, Chizarira, catena

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Introduction

The miombo woodlands in the southern, central and eastern parts of the African continent are the widest ranging deciduous woodlands in Africa and cover an area of 2. 7 million km² (Campbell *et al.*1996). Recently the miombo woodlands have been identified as one of the world's biodiversity hotpsots and are considered to be in need of a global conservation strategy (Mittiermeier *et al*. 2003). The miombo woodlands are rich in higher plant species diversity with a known 8 500 species of which 54% are endemic (Campbell *et al.*1996). There is concern that elephant impacts may be affecting species composition, richness and structure of vegetation in southern African protected areas (D. Cumming. pers.comm. 2008). In this study site, the last elephant density survey numbers were lower than earlier surveys and are currently 1.5 km^{-2} in the miombo research area of Chizarira National Park (Dunham *et al.* 2006). Biodiversity conservation is a key priority for most protected areas where a high number of elephants occur (Cumming *et al*. 1997, O' Connor *et al*. 2007). Elephants modify vegetation structure and are known to reduce plant diversity, canopy volume and height (Laws 1970, Owen-Smith 1988, Stuart-Hill 1992, Chafota & Owen-Smith 1996, Johnson *et al*. 1999).

Termites parallel elephants as 'ecosystem engineers' (Dangerfield *et al.* 1991, Jones *et al.* 1994) in tropical ecosystems and play an important role in the distribution of species diversity and plant biomass in nutrient-poor landscapes (Lopez-Hernandez *et al.* 2006). Large termite mounds built by the species of *Macrotermes* are conspicuous in the miombo landscape (Malaisse 1978, Loveridge & Moe 2004). In Africa, specific vegetation is associated with the mounds of some *Macrotermes* species (Wild 1952, Malaisse 1978). Sizes and the estimates of the ages of mounds vary considerably, and mounds 30 m in diameter and 6 m in height have been recorded (Pomeroy 1977, Lepage 1979). The building of the mounds is strongly related to soil properties.

Termites modify the structure of soil (Lee & Wood 1971, Greig-Smith 1979). At a fine scale, termites influence the soil water availability, fertility, mineral content and nutrient concentration in mounds (Lee & Wood 1971, Pomeroy 1976, Dangerfield *et al*. 1991, Konate *et al*. 1999). Their foraging activity concentrates nutrients (N, P, C, and Mg) from the nearby surrounding areas (Lopez-Hernandez *et al*. 2006), and results in a high plant biomass on mounds (Pomeroy 1976). Mound soils accumulate carbon (Konate *et al*. 1999), and consequently have a higher pH and bases than the surrounding soils (Watson 1967). The high concentration of nutrients and trace elements results in a distinct plant assemblage on termitaria than the adjacent woodland area in the miombo landscape (Fanshawe 1968).

The size, shape and spatial distribution of high plant-cover patches typify vegetation patterns (Aguiar & Osvaldo 1999). Patches provide refugia for certain species of plants in communities (Levin 1992, Hobbs & Mooney 1995) and contribute directly or indirectly to the survival of some plant species (Hansell 1993). Mounds form highly productive patches (Spain & McIvor 1988) and are important sources of spatial heterogeneity in the miombo woodlands (Scholes 1990, Frost 1996, Holdo & McDowell 2004).

Termitaria function as islands of local diversity in the miombo system (Fleming & Loveridge 2003). Mounds are an important resource used by small mammals (Fleming & Loveridge 2003) and large ungulates (Mobaek *et al*. 2005) and support a higher diversity of plant and animals than the surrounding matrix (Malaisse 1978). In 1952, Wild identified 72 different plant species on termitaria in Zimbabwe. An inventory of woody plants on termitaria in Zambia listed 129 species (Wild 1952) which increased to 208 species in 1969 (Fanshawe 1968). *Macrotermes falciger* mounds in southern Zambia supported more than 50% of the woody plant species in miombo woodland (Timberlake 1995). More recently Fleming and Loveridge (2003) recorded 93 species on termitaria compared to 83 species in the adjacent miombo woodland areas.

The high nutrient (Ca, Mg, K and P) content of trees on mounds makes them attractive to African megaherbivores, particularly to elephants (*Loxondonta africana*) and other large browsing herbivores (Ruggerio & Fay 1994, Holdo 2003, Holdo & McDowell 2004). Elephants litter the area around termitaria with dung and broken off plant material which provides termites with food resources (Holdo & McDowell 2004). Thus, termitaria sustain populations of herbivores in woodlands (Loveridge & Moe 2004) and elephants assist in regenerating species turnover and nutrient concentrations on mounds as positive feedback (Holdo & McDowell 2004). Despite the influence of elephants on vegetation structure there is still a lack of knowledge about the dynamics of species structure in modified and regenerating miombo (Chidumayo 1987, Frost 1996).

In the last 40 years termitaria in Chizarira National Park and other national parks in Zimbabwe have begun to show white rings around the base of the mounds. Glover (1949) observed similar white rings around termite mounds on the edges of ‘dambos’ (open seasonal swamps) in *Brachystegia* woodland in Zambia. As the termitaria aged, the hard outside surface eroded, the mounds flattened out and deposited salts and colloids around their bases (Glover 1949). This process resulted in a miniature ‘hardpan’ around the exterior of the mound devoid of plant growth. A large majority of the termitaria in Chizarira National Park have white rings, referred to as halos in this paper, whereas very few show no sign of a halo. It has been proposed that the cause of the halos is due to high herbivore densities; however the actual cause is unknown. Termitaria in the miombo woodland have a significant effect on the ecology of the area (Fleming & Loveridge 2003) and may also function as potential indicators of change in the miombo system.

The work presented here focused on species composition and vegetation height structure on termitaria with and without halos and in the surrounding woodland matrix. The objectives of this study were (1) to assess how woody plant species composition on termitaria and in the woodland matrix varies with the position of the mounds in the catena, (2) to explore the differences in woody plant species composition between termitaria and the woodland matrix, (3) to determine if woody plant diversity and vegetation height structure varies with the presence or absence of halos on termitaria on termitaria and in the surrounding woodland matrix.

My three main hypotheses were 1) woody plant species composition varies with the position of the mounds in the catena 2) large termitaria increase woody plant species diversity in nutrient poor ecosystems; 3) woody plant species composition and tree height structure varies with the presence or absence of halos on termitaria.

Methods

THE STUDY AREA

The study was conducted in October and November 2007 in Chizarira National Park (17º 32’ - 18º 1’ S, 27º 35’ - 28º 13’ E) which covers an area of 1 910 km² (Fig. 1). Chizarira National Park is in north western Zimbabwe and consists mainly of a plateau as part of the southern escarpment of the Zambezi valley and slopes to the Busi/Sengwa valley in the south (Thomson 1974). The landscape in Chizarira is highly dissected by drainage lines and rugged with an undulating terrain. Altitude varies from 760m to 1 445m above sea level (Thomson 1974). It is bounded by communal lands of the Binga and Gokwe Districts and shares a boundary with Chirisa Safari

Area to the south. Mean annual temperature is 23.2ºC and rainfall is about 713mm (Hutchinson *et al*. 1995). The area experiences three seasons: a hot wet season from November to April, a cool dry period through the winter months from May to July, and a hot dry period from August to October (Mapaure & Campbell 2002). The soil structure consists of luvisols bedrock, is derived from Sijarira quartzites (Late Precambrian) (Thomson 1974), and is characterized by low mineral reserves and limited fertility (Cole 1963, Menaut *et al*. 1985).

Herbivores in Chizarira National Park include elephant, buffalo, sable, kudu, waterbuck, eland, impala, zebra and warthog (Dunham *et al*. 2006). A wildlife aerial survey conducted in 2006 showed the population density of elephant (1.5 km^{-2}), buffalo (1.17 km^{-2}) and kudu (0.22 km^{-2}) (Dunham *et al.* 2006) to be relatively high in comparison to the other herbivores in the park.

The vegetation at Chizarira is dominated by the miombo tree genera *Brachystegia* and *Julbernardia* (Fabaceae, subfamily Caesalpiniodeae) (Desanker *et al*. 1995, Campbell *et al.* 1996, Frost 1996). Other common vegetation types are mixed *Combretum* and *Colophospermum mopane* woodlands (Campbell *et al* .1996). The *Colophospermum mopane* woodland covers approximately 5 % of the study area and occurred in the basin below the escarpment. *Combretum* woodlands were interspersed between mopane and the two miombo tree genera and covered on average 20 % of the study area. Both *Brachystegia* and *Julbernadia* mixed communities occurred in variable relative proportions (10 %) and were confined to the higher altitude sandy soils. In 1972 large areas of *Brachystegia boehmii* woodlands in Chizarira were reduced by elephants and fire and converted into shrublands (Thomson 1974). The more intact woodlands in Chizarira were dominated by *Julbernardia globiflora.*

Termitaria of the genus *Macrotermes* form distinctive structures and patterns in the miombo landscape (Fanshawe 1968, Lee & Wood 1971) and typically occur in *Brachystegia/Julbernardia*, *Acacia* and *Colophospermum mopane* woodlands (Loveridge & Moe 2004). Large termitaria occur predominantly in the *Brachystegia* shrublands with mostly small mounds in the *Julbernardia* woodland areas of Chizirira (personal observation). The mounds in the study site were constructed by *Macrotermes falciger* and showed structures typical of this species, evident by their extremely large size. *Macrotermes falciger* are characteristically large termitaria and were formerly known as *Macrotermes goliath* (Malaisse 1978).

Termitaria in Chizarira are clearly seen in aerial photographs and appear as dark areas where dense vegetation covers the mound, or more recently as whitish domes in the landscape (Fig. 2). The white rings are hard, bare and compacted. The termitaria are either circled entirely by a white ring or only partially where the ring forms a crescent shape around half the mounds' circumference. There are mounds without a white ring. For the purpose of this paper an entire white ring around a mound will be referred to as a full halo, a half a ring as a partial halo and mounds without a ring as non-halo.

Fig. 1. Location of Chizarira National Park, Zimbabwe

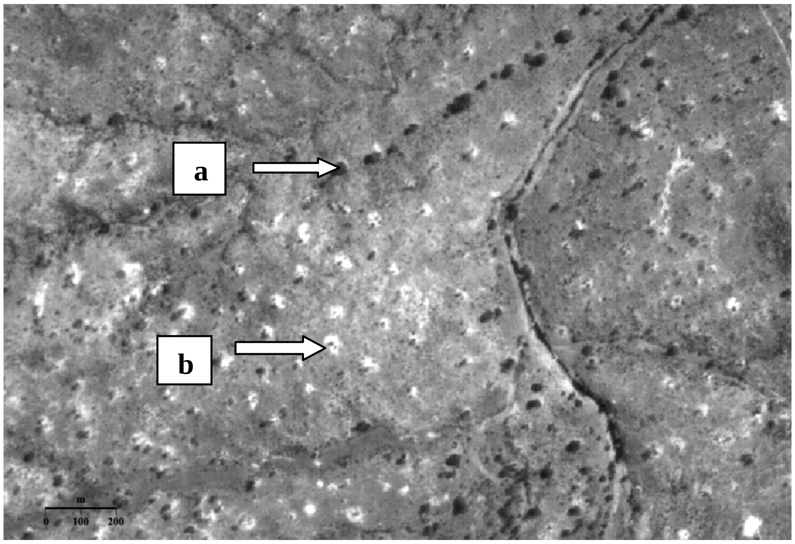

Fig. 2. Aerial photograph (WWF Southern Africa Regional Programme Office 1993) of a small area within Chizarira National Park showing (a) termitaria (dark patches of dense vegetation) and the (b) halos around mounds (white circles) in the miombo woodlands.

Aerial photographs (1: 25 000) from 1993 were used to identify areas with termite mounds (WWF Southern Africa Regional Programme Office 1993). Four major vegetation types were recognized in this study area and were considered as the dominant habitat types found within Chizarira and were classified into (i) mixed *Brachystegia* and *Combretum* woodland, (ii) *Colophospermum mopane*, (iii) *Julbernardia globifora* and (iv) riparian.

Plots covered an area of 20 000 m^2 (2ha) each and encompassed a total area of 360 000 m^2 in Chizarira. Eighteen plots, comprising 13 rectangular plots (200 x 100 m) and five road plots (500 x 40 m) were randomly selected and stratified for sites with termitaria in different vegetation types and catenal positions in the miombo landscape. Road plots comprised habitat parallel to each side of a road. Road plots were measured in 20 m strips from the edge of both sides of the road and were 500 m in length. Two different plot dimensions were used because the riparian area which was sampled was confined to a narrow valley which was parallel to the road.

Eight catenal positions were identified in the Chizarira landscape: lower midslope (LM); upper slope (US), primary plateau (PP), lower plateau (LP), middle plateau (MP) upper plateau (UP), valley bottom (VB) and drainage line to midslope (DLM). The lower and midslope catenal positions were representative of the hillsides, the valley bottom of the riparian area, the plateau catena positions primarily of the flat *mopane* woodland areas, and the drainage line to midslope of a steep gradient in Chizarira National Park.

All large termitaria (basal diameter > 10 m or a height ≥ 2 m; n = 86) located within the 18 plots were sampled. The short and long diameters and height of each mound were measured. The presence or absence of a halo and the status of the halo was recorded (i.e. full, partial or non-halo). All partial halo mounds were a fraction of 0.5 of a full halo. The distance of the halo in meters from the base of the mound was recorded and the mean distance in meters was noted. Full and/or partial halo mounds on a flat surface or on a downslope were recorded. The position of each termite mound was recorded with a GPS.

The numbers and heights of trees and shrubs of each woody plant species on the mound were recorded. Woody plant species were considered because they comprise 95-98 % of the aboveground biomass in the miombo woodlands (Campbell *et al*. 2006), with grasses and herbs constituting the remainder (Malaisse 1978). Trees were defined as woody plants > 3 m in height (Anderson & Walker 1974). Anderson & Walker (1974) identified a category 'converted trees' which were trees reduced to a height of less than 3 m due to elephant damage. Shrubs were defined as woody plant species with live foliage without evidence of damaged stems or branches which were < 3 m in height (Anderson & Walker 1974). To assess tree height structure on mounds and in the surrounding woodland matrix, two height categories were selected: (i) > 6 m, and (ii) 3 – 6 m. All trees that were reduced to a lower height structure on mounds were excluded in the analysis of the two height categories. The species, numbers and heights of trees > 6 m with a basal circumference of > 32 cm (measured above the buttress swelling) (Anderson & Walker 1974) and between 3 − 6 m in height were recorded on mounds. Trees greater than 6 m in height on mounds were considered tall, mature trees, whereas trees between 3 – 6 m in height were considered an intermediate height category.

An estimate of the anticipated vegetation volume removed (VVR) from the upper canopy trees and the vegetation cover removed (VCR) from the surface of the mound was recorded. A visual assessment of VCR was assessed by the proportion (%) of woody plant material removed from the base of the mound by herbivores browsing woody vegetation, trampling the area around the mound and their use of regular pathways to access vegetation on termitaria. Intact mounds are generally covered by a dense ground cover of grass and woody plant species and a full crown of upper canopy trees (personal observation). VVR was estimated by a visual assessment of the proportion (%) of volume absent from the upper tree canopy if the upper canopy consisted of a full crown of foliage. The visual assessments of VVR and VCR were derived by standing 20 m away from the mound and estimating the amount of vegetation volume and cover absent from the mound. No difficulty was experienced in estimating VVR and VCR due to obstructing vegetation between the observer and the mound. VVR and VCR were ranked according to five percentage classes, namely (1 =20 %; 2 = 40 %; 3 = 60 %; 4 = 80 % and 5 = 100 %).

A visual assessment of elephant damage and other herbivore damage to trees and shrubs were estimated by evaluating the proportion of damaged trees converted to shrubs, the amount of dead or fallen over trees and stripped foliage from branches. Damage was estimated as excessive vegetation destruction, but also noticeable utilization of woody material of trees and plants. Elephant browsing was identified by the size of the branches broken off and the shredded appearance of the leaves stripped off the branches (Dierenfield *et al*. 1995, Holdo 2003). Other herbivore browsing was identified as branches with browsed branch tips. Trees and shrubs on the mound were ranked into 1 of 7 damage classes, which include (1) 0 – 10, (2) 11 -25, (3) 26 -50, (4) 51 – 75, (5) 76 – 90, (6) 90 – 99, and (7) 100 % (Anderson & Walker 1974). The trees and shrub species were recorded where browsing was evident and whether the browsing damage was caused by either an elephant or other browsing herbivores. Damage to vegetation was either recorded as elephant damage rating (EDR) or other herbivore damage rating (OHDR).

Woodland transects (n = 86) were randomly selected using a compass bearing radiating from each termite mound and were situated 5m away from the base of the mound perimeter. Each woodland transect were measured as 50 x 2 m (0.1 ha). The start and end position of each woodland transect was recorded with a GPS.

The number of each species of woody plant was recorded in each of the woodland transects. All trees greater than 6m with a basal circumference of 32 cm and trees in a height class of 3 – 6 m were recorded in the woodland matrix.

STATISTICAL DATA ANALYSES (Appendix A)

REPRESENTATIVENESS OF SAMPLED VEGETATION

Species-accumulation curves and sample-based rarefaction curves for woody plant species were complied for termitaria and the woodland matrix separately to determine the degree of species representativeness of the sampled plant population on mounds and in the woodland matrix (PRIMER V6 Clarke & Gorley 2006). The species-accumulation curve was plotted using the number of woody plant species, S_{obs} (species density per unit area) versus the number of samples for the termitaria and the woodland matrix (total n = 86 paired sites). This approach follows the concept of the species-area curve which ensures that the area is adequately sampled. A species-accumulation curve is defined as the average number of species per unit area under all possible permutations of the samples and infers that the samples are independent (Ugland *et al*. 2003). In most experimental studies $S_{obs,}$ the observed number of species is used as a surrogate for $S_{true'}$, the true number of species (Brose *et al*. 2003, Brose & Martinez 2004). S_{obs} often excludes the presence of rare species and underestimates $S_{true'}$, thus nonparametric extrapolation estimators have been developed to reduce this bias (Brose *et al*. 2003). Two nonparametric estimators, the Michaelis-Menten (MM) richness estimate and a jacknife estimate, were used to assess sample size adequacy (Colwell & Coddington 1994). The jacknife estimate is a function of the number of species that occur in one and only plot (Heltshe & Forrester 1983). The jacknife procedure is a simulation affected by the plot size, sample size and the sampling area (Heltshe & Forrester 1983). The MM model and jacknife procedure were used to assess species richness in this study because they perform best in highly sampled communities (Brose & Martinez 2004). If the sample rarefaction curves and the estimators approximate each other at the highest observed values, then sampling size is considered adequate (Botes *et al*. 2006a). If the sampling size is adequate, datasets can be compared and standardized (Gotelli & Colwell 2001). The samples were randomly permuted 999 times for each site. Sample-based rarefaction curves were computed using PRIMER 6.0 (Clarke & Gorley 2006).

EFFECT OF EXPLANATORY VARIABLES ON SPECIES RICHNESS

Since area has an effect on species richness patterns (Rosenzweig 1995), the species-area relationship was determined for species richness across categorical catenal positions using a Generalized Linear Model (GLM). A GLM was performed to determine if the explanatory variables had an effect on species richness on termitaria. GLM Type III model was used. The dependent variable used in the GLM was termitaria species richness. The explanatory variables used in the analysis include termitaria area, VVR, VCR, OHDR, EDR and presence/absence of a halo, with the catenal position as the categorical predictor in the model. The analysis detects any variance in species richness that can be explained 'best' by the observed explanatory variables. SPSS Version 16.0 for Windows (Jöreskog & Sörbom 1989) was used for this analysis.

DIFFERENCES IN SPECIES COMPOSITION BETWEEN TERMITARIA AND THE WOODLAND MATRIX AND IN RELATION TO CATENAL POSITION

Woody plant species composition between termitaria and the woodland matrix were assessed using multivariate analyses. Multivariate community analysis was used to assess differences in woody plant community composition (PRIMER V6) (Clarke & Gorley 2006). Bray Curtis similarity measures (Bray & Curtis 1957) were used to determine whether woody plant composition differed between the termitaria and the woodland matrix. Woody plant species abundance data were used to investigate any difference in species composition. The abundance data were fourth-root transformed before analysis to reduce the weight of common species (Clarke & Warwick 1994). The relationships between woody plant assemblages on the termitaria and in the matrix were displayed using non-metric multi-dimensional scaling (nMDS) ordinations (Clarke 1993). Multi-dimensional scaling (MDS) was used to generate an ordination of the similarity of woody plant species composition between termitaria and the woodland matrix. The Bray−Curtis index was used to describe the dissimilarity between both areas. Stress levels are a measure of goodness of fit of data points in the nMDS, and stress levels equals zero when data are perfectly represented (Clarke 1993). Differences in species composition between termitaria and woodland matrices were compared using ANOSIM (one way analysis of similarity) and pairwise tests were used to determine whether there were significant differences between the woody plant assemblages on the termitaria and the matrix along eight catenal positions in the miombo landscape. The data were standardized and transformed to the 4th root to account for and downweight any highly abundant species. The ANOSIM procedure of PRIMER is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke 1993). This method generates a global R-statistic, which is a measure of the distance between groups. An R-value that approaches one indicates strongly distinct species composition, whereas an R-value close to zero indicates that the species compositions are similar (Clarke 1993). These R-values were used to compare woody plant composition between termitaria and the matrix.

Indicator species among eight catenal positions for termitaria and the woodland matrix were calculated using the species Indicator value index (*IndVal*) (Dufrene & Legendre's 1997) using PCORD V5 (McCune & Mefford 2006). Woody plant species abundance data in the 18 plots on termitaria and in the woodland matrix among eight of the catenal positions and between the four classified vegetation types was used to identify the indicator species. Indicator species are defined as the main species specific to a group of typology and present at the majority of sites belonging to that group (Dufrene & Legendre 1997, Legendre & Legendre 1998). This method combines a species relative abundance with its relative frequency of occurrence in a particular habitat type to obtain the maximum indicator value for the habitat type (Dufrene & Legendre 1997, Legendre & Legendre 1998).

A cluster analysis (PCORD V5 McCune & Mefford 2006) was used to assess the difference in species composition between the two habitat types, the termitaria and the woodland matrix. Species turnover between habitats was analyzed calculating the widely used 'Sorensen' (Bray-Curtis) distance and beta linkage (-0.25) (McCune & Mefford 2006). The presence and absence of woody plant species data in each of the 18 plots were used in this analysis.

The difference in vegetation structure of termitaria and the woodland matrix was classified using a two-way indicator species analysis, TWINSPAN (Hill 1979). This clustering program constructs an ordered two way table from a sites by species matrix (Jongman *et al*. 1995) approximating a Braun−Blanquet table (Dufrene & Legendre 1997). The presence or absence of species was used to assess the difference in species composition between termitaria and the woodland matrix. Three levels of division levels were used to distinguish the clusters representing different vegetation types. A few species were reorganized manually by shifting them to other clusters (Jongman *et al*., 1995) where according to the field data, they fitted better. Thirty six plots comprising 104 woody plant species (PCORD V5 McCune & Mefford 2006) were used for this analysis.

The total number of woody plant tree species > 6 m and between 3 − 6 m in height on termitaria and in the woodland matrix were analysed by counting the number of species in each height category.

VARIATION IN TREE HEIGHT STRUCTURE, TREE/SHRUB DENSITY BETWEEN TERMITARIA AND THE WOODLAND MATRIX AND ON HALO AND NON-HALO MOUNDS

Differences in shrub density and trees between 3 – 6 m were analyzed using *t*-tests (independent by groups) as the data were normally distributed. Mann-Whitney U tests was used to compare the medians of the height of trees greater than 6 m and total tree and shrub densities on termitaria and in the woodland matrix. Differences in height distributions of trees > 6 m and trees between 3 – 6 m between full, partial and non-halo mounds were tested using a Kruskal-Wallis One Way ANOVA by ranks test as the data were not normally distributed and between non-halo mounds, halo mounds on a downslope gradient and mounds on a flat surface. Nonparametric analyses were used with non-normal data that could not be transformed reliably. Statistica 7 (Statsoft 2004) was used for the *t*-test analyses.

VARIATION IN SPECIES COMPOSITION IN RESPONSE TO HALOS

nMDS ordinations were used to test for the relationships between termitaria vegetation and the halo and non halo mounds and partial, full and non-halo mounds. Analyses of similarity (ANOSIM – Clarke 1993) and pairwise tests were used to determine whether there were significant differences between the woody plant composition on the termitaria for 1) halo and non−halo mounds, and 2) for full, partial and non-halo mounds. The pairwise tests were used to compare the difference between paired halo statuses to detect the largest difference (R value) in species composition between the halo statuses.

PROCEDURE FOR CALCULATING THE MOUND SURFACE AREA

The total surface area of the mound, including the halo, was calculated as: Area of the halo + Area of the termitaria (ref 1). The procedure for calculating the total surface area of the mound was as follows: Area of the halo: a circle of halo size, minus the area within that circle that was occupied by the termitarium.

$$\left(\pi Rm^2 - \pi(Rt - Hw)^2 + \left(\frac{Mh}{Md}\right)\pi(Rt - Hw)^3\right) \qquad (1)$$

Where πRm^2 = area of a circle of halo size, let Rt = radius of the termitarium and Hw = halo width, which is the distance from the edge of the halo to edge of the mound (i.e. Rm – Rt). The termitarium radius was calculated as the mound radius minus the halo radius. Termite mounds were treated as partially exposed spheres. The termite mound area was calculated by multiplying the sphere surface area (πRm^3) by the fraction of the sphere “exposed” above the ground (Fig. 3). The fraction was determined by dividing mound height by mound diameter, where Mh = mound height and Md = mound diameter. This fraction was multiplied by the surface area of the mound, calculated as πRm^3 plus the halo to account for the spherical shape of the mound.

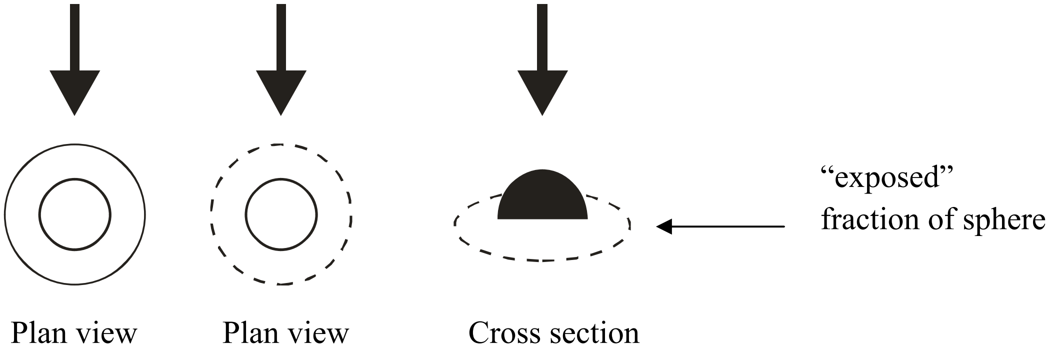

Fig. 3. Schematic representation of a termite mound with a halo (broken lines) and a cross section of a mound showing the 'exposed fraction of a sphere (half a sphere).

Results

REPRESENTATIVENESS OF SAMPLED VEGETATION

The species accumulation curves/sample-based rarefaction curves approximated asymptotes and leveled off indicating that the number of plant species collected on termitaria and in the woodland matrix was sufficient in this study (Appendix B). The rarefaction curves for the termitaria and the woodland matrix show that the MM model estimator, S_{obs} and the UGE converged at the highest observed density for each site. The species density estimates on termitaria and the woodland matrix are considered representative of the plant population in the study area within Chizarira National Park.

EFFECT OF EXPLANATORY VARIABLES ON SPECIES RICHNESS

None of the explanatory variables had an effect on species richness on termitaria (Table 1) * ($p >$ 0.05) when placed in the same model. However, a stepwise backward deletion of the explanatory variables with the least effect on species richness showed catenal position as the only significant factor on woody plant species richness on termitaria (GLM, $F_{7\ 78} = 2.398$, $p < 0.05$).

Table 1. Generalized linear model (Type III model) for the dependent variable termitaria species richness and explanatory variables.

Variable	*Sum of squares*	*d.f.*	*Mean square*	*F*	*p-value*
OHDR	26.726	2	13.363	.517	.599
EDR	55.685	5	11.137	.431	.825
VVR	57.201	4	14.300	.554	.697
VCR	50.888	4	12.722	.493	.741
Catenal position	277.608	8	34.701	1.343	.240
Halo Y/N	.051	1	.051	.002	.965
Termitaria area	1.014	1	1.014	.039	.844

EDR, elephant damage rating; OHDR, herbivore damage rating, VCR, vegetation cover removed, VVR, vegetation volume removed; Halo P/A, halo presence /absence

Catenal positions have distinct woody plant species assemblages on termitaria and in the woodland matrix in Chizarira National Park (Figs. 4 and 5). The MDS ordination plot based on similarity and ANOSIM tests revealed a significant difference ($p < 0.05$) of 38.9 % between the plant species composition among the eight catenal gradients on termitaria and a 47.3 % significant difference in the woodland matrix. The valley bottom (riparian area) is distinct from the plateau and midslope catenal positions on termitaria and in the woodland matrix (Figs. 4 and 5).

The primary plateau formed a distinct cluster from the valley bottom on termitaria (Fig. 4). *Diospyros lycioides* (75)* was the main indicator species of the lower midslope on termitaria. *Boscia salicifolia* (30) and *Burkea africana* (40) were characteristic of the upper slope catenal positions. The upper plateau indicator species were *Bauhinia petersiana* (56)*,*Ozoroa insignis* (38) and *Terminalia stenostachya* (31). *Berchemia discolor* (40), *Diospyros senensis* (82)*, *Diospyros mespiliformis* (67)*, *Feretia aeruginescens* (75)*, Allophylus africanus* (78)*, *Philenoptera violacea* (75), *Pavetta gardenifolia* (64)*, *Stychnos potatorum* (86)* were the predominant indicator species on the valley bottom. *Colosphospermum mopane* (56)* was characteristic of the primary plateau on termitaria.

Drainage line to midslope, middle plateau and primary plateau catenal positions formed separate clusters from the valley bottom in the woodland matrix (Fig. 5). An indicator species in the drainage line to midslope areas was *Diospyros quiloensis* (48). *Burkea africana* (31) was prominent on the lower plateau. The middle plateaus main indicator species was *Julbernadia globiflora* (44)*. The primary plateaus main indicator species were *Brachstegia boehmii* (43)*, *Colophospermum mopane* (47) and *Peltophorum africanum* (39). The valley bottom was characterized by *Diospyros* *lycioides* (67), *Diospyros senensis* (67)*, *Friesodielsia obovata* (87)*, *Pterocarpus rotundifolius* (45), *Terminalia sericea* (47), *Terminalia trichopoda* (41), *Philenoptera violacea* (60), *Brachystegia spiciformis* (65), *Ziziphus mucronata* (48) as indicator species in the woodland matrix. The lower midslope indicator species were *Catunaregum spinosa* (35)*, *Crossopteryx febrifuga* (47) * and *Diospyros kirkii* (35). .*Xeroderris stuhlmanni* (40) was characteristic of the upper slope catenal position and *Kirkia acuminata* (40) of the upper plateau.

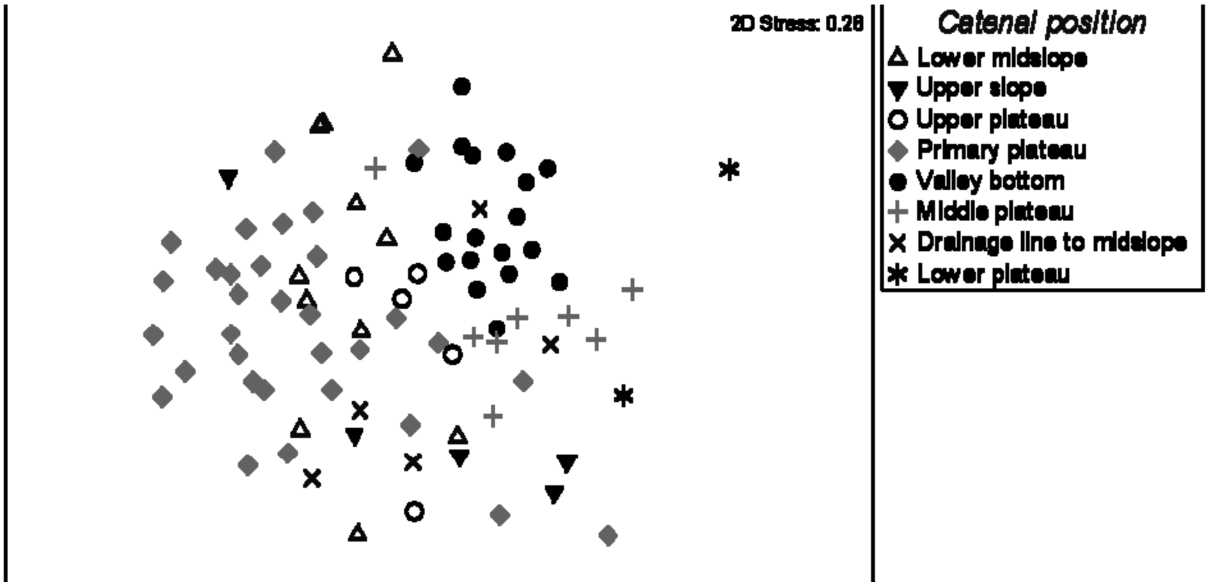

Fig. 4. Variation in species composition on termitaria among eight catenal positions. MDS ordination plot based on Bray−Curtis similarity measures showing the difference in species composition among eight catenal positions on termitaria. (R = 0.389). Stress = 0.26. *($p < 0.05$).

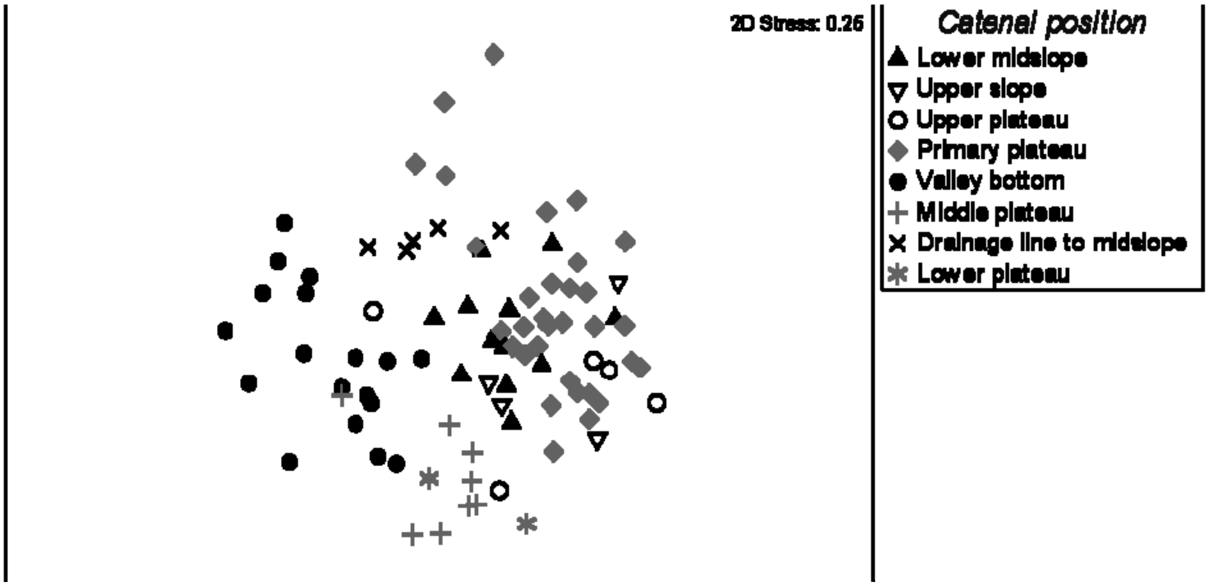

Fig. 5. Variation in species composition in the woodland matrix among eight catenal positions. MDS ordination plot based on Bray−Curtis similarity measures showing the difference in species composition among eight catenal positions in the woodland matrix. (R = 0.473). Stress = 0.25. *($p < 0.05$).

Catenal positions in proximity to each other show a large similarity (e.g. primary plateau and middle plateau) in comparison to catenal positions distal from each other, which show a greater difference (e.g. valley bottom and lower plateau) (Table 2). Based on Bray-Curtis similarity indices, there was a significant difference in species composition among the eight catenal gradients between termitaria and the woodland matrix (ANOSIM), with none of the 999 random permutations exceeding the global *R* statistic (0.943). Fifteen of the pairwise comparisons differed significantly ($p < 0.05$) in eight catenal positions on termitaria and 20 in the woodland matrix (Table 2).

Table 2. Pairwise tests of species composition on termitaria and in the woodland matrix along eight catenal positions in the miombo landscape. *($p < 0.05$)

Termitaria			Woodland matrix		
Groups	R statistic (%)	*p* - value	Groups	R statistic (%)	*p* - value
VB, LP	94.0	0.005	US, DLM	94.4	0.008
LM, LP	84.0	0.013	LM, LP	87.6	0.011
UP, LP	83.6	0.048	LM, UP	86.2	0.002
US, VB	82.2	0.001	LM, DLM	81.1	0.001
DLM, LP	80.0	0.048	DLM, LP	78.2	0.048
VB, DLM	63.0	0.001	LM, MP	72.6	0.001
MP, DLM	58.3	0.002	US, MP	72.1	0.002
LM, MP	56.6	0.001	PP, VB	69.6	0.001
LM, VB	56.5	0.001	UP, VB	66.6	0.002
US, MP	54.3	0.002	VB, LP	64.2	0.005
PP, VB	51.7	0.001	UP, MP	63.0	0.003
UP, VB	46.8	0.001	LM, VB	62.2	0.001
PP, MP	46.3	0.001	UP, DLM	62.0	0.008
VB, MP	46.3	0.001	PP, LP	60.0	0.018
LM, UP	42.0	0.003	US, VB	58.3	0.001
			VB,DLM	55.0	0.001
			PP, MP	51.6	0.001
			PP, DLM	48.0	0.004
			LM, UP	45.1	0.001
			VB, MP	43.8	0.001

LM: lower midslope, US: upper slope; LP: lower plateau; PP: primary plateau; MP: middle plateau; UP: upper plateau; VB: valley bottom; DLM: drainage line to midslope

There was a considerable difference in community composition between termitaria and the surrounding woodland matrix (Fig .6, Table 3 and 4).

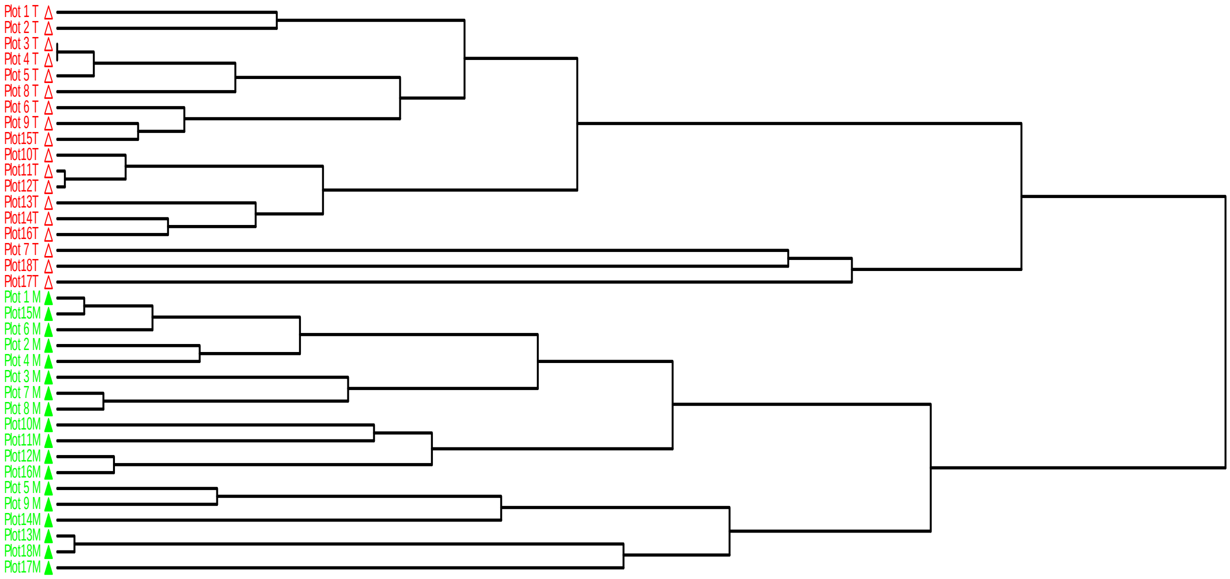

Fig. 6. Cluster Dendogram showing the divisive split in species composition between termitaria and the woodland matrix.

Table. 3. Two way indicator table showing species composition of the four dominant vegetation types on termitaria in Chizarira.

Vegetation type	Species	Plot
Brachystegia/Combretum woodland	*Acacia nilotica*	1,2,3,4 ,5, 15 and 16
	Burkea africana	
	Capparis tomentosa	
	Cassia abbreviata	
	Combretum molle	
	Combretum zeyheri	
	Commiphora africanus	
	Commiphora karibensis	
	Commiphora mossambicense	
	Dalbergia melanoxylon	
	Dichrostachys cinerea	
	Diospyros batocana	
	Diospyros quiloensis	
	Grewia monticola	
	Maerua prittwitzii	
	Margaritaria discoidea	
	Maytenus putterlickioides	
	Maytenus senegalensis	
	Ozoroa insignis	
	Terminalia stenostachya	
	Xeroderris stuhlmannii	
	Ximenia americana	
	Ximenia caffra	
Mopane woodland	*Acacia gerrardii*	6,7,8,9
	Acacia nigrescens	
	Albizia harveyi	
	Bauhinia peterisiana	
	Boscia angustifolia	
	Colophospermum mopane	
	Commiphora mollis	
	Erythroxymum zambesiacum	
	Euclea divinorum	
	Euphorbia ingens	
	Gardenia resiniflua	
	Gardenia spathulifolia	
	Jasmine stenolubum	
	Maerua kirkii	
	Markhamia acuminata	
	Pterocarpus rotunidifoilus	
	Rhoicissus revoilli	
	Schrebera trichoclada	
Riparian area	*Allophylus africanus*	10, 11 and 12
	Berchemia discolor	
	Boscia salicifolia	
	Combretum adenogonium	
	Combretum hereroense	
	Combretum mossambicense	
	Commiphora pyracanthoides	
	Diospyros lyciodes	
	Diospyros mespiliformis	
	Diospyros senesis	
	Ehretia caerulea	
	Feretia aeruginescens	

	Ficus ingens *Fluegea virosa* *Friesodielsia obovata* *Grewia flavescens* *Lannea discolor* *Lannea schweinfurthii* *Manilkara mochisia* *Markhamia zanzibarica* *Maytenus heterophylla* *Pavetta gardenifolia* *Philenoptera violaceae* *Strychnos potatorum* *Vangueria randii* *Ziziphus mucronata*	
Julbernadia globiflora	*Bridelia carthartica* *Crossopteryx febriguga* *Diplorhynchus condylocarpon* *Grewia bicolor* *Psuedolachnostylis maproueneifolia* *Senna singueana* *Strhychnos cocculoides* *Terminalia brachystemma* *Terminalia trichopoda* *Vangueria infausta*	13,14,17 and 18

Table. 4. Two way indicator table showing species composition of the four dominant vegetation types in the woodland matrix in Chizarira.

Vegetation type	Species	Plot no.
Brachystegia/Combretum woodland	*Acacia gerraradii* *Acacia nilotica* *Allophylus alnifolius* *Brachystegia boehmii* *Bridelia carthartica* *Catunaregum spinosa* *Combretum zeyheri* *Commiphora mollis* *Crossopteryx febrifuga* *Dichrostachys cinerea* *Diospyros lycoides* *Diospyros quiloensis* *Diospyros senensis* *Flacourtia indica* *Grewia monticola* *Jasmine stenolubum* *Kirkia acuminata* *Lannea discolor* *Lannea edulis* *Maerua prittwitzii* *Markhamia acuminata* *Ormocarpum kirkii* *Sclerocarya birrea* *Terminalia stenostachya* *Vangueria spp.* *Xeroderris stuhlmanni*	1,2,3,4,5, 15 and 16
Mopane woodland	*Colophospermum mopane* *Bauhinia petersiana* *Cassia abbreviata* *Cissus confolia* *Combretum molle* *Diplorhynchus condylocarpon* *Erythroxymum zambesiacum* *Maytenus heterophylla* *Pavetta schummanii*	6,7,8 and 9
Riparian area	*Acacia galpinii* *Albizia harveyi* *Allophylus africanus* *Brachystegia spiciformis* *Combretum apiculatum* *Combretum adenogonium* *Combretum collinum* *Combretum hereroense* *Combretum mossambicensis* *Commiphora mossambicense* *Dalbergia melanoxylon* *Diospyros mespiliformis* *Euclea divinorum* *Feretia aeruginescens* *Fluegea virosa* *Friesodielsa obovata* *Grewia flavescens* *Lannea schweinfurthii*	10,11 and 12

	Margaritaria discoidea *Ozoroa insignis* *Peltophorum africanum* *Periocarpus angolensis* *Philenoptera violaceae* *Piliostigma thonni* *Pterocarpus rotunidifolius* *Terminalia mollis* *Terminalia sereicea* *Ximenia americana* *Ximenia caffra* *Ziziphus mucronata*	
Julbernadia globiflora	*Annona stenophylla* *Burkea africana* *Gardenia spathulifolia* *Julbernadia globiflora* *Maytenus senegalensis* *Ochna schweinfurthiana* *Pseudolachnostylis maprouneifolia* *Terminalia brachystemma* *Terminalia trichopoda* *Turrea nilotica* *Vangueira infausta* *Ziziphus abyssinica*	13,14, 17 and 18

A total of 104 woody plant species, representing 63 genera were identified on termitaria and in the woodland matrix in the miombo woodlands of Chizarira National Park (Appendix C).

Species richness between termitaria and the woodland matrix was similar with 90 plant species found on termitaria and 86 in the woodland matrix**.** However, termite mounds differed from the woodland sites in species composition: of the 90 species recorded on termite mounds, 18 were specific to termite mounds, with 13 species found only in the woodland transects and not on the mounds (Table 3). Sixty seven woody plant species were shared between termitaria and the woodland matrix. Based on the Bray−Curtis similarity index there was a 66. 5% significant difference in species composition between the termitaria and the woodland matrix (ANOSIM, $p < 0.05$; Fig. 7).

Table 3. Woody plant species which were exclusive on termitaria and in the woodland matrix.

Termitaria	Woodland matrix
Acacia nigrescens	*Acacia galpinii*
Azanza garckeana	*Allophylus alnifolius*
Berchemia discolor	*Annona stenophylla*
Boscia angustifolia	*Lannea edulis*
Commiphora pyrancanthoides	*Ochna schweinfurthiana*
Diospyros batocana	*Ormocarpum kirkii*
Ehretia caerulea	*Pavetta schumanniana*
Euphorbia ingens	*Peltophorum africanum*
Ficus ingens	*Terminalia mollis*
Gardenia resiniflua	*Terminalia sericea*
Maerua kirkii	*Turraea nilotica*
Markhamia zanzibarica	*Vangueria spp.*
Manilkara mochisa	*Ziziphus abyssinica*
Maytenus putterlickioides	
Senna singueana	
Strychnos cocculoides	
Strychnos potatorum	
Vangueria randii	

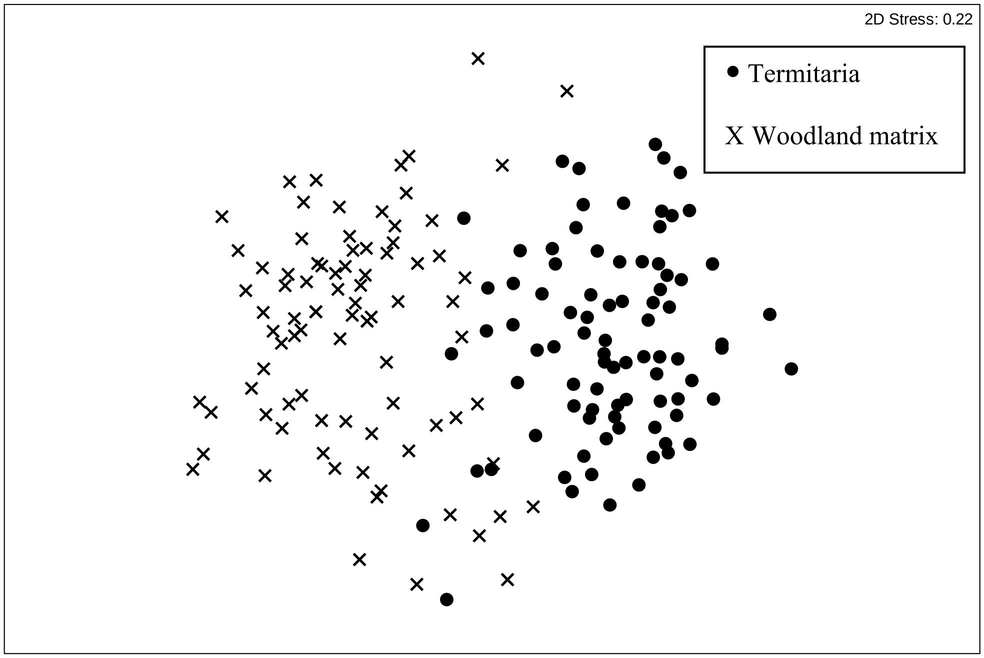

Fig. 7. Difference in species composition between termitaria and the woodland matrix. MDS ordination plot based on Bray−Curtis similarity measures showing the difference between termitaria and the woodland matrix in species composition. (R = 0.665). Stress = 0.22. *($p <$ 0.05). Species compositions were significantly different between termitaria and the woodland matrix.

Although the stress levels are high and should be close to 0 to show perfect representation of the population sampled (Fig. 7) the differences in species composition between termitaria and the woodland matrix were considerable (see Fig. 6, Fig. 7, Table 3 and 4 , Appendix C). The main indicator species on termitaria and in the woodland matrix in four of the dominant vegetation types differed (Table, 4 and 5).

Table. 4. Summary of the main indicator species on termitaria in the dominant vegetation types in miombo woodlands of Chizarira.

Vegetation type	Species	*IndVal* (%)
Brachystegia/Combretum	*Acacia nilotica*	66*
	Commiphora africanus	57*
	Diospyros quiloensis	77*
Mopane	*Azanza garckeana*	75*
	Colosphospermum mopane	83*
	Euclea divinorum	57*
	Erythroxylum zambesiacum	60*
Riparian	*Allophylus africanus*	76*
	Berchemia discolor	55*
	Diospyros mespiliformis	81*
	Diospyros senensis	90*
	Feretia aeruginescens	86*
	Fluegea virosa	66*
	Lannea schweinfurthii	47*
	Pavetta gardenfolia	81*
	Philenoptera violacea	83*
	Strychnos potatorum	93*
	Friesodielsia obovata	60
	Grewia flavescens	47
Julbernadia globifora	*Diplorhynchus condylocarpon*	50
	Pseudolachnostylis maprouneifolia	25

*significant indicator species

Table. 5. Summary of the main indicator species in the woodland matrix in the dominant vegetation types in miombo woodlands of Chizarira.

Vegetation type	Species	*IndVal* (%)
Brachystegia/*Combretum*	*Brachystegia boehmii*	63*
	Diospyros kirkii	73*
Mopane	*Colosphospermum mopane*	65*
	Commiphora africanus	56*
	Terminalia stenostachya	47*
	Pavetta schumanniana	65*
Riparian	*Brachystegia spiciformis*	84*
	Combretum apiculatum	63*
	Combretum collinum	75*
	Diospyros lycoides	66*
	Diospyros senensis	67*
	Friesodielsa obovata	96*
	Pterocarpus rotunidifolius	70*
	Terminalia sereicea	52*
	Philenoptera violaceae	64*
Julbernadia globiflora	*Burkea africana*	63*
	Julbernadia globiflora	66*

*significant indicator species

Table 6. Summary of the total number of shared and unshared tree and species > 6 m and between 3 – 6 m on termitaria and in the woodland matrix in all 18 plots

Height category	Termitaria	Woodland matrix
Trees > 6 m	23	14
Trees 3 – 6 m	41	24
No. of ‘unshared tree species > 6m	18	9
No. of ‘unshared tree species 3 – 6 m	28	11
No of shared tree species	5	16

*(see Appendix D, 1 and 2 for a list of tress > 6 m and between 3 – 6m)

VARIATION IN TREE HEIGHT STRUCTURE AND TREE/SHRUB DENSITY ON TERMITARIA AND IN THE WOODLAND MATRIX

Termitaria tree height structure and total tree density are significantly different from the woodland matrix (Table 7). Trees were taller and were at a higher density on termitaria than in the woodland matrix. Termitaria support more trees greater than 6 m and trees between 3 – 6 m in height than the woodland matrix (Tables 7 and 8). Total tree density and density of trees > 6 m are higher on termitaria than in the woodland matrix. Smaller trees and shrubs did not differ in height or density between the termitaria and the woodland matrix. There is an insignificant difference in density of trees between 3 – 6 m and shrub density on termitaria and in the woodland matrix (Table 7). However, the mean densities of both these categories were higher on termitaria than in the woodland matrix (Tables 7 and 8).

Table 7. Tree height and trees per unit area (ha) greater than 6 m on termitaria and in the woodland matrix (n = 86), Mann Whitney U tests *($p < 0.05$)

	Termitaria			Woodland matrix				
Category	Median	Mean	±SD	Median	Mean	±SD	U	*p -value*
Tree height > 6 m	8.03	9.32	4.52	0	6.63	4.02	1733.5	$p < 0.05$*
Trees per unit area > 6 m	102.54	78.68	90.7	33.33	43.02	77.5	2631	$p < 0.05$*
Total trees per unit area (ha)	368.15	535.52	464.72	287.83	320.93	287.83	2675.5	$p < 0.05$*

Table 8. Tree height and trees per unit area between 3 - 6m and total shrubs per unit area (ha) on termitaria and in the woodland matrix (n = 86), *t* tests *($p < 0.05$)

	Termitaria		Woodland matrix				
Category	Mean	±SD	Mean	±SD	*F*	*p -value*	*d.f.*
Tree height 3 − 6 m	4.09	1.14	3.27	1.92	2.84	$p < 0.05$*	170
Trees per unit area 3 − 6 m	361.34	340.64	270.93	259.35	1.72	$p > 0.05$	170
Total shrubs per unit area (ha)	4944.25	3806.66	3644.65	1640.99	5.38	$p > 0.05$	34

VARIATION IN TREE HEIGHT STRUCTURE ON HALO AND NON-HALO MOUNDS

The white rings (halos) observed around the bases of termitaria in protected areas have been associated with high densities of elephants, suggesting that elephant impacts may be affecting species composition, richness and structure. To test this, species composition and vegetation tree height structure were sampled and comparisons made using between 3 halo statuses (halo, non-halo and partial halo) on mounds. Differences in tree height structure of trees > 6 m and between 3 – 6 m between non-halo mounds, mounds on a downslope and on a flat surface were tested using a Kruskal- Wallis One way ANOVA by rank test and a Mann-Whitney U test was used to compare the medians of heights of trees between full and non halo mounds.

There is a significant difference between trees > 6 m on non-halo and halo mounds (Mann Whitney U test, U = 499.5, $p < 0.05$) (Fig. 8), however, no difference was found between trees of 3 – 6 m on full and non-halo mounds.

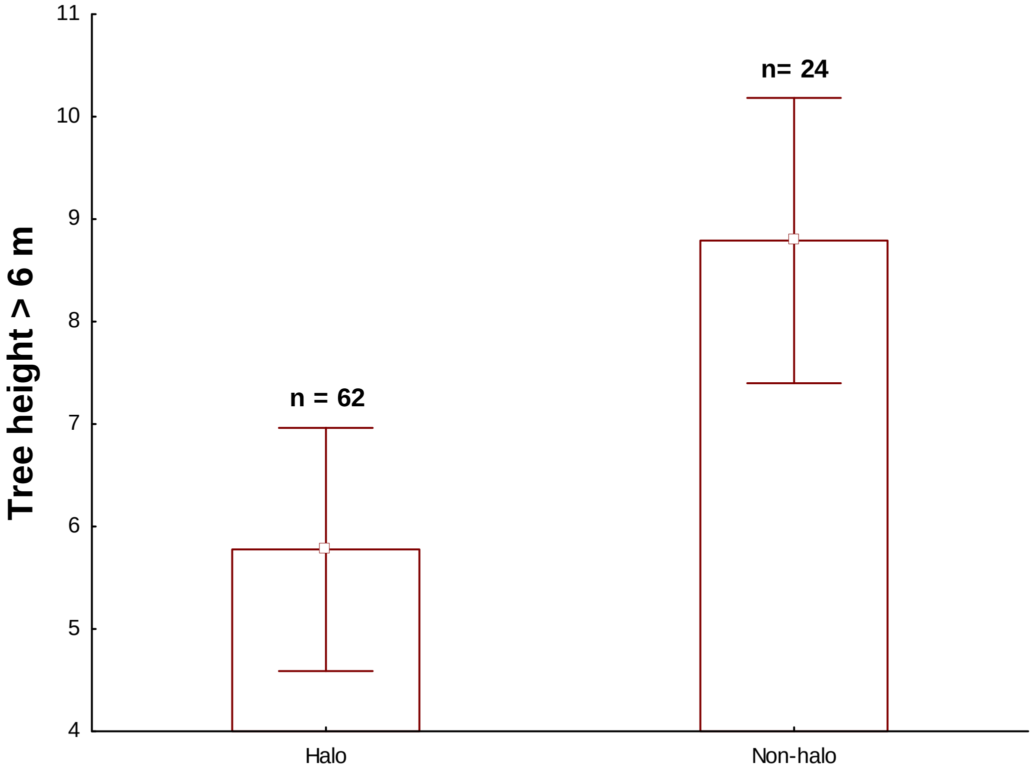

Fig. 8. A comparison of tree height between non-halo (mean = 8.79, ± SD = 3.29) and halo mounds (mean = 6.61, ±SD = 4.67). The inner 'box' indicates the mean, the 'whiskers' show the 1.96*SE

Non-halo mounds supported taller trees then mounds with a full halo on flat ground (Kruskul-Wallis ANOVA by ranks (H= 6.44, $\chi^2 = 6.09$, $p < 0.001$, *d.f.* = 2). Tree height on mounds with a downslope halo was intermediate between the two and did not differ significantly from either (Fig. 9). There was no significant difference in trees between 3 – 6 m in height between non-halo, halo mounds on a flat or on a downslope or between full and non-halo mounds.

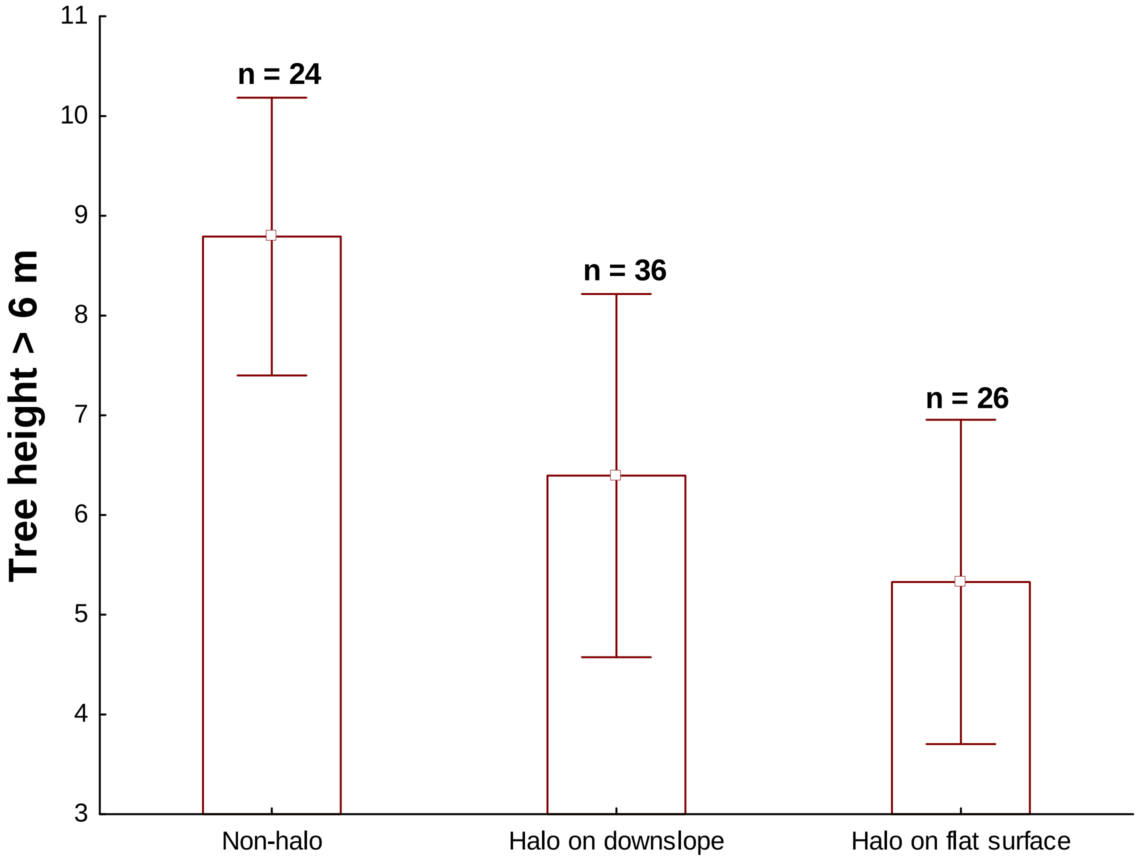

Fig. 9. A comparison of tree height > 6 m on non-halo mounds, halo mounds on a downslope gradient and halo mounds on a flat surface. The inner 'box' indicates the mean, the 'whiskers' show the 1.96*SE.

VARIATION IN SPECIES COMPOSITION IN RESPONSE TO HALOS

There is a significant difference, but only 12.5% in species composition between halo and non-halo mounds (p <0.05) (Fig. 10). This shows that there is an 87.5% similarity in the species composition between mounds which have halos and mounds without halos. The largest difference in species composition was expected between full halo and non-halo mounds because mounds without halos were more densely vegetated than full halo mounds in Chizarira.

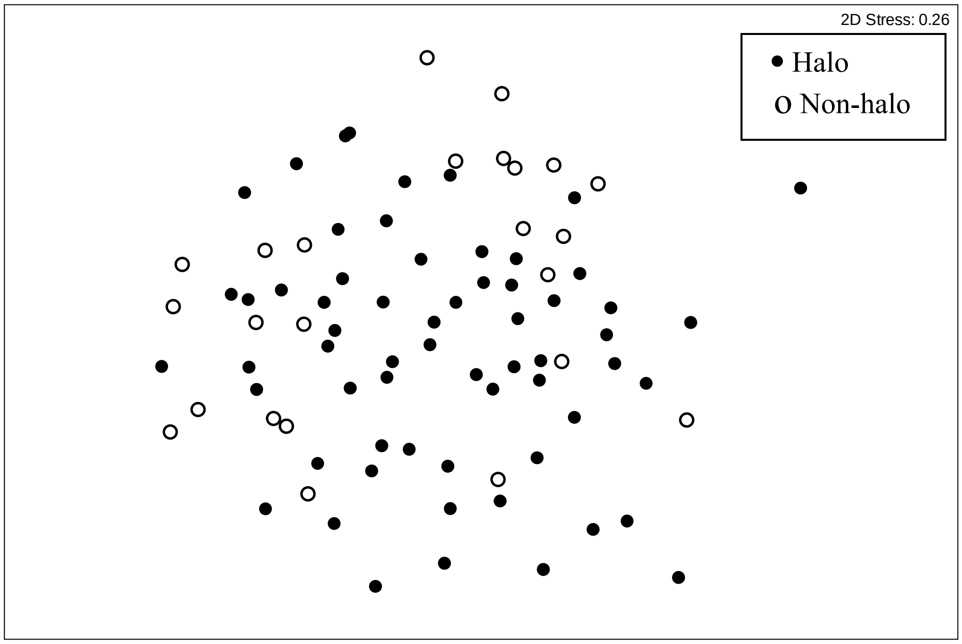

Fig. 10. Variation is species composition between halo and non - halo mounds. MDS ordination plot based on Bray−Curtis similarity measures showing difference in species assemblages between halo and non-halo mounds on termitaria. (R = 0.125). Stress = 0.26. *($p < 0.05$)

There was only a 6 % difference in species composition between mounds which were full, partial and non-halo mounds on termitaria (Fig 11).

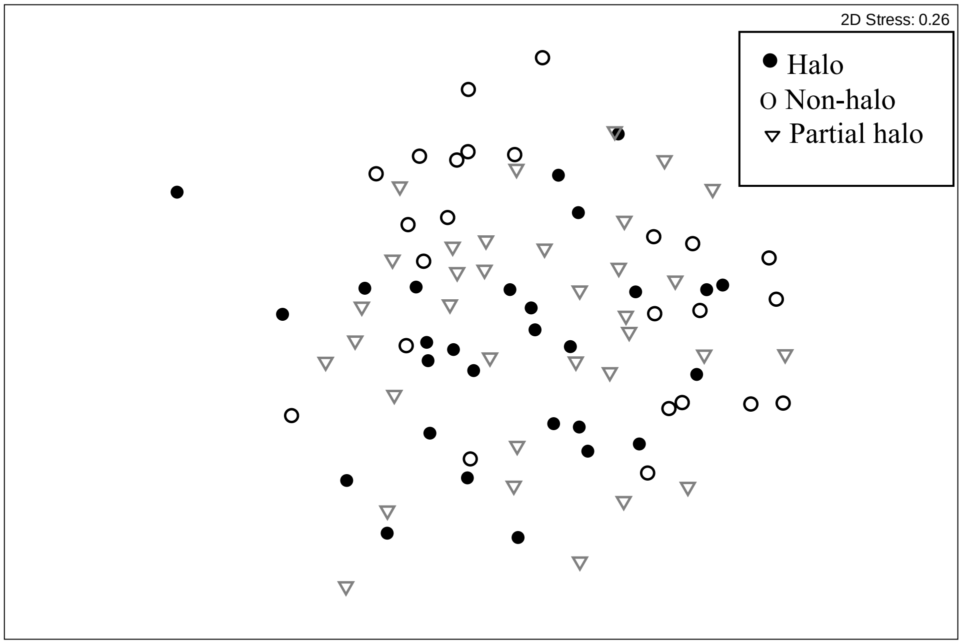

Fig. 11. Differences in species composition between full, partial and non - halo mounds on termitaria. MDS ordination plot based on Bray−Curtis similarity measures showing differences in species composition between full, partial and non-halo mounds on termitaria. (R = 0.06). Stress = 0.26.

Full and partial halo mounds were the most similar, with a 7 % difference in species composition. There was no difference between partial and non-halo mounds (49 %). The pairwise tests show a significant difference of 14.5 % between mounds with a full halo and mounds with no halo (Table 9). Halos around three termitaria in the *Julbernardia globiflora* woodland had grass growing on the haloed area.

Table 9. Pairwise tests show the difference in species composition between mounds which have a full or partial halo and non−halo on termitaria. *($p < 0.05$)

Group	R Statistic (%)	*p* value
Partial, full	7.0	0.339
Partial, non-halo	49.0	0.073
Full, non-halo	14.5	0.04*

*statistically significant

In total 72 % of the termitaria were surrounded by halo, of which 24 were partial and 62 were full halo mounds. There was an insignificant difference between the number of mounds which had a full or a partial halo. The number of partial halo mounds on a downslope gradient where almost twice the amount of full halos on a downslope. Mounds on a flat surface either had a full halo or a partial halo (Table 10). Of these 72%, 26 were on a downslope and 36 were on a flat surface.

Table 10. Number of full, partial halo mounds and mounds on a downslope and on a flat surface

Mound status	Number of observations	Percentage (%)
Full halo	29	46
Partial halo	33	53
Full halo downslope	9	31
Partial halo downslope	17	51
Full halo on flat surface	20	69
Partial halo on flat surface	16	48

Discussion

SPECIES COMPOSITION IN RELATION TO CATENAL POSITION

Catenal position had a significant influence on species richness and composition on a local scale on termitaria and in the woodland matrix in Chizarira National Park. Generally, differences in species composition and structure in miombo woodlands are apparent at a local scale (Campbell 1996). Chidumayo (1987) inferred that site specific, spatial gradients may be important in determining patterns of species richness in miombo woodlands. The main indicator species among eight catenal positions on termitaria and in the woodland matrix were substantially different from each other. Particular species formed indicator species which were mostly common on termitaria or in the woodland matrix, and were therefore indicative of the habitat being sampled (i.e. the mound or the matrix). However, certain species, such as *Colophospermum mopane* were common to both termitaria and the woodland matrix in mopane woodland, and similarly for *Philenoptera violacea* in the valley bottom catena in both habitats. Termitaria had a higher number of significant maximum indicator values for certain species than the woodland matrix. This perhaps indicates that termitaria are largely more heterogeneous in species diversity in comparison to a more homogenous woodland matrix. Overall, catenal position described the highest variance in species richness in Chizarira.

Catenal positions that differ along a variety of spatial gradients are important in determining species composition in Chizarira National Park. The valley bottom catena representative of the riparian area of Chizarira showed a distinctive cluster of species in relation to the upper slopes, to the lower and middle plateaus on termitaria and in the woodland matrix. At a landscape level, catenal processes result in major fertility differences between high ridges and valley bottom positions where the most fertile soils are found (Scholes 1990). This observation was implicit in the comparison of species composition between termitaria and the woodland matrix in Chizarira among eight catenal positions. Differences in species composition were highly significant between catenal positions close to each other and far from each other on termitaria and in the woodland matrix. At the fine scale termitaria were sites of different species composition than the matrix, and at the landscape level the catena, in the woodland matrix showed a greater contrast in species composition when compared to the termitaria (fig 4 and 5). Thus, edaphic factors, such as soil, water and nutrients most likely have a significant influence on vegetation composition in the Chizarira area.

SPECIES COMPOSITION ON TERMITARIA AND IN THE WOODLAND MATRIX

The number of woody plant species recorded on termitaria (90) and in the woodland matrix (86) is comparable to other studies conducted in the miombo regions (Wild 1952, Chidumayo 1987, Fleming & Loveridge 2003). In Chizarira, there was no difference in species richness between termitaria and the woodland matrix, however differences in species composition were highly significant (66.5%). Specific species of woody plants were exclusive to termitaria and the woodland matrix, however these species were typically rare and occurred infrequently in both habitats. However, *Allophylus africanus* was common to both termitaria and the matrix, but occurred in different vegetation types; it occurred on termitaria in the riparian area and in mixed *Brachystegia/Combretum* woodland in the matrix. The combination of water availability, nutrient concentration and spatial heterogeneity on mounds and in the woodland matrix facilitate this difference in species composition, resulting in distinct plant assemblages on termitaria in comparison to the woodland areas (Fanshawe 1968, Fleming & Loveridge, 2003).

Termitaria were dominated largely by *mopane, Diospyros*, *Combretum* and *Commiphora* genera, whereas the woodland matrix by *Julbernadia, Brachystegia, Combretum, mopane* and *Terminalia* genera. The *mopane* woodland on termitaria had greater species richness than the *mopane* area in the woodland matrix. The *Julbernadia* and the riparian area on termitaria and in the woodland matrix comprised unique species richness in each of these vegetation types. *Jasmine stenolobum* frequently occurred as a forb in all 18 plots. *Diospyros mespiliformis* was a common tree characteristic of termitaria in the riparian area. Other common trees in the riparian area on termitaria were *Berchemia discolor*, *Diospyros senensis, Manilikara mochisa, Lonchocarpus capassa* and *Pterocarpus rotundifolius*. *Friesodielsia obovata* and *Maerua prittwitzii* frequently occurred as shrubs on mounds. Notable species in the woodland matrix were *Diospyros kirkii, Diplorhynchus condylocarpon, Pseudolachnostylis maprouneifolia*, *Terminalia stenostachya* and *Burkea africana*. Differences in species composition were considerable between termitaria and the woodland matrix; however certain species were widespread and common in both. Common species include *Bauhinia petersiana*, *Colophospermum mopane, Combretum mossambicense, Diospyros quioensis, Erythroxylum zambesiascum* and *Philenoptera violacea.*

TERMITARIA: REFUGIA FOR SPECIES DIVERSITY, TALL TREES AND DENSITY OF TREES

Mounds harbor a high diversity of tree species taller than 6 m and between 3 – 6 m than the woodland matrix. The woodland matrix supports half the number of tall tree species than termitaria (Table 4). Trees common to termitaria > 6 m in height were *Diospyros mespiliformis*, *Colophospermum mopane*, *Lannea schweinfurthii*, *Erythorxylum zambesiacum* and *Berchemia discolor.* Another notable feature was the presence of a creeper *Capparis tomentosa*, largely associated with termitaria, as a woody climber and only occasionally a shrub or small tree on mounds in Chizarira. Mounds are critical to the survival of tall trees and plant species diversity, given that a great proportion relative to the woodland matrix occur on mounds in Chizarira National Park. Since, most tall trees are no longer present in the depauperate woodland matrix, termitaria are foci for the establishment of tall tree species diversity in the miombo woodlands. Thus, mounds provide refugia for the structure of trees > 6 m and between 3 to 6 m in height. Termitaria are islands of high plant diversity of tall trees with a distinct plant assemblage in Chizarira National Park by contrast with the woodland matrix which consists mainly of regenerating, coppicing *Brachystegia boehmii* shrubs and *Combretum* species.

Mounds also support a greater density of trees > 6 m and trees with a height of over 6 m than the adjacent woodland matrix. This finding supports Loveridge & Moe's (2004) study, where the mounds supported twice the density of trees than the adjacent woodland plots. The termite mound ecosystem with its concentration of nutrients, organic matter and modified soil structure (Lee & Wood 1971, Pomeroy 1976, Dangerfield *et al*. 1998) supports the growth of woody plant species, and hence a higher density of trees than the adjacent woodland matrix. Mounds form dense vegetative patches in the landscape as well as create spatial heterogeneity for a taller tree height structure in the woodlands in Chizarira National Park relative to the woodland matrix.

The woodland matrix supports trees between 3 and 6 m in height and a high shrub density. However, very few tall trees remain in the woodland matrix in Chizarira National Park. The majority of trees remaining in the woodland matrix were mostly *Combretum spp.*, a hard wood which appears to be resistant to the impacts of elephants (personal observation). The closed canopy *Brachystegia/Julbernardia* woodlands of the past are now regenerating, coppicing stands of *Brachystegia* and *Combretum* shrubs in Chizarira National Park and few areas of *Brachystegia/Julbernardia* woodlands remain in Chizarira currently. The concentration of elephants and the frequency of fire may be preventing the *Brachystegia boehmii* shrubs from developing into tall trees in Chizarira. A situation could take place where *Brachystegia/Julbernardia* woodlands diminish over time and be replaced by resilient species such as *Combretum*. A study in Sengwa Wildlife Research Area (SWRA) found that two species of *Combretum* and a species of *Terminalia* proliferated in response to elephant disturbance because they were more resilient than *Brachystegia* (Mapaure 2001). In the woodland matrix in Chizarira, two of the same species which emerged as a response to elephant disturbance in Sengwa, *Combretum collinum* and *Termianlia sericea* as well as *Combretum apiculatum* were significant indicator species in the riparian area of Chizarira. This indicates that the riparian area is disturbed by elephants. *Brachystegia boehmii* is particularly vulnerable to debarking by elephants (Anderson & Walker 1974), however their large lignotuber roots penetrate to great depths in the soil (Cole 1963), which may prevent elephants from removing them from the ground. As in many other areas of Zimbabwe (Thomson 1974, Guy 1981, Guy 1989, Mapaure 2001, Mapaure & Campbell 2002), the synergy of fire and elephants has had an effect on woodland vegetation structure in Chizarira. Woodlands converted by elephants and fire are typically maintained in that state (Mapaure 2001). Elephants and fire are important disturbance factors in miombo woodlands, however, create spatial heterogeneity (Gambiza *et al*. 2000, Holdo & McDowell 2004).

Fire is frequent in miombo and moves through the understory every 3 years (Boaler 1966, Frost 1996). Trees < 3 m are vulnerable to fire (Swaine 1992, Higgins *et al*. 2000). The woodland matrix transects showed evidence of recent fire evident in the understory layer of burnt grass and a few trees, which were damaged and burnt to the base resulting in death. Evidence of fire was prevalent on trees in the woodland matrix, whereas trees on mounds appeared unscathed. Trees in the woodland matrix of Chizarira are unlikely to grow beyond 6 m in height as elephants and fires continue to denude and alter the woodland matrix. Whilst, the high nutrient and water content in soils on termitaria in comparison to the woodland matrix (Watson 1969, Lee & Wood 1971, Pomeroy 1976, Dangerfield 1991, Dangerfield *et al.* 1998) provides an environment conducive to the growth of tall trees, the particularly high water moisture in soils prevents the effects of fire on trees on mounds (Harrington 1991). The large number of *Macrotermes* in Chizarira may provide protection to tall trees from elephants and fire. Thus, the elevation of termitarium, the high nutrient and soil moisture availability can protect tall trees from both fire and elephants in this system. However, only the tall, mature growth forms of trees which have reached a certain height at the apex of a mound are safe from the browsing habits of elephants. Trees at the base of mounds may be impacted on by elephants more so than trees at the apex of a mound, which are out of reach to elephants due to the steep gradient and height of the termitaria. The high occurrence of both fire and elephants magnifies the role termitaria play in the miombo landscape as structures which preserve tall trees and woody plant species diversity in Chizarira.

VARIATION IN TREE HEIGHT STRUCTURE ON HALO AND NON-HALO MOUNDS

Mounds without halos had taller trees than mounds with halos. The uprooting of trees by elephants reduces the density of mature canopy trees and alters their structure in woodlands (Mapaure 2001). Even though termitaria are refugia, allowing trees to gain height at the apex of mounds, some trees are exposed to herbivore browsing and damage at the base of mounds and notably, not all trees on mounds are inaccessible due to termitarium height in Chizarira. Hence, not all trees are out of reach of herbivore damage on termitaria. A reduced tree height structure on haloed mounds relative to non-halo mounds suggests that elephants alter tree structure and may trample the surrounding soil and facilitate the compaction of the area around mounds. The rate and extent of trampling and dung deposits can have marked effects on soil erosion, and compaction, water infiltration, seedling recruitment, nutrient cycling and plant growth (Gifford & Springer 1980, Plumptre 1993). Grazing and trampling compact the soil between patch areas, prevent water from filtering into the soil and increase water run-off (Aguiar & Osvaldo 1999). Animal paths were evident on some mounds (personal observation). Elephants have also been seen eating and excavating the mineral and clay rich soils from old termitaria (Ruggerio & Fay 1994).

Non-halo mounds had a taller height structure than halo mounds on a flat surface in Chizarira National Park. Evidence of reduced tree height structure on the flat surface halo mounds suggests that mound structure and slope angle (i.e. steep gradient) affect an elephant's ability to feed off tall trees on termitaria in Chizarira National Park. A steep slope is a physical constraint and can limit access to high resource areas (Coughenour 1991). Tall trees on mounds situated on the apex of a steep gradient are mostly out of reach from elephants (personal observation). Recent research has shown that elephants in Kruger National Park are reluctant to feed on steep gradients and rocky ridges and have a preference for browsing on baobabs (*Adansonia digitata*) in low lying areas (Edkins *et al*. 2007).

Spain and McIvor (1988) hypothesized that preferential grazing of vegetation near mounds by mammals can cause changes in vegetation composition. The difference in height structure between halo and non-halo mounds indicates that elephants have altered the structure of vegetation on mounds which can result in a change in species composition on termitaria. Recent research shows changes in bird species diversity (Herremans 1995), decline in mountain Acacia (*Brachystegia glaucescens*) in Zimbabwe (Tafangenyasha 2001), reduction in bird and ant species richness (Cumming *et al*. 1997) and a lowering of dung beetle species richness (Botes *et al*. 2006 b) where elephants have reduced tree biomass and opened up the tree canopy (Mapaure 2001). Mounds in Chizarira are increasingly showing signs of erosion, perhaps as synergistic consequences of high elephant impacts and the age of the mound. The high density of elephants in this system could result in the loss of species diversity of tall tree on mounds as more trees and nutrients are removed from the woodland matrix. If the population of elephants continues to expand in the park, the situation might develop where elephants are left little choice but to feed off mounds more frequently than in the past.

Recent research has shown that termitaria support browsing African megaherbivores in tropical savannas and woodlands in Uganda (Mobaek *et al*. 2005), Zimbabwe (Loveridge & Moe 2004, Holdo & McDowell, 2004, Fleming & Loveridge, 2003), and the Central African Republic (Ruggiero & Fay 1994). It is apparent in aerial photographs from 1965 that there were none, or very few large termitaria with halos, however on a time scale of 40 years, halos have appeared around many more termitaria (Thomson 1974). An examination of aerial photography of the Sebungwe region at a scale of 1: 25, 000 indicates an absence of halos in areas with few or no elephant and no livestock. Settled areas carrying high densities of livestock also show halos. The presence of elephants in confined protected areas may be a contributing factor to the halo effect around mounds. Termitaria in communal areas of Zimbabwe have halos which may be a result of high livestock densities and agricultural tilling (D. Cumming pers.comm. 2008).

VARIATION IN SPECIES COMPOSITION IN RESPONSE TO HALOS

Full and non- halo mounds were the most distinct from each other in species composition. Species composition between halo, partial and non-halo mounds showed a high level of similarity (87.5 %) and partial and the full halo mounds were the most similar (93 %). In a time scale of 40 years halos have appeared around termitaria in Chizarira National Park. The significance between the full and non-halo mounds indicates that eroded halo mounds have a different species composition than perhaps non-halo mounds which have not been subject to erosion. Woody plant species may diminish as the termitaria age over a period of time. The combination of the compaction and the trampling of mounds by elephants and erosion of mounds along an age gradient might explain the difference in species composition between halo and non-halo mounds in Chizarira National Park. Glover (1949) recorded the presence of 'hardpans' at the base of termitaria in Northern Rhodesia which were associated with an inhibited plant growth. Partial and full halo mounds are probably in a similar state of erosion and hence are alike in species composition. The early stage of erosive processes in the small time scale of 40 years might explain the lack of significant differences in species composition between the halo, partial and non-halo mounds in Chizarira National Park. The variation in species composition has not been explained by the measured variables in this study, indicating that other unmeasured factors such as soil structure, soil nutrients and age gradients (i.e. active to abandoned mounds) may also be important. Mounds are ancient structures in the miombo landscape. Although little is known about the longevity of termite mounds (de Bryn & Conacher 1990), the mounds in Chizarira National Park may be up to a 1 000 year old (Watson 1967). So, it is interesting that the first signs of erosion have appeared only in the last 40 years. Since, fire and high densities of elephants have facilitated disturbance in the miombo woodlands for the last three decades, they are important factors to consider in understanding the effect of halos on species composition in Chizarira.

Partial mounds situated on a downslope gradient were observed more frequently than full halo mounds on a downslope gradient (Table 10). This observation suggests that mounds on a downslope gradient might be caused by erosion. A study of vegetation patterns around mounds in the Loita plains in Kenya showed that the surrounding mound area was affected by rain wash from the mounds (Glover *et al*. 1964). Ninety five percent of the annual rainfall falls within a 5-7 month wet season in the miombo woodlands (Campbell *et al.*1996) and frequently in the form of afternoon downpours. Water input to the soil around mounds can be affected by soil surface penetrability, vegetation cover and the shape of the mound by affecting rainfall interception and runoff (Konate *et al*. 1999). The compaction and trampling of soil by browsing herbivores (Glover *et al.* 1964, Spain & McIvor 1988) may reduce the water infiltration around mounds. Thus, interacting factors, such as the compaction of soil by browsing herbivores, mound vegetation cover, the mound profile and rain wash may facilitate the formation of halos around mounds in Chizarira.

A combination of erosion, fire and high numbers of elephant in Chizarira National Park may accelerate the loss of species diversity over time in the miombo woodlands. Research on the nutrient concentrations on mound soils and the comparison of areas without high densities of herbivores will provide further insight into halos around termitaria. This study is the first to identify the importance of termitaria as islands or refugia for tall trees, allowing the maturation and growth of trees in an area impacted by elephants and fire. Termitaria as features of spatial heterogeneity in the miombo landscape may function as indicators of any change in plant species diversity and woodland structure in this system. Protection of the miombo woodlands from fire is an impractical ideal (Sileshi & Mafongoya 2006). It seems that elephants at high densities will continue to threaten species diversity in the miombo woodlands unless effort is made to put the appropriate control measures in place.

Conclusion

Catenal position has a significant influence on species richness in the miombo woodlands. The differences in species composition were largely evident at the local scale in the catena in Chizarira National Park.

Termitaria form refugia for the growth of tall trees in the miombo woodland matrix highly altered by the presence of high elephant densities and fire. A high density of tall trees > 6 m is characteristic of termitaria, while the woodland matrix area is predominantly characterized by a lower density of trees that are mostly less than 6 m in height and shrubs in this study site. It is apparent that elephants are maintaining the woodland matrix trees in perpetual state of coppicing and resprouting *Brachystegia* shrubs and *Combretum* species in Chizarira National Park.

The variations of tree height on termitaria and the evidence of a higher trees on non-halo mounds suggests that elephants may be one contributing factor that is accelerating the process of erosion and the formation of halos around termitaria in the miombo woodlands.

Mounds play an important role in preserving vegetation height structure and plant species richness of tall trees in comparison to the depauperate woodland matrix. Thus, termitaria in the landscape are important factors that enhance biodiversity in the miombo system. This study shows that a high population of herbivores may accelerate species loss in the woodland matrix, together with the erosion of termitaria. The loss of certain tree species and localized woodland damage can occur at elephant densities < 0.2 km^2 in a wide range of woodlands (Spinage 1990). A high number of elephants can reduce species richness and alter species composition if not managed appropriately. The elephant densities at the time of the study in Chizarira were approximately 1.5 ^{km2}, which suggests that long term planning and better management of elephant populations is urgently needed in Chizarira National Park given the long time scale vegetation takes to regenerate in degraded systems such as the miombo woodlands.

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Appendix A.

Assess plant representativeness on termitaria and in woodland matrix

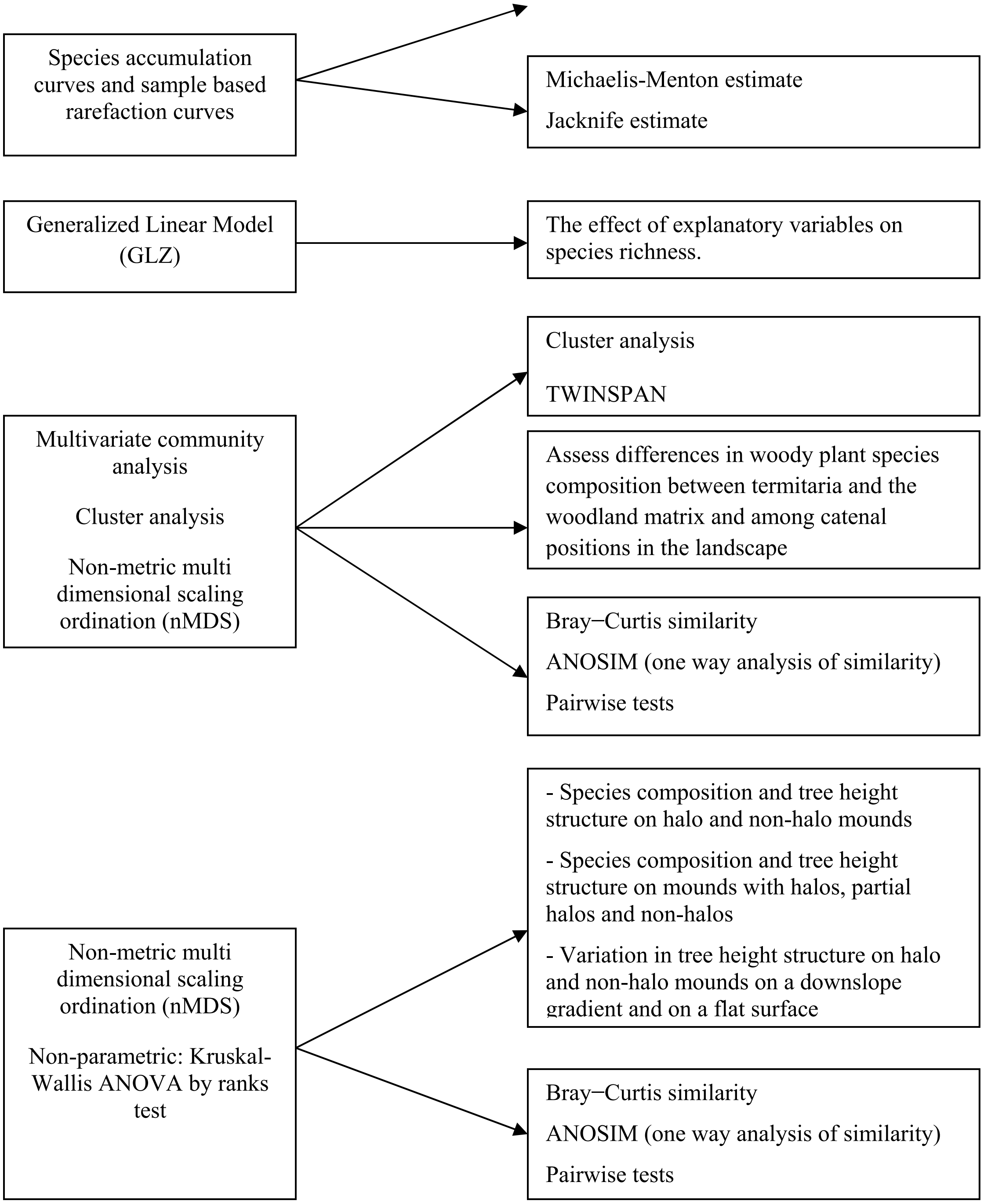

Fig. 1. Diagram of analysis steps for the difference in species composition between termitaria and woodland matrix in relation to catena and in response to halos on termitaria.

Appendix B

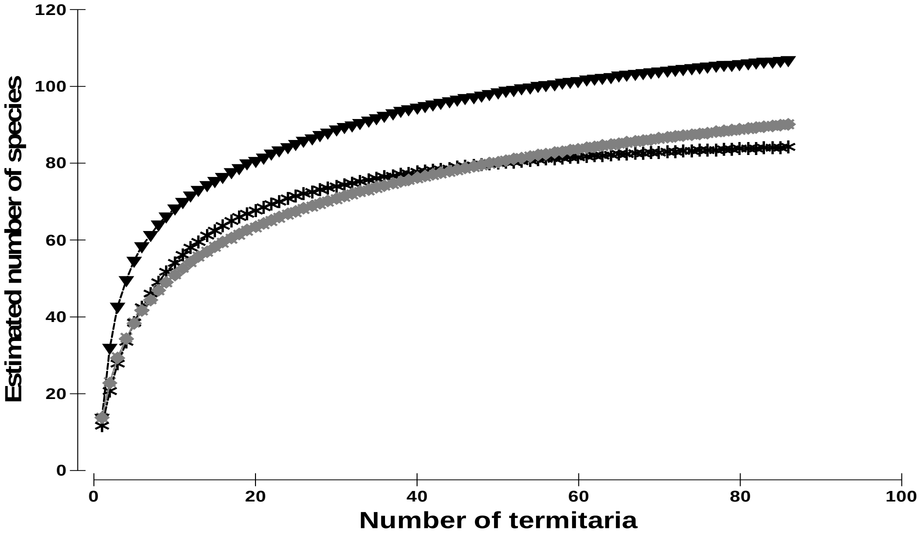

Fig. 2. Species-accumulation curve extrapolating woody plant species density versus sample size data (n = 86) of termitaria. (MM = Michaelis-Menton estimator [star line], S_{obs} = observed number of species [x line], Jacknife1 = richness estimator [line], UGE = mean curv▲[gray line].

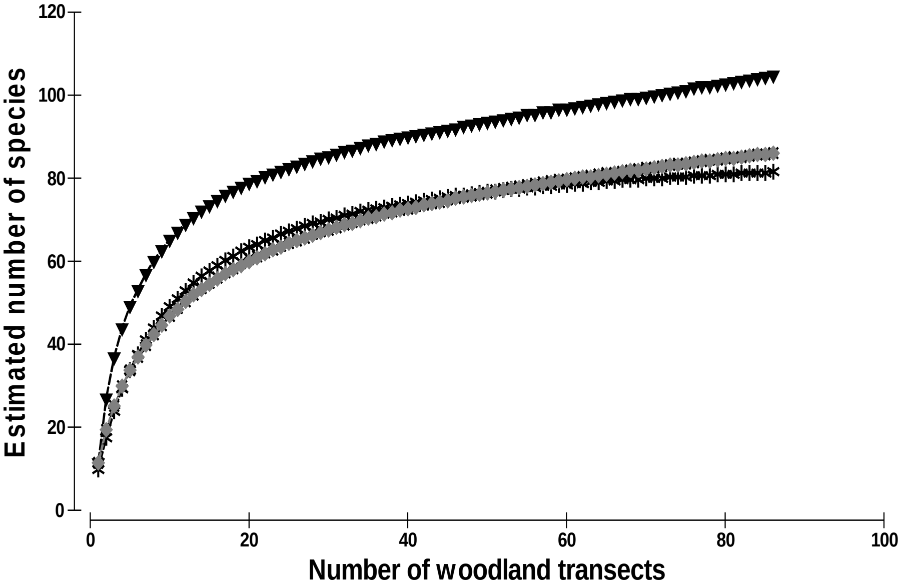

Fig. 3. Species-accumulation curve extrapolating woody plant species density versus sample size data (n = 86) of woodland matrices. (MM = Michaelis-Menton estimator [star line], S_{obs} observed number of species [x line], Jacknife1 = richness estimator [▲ne], UGE = mean curve [gray line].

Appendix C. Species, author (family) of woody plant species found on termitaria and in the woodland areas of miombo woodland. Nomenclature follows Palgraves (1981). ^{t} recorded only on termitaria; ^{w} recorded only in the woodland matrix; $^{t/w}$ shared species between termitaria and woodland matrix.

Acacia gerrardii Benth (Acacia)$^{t/w}$
Acacia galpinii Burtt Davy (Acacia)^{w}
Acacia nigrescens Oliver (Acacia)^{t}
Acacia nilotica Wild. Ex Delile (Acacia)$^{t/w}$
Albizia harveyi Fourn. (Mimosoideae)$^{t/w}$
Allophylus africanus Beauv. (Sapindaeae)$^{t/w}$
Allophylus alnifolius (Baker) Radlk. (Sapindaeae)^{t}
Annona stenophylla Engl & Diels (Annonaceae)^{w}
Azanza garckeana (F. Hoffman) Exell & Hillcoat (Azanza)^{t}
Bauhinia petersiana Bolle (Caesalpinioideae)$^{t/w}$
Berchemia discolor (Klotzsch) Hemsley (Rhamnaceae)^{t}
Boscia angustifolia A. Rich (Capparaceae)^{t}
Boscia salicifolia Oliver (Capparaceae)$^{t/w}$
Brachystegia boehmii Taub. (Caesalpinioidaea)^{w}
Brachystegia spiciformis Harms. (Caesalpinioidaea)^{w}
Bridelia cathartica Bertol.f. (Euphorbiaceae)$^{t/w}$
Burkea africana Hook (Caesalpinioidaea)$^{t/w}$
Capparis tomentosa Lam. (Capparaceae)$^{t/w}$
Cassia abbreviata Oliver (Caesalpinioidaea)$^{t/w}$
Catunaregam spinosa (Rubiaceae)$^{t/w}$
Cissus confolia (Vitaceae) $^{t/w}$
Combretum zeyheri Sonder (Combretaceae)$^{t/w}$
Colophospermum mopane (Kirk ex Benth.) Kirk ex. J. Léonard (Caesalpinioidaea)$^{t/w}$
Combretum adenogonium F. Hoffm.(Combretaceae)$^{t/w}$
Combretum apiculatum Sonder (Combretaceae)$^{t/w}$
Combretum collinum Sonder (Combretaceae)$^{t/w}$
Combretum hereroense Schinz (Combretaceae)$^{t/w}$
Combretum molle R. Br. ex. G. Don (Combretaceae)$^{t/w}$
Combretum mossambicense (Klotzsch) Engl. (Combretaceae)$^{t/w}$
Commiphora africana (A. Rich.) Engl (Burseraceae)$^{t/w}$
Commiphora karibensis Wild (Burseraceae)$^{t/w}$
Commiphora mollis (Oliver) Engl. (Burseraceae)$^{t/w}$
Commiphora mossambicensis (Oliver) Engl. (Burseraceae)$^{t/w}$
Commiphora pyracanthoides Engl. (Burseraceae)^{t}
Crossopteryx febrifuga (Afzel.ex. G. Don) Benth. (Rubiaceae)$^{t/w}$
Dalbergia melanoxylon Guillemin & Perrottet (Papilionoideae)$^{t/w}$
Dichrostachys cinerea Wight & Arn. (Mimosoideae)$^{t/w}$
Diospyros batocana Hiern (Ebenaceae)^{t}
Diospyros kirkii Hiern (Ebenaceae)$^{t/w}$
Diospyros lycioides Desf. (Ebenaceae)$^{t/w}$

Diospyros mespiliformis Hochst (Ebenaceae)$^{t/w}$
Diospyros quiloensis (Hiern) F. White (Ebenaceae)$^{t/w}$
Diospyros senensis Klotzsch (Ebenaceae)$^{t/w}$
Diplorhynchus condylocarpon (Muell. Arg.) Pichon (Apocynaceae)$^{t/w}$
Ehretia caerulea Gurke (Boraginaceae)^{t}
Erythroxylum zambesiacum N. K. B. Robson (Erthroxylaceae/balanticeae)$^{t/w}$
Euclea divinorum Hiern (Ebenaceae)$^{t/w}$
Euphorbia ingens E. Meyer ex Boiss. (Euporbiaceae)^{t}
Feretia aeruginescens Stapf (Rubiaceae)$^{t/w}$
Ficus ingens (Miq.) Miq. (Moraceae)^{t}
Fluegea virosa (Roxb. Ex Wild.) Baillon (Euphorbiaceae)$^{t/w}$
Flacourtia indica (N. L. Burm.) Merr. (Flacouticaea)$^{t/w}$
Friesodielsia obovata (Benth.) Verdc. (Annonacea)$^{t/w}$
Gardenia resiniflua Hiern (Rubiaceae)^{t}
Gardenia spathulifolia K. Schum. (Rubiaceae)$^{t/w}$
Grewia bicolor Juss. (Tiliaceae)$^{t/w}$
Grewia flavescens Juss. (Tiliaceae)$^{t/w}$
Grewia monticola Sonder (Tiliaceae)$^{t/w}$
Jasminun stenolobum Linnaeus (Oleaceae) $^{t/w}$
Julbernardia globiflora (Benth.) Troupin (Caesalpiniodeae)^{w}
Kirkia acuminata Oliver (Simaroubaceae/Burseraceae)$^{t/w}$
Lannea edulis Sond. Engl (Anacardiaceae)^{w}
Lannea discolor (Sonder) Engl. (Anacardiaceae)$^{t/w}$
Lannea schweinfurthii (Engl.) Engl. (Anacardiaceae)$^{t/w}$
Maerua kirkii (Oliver) F.White (Capparaceae)^{t}
Maerua prittwitzii Gilg & Benedict (Capparaceae)$^{t/w}$
Manilkara mochisa (Baker) Dubard (Sapotaceae)^{t}
Margaritaria discoidea (Baillon) Webster (Euphorbiaceae)$^{t/w}$
Markhamia acuminata (Klotzsch) K.Schum (Bigoniaceae)^{w}
Markhamia zanzibarica (Klotzsch) K. Schum (Bigoniaceae)$^{t/w}$
Maytenus heterophylla (Ecklon & Zeyher) N. K. B. Robson (Celastraceae)$^{t/w}$
Maytenus putterlickioides (Loes)Excell & Mendonça (Celastraceae)^{t}
Maytenus senegalensis (Lam.) Excell (Celastraceae)$^{t/w}$
Ochna schweinfurthiana F. Hoffm (Ochnaceae)^{w}
Ormocarpum kirkii S. Moore (Papilionoinodieae)^{w}
Ozoroa insignis Delile (Anacardiaceae)$^{t/w}$
Pavetta gardenifolia Hochst. Ex A. Rich (Rubiaceae)$^{t/w}$
Pavetta schumanniana F. Hofman. Ex. K. Schum. (Rubiaceae)^{w}
Philenoptera violacea Rolfe (Violacea)$^{t/w}$
Pericopsis angolensis (Baker) van Meeuwen (Papilionoideae)$^{t/w}$
Peltophorum africanum Sonder (Caesalpinioideae)^{w}
Piliostigma thonningii Schumacher (Caesalpinioideae)^{w}
Pseudolachnostylis maprouneifolia Pax (Euphorbiaceae)$^{t/w}$
Pterocarpus rotundifolius (Sonder) Druce (Papilionoideae)$^{t/w}$

Rhoicissus revoilli Planchon (Vitaceae)^{t}
Schrebera trichoclada Welw. (Oleacae)$^{t/w}$
Sclerocarya birrea (A. Rich.) Hochst. (Anacardiaceae)^{w}
Senna singueana Delile (Caesalpinioideae)^{t}
Strychnos cocculoides Baker (Loganiaceae)^{t}
Strychnos potatorum L.f. (Loganiaceae)^{t}
Terminalia brachystemma Welw. ex Hiern (Combretaceae)$^{t/w}$
Terminalia mollis C. Lawson (Combretaceae)^{w}
Terminalia sericea Burch. ex DC (Combretaceae)^{w}
Terminalia stenostachya Engl. & Diels (Combretaceae)$^{t/w}$
Terminalia trichopoda Diels (Combretaceae)$^{t/w}$
Turraea nilotica Kotschy & Peyr. (Meliaceae)^{w}
Vangueria infausta Burch. (Rubiaceae)$^{t/w}$
Vangueria randii S. Moore (Rubiaceae)^{t}
Vangueria spp.
Xeroderris stuhlmannii (Taub.) Mendonça & E. P. Sousa (Paiplionideae)$^{t/w}$
Ximenia americana L. (Olacaceae)$^{t/w}$
Ximenia caffra Sonder (Olacaceae)$^{t/w}$
Ziziphus abyssinica Hochst. ex. A. Rich (Rhamnaceae)^{w}
Ziziphus mucronata Wild. (Rhamnaceae)$^{t/w}$

Appendix D. (1). Tree species > 6m on the termitaria and in the woodland matrix; $^{t/w}$species of trees > 6m recorded on both termitaria and in the woodland matrix.

Termitaria	Woodland matrix
Acacia nigrescens	*Acacia galpinii*
Acacia nilotica$^{t/w}$	*Acacia nilotica*$^{t/w}$
Berchemia discolor	*Burkea africana*
Capparis tomentosa	*Colophospermum mopane*$^{t/w}$
Cassia abreviata	*Combretum hereoense*$^{t/w}$
Colophospermum mopane$^{t/w}$	*Combretum adenogonium*
Combretum apiculatum$^{t/w}$	*Combretum apiculatum*$^{t/w}$
Combretum collinum	*Combretum mollis*$^{t/w}$
Combretum hereroense$^{t/w}$	*Julbernardia globiflora*
Combretum mollis$^{t/w}$	*Piliostigma thonningii*
Combretum mossamibicense	*Scleocarya birrea*
Commiphora mollis	*Schrebera trichoclada*
Commiphora mossambicensis	*Terminalia sericea*
Diospyros kirki	*Terminalia stenostachya*
Diospyros mespiliformis	
Diospyris quiloensis	
Erythoxylum zambesiaccum	
Lannea schweinfurthii	
Philenoptera capassa	
Manilkara mochisia	
Rhoissuss revoilli	

Strychnos potatorum
Xeroderris stuhlumani

Appendix D. (2). Tree species between 3-6m on termitaria and in the woodland matrix. $^{t/w}$Species of trees between 3 – 6 m recorded on both termitaria and in the woodland matrix.

Termitaria	Woodland matrix
Acacia gerrardii	*Capparis tomentosa*$^{t/w}$
Acacia nilotica	*Brachystegia boehmii*
Berchemia discolor	*Burkea africana*
Boscia angustifolia	*Colophospermum mopane*$^{t/w}$
Bridelia cathartica	*Combretum adenogonium*$^{t/w}$
Capparis tomentosa$^{t/w}$	*Combretum apiculatum*$^{t/w}$
Cassia abreviata	*Combretum collinum*$^{t/w}$
Cissus confolia	*Combretum hereroense*$^{t/w}$
Colophospermum mopane$^{t/w}$	*Combretum mollis*$^{t/w}$
Combretum adenogonium$^{t/w}$	*Combretum mossamibicense*$^{t/w}$
Combretum apiculatum$^{t/w}$	*Commiphora mollis*$^{t/w}$
Combretum collinum$^{t/w}$	*Crossopteryx febrifuga*
Combretum hereroense$^{t/w}$	*Diospyros senensis*$^{t/w}$
Combretum mollis$^{t/w}$	*Erythroxylum zambesiacum*$^{t/w}$
Combretum mossamibicense$^{t/w}$	*Euclea divinorum*$^{t/w}$
Combretum zeyheri	*Julbernardia globiflora*$^{t/w}$
Commiphora karibensis	*Peltophorum africanum*
Commiphora mollis$^{t/w}$	*Pseudolachnostylis maprouneifolia*
Commiphora mossambicensis	*Fluegea virosa*$^{t/w}$
Diospyros kirki	*Terminalia sericea*
Diospyros mespiliformis	*Terminalia stenostachya*$^{t/w}$
Diospyros lycioides	*Terminalia trichopoda*$^{t/w}$
Diospyros senensis$^{t/w}$	*Turrea nilotica*
Erythroxylum zambesiacum$^{t/w}$	
Euclea divinorum$^{t/w}$	
Feretia aeruginescens	
Julbernardia globiflora^{w}	
Lannea schweinfurthii$^{t/w}$	
Manilkara mochisia	
Maytenus heterophylla	
Pavetta gardenifolia	
Rhoicissus revoilli	
Fluegea virosa$^{t/w}$	
Strychnos potatorum	
Terminalia brachystemma	
Terminalia stenostachya$^{t/w}$	
Terminalia trichopoda$^{t/w}$	
Xeroderris stuhlumani	
Ximenia americana	
Ximenia caffra	