Landscape heterogeneity facilitated by termitaria and its effect on ant community composition in the miombo woodlands of Chizarira National Park, Zimbabwe

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Abstract

Within the miombo woodlands of Chizarira National Park, Zimbabwe, *Macrotermes* termites create large, vegetated mounds and nutrient rich patches in a system that has been transformed and simplified by high elephant densities and fire. These termitaria have been shown to provide refugia for cavity nesting birds, small mammals and plant species. I tested how the landscape heterogeneity associated with termitaria affects ant community composition on the mounds and in the matrix within this modified habitat. I surveyed 12 sites, each comprised of a mound and an adjacent matrix plot. The 12 pairs consisted of three different types of vegetation cover; four mounds with high canopy cover and high ground cover, four with low canopy cover and low ground cover and four with high canopy cover and low ground cover. One hundred and twenty pitfall traps were used to collect the ant samples across all treatments, with five traps per mound and matrix plot. Over four days of sampling 24,168 ants were caught, comprising 43 species. Species richness (p-value .0159) and abundance (p-value .0029) was significantly higher on the mound sites, while species evenness (p-value .0027) and diversity (p-value .0168) was higher in matrix sites. Vegetation coverage of sites could not be used to predict ant assemblages due to a recent fire that had burned three of the matrix sties and four of the mound sites, therefore falsifying coverage data that was obtained since it reflected the habitat in a post-fire state. The most interesting result was how different the ant assemblages were on and off mounds. The species found between these sites formed entirely different communities. By providing heterogeneity in a transformed environment through elevated nutrient concentrations, termitaria are creating the niche partitioning needed for a great number of ant species to coexist in an intensely competitive environment. Ants are becoming increasingly important to science as bioindicators in disturbed environments and biodiversity surrogates. Thus, elements within an environment, like termitaria, that preserve the coexistence and therefore facilitate species richness of various taxa, become increasingly important as habitats become transformed.

Chapter 1: Introduction and Literature Review

1.1 Consequences of Elephant Over-population

The 20th century brought many changes to Africa, one of the most ubiquitous being the rapid increase in the human population. The unprecedented expansion of the population put severe strain on the limited land, water and other resources that needed to be shared by millions of both people and wild animals. As more land was converted for subsistence agriculture and infrastructure development, massive reductions in the ranges of wild animals seemed imminent. Many countries attempted to solve the impending crisis by putting up fences and partitioning off land reserves for wild animals. Fencing as a form of wildlife management and conservation is a feature of South Africa, but not most of southern Africa (South African Savannas Network 2001, Grant et al. 2008). Once implemented over southern Africa these fences blocked historical migration patterns for many animals and the new barriers quickly became a problem, especially for elephants (Hanks 1979, Owen-Smith 1988).

Historically, elephant populations in southern Africa were reduced to very low levels by 1890 by means of hunting and the ivory trade. An estimated number of only 4,000 elephants populated Zimbabwe in 1900 (Child 2004). However, exponential growth of herds in Zimbabwe and South Africa of between 5-7% p.a. in the 20th century and a lack of efficient management, caused Zimbabwe's elephant population to soar to around 100,000 individuals by 2003 (Child 2004). Under natural conditions, such intense population pressure that is well beyond local carrying capacity would cause elephant herds to go through a range expansion or shift in distribution (Laws 1970). However, besides fences, other forms of range restrictions due to explosive human population growth coupled with agriculture expansion have been too rapid for adaptation, population dispersal or natural intra-regulatory mechanisms of elephant populations (Laws 1970). Small patches of fenced land were now forced to cater to expanding elephant populations that could no longer disperse and as a result the overpopulation problem was exacerbated (Hall Martin 1990).

Elephants, which are generalist herbivores, are capable of altering entire ecosystems (Owen-Smith 1988, Hall Martin 1990, Cumming et al. 1997, Joseph 2007). The unprecedented densities of elephant populations within some of the reserves of southern and central Africa have caused natural woodland habitat to become more marginalized and simplified, thus generating changes in ecosystem dynamics (Cumming 1982, Jones et al. 1994, Meysman et al 2006). Subsequently, a severe decline in the quality, health and extent of woodland habitat has been demonstrated, including a loss of canopy cover and a decline of biodiversity, in many reviews and studies (Guy 1981, Cumming 1981, Conybeare 1989, Mapaure and Campbell 2002). Elephant herbivory is an important mechanism in the structuring of plant communities (Trollope et al. 1998, Mapaure and Campbell 2002). In one specific habitat, the miombo woodlands, complex canopies with both vertical and horizontal heterogeneity have been transformed into more uniform bushlands or savanna-type environments due to extensive elephant herbivory (Cumming et al. 1997). In the Sengwa Wildlife Research Area in Zimbabwe a strong negative correlation was found between elephant densities and woody cover, where there was an overall decrease of mean woody cover by 28.4% between 1958 and 1996 (Mapaure and Campbell 002). These changes considerably alter the dynamics of the ecosystem, due to secondary effects, feedback mechanisms and a loss of biodiversity, as the land becomes more homogeneous at all spatial scales (Guy 1981, Herremans 1995, Mapaure 2001).

1.2 Termites Facilitate Landscape Heterogeneity

Termites show considerable resistance to environmental disturbances (Eggleton et al. 1995, Eggleton et al. 1996). Within the miombo woodlands termitaria are capable of creating refugia, or foci of diversity, for species in a mega-herbivore dominated or transformed environment (Fleming and Loveridge 2003). For many taxa, termitaria create nutrient rich island hotspots, within the modified matrix environment, which contribute to the landscape heterogeneity and promote and maintain species diversity and abundance. Plants, small mammals and cavity-nesting birds have already been shown to be benefactors of termitaria (Arshad 1982, Fleming and Loveridge 2003, Joseph 2007).

Termites are dominant invertebrates, both in terms of their overall biomass and in their ability to alter their environment (Wood and Sands 1978, Eggleton et al. 1996, Fall et al. 2001) Termites are ecosystem engineers; they have a strong influence on water availability for many organisms and on the soil physico-chemical characteristics (Jones et al. 1994, Konate et al. 1998, Dangerfield et al. 1998). Termites have a long-term influence on nutrient availability, flow-rates and concentration. They have the ability to mediate nitrogen fixation and decomposition and also modify the texture and structure of the soil (Eggleton et al. 1996). Soils on termitaria have been found to have elevated concentrations of Ca, Mg, K and Na compared to surrounding soils (Lobry de Bryn and Conacher 1990, Folgarait 1998, Jouquet et al. 2006). More importantly, these soil modification processes appear to persist long after the lifetime of a colony (Lavelle et al. 1993, Hedde 2005). Many studies of various species of termites have found that abandoned mounds often are preferred sites for successive colonies, which perpetuates this nutrient concentration (Collins 1981, Wood et al. 1982, Schuurman and Dangerfield 1996, 1997, Dangerfield et al. 1998)

Termites also concentrate finer particles within their mounds, increasing the clay content two to three times that of which can be found on a matrix patch, which increases soil water retention (Boyer 1982, Lavelle et al. 1993, Konate et al. 1998). This is a key determinant of vegetation structure and composition, in a dry, savanna-like environment. Consequently, vegetation structure and dynamics influence the spatial and temporal distribution of many other species that are dependent upon the presence of specific plant species (Frost et al 1986, Konate et al 1998).

The growth rate, morphology and composition of vegetation species is directly and indirectly influenced by the presence of termitaria, through moisture retention and elevated nutrient concentrations and feedbacks, therefore vegetation on mounds is often more diverse and has a higher biomass than in the nutrient-poor matrix (Arshad 1982, Jouquet et al 2006). Species richness of woody plants is two to three times higher on mounds than in the surrounding matrix in a typical savanna environment (Abbadie et al. 1992, Konate et al. 1999). In a study done in central Zimbabwe, on the Iwaba Wildlife Estate, which is characterized by high herbivore browsing, tree densities on mounds were shown to be twice that of the surrounding matrix (Loveridge and Moe 2004). Termite mounds create spatial patterns on a local scale that influence overall habitat structure and preserve landscape heterogeneity on a regional scale (Abbadie et al. 1992, Konate et al. 1999, Palmer 2003). Termites are capable of both directly and indirectly modulating the intake of resources of other organisms, which creates landscape patterns by fostering more functional niches for species in an otherwise homogeneous environment.

Studies have already demonstrated how vegetation diversity is influenced by the nutrient enrichment created by the presence of termitaria and, a greater number of small mammal and cavity-nesting bird species are also found on termite mounds versus the surrounding matrix environment (Arshad 1982, Fleming and Loveridge 2003, Joseph 2007). What this study seeks to explore is whether termitaria are refugia for other species as well. I would like to determine if other taxa, in this case ants, are also affected by the presence of termitaria and the termite's ability to modulate resources and transform various aspects of their environment.

1.3 The Impact of Landscape Heterogeneity on Ant Diversity

Many studies have shown how termite activity generates hotspots of productivity surrounded by less productive matrix areas (Hansell 1993, Hopper et al 2000, Palmer 2003). In intensely competitive ant communities termitaria create habitat structural complexity and patchiness that contributes to the coexistence of more species than uniform habitats (Palmer 2003, Santos et al. 2008). Soil invertebrates, many ant species included, are known to be specific in terms of their diet (Anderson 1987, Hopper et al. 2000). As a result, the spatial mosaic of resources created by termite activity fosters the development of a wider range of habitat niches, which can create more habitat specialist species and alleviate competitive exclusion (Schoener 1974). Habitat heterogeneity increases the multidirectional complexity within competitive interactions that limits such exclusion (Anderson 2008). Such environmental variation is critical for niche partitioning so that both specialists and generalists species, subordinate and dominant species are able to exploit the same habitat. For example, not all patches in a landscape are equal qualitatively, (Schoener 1974) but, subordinate species can fill the gaps created by a heterogeneous landscape, since even dominate species cannot occupy all possible niches within a range of all temporal and spatial scales. Thus, heterogeneity, especially at the local level, promotes differential responses and interspecific trade-offs among ants. This allows a wide range of species, both competitively dominant and subordinate, to utilize different aspects and take advantage of the varying conditions of their environment (Speisman and Cumming 2008).

Clay content on termite mounds is much more concentrated than in the surrounding matrix (Boyer 1982, Lavelle et al. 1993, Konate et al. 1998), and in a study done by Debuse et al. (2007), it was found that clay content in the soil was the most important habitat predictor for variation and species coexistence in ant communities. Clay is very important for some ant species for the construction of their nests (Davis-Carter and Sheppard 1993) but it also aides significantly in resource productivity and water retention (Parr et al. 2004, Debuse et al. 2007). Higher resource availability near termite mounds has been shown to increase the average growth rate and overall size of many ant species colonies, especially competitively dominant ones (Palmer 2003). Since the presence of water appears to be a very critical factor for ant colonies, species diversity is most likely preserved by environmental temporal variation as well as spatial heterogeneity. Since many ants are thermophilic, temporal niche separation is especially pronounced in hot, dry environments (Andersen 2008).

Termite mounds may also preserve the diversity of ants through ‘spatial mass-effects’ (Shmida and Ellner 1984). Within a heterogeneous landscape, high and persistent immigration from more favorable sites, the mounds, to less favorable sites, the matrix, can prevent the extinction of competitively inferior species (Shmida and Wilson 1985, Andersen 2008). Spatial mass effects predicts that due to this constant influx of colonizers from a community with a higher equilibrium species number, chance establishment of subordinate species will take place in less productive patches (Shmida and Wilson 1985, Andersen 2008). As a result, termitaria have the ability to influence the environment on a landscape level.

There is a distinct lack of congruence within the literature with respect to the effect of bare ground, ground vegetation cover and canopy cover on ant communities. While some research cites the importance of vegetation cover for ant species coexistence (Chase and Leibold 2003, Leibold et al 2004), others refer instead to the importance of bare ground since many species of ants are thermophilic (Holldobler and Wilson 1990, Parr et al. 2004, Debuse et al. 2007). Due to these gaps in the literature, vegetation cover was an important factor that I wanted to test in this study.

1.4 Key Questions and Hypotheses

It is common throughout the literature that the coexistence of species with similar requirements, like ants, is dependent on the spatial dynamism of a habitat (Amarasekare 1993). Therefore, spatial heterogeneity within a landscape is critical for the maintenance of coexisting ant species (Spiesman and Cumming 2007). I tested whether termitaria are creating the spatial structure and division needed to partition the local niches of ants to foster the development of very different ant communities and facilitate the coexistence of more species than one would assume would could co-habitat a local environment together (Holldobler and Wilson 1990). The diversity of ant communities depends on environmental heterogeneity at multiple scales (Spiesman and Cumming 2007), but due to the short duration of this study, I focus on the local scale. At the local scale, I wanted to test whether ant community composition was dependent upon its location (on a mound or in the matrix) and vegetation cover. Here are some questions I addressed and used to shape my predictions:

- How do termitaria affect the diversity, evenness, abundance and richness of ant communities in Chizarira?
- Do termitaria spatially divide a habitat to support more niches and therefore more ant species compared to the matrix?

- Will more specialist or generalist ant communities be found on termitaria?
- How will the canopy cover and ground cover impact the composition of the ant communities on and off mounds?
- How will the ant species composition differ between matrix and mounds?

My hypotheses are as follows: (1) the diversity, evenness, abundance, (i.e. number of individuals), and richness of ant species will be significantly different between the termitaria and matrix sites; (2) the diversity, abundance, and richness of ant communities will be greater on the termitaria than in the matrix (3) the evenness of the ant communities will be greater in the matrix (4) there will be a significant different between the composition of ant communities of the mounds and matrix sites and (5) vegetation cover will be a significant variable influencing the composition of ant communities.

Chapter 2: Study Area and Methods

2.1 Study Area

The field work for this study was carried out in Chizarira National Park, Zimbabwe (17° 42' S, 27° 55' E) over a two week period in September-October 2009. Located on the Zambezi Escarpment in North-western Zimbabwe, this park, part of which was gazetted in 1958 as a non-hunting reserve, became a Game Reserve in 1963, was extended in 1968 and became a National Park in 1975 (Zimbabwe Parks and Wildlife Authority 2009). It is 1,910km^2 and has an elevation of between 700 and 1400 m. Chizarira National Park is located within the miombo woodland biome, which is a woodland dominated by broad-leafed deciduous trees. This woodland covers an area of 2.8 million km^2 over southern and central Africa and consists predominantly of trees within the genus *Julbernardia* and *Brachystegia* (Guy 1981, Frost 1996, Cumming et al. 1997). The study was conducted near the Kaswisi Camp, which is located 6 km from the park headquarters at Manzituba (17°45′S 28°10′E). Upon arrival, I was informed by a ranger that a fire set by poachers had burned through my study site in August. The specific date is not known.

The mounds of Macrotermitinae, a common sight over most of eastern and central Africa, reach densities between 2 and 5 mounds per ha^{-1} in Chizarira. Chizarira's landscape is densely covered with large, conspicuous and densely vegetated mounds of the species *M. falciger* (Fleming and Loveridge 2003). The temperature range for the region varies from an average maximum temperature of 29. 5°C in November to an average minimum temperature of 16.9°C in July and an overall annual temperature of 23.2°C. Annual precipitation is approximately 700 mm and falls during a single rainy season extending from November through to April (Hutchinson et al. 1995).

2.2 Field Set-up and Sampling

The first step in the study was to pick the termite mounds that ant trapping would take place on. I was constrained in what locations to pick since I did not have a vehicle, so all the mounds had to be located within walking distance of the camp and each other. The initial process of selecting mounds for the paired mound-matrix sampling design required a vegetation survey of percentage cover of 20 mounds that were approximately the same size. Many invertebrates, including ants, are affected by the presence/absence of vegetation cover, including both the amount of vegetation covering the ground, but also the amount of tree canopy cover that creates shade. To take both factors into account I wanted to diversify the mounds I choose based on the amount of ground cover and canopy cover they had, to see how the variable of cover would impact the ant community composition of the area.

To assess cover for the mounds three parallel 15 m-long line transects were conducted on the ground, with one transect going directly over the center of the mound and the other two transects three meters on either side of the center transect on both sides of the mound. Ground cover and canopy cover along each transects were recorded, noting in centimeters where the ground cover and canopy cover intercepted directly with the transect line. After getting the two different measurements of cover data for the 20 mounds the centimeters of vegetation intersection points from each transect were added together and then divided by 15 to get an average percentage cover per m^2 for each transect. The three transects for each mound were then averaged together to provide an average percent canopy cover and ground cover for each mound.

Twelve mounds were then selected for the study based on three distinct cover categories that were extracted from the cover data. These included four mounds with low ground cover and low canopy cover (low coverage) and four mounds with low ground cover and high canopy cover (intermediate coverage) and four mounds with high ground cover and high canopy cover (high coverage). A fire had burned through the study site in August, influencing the coverage of some of the mounds and matrix sites. Three of the intermediate coverage mounds had been burned by a fire in August, which is most likely the reason for a high percentage of canopy cover but low percentage of ground cover. The three matrix plots for these mounds were burned also, as well as one of the low coverage mounds. Therefore a total of four mound and three matrix plots were burned by the fire.

The following criteria were used to separate mounds into different cover categories: Low ground cover < 20%, high ground cover > 30%, low canopy cover < 40% and high canopy cover >50%. Using the cover data from the twelve surveyed mounds I choose four mounds to fit into the three cover categories, low, intermediate and high cover, based on the above percentages (Cover data in Appendix 1). Besides the cover data, all of the chosen mounds had to be at least 20 m away from any other mound, whether it was one in the study or not.

Pitfall traps were used (100 mm in depth and 80 mm in diameter) to sample ground dwelling ant species. Figure 1 shows an example of a termite mound and pitfall trap. One trap was placed roughly in the center of each mound with four placed in a 2m x 2m square around the center one (Figure 2). The traps were filled with water with a trace amount of soap in it to break the surface tension.

Figure 1. The picture on the left is a typical termite mound in the study area. On the right is one of the 120 pitfall traps.

The pitfall traps in the matrix were set up in the same manner as on the mounds. The center trap was 20 m from the base of its corresponding mound with the 2m x 2m square around it. Matrix plots had to be not only 20 m away from its paired mound but 20 m from any other mound as well. A vegetation survey was conducted for the matrix plots, but unlike the mound cover data, the matrix cover data was not used to choose sites.

Two parallel 15 m transects, five meters on either side of the center pitfall trap, were used to asses canopy cover and ground cover. Cover data for the twelve paired sites in (Appendix 1). A survey of dominant plant species was also done for all mound/matrix sites (Appendix 2).

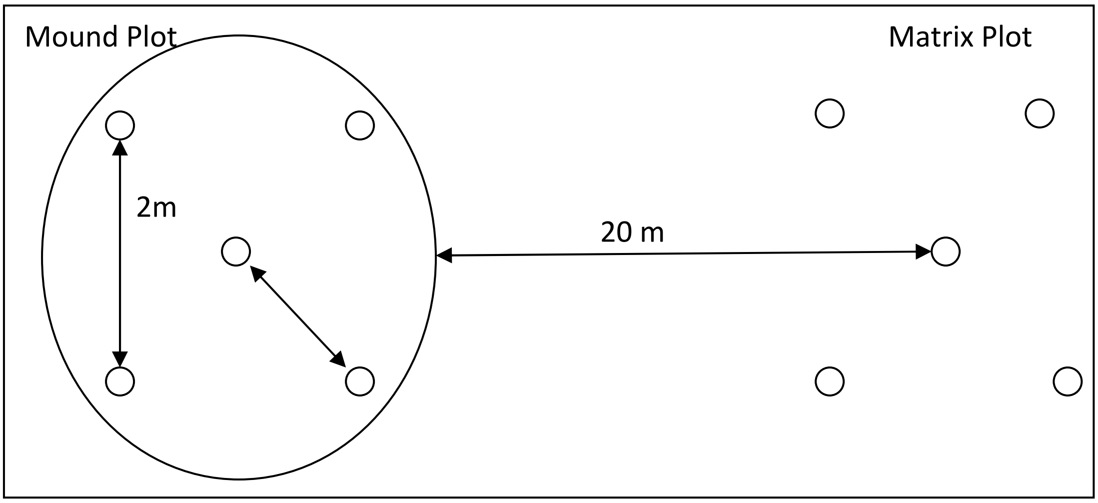

Figure 2. Schematic representation of one of twelve study plots. Center mound pitfall traps were placed as close to the center of the mound as possible. Center matrix pitfall trap was 20 m from the base of the corresponding mound. All outer pitfall traps were 2 m from each other. Both plots had to be at least 20 m from any other termite mound whether it was in the study or not.

2.3 Data Collection

A total of 120 pitfall traps was used in the experiment, ten for each of the twelve mound/matrix pairs. After they were dug, traps were left for 48 hours before they were filled with soapy water to reduce the affect of ground disturbance on ant behavior (Bestelmeyer et al. 2000). Based on other similar experiments pitfall traps should be left in the field 2-4 days to get a clear indication of all the ant species in the immediate area (Holldobler and Wilson 1990, Andersen 1991, Folgrait 1998).The 120 pitfall traps in this experiment were emptied and refilled every morning at dawn for a total of four days of collecting. Ants were preserved in a 90% ethanol solution and transferred back to the University of Cape Town, South Africa. They were sorted into morpho species at the university and later classified by name at the Iziko Museum of Cape Town with the help of Hamish Robertson.

2.4 Data Analysis

Data were analyzed using Statistica version 8, PRIMER version 5, PC-ORD and Microsoft Excel. The 12 mound/matrix pairs were compared in Statistica, first without using the ground and canopy cover variable. The 12 matrix sites were compared against the 12 mound sites using non-parametric tests, the Wilcoxon test for matched pairs, which compares the medians of two matched samples. Four of these tests were conducted in Statistica comparing species richness, abundance, evenness and Shannon-Wiener Diversity Index between the mound sites and matrix sites.

A general linear model (GLM) analysis was run to determine the influence of ground cover and canopy cover versus the site, mound or matrix, on ant species richness. This test was used to demonstrate what factor had the most influence on species composition. Microsoft Excel was used for regression analyses. These were conducted using canopy cover and ground cover percentages to determine the extent of the relationship between vegetation cover and ant abundance and diversity on termitaria and in the matrix sites.

The species composition of ant assemblages on mounds and in the matrix plots were compared in PRIMER (Clarke &Gorley 2001) by constructing a triangular similarity matrix, using a Bray-Curtis similarity measure on square-root transformed data. Data was square-root transformed to reduce the effect of very common and very rare species (Clarke and Green 1988). Analysis of similarity (ANOSIM) was used to produce a global R-statistic, which is an absolute measure of the distance between the species compositions of the two groups, mound and matrix plots (Parr et al. 2004). A cluster analysis, using the presence of species at each site and Bray-Curtis similarity measures, was used to assess which sites were most similar to each other based on the ant species composition. To reduce the weight of common species, the data was square-root transformed. In PRIMER, a BioEnv analysis

(Clarke & Ainsworth 1993) was performed to identify which environmental variables might be driving the observed similarities in ant assemblage species composition. BioEnv correlates environmental variables with assemblage similarity between sites, thus an environmental variable that correlates highly with similarities is considered one that may drive similarity in species composition.

Finally, PC-ORD (Kruskal 1964, Mather 1976) was used to develop a species accumulation curve to evaluate sample adequacy based on repeated sub-sampling of a fixed sample size, in this case ant communities. PC-ORD was also used to assess indicator species within the ant species that were sampled to determine relationships between specific species and environmental variables. Indicator values were calculated with the method of Dufrêne and Legendre, 1997. Lastly, PC-ORD was implemented to run a nonmetric multidimensional scaling (NMS) test. NMS is an ordination method used to assess community data that is on a discontinuous scale. I used a NMS analysis to produce a graphical view of the community relationships in order to see how assemblages of ants grouped together in relation to what type of environmental variable. I tested location i.e. mound/matrix, vegetation cover or whether or not the location had been burned to decipher what was influencing them most strongly.

Chapter 3: Results

3.1 *Overview of Ant Assemblages*

A total of 24, 168 ants were collected over the 4 day period, comprising 43 species (Appendix 3). Species accumulation curve shown below in Figure 3.

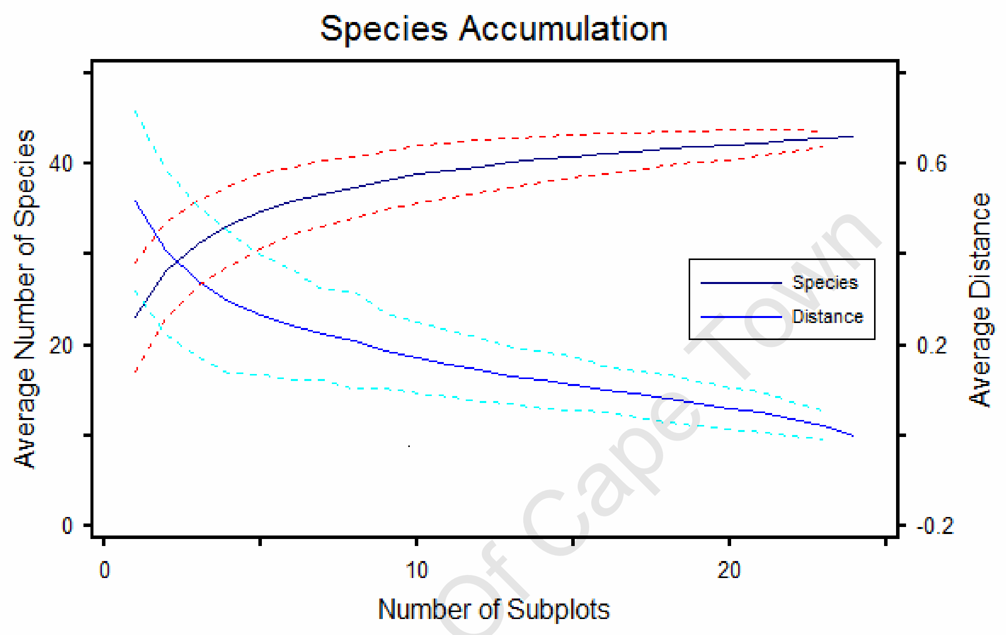

Figure 3. A species accumulation curve by site and number of species. Sampling effort was sufficient. Estimates of total number of species: 43.0 = Number of species observed, 47.8 = First-order jackknife estimate, 51.5 = Second-order jackknife estimate.

There was a substantial difference in abundance with 17,766 individuals caught on mound sites and 6,402 in matrix sites. 38 species were caught on mound sites and 39 were caught in matrix sites. Table 1 shows a breakdown of maximum species caught and accumulation per day and site (mound/matrix).

Table 1. Maximum number of species and individuals caught per day and per site. Note how almost half of the total number of individuals were caught on the first day.

	Day 1	Day 2	Day 3	Day 4
Species Caught on all Mound Plots	30	32	30	35
Species Caught in all Matrix Plots	32	29	32	30
Total # of New Species Caught	37	4	1	1
Total # of Individuals Caught on Mounds	8596	4660	1947	2563
Total # of Individuals Caught in Matrix	2419	1518	1278	1187
Total # of Individuals	11015	6178	3225	3750

Number of individuals trapped per site varied widely. The most were caught on mound #12, which had 4,197 individual ants over the four day period; the least were caught on mound # 2, with 231 individuals. The most species were caught on mounds # 9 and 10 with 29 species each, and the least in matrix #2, with 17 species. For the full count of the combined number of species and individuals caught at each site over the four days refer to Appendix 4. Figure 4 show a graphical representation of number of species and individuals caught per day.

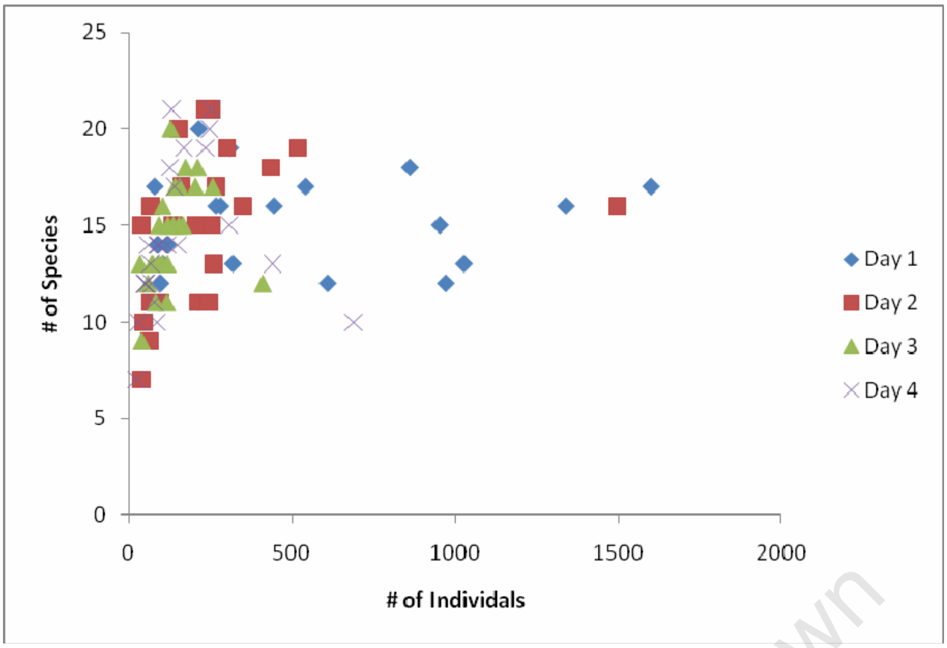

Figure 4. Number of species and individuals caught per day. Each point represents a site.

3.2 Species Specific Results

The most common species caught in the pitfall traps was *Monomorium* sp. 1, with 6,224 individuals. *Monomorium* ant species are very common and are warm climate specialists known to be active during the heat of the day. This is most likely the reason they were the most abundant species. When looking at the total number of ants for all mound and matrix sites together, four ant species were only represented by one individual; *Crematogaster* sp. 1, found on a mound and *Anochetus* sp. 1*, Polyrhachis* sp. 1 and *Cataulacus* sp. 1*,* all found in matrix sites. There were two individuals trapped of *Aenictus* sp. 1 and four of *Anochetus* sp. 2 in the matrix. *Crematogaster* sp.1, *Polyrhachis* sp. 1 and *Cataulacus* sp. 1 are all arboreal species; therefore they are not commonly caught in pitfall traps.

An indicator species analysis was run in PC-ORD to show the relationships of certain species to environmental variables within a larger community of species. These species have a certain value attached to them for indicating environmental conditions they are linked to. In this study, a species of ant that is a perfect species indicator (value of 100) will always be faithful to specific environmental attributes of a pre-assigned group (will always be always present in that group) and should also be exclusive to that group. Group values (i.e. environmental condition) were based on vegetation cover and site and were assigned as follows: group 1, matrix sites 1-4 (low coverage); group 2, mound sites 1-4 (low coverage); group 3, matrix sites 5-8 (high coverage); group 4, mound sites 5-8 (high coverage); group 5, matrix sites 9-12 (intermediate coverage); and group 6, mound sites 9-12 (intermediate coverage). Table 2 shows the indicator species for this study.

Table 2. Group value represents species that are indicators of a type of environmental condition (coverage and site). 12 matched pair sites by 43 species. Perfect indicator is equal to 100, but it is significant it greater than 50, with a p-value <.05. Species that do not have these values are not shown. For example Camponotus sp. 2 is an indicator for group 4, which means that they are expected to be found on mound sites with high coverage.

Species	Group Value	Observed Indicator Value (IV) out of 100	IV from randomized groups (Monte Carlo) mean	IV from randomized groups (Monte Carlo) S. Dev.	p-value
Camponotus sp. 2	4	57.8	43.3	9.29	0.05
Camponotus sp. 5	6	53.1	29.1	10.43	0.04
Monomorium sp. 5	4	50	26.6	8.15	0.01
Tetramorium weitzeckeri	1	77.5	42.2	16.96	0.047
Lepisiota sp. 2	4	65.3	32	9.08	0.003

3.3 Results without Cover Data Variable

Four Wilcoxon tests for matched pairs were conducted. These tests compared the medians of multiple variables of all the mound sites against the medians of all matrix sites. Species abundance, (i.e. number of individuals), and richness was greater on mound sites and species evenness and diversity was greater in matrix sites. The values represented in the following four graphs are the mean values for the four day period.

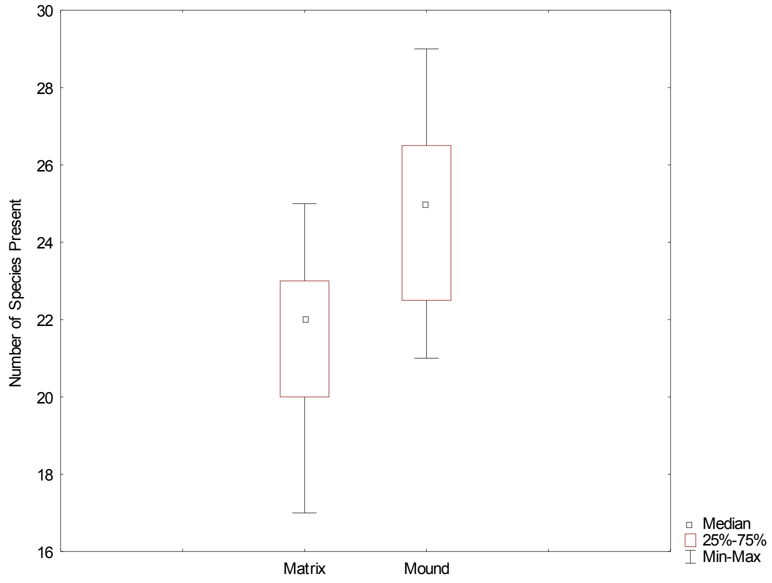

Figure 5. Box and Whisker graph showing results of species richness between all mound and matrix sites. Number of species present represents an average between 12 mound sites and 12 matrix sites. The difference between mound and matrix sites is significant (p-value .0159) with higher species richness on average per site on the mounds.

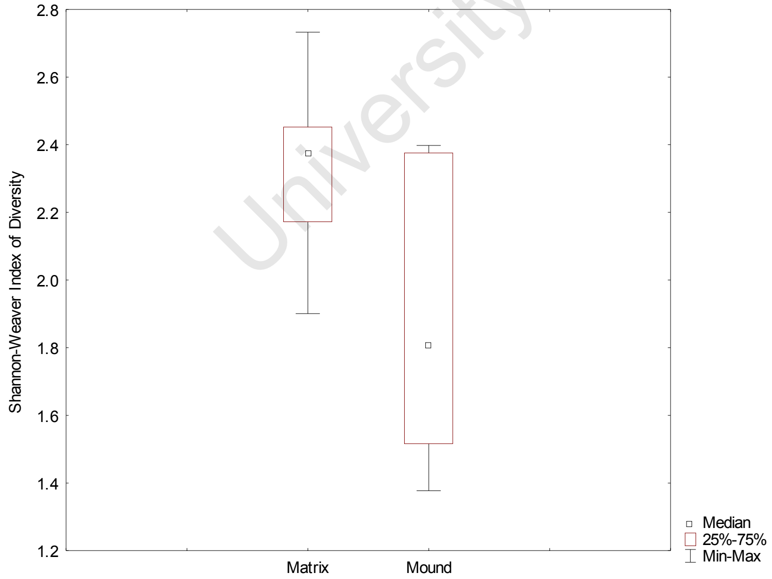

Figure 6. Box and Whisker graph showing results of species diversity between all mound and all matrix sites. Shannon-Wiener *Diversity used to indicate a significant difference between sites (p-value .0168) and shows how there was higher species diversity on average per site in the matrix.*

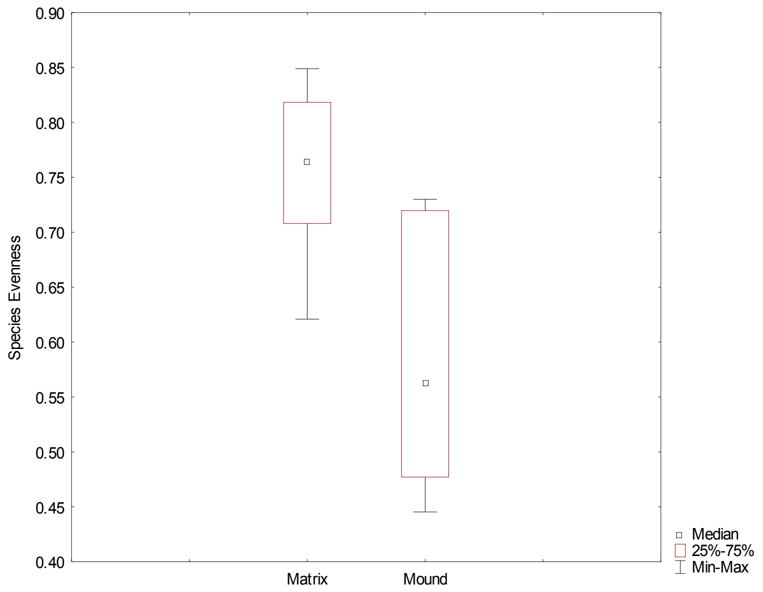

Figure 7. Box and Whisker graph showing results of species evenness between mound and matrix sites. The graph demonstrates how there was a significant difference (p-value .0027), with the species evenness higher on average per site in the matrix.

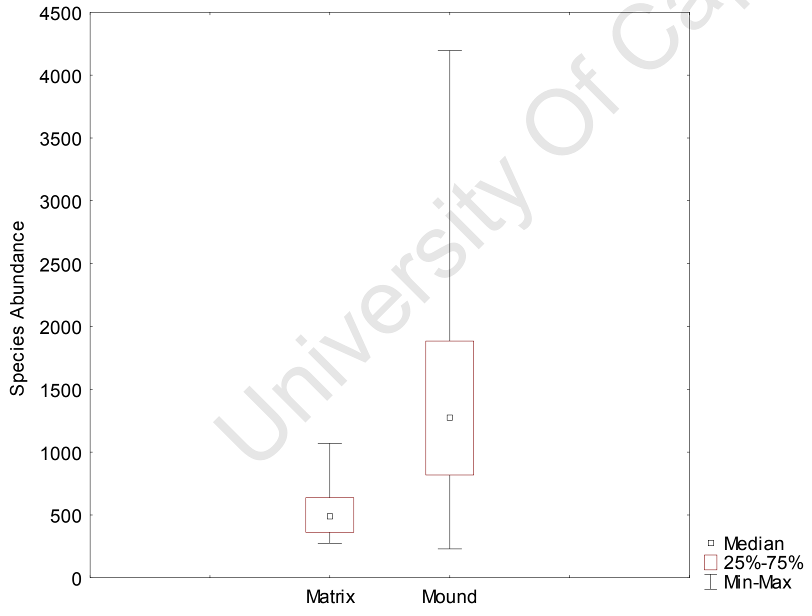

Figure 8. Box and Whisker graph showing results of species abundance within the mound and matrix sites. There is a significant difference between plots (p-value .0029), with ant abundance higher on average per site on the mounds.

The difference between the compositions of ant communities was significant (p-value .0021). In PRIMER, an ANOSIM analysis, measuring the similarity between the assemblages of ant communities on mound and matrix sites, produced a global R-statistic value of 0.553

and a highly significant p-value of 0.001, distinctly separating the ant communities plots on mounds and in the matrix. Also in PRIMER, a cluster analysis, performed by subjecting the similarity matrix to a group-average sorting method, grouped similar sites together based on the ant species caught at each site to determine whether ant assemblage structure varied between sites (Figure 9).

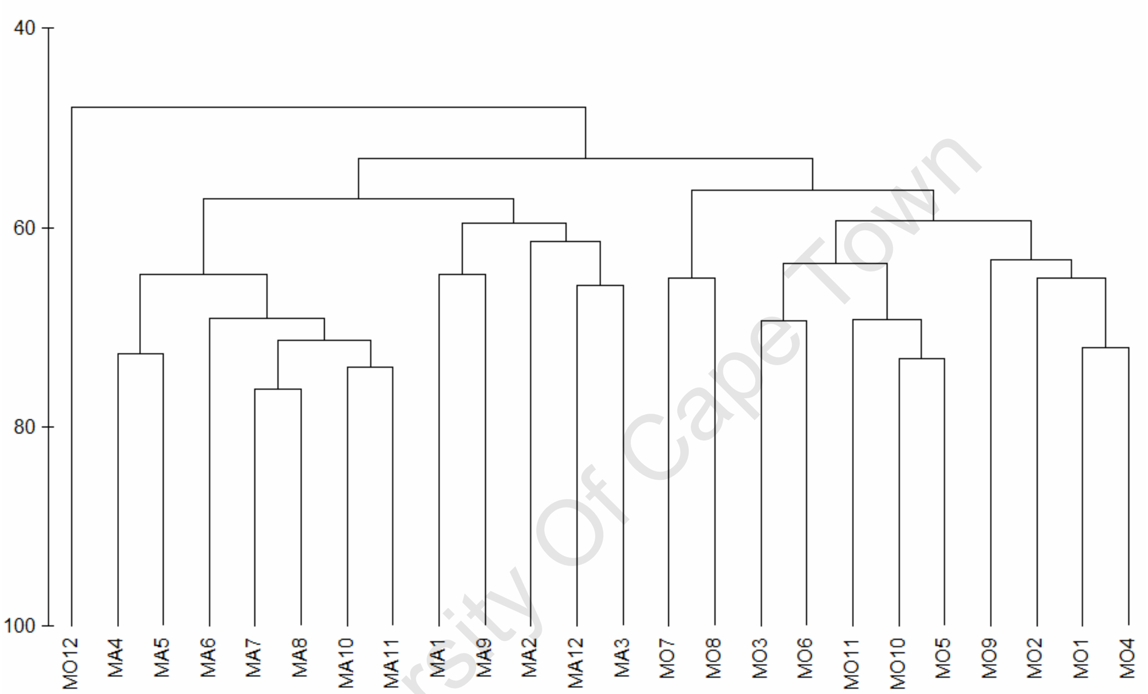

Figure 9. (MO=mound site, MA= Matrix site) Dendrogram created from a cluster analysis using Bray-Curtis similarity measures and square-root transformed data to reduce the weight of common species. Ant communities show a clear distinction between species composition on mounds versus matrix sites. The ant assemblages have formed two groups; mound and matrix sites have almost completely grouped separately from each other, with the exception of mound 12.

3.4 Results with Cover Data Variable

Table 3 shows a breakdown of maximum overall number of ants caught and number of species in terms of the three different vegetation covers.

Table 3. Sites 1-4 low coverage, sites 5-8 high coverage, sites 9-12 intermediate coverage. Note how the most species and individuals were caught on mounds with high canopy cover and low ground cover (intermediate coverage). Numbers shown represent the maximum number caught over the four day period.

	# of Ants	**# of Species**
Sites 1-4 (Low Canopy Cover and Low Ground Cover)		
Matrix	1651	30
Mounds	3034	29
Sites 5-8 (High Canopy Cover and High Ground Cover)		
Matrix	2690	34
Mounds	6799	33
Sites 9-12 (High Canopy Cover and Low Ground Cover)		
Matrix	2061	28
Mounds	7933	38

The PRIMER results of the BIOENV test indicated that of the possible cover types, the variable most influencing the patterns of ant species composition in all sites was canopy cover with a correlation of 20.4%.

The general linear model (GLM) run in Statistica compared ground cover and canopy cover using the site, mound or matrix, as a random term to see if site or cover was a more important factor for ant species richness. Out of the possible vegetation covers and sites the results indicate canopy cover to be the attribute most influencing ant species richness (p-value=0.0197). P-values for ground cover and site were not significant with values of 0.5404 and 0.7585 respectively.

Species diversity showed the strongest correlation with canopy cover, but only on the mounds, with an R^2 value of 0.4167 (Figure 10a). Species abundance showed the strongest correlation with canopy cover, but only in the matrix, with an R^2 value of .3924 (Figure 10b). All other correlations are not shown and were below R^2 values of .12.

Figure 10

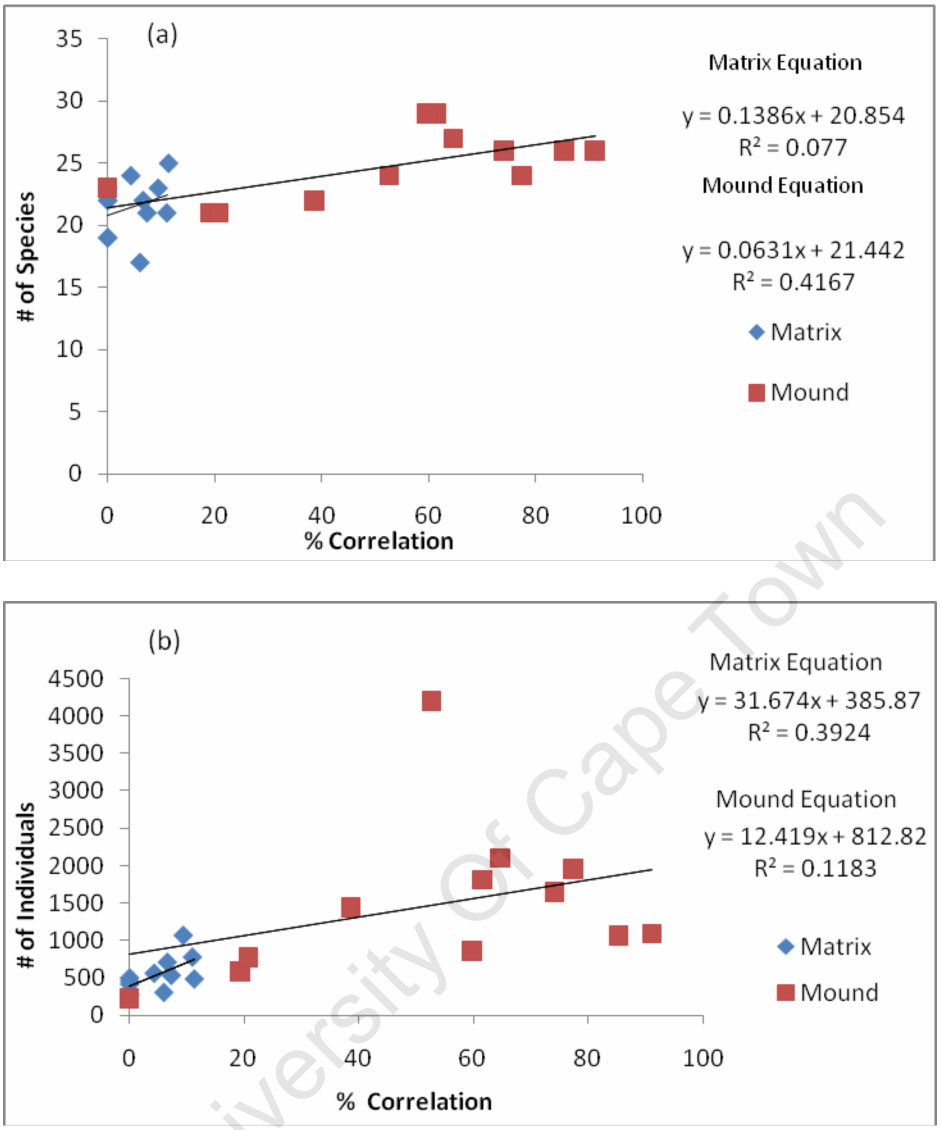

Figure 10 (a) Regression line showing correlation between canopy cover species diversity on mound and matrix plots (b) Regression line showing correlation between canopy cover and species abundance on mound and matrix plots.

Finally, multiple nonmetric multidimensional scaling test (NMS) produced in PC-ORD were used to determine the relationships of the ant communities and the influence of vegetation cover and the fire on the composition. The first NMS showed a strong correlation between the ant communities on termitaria and canopy cover (Figure 11). Because the amount of rare species caught in the traps was quite high (when looking at the sites separately the mounds have 10 species of ant represented with five or fewer individuals and the matrix has 12 species represented with five or less individuals), in order to account for the bias that rare species can present in analyses, I decided to not included these species for the first test run in PC-ORD. The ordination in Figure 11 is based on the 31 species that represented more that one percent of the total population and 12 sites. Site numbers were assigned as follows: group 1, matrix sites 1-4 (low coverage); group 2, mound sites 1-4 (low coverage); group 3, matrix sites 5-8 (high coverage); group 4, mound sites 5-8 (high coverage); group 5, matrix sites 9-12 (intermediate coverage); and group 6, mound sites 9-12 (intermediate coverage). Canopy cover is shown to be the most significant driver of ant community composition on the mounds (p-value = 0.012), indicating that ant abundance increases with increasing canopy cover. With the exception of mound #2, mound and matrix communities have separated completely from each other, forming two distinct species assemblages.

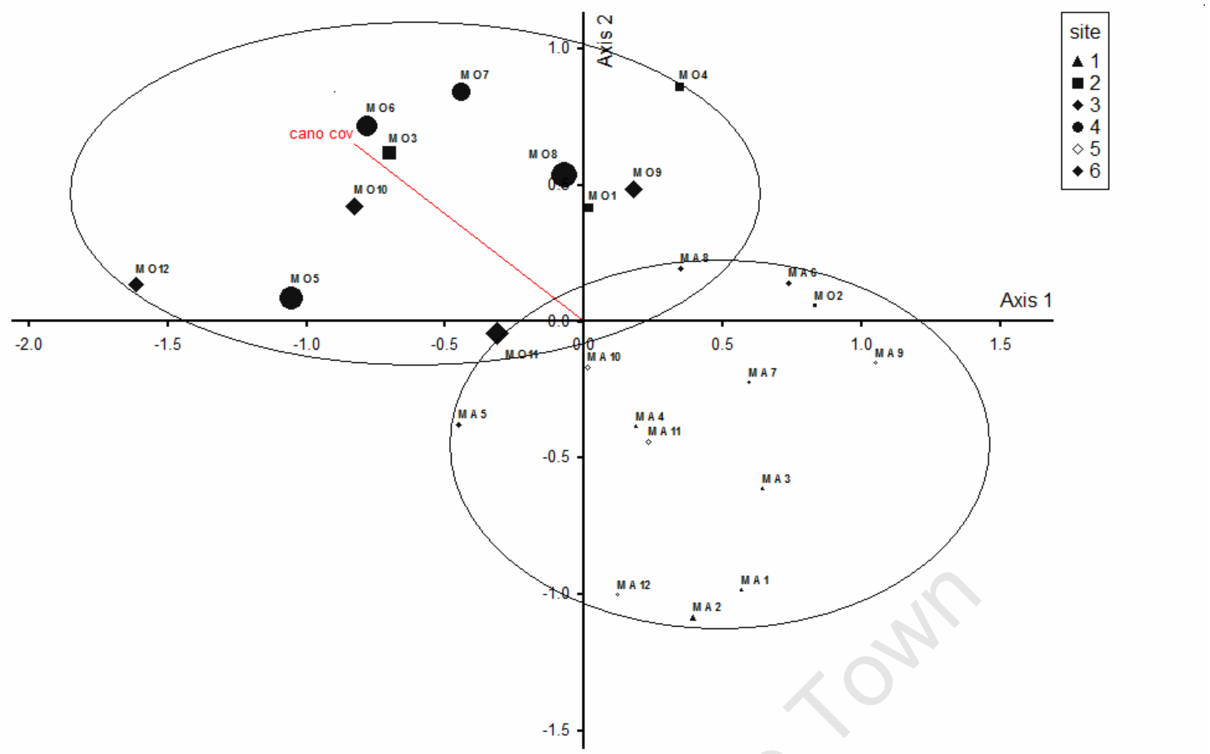

Figure 11. Canopy cover shown to be the most significant driver of ant community composition on the mounds (p-value = 0.012).Ellipses drawn around similar communities. The following options were selected for this analysis: S ørensen Distance Measure, random starting coordinates, 250 runs with real data, 3-dimenstionality of data, 500 iterations in final solution. The stress in real data of the final solution (250 runs) was 47.54. The stress in randomized data Monte Carlo test (250 runs) was 45.26.

To determine if rare species were in fact biasing the results of this test, another NMS test was run with all 43 species included. This test also included the fire variable to see if ant communities separated into distinct species assemblages based on whether or not a site had been burned (Figure 12). Mounds #3, 9, 10 and 11 had been burned in the fire as well as matrix sites # 9, 10 and 11. With the exception of mound #8 (as opposed to mound # 2 in Figure 11), mound and matrix sites are again separating distinctly from each other when all 43 species are included. Canopy cover (significance shown by size of marker on graph) is shown again to be the biggest factor in abundance of ants on mounds, the p-value didn't change from the previous test (p=0.012). Whether or not the site was burned, however, does not appear to be a driving factor of species composition. Burned sites (the triangles) are not clumping

together.

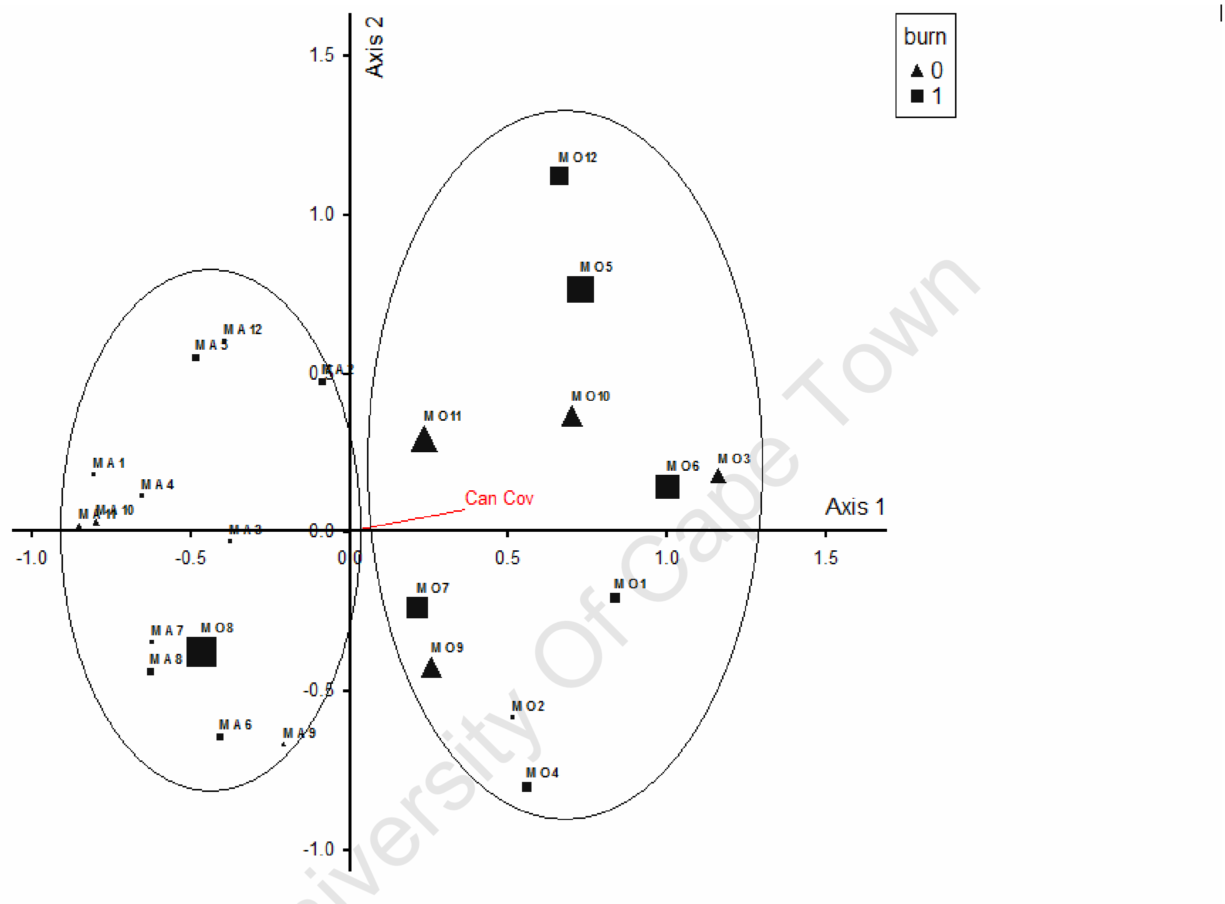

Figure 12. Canopy cover shown to be the most significant driver of ant community composition on the mounds (p-value = 0.012).Ellipses drawn around similar communities. The following options were selected for this analysis: S ørensen Distance Measure, random starting coordinates, 250 runs with real data, 3-dimenstionality of data, 500 iterations in final solution. The stress in real data of the final solution (250 runs) was 47.366. The stress in randomized data Monte Carlo test (250 runs) was 45.997.

Chapter 4: Discussion

The box and whisker graphs indicate that when the numbers of ants are averaged together over the four day period ant species richness and abundance were both significantly higher on the mounds than in the matrix, an expected outcome. Also expected, and shown to be accurate in the analysis was that species evenness was significantly higher in the matrix. This was a predicted outcome for one simple reason. In one study looking at the subterranean termites *Odontotermes*, the density of ant nests has been shown to increase with increasing proximity to the mounds (Palmer 2003). In Chizarira the mounds are above-ground and vegetated but the foraging behavior of all termites concentrate nutrients within their mounds (Collins et al. 1984). Therefore, one would expect the abundance of individual ants on the mounds to be greater because of the higher nutrient availability, which the ants utilize indirectly. As already discussed in the introduction, high clay content in the soil, facilitated by termites, has been shown to be the most important habitat predictor for ant species coexistence (Debuse et al 2007), nest construction (Davis-Carter and Sheppard 1993), resource productivity and water retention (Parr et al 2004, Debuse et al. 2007), which has been demonstrated to increase average growth rate and size of many ant species colonies (Palmer 2003). Because of the expected higher density of nests, there was a greater chance that traps on the mounds were more likely to be placed in very close proximity to one particular species' nest than in the matrix. If this happened, a large amount of this one species would fall in the trap, thus biasing the results by decreasing the species evenness, since one species becomes over-represented on a particular mound. Although not confirmed, there is evidence of this occurring in the study. For example, on mound 12, 550 individuals of *Pheidole* sp. 2 were caught on day one and 1093 of *Pheidole* sp. 2 on day two, which clearly indicates that a nest of *Pheidole* sp. 2 had to be on or very near mound 12. Such high numbers of ants were never caught in one site on any of the days in the matrix. In the matrix it is a lot less likely that one of my pitfall traps was placed by a particular species nest, therefore numbers of ant species caught were generally more equally represented, which is why the species evenness is significantly higher for those sites.

4.1 Sampling Effort

Almost half of the total number of individuals, 11,015 out of 24, 168, were trapped on the first day of sampling. None of the sampling days varied from each other in terms of temperature nor was there rain any of those days. The reason for these sampling results could be that many pitfall traps were located quite close to ant nests, leading to the majority of individuals trapped falling in on the first day. My sampling effort was sufficient for the area; I caught 37 species the first day, followed by four new the second, one new the third and one new the last day. Although Figure 3 and 4 demonstrate that I sampled enough, Andersen and Yen (1985) did a study showing how there can be a sampling bias when using pitfall traps after a fire. York (2000) showed that 22% of the ant species he caught were collected by litter sampling and not pitfall trapping. However, a longer study period would be necessary to incorporate different techniques of sampling if there was a bias as a consequence of the fire.

4.2 Ant Community Composition of the Mounds and Matrix

The results indicate that different assemblages of species occur on mound and matrix sites. The cluster analysis strongly supports the hypothesis that ant species community composition on the mound sites and in the matrix sites are distinctly different from each other. PC-ORD tests reveal very different assemblages between the two types of sites as well. This is not surprising considering how the different habitats have specific characteristics that favor some ant species over others, a fact that is in fact even more pronounced in extreme climates like the miombo. The ANOSIM results indicate a similar trend. The ant species composition on all mound sites are more similar to each other than any of the matrix sites and the ant species composition on all the matrix sites are more similar to each other than to any of the mound sites. These primary groupings were statistically significant, with a global R statistic of 0.553 and a p-value of 0.001. This indicates that the mound and matrix environments are supporting very different ant communities is one of the most interesting results of this study.

4.3 Influence of Fire

A moderate fire had burned through the study site in August. Most of the brush, small plants and grasses were cleared away on three of the matrix patches and four of the mounds, but if there were large trees on the mounds they were unaffected. Fires generally simplify natural habitats by transforming woodlands to grasslands (Mapaure 2001). Fires are capable of maintaining grassland environments by preventing the recruitment of trees and other woody species by burning samplings and seeds (Trollope 1982, 1984). Simplification of the environment creates a more homogeneous landscape where one would expect species diversity to decline. However, the effect of a disturbance, such as fire, is highly dependent on habitat characteristics such as structural complexity and vegetation morphology and some studies have found that fire actually increases species richness (Folgarait 1998, York 2000, Hoffman 2003, Debuse et al. 2007, Santos et al. 2008), while others have found it decreases species richness (Andersen and Yen 1985). Other studies have found that soil type had a much greater influence on ant communities than fire did (Hoffman et al. 2000, Bestelmeyer and Wiens 2001, Woinarski et al. 2002, Hoffman 2003), due to the fact that soil type dictates vegetation structure and therefore fire causes differential impacts on habitat suitability for ants (Pickett and White 1985, Pimm 1991).

The effect of fire on ants operate through a variety of complex, but usually indirect mechanisms, which include changing the composition of the vegetation on the ground, foraging for food supplies and interspecific competition (Levieux 1983, Andersen and Yen 1985, Andersen 1988). A lack of definitive evidence suggesting that the fire in this study had an impact on ant communities could be due to the short time lapse since the fire. There is a lot of literature on the impact of disturbance on ant assemblages. While the direct impact of fire on ants is generally not severe, because many of their nests are subterranean, as mentioned above, many of the effects are indirect and take time to manifest (Anderson 1991, Hoffman 2003). For example, many subordinate and opportunistic species have broader levels of physiological tolerances than dominant or specialist species, which gives them the competitive advantage in situations of disturbance (Fellers 1987, Anderson 1992, Cerda et al. 1997, Bestelmeyer 2000, Farji-Brener 2002). Ant colonies have an uncanny ability to persist; once established, instead of going locally extinct when they are dominated by other species, they can persist in very low numbers for long periods of time (Andersen 2008). Due to a disturbance, fire in this case, these subordinate species surviving in low numbers are now given the opportunity to utilize their competitive advantage when the habitat becomes too extreme for other ants to exploit anymore (Farji-Brener 2002).

Not only is fire a disturbance in itself, it has long term impacts on the vegetation structure as well. Many studies have found a decline in the activity of dominant species after a fire due to simplifications in vegetation structure and complexity (Andersen and Yen 1985, Andersen 1991, Farji-Brener 2002). When vegetation has been cleared, the natural soil temperature buffer and protection from direct sunlight is gone, allowing subordinate ants that are thermophilic and operate under extreme heat to take advantage of being able to exploit resources for longer periods during the day. This has been shown to be especially true in arid environments, due to their intense climate, where dominant species that are intolerant of habitat alteration reduce in both relative abundance and number of species accompanied by an increase in diversity of subordinate species (Farji-Brener 2002). This process as a form of competitive release has been demonstrated in a few different studies; after the fire the subordinate species with broader physiological tolerances can expand their ranges and have the opportunity to increase in relative abundance (Flogarait 1998, Farji-Brener 2002, Andersen 2008). Although there has been many studies done on the impacts of fire on ant communities (Andersen and Yen 1985, Andersen 1991, Farji-Brener 2002), a specific study in this area would need to be conducted on differential fire regimes to validate this hypothesis since the effects of fire are indirect and take many months or years to develop, also pre-fire vegetation structure is an important determinant of the outcome of a fire (Andersen 1991, Farji-Brener 2002, Parr et al. 2004 Santos et al. 2008).

While no tests were run on species diversity in this study of burned versus unburned sites, the test run in PC-ORD showed that ant species are not grouping together in any coherent pattern based on whether or not a site was burned (Figure 12). It would be very interesting to see if a pattern would emerge in a longer study when more replicates of burned and unburned sites could be tested. Based on other studies of burned and fire-exclusion plots, two distinct communities of species form based on the different species' responses to separate treatments (Andersen 1991, Hoffman 2003). While this was not shown in this study, a larger sample size and more of a time lapse since burn might produce a discernable pattern. Information on environmental conditions (i.e. rainfall, soil moisture content), would be important as well since the strength of response by an ecological community, the ants, to disturbance, the fire in this case, will vary relative to detected conditions (Ash et al. 1996, Dyer et al. 1997)

4.4 Influence of Vegetation

It could appear that vegetation cover is having an impact on the composition of ant communities. All the analyses show that high canopy cover, not ground cover or site (mound/matrix), was the most influential factor driving the recorded species composition, especially on mounds. Table 3 shows how the mounds with high canopy cover and low ground cover had the most ant species and the highest overall abundance of individual ants. Both PC-ORD ordination analyses produced a highly significant p-value of 0.012 which indicates a strong influence of canopy cover on ant species composition on the mounds. The BIOENV showed the highest correlation with canopy cover, at 20.4%. The regression analysis produced the strongest correlation with species diversity and canopy cover on mounds, with an R^2 value of 0.4167, which is significant, and species abundance with canopy cover in the matrix, with an R^2 value of 0.3924. The general linear model confirmed canopy cover as having the strongest explanatory value on community composition when considering both site (mound/matrix) and type of vegetation cover, with a p-value of 0.019686. These various tests all show the same pattern, that canopy cover is an important correlate driver, specifically on mounds, of species assemblages in Chizarira.

I believe many of the variables influencing ant communities are inter-correlated. As mentioned in the introduction, some studies have found clay content of the soil to be the most important habitat predictor for coexistence and variance in ant communities (Debuse et al. 2007). More clay positively correlates with higher moisture retention and therefore more vegetation (Boyer 1982, Lavelle et al. 1993, Konate et al. 1998). Consequently, vegetation cover should be positively correlated with clay content of the soil, making it difficult to separate one variable from the other as a more important factor for ant community composition. Productivity of resources has been demonstrated to be a major structuring force in ant communities (Kaspari et al. 2000) and while some ants are tied to specific species of plants (Palmer 2003), it would appear that the vast majority of species depend more on mere presence of vegetation, which is a product of higher nutrient concentrations, clay content and water retention (i.e. because of the termitaria).

However, in this study vegetation categorization is falsely represented based on post-fire coverage, and there is no way to decipher what the basal coverage was before the fire in August. Many studies looking at the responses of ants to fires have stressed the importance of the vegetation cover in its pre-fire state (Parr et al. 2004, Santos et al. 2008). Differences in the vegetation structure and coverage before the fire influence the extent to which the fire affects ant assemblages. For instance if biomass loads were small before the fire, the changes induced by the burn on basal cover is reduced therefore the degree of impact of ant assemblages is smaller (Fraji-Brener et al. 2002, Parr et al. 2002, Hoffman 2003). If biomass loads were large, however, degree of impact on vegetation can become much more acute and impact on ants greater. Thus, it is impossible to interpret the extent of the importance of vegetation cover, ground or canopy, on ant assemblages since the cover data reflects the habitat in a post-burn state, where the influence of vegetation characteristics, i.e. ground cover, have potentially been over-looked on burned sites.

4.5 The Synergy between Fire and Herbivory

The miombo woodlands are accustomed to wildfires and a few studies have confirmed the rapid recovery rate of many invertebrate populations, including ants, in arid environments (Friend and Williams 1996, Gunawardene and Majer 2005). Nevertheless, it has also been shown that in elephant-degraded woodlands, such as the miombo, the influence of fire is much more acute (Mapaure 2001). The increase in small brush and grass biomass, due to the decrease in canopy cover because of the heightened herbivory, increases the fuel load and results in hotter, more intense fires. Woodland change due to the promotion of grassland and ticket formation because of the interactive feedback effects between fires and herbivory has been documented in numerous studies (Dublin et al. 1990, Norton-Griffiths 1979; West 1972). The synergy between elephant herbivory and fire has the potential to be changing the species composition of the miombo and which can lead to multi-scale impact on many taxa, including ant communities. However, long-term studies and burn records in this area would be required to come to a definitive conclusion.

Conclusion

In the miombo woodlands of Chizarira National Park termite-induced habitat heterogeneity contributes to the coexistence of ant communities. What is evident from this study is that very different processes are operating on the termite mounds and in matrix sites. Even though the difference between number of species on and off mounds isn’t very substantial, the species composition of the communities between sites indicates two very distinct assemblages. While there had been a recent fire on some of the sites, not enough time had elapsed to influence species assemblages since most of the impacts of fire are indirect and take time to manifest (Anderson 1991, Hoffman 2003). The fire did however, have an impact on basal coverage, making it impossible to provide a link between ant communities and vegetation cover.

One strong correlation appears to be that mounds, due to termite activity, have the higher nutrient concentrations needed to create more resources and therefore support a greater abundance and richness of ants. Termitaria appear to be promoting higher species richness on the mounds, but are not promoting higher species diversity on the mounds, which was one of my hypotheses. In fact, I believe that termitaria are maintaining higher species diversity within the entire habitat in general, by means of facilitating interspecific trade-offs among ants by creating resource rich-versus resource-poor patches. While ant species are not confined to forage entirely where their nests are, (many species can actually forage great distances), these patches, which are varying substantially in levels of resource productivity (Lobry de Bryn and Conacher 1990, Folgarait 1998, Jouquet et al. 2006), are supporting entirely different species assemblages. This supports previous studies indicating how different taxa with similar requirements, ants and other species, are naturally better adapted to exploit different aspects of a habitat to limit competitive exclusion (Kotler and Brown 1988, Hanski 1989, Palmer 2003). Within an elephant transformed environment termitaria are essential for providing a refuge for diverse ant communities because such different species are found on and off mounds. It appears that the termitaria are helping drive the dynamics of competitive ant communities by spatially sub-dividing the habitat and facilitating the coexistence of species between sites through providing landscape heterogeneity in the form of resource-rich patches.

Maintaining a diverse assemblage of ant communities is essential to a healthy environment (Levieux 1983, Andersen 1991, Folgarait 1998). Ants have also been classified as ecosystem engineers; they have been shown to be just as essential as termites in nutrient cycling (Jones et al. 1994, Flogarait 1998, Jouquet 2005), are key players in the decomposition of organic matter and bioturbation (Folgarait 1998) and have been demonstrated to be useful bioindicators in various studies (Majer 1983, 1996, Majer et al. 1984, Andersen 1997, Andersen et al. 2002). Bioindicators have generally been used to assess ecosystem responses to environmental disturbance (Noss 1990, Spellerburg 1993, McKenzie et al. 1995, Andersen 1997). Ant functional groups respond quite differently to environmental perturbations, both natural and human-induced, and can therefore give us a predictive understanding of how various species may react to a disturbance (Andersen 1997, Andersen et al. 2002). In a few case studies ant functional groups have also demonstrated clear successional patterns in relation to time since a disturbance (Andersen 1993, Andersen et al. 2002). In Australia, they have been used to monitor mine restoration efforts (Andersen 1993). More studies are needed, but as our knowledge base expands, ant assemblages should be able to give an indication as to the state of an ecosystem after many different types of disturbances, be it due to deforestation for subsistence agriculture or high elephant herbivory.

Ants are also starting to be used as biodiversity surrogates (Andersen 1997). As surrogate taxa, ants can give scientists an indication as to the total species diversity in an area (Andersen 1995, Abensperg-Traun et al. 1996, Oliver and Beattie 1996, Andersen 1997). For conservation biology and the allocation of land for reserves, this information is not only vital for the biology field itself, but could potentially offer a way to cut down on cost and time in the reserve establishment phase.

The miombo woodland is playing host to some very interesting biological interactions. The patchiness of the landscape, created by the termitaria, offers a fascinating look at the processes involved in creating and preserving the composition of many species. By facilitating the establishment of specialist species to providing niches for subordinate species thus relaxing competitive exclusion, these termitaria are essential for the continuation of vital ecological processes. However, as subsistence agriculture increases, as it is rapidly in Zimbabwe, (Nyamapfene 1986, Kamusoko et al. 2009) dependence on the land and its resources will only continue to grow. This will no doubt exacerbate the problem of high elephant densities and the damage they cause to the landscape and ecosystem in Chizarira National Park and others like it. The tribulations of other disturbances are also likely to grow more acute as the land becomes more crowded. The importance of not only proper elephant management, but interactive regional park management, thus becomes imperative for maintaining the health and stability of the miombo ecosystem.

This paper is one of only a few to come out of this region of Zimbabwe. In order to have a better understanding, and then be able to act on the complex processes and patterns involved in how termitaria shape local to landscape level habitats, much more research needs to be carried out in this region. Due to time constraints in this study, ant assemblages were only looked at on a local level, but termitaria are structuring the environment on a landscape level as well, so research looking at ant assemblages on that level would be fascinating and important to undertake. Also incorporating data from the wet season to see what differences there are is necessary. A longer study would help alleviate some of these biases that were in this study.

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Appendices

Appendix 1. Cover data for 12 mound and matrix sites. Sites 1-4= low coverage, sites 5-8= high coverage, sites 9-12= intermediate coverage. Three 15 m transects were done on each mound and two in the matrix. Measurements were averaged together to get a single percentage cover per mound and matrix site.

Mound # 1-4 Low Ground Cover and Low Canopy Cover				Height (m)	Length/Width (m)
		Ground Cover %	Canopy Cover %		
MO #1	unburned	7.02	19.27	1.8	11 x 11.8
MA #1	unburned	46.56	0		
MO #2	unburned	19.85	0	2.3	12.1 x 12.3
MA #2	unburned	9.6	6		
MO #3	burned	12.67	38.63	1.6	12.85 x 13
MA #3	unburned	24.5	0		
MO #4	unburned	6.19	20.81	1.85	12.3 x 11.9
MA #4	unburned	10.16	4.3		
Mounds # 5-8 High Ground Cover and High Canopy Cover					
		Ground Cover %	Canopy Cover %		
MO #5	unburned	34.82	77.4	2.2	11.6 x 14.3
MA #5	unburned	36.54	9.4		
MO #6	unburned	40.15	74.12	2.1	13.05 x 14.3
MA #6	unburned	20.5	11.33		
MO #7	unburned	54.88	64.6	1.65	12.5 x 11.8
MA #7	unburned	34.5	0		
MO #8	unburned	38.57	91.1	2.8	14.46 x 16.1
MA #8	unburned	45.1	6.6		
Mounds # 9-12 Low Ground Cover and High Canopy Cover					
		Ground Cover %	Canopy Cover %		
MO #9	burned	19.72	59.73	2.6	13.45 x 14.7
MA #9	burned	16.83	0		
MO #10	burned	8.95	61.51	3	16.62 x 16.12
MA #10	burned	64.3	11		
MO #11	burned	11.7	85.31	1.2	12.78 x 12.72
MA #11	burned	12.26	7.3		
MO #12	unburned	19.1	52.66	2.4	12.4 x 12.54
MA #12	unburned	100	0		

Appendix 2. Vegetation species found on all mound and matrix sites. P=present.

Mound Species	MO1	MO2	MO3	MO4	MO5	MO6	MO7	MO8	MO9	MO10	MO11	MO12
Acacia nilotica					p		p	p				p
Adropogon gayanus				p								
Allophylus africanus				p				p		p		
Aristida bicolor												
Aristida leucophaea												
Berchemia discolor			p					p		p	p	p
Boscia angustifolia												p
Boscia salicifolia												p
Brachystegia boehmii		p	p									
Brachystegia spiciformis												
Bridelia cathatica												
Bridelia micrantha												
Burkea africana												
Capparis tomentosa		p	p	p	p	p	p	p	p	p	p	p
Cassia abbreviata			p			p	p	p		p	p	
Catuneragum spinosa												
Cissus cornifolia			p									
Colophospermum mopane												
Combretum												
Combretum apiculatum			p							p		
Combretum collinum	p	p		p	p		p		p	p	p	p
Combretum hereroense			p		p	p		p			p	p
Combretum molle			p	p	p	p		p		p		p
Combretum mossambicense	p	p		p			p	p	p	p	p	
Combretum xeyheri		p							p			
Comiphora mollis				p								
Commiphora mossambicensis	p			p								
Crossopteryx febrifuga												
Dalbergia melanoxylon		p										
Dichrostachys cinerea											p	
Diospyros kirkii			p						p			
Diospyros quiloensis		p	p			p	p		p			
Diospyros senensis							p					p
Diplorynchus condylocarpon												
Erythroxylum zambesiacum								p				p
Euclea divinorum	p	p	p			p	p	p	p	p		p
Feretia aeruginenscens										p		
Flacourtia indica												
Flueggea virosa	p	p		p					p	p	p	p

Friesoldielsia obovatum			p	p		p		p	p		p	p
Grwria monticola				p					p	p		
Hyparrhenia filipendula												
Jubinardia globiflora												
Lannea edulis												
Lannea discolor												
Lannea schweinfurthii												p
Lannea stuhlmannii	p	p	p	p		p		p	p		p	
lonchocarpus capassa									p			
Loudetia flavida												
Maerua prittwitzii	p	p	p	p			p	p	p	p	p	p
Manilkara mochisia			p	p		p	p					p
Markhamia zanzibarica											p	
Ozoroa insignis												
Pavetta schumanniana												
progonathria squarrosa												
Pseudolachnostylis maprouneifolia												
Pterocarpus rotundifolius			p			p						
Sclerocarya birrea												
Strychnos potatorum												p
Terminalia brachystemma												
Terminalia sericea												
Terminalia sternostachya												
Turrea nilotica												
Xeroderris stuhlmannii						p	p		p			
Ximenia americana					p			p				p
Ximenia caffra											p	
Ziziphus abyssinica												
Ziziphus mucronatum										p		

Matrix Species	MA1	MA2	MA3	MA4	MA5	MA6	MA7	MA8	MA9	MA10	MA11	MA12
Acacia nilotica	p											
Adropogon gayanus		p										
Allophylus africanus												
Aristida bicolor	p	p										
Aristida leucophaea										p	p	
Berchemia discolor												
Boscia angustifolia												
Boscia salicifolia												
Brachystegia boehmii	p	p	p	p		p	p	p	p	p	p	p
Brachystegia spiciformis		p									p	
Bridelia cathatica							p					p
Bridelia micrantha												
Burkea africana		p										
Capparis tomentosa												

Cassia abbreviata												
Catuneragum spinosa		p	p	p		p	p				p	p
Cissus cornifolia												
Colophospermum mopane												
Combretum												
Combretum apiculatum	p	p		p	p		p	p				p
Combretum collinum		p				p						
Combretum hereroense												p
Combretum molle							p	p	p	p	p	p
Combretum mossambicense												
Combretum xeyheri	p										p	
Comiphora mollis												
Commiphora mossambicensis												
Crossopteryx febrifuga		p						p			p	p
Dalbergia melanoxylon												
Dichrostachys cinerea		p					p					
Diospyros kirkii	p		p			p	p	p		p	p	p
Diospyros quiloensis												
Diospyros senensis												
Diplorynchus condylocarpon		p	p	p		p		p	p			p
Erythroxylum zambesiacum												
Euclea divinorum												
Feretia aeruginenscens												
Flacourtia indica		p						p				
Flueggea virosa												
Friesoldielsia obovatum												
Grwria monticola												
Hyparrhenia filipendula	p	p	p	p		p		p	p	p	p	p
Jubinardia globiflora		p				p			p	p		
Lannea edulis									p			
Lannea discolor	p	p		p						p		
Lannea schweinfurthii												
Lannea stuhlmannii												
lonchocarpus capassa										p		
Loudetia flavida												p
Maerua prittwitzii												
Manilkara mochisia												
Markhamia zanzibarica												
Ozoroa insignis	p			p	p	p	p	p	p	p		
Pavetta schumanniana				p								
progonathria squarrosa	p			p						p	p	
Pseudolachnostylis maprouneifolia	p		p	p	p	p	p	p	p	p	p	
Pterocarpus rotundifolius												
Sclerocarya birrea									p			
Strychnos potatorum												
Terminalia brachystemma						p		p			p	

Terminalia sericea												p
Terminalia sternostachya	p	p	p	p			p		p		p	
Turrea nilotica			p									
Xeroderris stuhlmannii		p							p	p		
Ximenia americana												
Ximenia caffra												
Ziziphus abyssinica												p
Ziziphus mucronatum												

Appendix 3. Total number of each species found on each mound and matrix site in alphabetical order. Note that the four days of sampling are grouped together.

Mounds	MO1	MO2	MO3	MO4	MO5	MO6	MO7	MO8	MO9	MO 10	MO 11	MO 12
Aenictus sp. 1	0	0	0	0	0	0	0	0	0	0	0	0
Anochetus sp. 1	0	0	0	0	0	0	0	0	0	0	0	0
Anochetus sp. 2	0	0	0	0	0	0	0	0	0	0	0	0
Camponotus sp. 1	66	36	198	55	16	49	39	85	71	127	68	83
Camponotus sp. 2	1	3	56	25	4	81	252	28	5	10	17	1
Camponotus sp. 3	1	4	86	11	2	113	307	74	7	299	18	0
Camponotus sp. 4	0	0	0	0	0	0	0	0	0	1	0	30
Camponotus sp. 5	0	0	0	0	0	1	1	1	8	1	2	15
Camponotus sp. 6	0	0	0	0	0	0	0	0	0	0	0	21
Camponotus sp. 7	4	4	7	4	3	7	0	1	0	2	4	8
Camponotus sp. 8	1	6	9	2	2	7	0	0	4	2	6	4
Camponotus sp. 9	0	2	0	0	3	2	9	0	1	0	4	0
Camponotus sp. 10	1	5	7	3	0	11	2	1	8	3	11	12
Camponotus sp. 11	9	6	43	18	16	10	12	8	23	14	15	5
Camponotus sp. 12	4	9	16	8	12	8	8	8	31	1	4	8
Camponotus sp. 13	2	2	8	3	18	4	1	7	7	12	7	1
Camponotus sp. 14	0	0	0	0	10	0	2	1	0	0	18	0
Cataulacus sp. 1	0	0	0	0	0	0	0	0	0	0	0	0
Crematogaster sp. 1	0	0	0	0	0	0	0	0	1	0	0	0
Dorylus sp. 1	0	0	0	0	0	0	5	0	1	3	0	0
Lepisiota sp. 1	0	0	0	1	0	0	0	1	2	0	0	0
Lepisiota sp. 3	2	3	2	2	17	15	37	34	41	24	5	42
Lepisota sp. 2	1	3	1	0	59	12	55	47	15	31	3	17
Monomorium sp. 1	391	104	934	237	1162	675	352	82	176	800	282	782
Monomorium sp. 2	20	2	3	16	98	7	284	34	7	47	92	70
Monomorium sp. 3	0	0	1	0	0	0	0	0	0	4	0	0
Monomorium sp. 4	10	2	9	15	57	19	222	370	8	48	34	98
Monomorium sp. 5	1	2	1	0	6	3	7	13	3	4	0	2
Myrmicaria natalensis sp.1	0	1	0	0	0	0	0	107	0	1	0	0
Ocymyrmex sp. 1	18	4	14	20	15	1	6	5	6	9	3	15

Odontomachus troglodytes sp.1	0	0	0	1	1	2	0	0	1	0	0	0
Pheidole sp. 1	9	0	1	7	42	6	15	3	32	12	112	50
Pheidole sp. 2	21	9	27	12	347	27	32	32	45	202	216	2325
Pheidole sp. 3	22	10	1	2	52	540	77	14	126	141	41	539
Phedole sp. 4	0	0	0	0	4	1	0	0	5	1	18	0
Polyrhachis schistacea sp.1	2	7	8	330	6	3	288	17	212	5	17	0
Polyrhachis sp. 1	0	0	0	0	0	0	0	0	0	0	0	0
Tapinoma sp. 1	0	0	0	1	0	0	1	1	7	2	0	0
Technomyrmes sp. 1	0	4	0	0	0	40	7	92	5	4	3	8
Tetramorium humbloti sp.1	0	0	0	0	0	0	54	0	0	0	0	39
Tetramorium sericeriventre sp.1	2	0	10	0	0	0	20	26	0	1	56	22
Tetramorium setuliferum sp.1	0	0	0	0	0	0	0	0	0	0	5	0
Tetramorium weitzeckeri sp.1	0	3	0	0	5	5	6	0	6	0	0	0
Matrix	MA1	MA2	MA3	MA4	MA5	MA6	MA7	MA8	MA9	MA10	MA11	MA12
Aenictus sp. 1	0	0	0	2	0	0	0	0	0	0	0	0
Anochetus sp. 1	0	0	0	0	1	0	0	0	0	0	0	0
Anochetus sp. 2	0	0	2	0	2	0	0	0	0	0	0	0
Camponotus sp. 1	14	26	75	39	110	70	23	55	106	35	16	24
Camponotus sp. 2	2	0	3	0	0	35	18	65	11	9	4	2
Camponotus sp. 3	4	1	1	2	1	46	7	96	22	16	46	3
Camponotus sp. 4	0	0	0	0	0	0	0	0	0	0	59	57
Camponotus sp. 5	0	0	0	4	8	4	0	0	1	0	1	2
Camponotus sp. 6	19	0	0	0	0	0	0	0	8	0	0	5
Camponotus sp. 7	6	3	12	1	0	12	20	5	8	9	12	16
Camponotus sp. 8	4	7	17	2	1	20	22	12	1	10	9	8
Camponotus sp. 9	0	0	0	0	0	21	0	2	5	1	4	1
Camponotus sp. 10	15	6	6	13	5	17	5	43	13	38	13	3
Camponotus sp. 11	4	4	5	9	11	9	10	7	4	9	5	1
Camponotus sp. 12	0	1	8	3	3	2	2	1	1	4	0	0
Camponotus sp. 13	0	0	0	0	0	0	0	0	0	0	0	0
Camponotus sp. 14	0	0	0	0	0	0	0	0	0	0	0	0
Cataulacus sp. 1	0	0	0	0	0	1	0	0	0	0	0	0
Crematogaster sp. 1	0	0	0	0	0	0	0	0	0	0	0	0
Dorylus sp. 1	0	0	0	0	0	0	5	2	0	0	0	0
Lepisiota sp. 1	0	0	0	0	0	1	0	0	0	0	0	0
Lepisiota sp. 3	0	1	0	2	6	18	2	0	0	4	5	4
Lepisota sp. 2	0	0	0	1	2	8	2	1	0	6	1	0
Monomorium sp. 1	4	27	11	4	35	10	35	32	25	20	18	26
Monomorium sp. 2	14	3	21	64	148	4	68	119	13	140	123	8
Monomorium sp. 3	0	0	0	0	0	0	0	0	0	0	0	2
Monomorium sp. 4	39	7	22	89	136	32	57	119	8	297	75	12
Monomorium sp. 5	0	0	0	4	0	4	0	0	0	7	0	1
Myrmicaria natalensis sp.1	0	0	179	0	0	0	2	0	1	0	0	61
Ocymyrmex sp. 1	24	5	11	14	8	9	15	20	22	13	8	4
Odontomachus troglodytes sp.1	8	0	0	1	0	6	0	0	3	0	0	0
Pheidole sp. 1	5	2	4	56	21	10	2	3	0	39	18	30
Pheidole sp. 2	65	109	51	56	445	19	42	15	24	29	44	104
Pheidole sp. 3	41	15	56	97	54	32	7	8	0	87	31	79

Phedole sp. 4	4	0	0	1	8	0	1	0	0	0	0	0
Polyrhachis schistacea sp.1	2	4	5	85	58	92	70	96	9	7	41	6
Polyrhachis sp. 1	0	0	1	0	0	0	0	0	0	0	0	0
Tapinoma sp. 1	0	0	0	0	0	0	0	0	0	0	0	0
Technomyrmes sp. 1	0	0	5	0	0	6	4	9	0	1	0	0
Tetramorium humblotic sp.1	0	0	0	0	0	0	0	1	0	0	0	0
Tetramorium sericeriventre sp.1	0	0	0	0	3	0	0	1	0	0	3	0
Tetramorium setuliferum sp.1	0	0	5	14	3	0	0	0	0	0	0	0
Tetramorium weitzeckeri sp.1	1	87	4	1	2	0	0	0	0	0	0	0

Appendix 4. Number of individuals and species caught per site. Number shown is all four days of trapping combined together.

Site	# of Individuals	# of Species
MA1	275	19
MA2	308	17
MA3	504	22
MA4	564	24
MA5	1071	23
MA6	488	25
MA7	419	22
MA8	712	22
MA9	285	19
MA10	781	21
MA11	536	21
MA12	459	23
MO1	588	21
MO2	231	23
MO3	1442	22
MO4	773	21
MO5	1957	24
MO6	1649	26
MO7	2101	27
MO8	1092	26
MO9	864	29
MO10	1811	29
MO11	1061	26
MO12	4197	24