How fast can you climb a mountain? Climate change, ant assemblages and a centre of endemism

By

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DECLARATION

I **THINANDAVHA CASWELL MUNYAI**, hereby declares that the dissertation for the degree of Master of Environmental Sciences at the University of Venda for Science and Technology, hereby submitted by me, has not been previously submitted for a degree at this university or any other university, that it is my own work in design and execution and that all reference material contained therein has been duly acknowledged.

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ABSTRACT

Elevational transects across mountains, although at a smaller scale, provide compressed versions of regional and continental variation and might be the most cost-effective measure of ecosystem response to global climate change in the tropics. The pattern of ant diversity along a proposed long-term elevational transect across the western Soutpansberg mountains in the north-east South Africa, is investigated to see if it can be related to spatial and environmental variables and the indicator species for each vegetation type and aspect is identified. Ants were sampled with pitfalls laid in 2 X 5 grids, replicated 4 times in each elevation zone (44 in total). Habitat structure (5), temperature (6) and soil parameters (20) were collected in each replicate. A total of 75 ant species representing 27 genera in seven subfamilies were collected. The high diversity of ants in subfamily Myrmicinae and Formicinae is common in other South African ant studies. The species estimators for the whole transect converged closely to each other, indicating that sampling was representative. There was no clear pattern of species richness and density along the whole transect but a mid-elevational peak in species richness and density was found at the northern aspect. The southern aspect had no clear pattern and this can be explained by a clear north-south dichotomy, characterised by the presence of three biomes along the southern aspect and one on the northern aspect. Ant assemblage structure of site 08N was distinct from other sites. Ant diversity patterns and assemblage structure were largely determined by regional environmental factors (32 – 56%) followed by spatially structured environmental factors (5 – 46%) with local processes explaining very little variation (1 – 4 %). Temperature, mean monthly and absolute minimum, in conjunction with percentage sand in the soil, presence of stone in the soil and pH, consistently explained significant amounts of species density, abundance and assemblage structure in particular. Only two of the vegetation types, *viz.* Arid North Bushveld and Leached Sandveld, and also the northern aspect had significant IndVal values larger than 70. The recent climate change predictions suggest that there will be an increased density of thickets on the southern aspect as induced by elevated CO_2 levels and rainfall. This will increase species associated with the thicket. The lower elevational indicator species of the northern slope will move uphill at a rate proportional to their thermal tolerance following the regional increase in temperature due to steeper adiabatic lapse of this aspect. The findings of this study provide baseline data for long-term monitoring of the impacts of climate change on ant diversity of this mountain.

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CHAPTER ONE: INTRODUCTION

Patterns of species diversity around the globe are of great interest to biologists, as are the factors that are responsible for explaining them. Various studies have examined the latitudinal patterns of species diversity (*inter alia* Rohde, 1992; 1999; Willig *et al*., 2003) and mechanisms that cause them. Similarly, other studies have examined species diversity along elevational gradients (Kusnezov, 1957; Stevens, 1992).

The relationship between species diversity pattern across elevational gradients is as general as that of latitudinal gradients (Rahbek, 1995). Studies have tested some of the hypotheses that explain latitudinal species diversity to see if they apply to elevational species diversity (Stevens, 1992; Jetz & Rahbek, 2001; Kessler, 2001; Sanders, 2002; Grytness, 2003; Bachman *et al*., 2004; McCain, 2005; Botes, 2006). Recently, Dunn *et al*. (2010) urged on the similarity between the elevational and latitudinal gradients due to the majority of processes operating along latitudinal gradients also applying to elevational gradients.

1.1 Background Information

One of the most widely recognised patterns in ecology is the latitudinal gradient of species diversity. Critical literature reviews by Rosenzweig (1995), Brown & Lomolino (1998), and Gaston & Blackwell (2000) presented patterns of species diversity along gradients (elevational and latitudinal). Various studies have been conducted across the globe to understand these patterns (*inter alia* Gaston, 1996; Whittaker *et al*., 2001; Willig *et al*., 2003).

Understanding patterns of species distribution along gradients can reveal many challenges facing biodiversity maintenance (Gaston, 2000) *inter alia* climate change. In different parts of the world, many studies have questioned what determines patterns of species diversity (Pianka, 1966; Brown, 1998; Rohde, 1992; Gaston & Blackwell, 2000). Many hypotheses have been developed and tested to identify mechanisms that underlie patterns of species diversity across gradients (Rohde, 1992). Dunn *et al.* (2010) argues that there are at least 30 hypotheses to explain patterns of diversity along gradients.

1.2 Problem Statement of the Research

There is a lack of knowledge about ant diversity and factors that determine ant diversity along environmental gradients in the Limpopo province, with the exception of studies done in the Kruger National Park (Parr *et al.*, 2004; 2005).

Despite some studies conducted on similar topics in South Africa, few of them looked at the distribution of species along elevational transect (especially both sides of the transect) and environmental variables that explain such patterns (Botes, 2006).

1.3 Research Questions

- What is the pattern of ant species richness, density, abundance, and assemblage structure across the transect?
- Which spatial and environmental determinants underlie these patterns (if any)?
- What are the indicator taxa for each of the vegetation types and aspects?

1.4 Research Objective

1.4.1 General Objective

- To determine ant assemblage structure and the spatial and environmental determinants that underlie the differences of the assemblages across an elevational transect.

1.5 Thesis Statement

Pattern of ant diversity and assemblage structure along an elevational transect differ as a result of variation in spatial and environmental variables found along it.

1.6 Justification of the Research

Despite many studies of the distribution of species along environmental gradients (*inter alia* Stevens 1992; Araújo & Fernandes, 2003; McCain, 2007a), there is a need to study elevational gradients. They provide compressed versions of regional environmental variables and might be the most cost-effective measure of ecosystem response to global climate change. Ideally this will require, in part, time-series data for some taxa and a substantial improvement in the understanding of the links between environmental variables and animal distributions (Erasmus *et al.*, 2002).

Botes *et al.* (2006) also points out that there is lack of studies into the effects of climate change on ecosystem dynamics in southern Africa. These likely effects should ideally be determined through experimentation but monitoring of elevational transects will reveal the pace and nature of these changes (Botes *et al.*, 2006; 2007).

There is no long-term monitoring of South African fauna, except aquatic surveys of ecosystem health (River Health Program*), and the impact of global climate change in the Limpopo province. This study, the first elevational monitoring site for this province, will provide baseline data which can act as a reference for long-term monitoring of this transect in future.

*www.csir.co.za/rhp

1.7 Delineation and Limitations

This study focused on the patterns of ground-dwelling ant (epigaeic ant) diversity along an elevational transect and, environmental and spatial variables that determined these patterns in the western part of the Soutpansberg mountains. It also only identified indicator species of vegetation types and aspects along the transect. Only epigaeic ants were sampled. The temporal scale of this study was constrained by the requirements of a master degree at the University of Venda and therefore represents only one season of sampling (September 2009 to January 2010).

1.8 Underlying Assumptions

The distributions of resources (biotic and abiotic variables) along the elevational transect differ and this determines ant diversity. Different vegetation types and aspects occurring along the Soutpansberg elevational transect have indicator species.

CHAPTER TWO: LITERATURE REVIEW

2.1 Introduction

Different environmental factors act in varying ways to shape the patterns of species richness along latitudinal and elevational gradients (Botes, 2006). Although, it has been suggested that processes responsible for causing differences in patterns of species richness along elevational and latitudinal gradients might be the same, it is difficult to assess the role of each environmental factor in determining species diversity along gradients as they do not act separately and are often correlated (Dunn *et al.,* 2010). Rohde (1992) recommended that further studies be undertaken to understand the correlation between factors that are responsible for shaping species diversity along both these gradients.

Over the past five decades, a number of hypotheses (Pianka, 1966; Brown, 1988; Rohde, 1992, 1999; Gaston, 1996; Whittaker *et al.,* 2001) have been proposed to explain the interdependence of species richness and latitude. Recent studies have tested some of these hypotheses (Araújo & Fernandes, 2003; Sfenthourakis *et al.,* 2005; Joshi *et al.*, 2008; Chetti *et al.,* 2010).

Rohde (1992) listed and discussed 28 hypotheses that attempt to examine species diversity across latitude, some circular, some based on insufficient evidence, and others are time hypotheses. Hawkins *et al.* (2003), however, claimed that these hypotheses exceed 30 to date. Other authors, McCain (2007a) and Pimm & Brown (2004) grouped these many hypotheses into three groups: namely null models, historical and ecological hypotheses.

2.2 Species Diversity Patterns along Environmental gradients

2.2.1 Species Diversity along Elevational and Latitudinal Gradients

2.2.1.1 Species Diversity along Latitudinal Gradient

Latitudinal distribution of species diversity has received considerable attention in the field of macroecology. The latitudinal gradient is believed to have existed since the age of dinosaurs

(Lomolino, 2002; Mittelbach *et al*., 2007). Across latitudinal gradients, species richness is generally higher in low latitudes e.g. warm latitudes (tropics) than in high latitudes e.g. colder poles (Samways, 1994; Rosenzweig, 1995; Gaston, 2000; Miller & Spoolman, 2009; Dunn *et al.,* 2010). This can be expected because warmer environments may increase mutation rates and allow for longer growing seasons which give rise to the establishment of more generations (Kaspari *et al.,* 2003; Gillman *et al.,* 2009).

This decline in species richness from the equator to the poles has been shown in different taxa of insects (Kusnezov, 1957; Cushman & Manly, 1993; Davidowitz & Rosenzweig, 1998; Lobo, 2000; Dunn *et al.,* 2009) plants (Gentry, 1988; Ellison, 2002; Hunter, 2005), mammals (Currie, 1991; Rosenzweig, 1992; Ruggiero, 1994; Kaufman, 1995; Cowlishaw & Hacker, 1997; Loyons & Willig, 2002) amphibians and reptiles (Kiester, 1971; Arnold, 1972; Schall & Pianka, 1978; Currie, 1991), and fishes (Rohde, 1992; Rosenzweig, 1992; Stevens, 1996).

Along latitudinal gradients, ant species richness patterns have been reported to decrease with increased latitude (Kusnezov, 1957; Cushman & Manly, 1993; Gotelli & Ellison, 2002; Dunn *et al.,* 2009). A latitudinal gradient in species richness for ground foraging ants has been found globally (Dunn *et al.,* 2009). In the same study, the southern hemisphere had higher local ant species richness when compared with the northern hemisphere after excluding the effects of sampling and contemporary climate.

2.2.1.2 Species Diversity Patterns along Elevational Gradients

Studies have found that species richness decreases as elevation increases (Stevens 1992; McCain, 2007b). However, this remains contentious because other studies (Rahbek, 1995; McCain, 2005; Escobar *et al.,* 2005) had reported a peak in species richness at mid-elevations and a few studies found an increased species richness with elevation (e.g. Sanders *et al.*, 2003).

Patterns of insect diversity along elevational gradients are controversial because there is no consensus about the pattern (McCoy, 1990). Navas (2003) admitted that a decline in diversity with elevation is a well-documented pattern in macroecology (Joshi *et al.,* 2008; Terhivuo & Saura, 2008). McCoy (1990) argued that the reported mid-elevational peak of insect species richness is the result of short-term sampling (e.g. Jansen, 1973; McCoy, 1990; Escobar, 2005) despite other studies reporting mid-elevation peaks as a common pattern for other taxa such as invertebrates, birds and small mammals (Chettri *et al.,* 2010).

Anthropogenic disturbances at low elevations have been reported to be responsible for a decrease in insect species richness at low elevation (McCoy, 1990). McCoy (1990) also argued that results from long-term studies concluded that insect species richness was likely to peak at lower elevation. Similarly, Röder *et al.* (2010) found that the proportion of beetle and bug spruce specialists significantly increased with elevation. At mid-elevations, Brühl *et al.* (1999) argued that species richness was high because of higher primary productivity.

Janzen (1973) found high insect species richness at intermediate elevations in the sweep samples of tropical insects. This pattern was thought to be a result of highly harvestable productivity from plant communities at intermediate elevations (Janzen, 1973).

Ant taxa in particular have been observed to peak at mid-elevations (Samson *et al.,* 1997; Sanders *et al.,* 2002; 2003). Other studies, however, observed ants to be more abundant at lower elevations, out numbering small mammals in the Asian tropical forest (Romdal & Grytnes, 2007).

Meanwhile, a study by Sanders *et al.* (2003) in an arid environment, suggested that species richness may be highest at high elevations which was explained by lower temperature and higher precipitation at these elevations. This is thought to support more taxa in the arid environment because it supports higher levels of primary productivity and causes lower levels of physiological stress (Sanders *et al.,* 2003).

Brühl *et al.* (1999) observed an exponential decrease of ant species in leaf litter of a primary rain forest with elevation and no evidence of a mid-elevational peak in species richness, although there were no ants sampled at the highest elevational sites of the transect. Species richness and ant abundance have been reported to be markedly reduced at higher elevations as compared with low elevational forest (Brown, 1973; Brühl *et al.,* 1999). In the tropics, Dunn *et al.* (2010) pointed out that several studies have observed a decline of ant species richness with elevation.

2.3 Hypotheses that have been Proposed to Explain Species Diversity Patterns along Environmental Gradients

For the purpose of this study, the many hypotheses proposed to examine species diversity across environmental gradients were divided into four general hypotheses. These are: area/spatial constraint, climatic, historical and ecological hypotheses.

2.3.1 Area/spatial constraint Hypotheses

These are spatial hypotheses, and they include: mid-domain effect, Rapoport's rescue effect, available area, and species-energy relationship.

2.3.1.1 Mid-Domain Effect

The mid-domain effect can be defined as "the increasing overlap of species ranges towards the centre of a shared geographic domain due to geographic boundary constraints in relation to the distribution of species' range sizes and the midpoints" (Colwell & Lees 2000; p. 72). This hypothesis tends to predict a humped species patterns when species are randomly distributed within a geographically constrained domain. Colwell & Lees (2000) coined the term mid-domain effect (Colwell & Hurt, 1994; Willig & Lyons, 1998) when they were using computer simulations.

Pimm & Brown (2004) reported that the mid-domain model served as an explanation of why South American birds peak equatorially. Pimm & Brown (2004), however, argued that there are difficulties in applying these models and that care should be taken in identifying the boundaries of domains.

2.3.1.2 Rapoport's Rescue Effect

The range size of species has been asserted to decrease with both decreasing elevation and latitude (Stevens, 1989; 1992). It is therefore thought that species have smaller ranges in both low latitudes and elevations because they experience smaller climatic variability. While at high latitudes and elevations species would have larger ranges as a result of their broader environmental tolerances (Dunn *et al.,* 2010). This hypothesis emphasises that species that are at lower elevation/latitude are more likely to be near the edge of their ranges. Although these species might not do very well at the edges, they are rather close to areas where they can be rescued through dispersal and this give rise to inflated species richness in area where species have small ranges (i.e. low elevations and latitudes).

Along elevational gradients, this rule has been presented as increasing distributional ranges with an increase in elevation for six different taxa: trees, mammals, birds, reptiles, insects and amphibians (Stevens, 1992). For insects in particular, Stevens (1989) hypothesised that because of dormancy during parts of the year, Rapoport's rule would not apply to these organisms and the same was argued for internal parasites and annual plants because they remain dormant during extreme environmental conditions.

2.3.1.3 Available Area

This hypothesis proposed that areas/regions with the largest available area will have more species (MacArthur & Wilson, 1963; Rosenzweig, 1992). McCain (2007) argued that testing this hypothesis along elevational gradients would reveal whether available area is positively related to diversity of given elevational bands. Several other studies tested regional area effects following evidence provided by Rahbek (1995), who had shown that the available area of regional elevational bands can influence the number of species found at each (Sanders, 2002; Sanders *et al.*, 2003; Bachman *et al.*, 2004).

The larger areas are believed to render immigration and emigration of species less vital, while the effects of speciation and global extinction would predominate (Gaston, 2000). This interpretation by Gaston (2000) further defended the idea that this difference in balance of speciation and immigration of species will increase species in an area. This hypothesis argues that speciation increases with area an and thereby reduced extinction rates, resulting in higher species richness. This had been argued by Dunn *et al.* (2010) to be a result of larger areas likely to have been subdivided by dispersal barriers (such as rivers and mountains) and species inhabiting these habitats have been predicted to have opportunities for larger populations and ranges.

2.3.1.4 Species-Energy Relationship

This hypothesis argued that there are more species at lower latitudes due to higher net primary productivity resulting from increased solar energy found towards the equator. The tropical environment in particular, as argued in Kaspari (2000), was more productive resulting from more photosynthesis and abundant water in these areas. This hypothesis suggested that due to higher energy available at low latitude (tropics in particular), more individuals will be supported by these areas hence there will be more species in the area, generally known as the "more individuals" hypothesis.

Strivastava & Lawton (1998) argued that it is based on insufficient data and they found no support for this hypothesis when testing the productivity theory using tree-hole communities. Conversely, a study by Gotelli & Ellison (2002) strongly point to the importance of this hypothesis when studying ant species richness across environmental gradients.

Sanders (2002) hypothesised that productivity is highest at mid-elevations because of increased photosynthesis and tolerable conditions (day-time temperature and cool evenings) that stimulate plant growth along elevational gradients and this tended to increase diversity at mid-elevations. Similarly, Huston (1979) mentioned many studies that have found positive correlations between diversity and productivity.

2.3.2 Climatic Hypotheses

These hypotheses suggest that climatic conditions could set limits to species diversity patterns along gradients. Harsh conditions at higher latitudes and elevation (which are usually colder) limit the survival of species in these areas. Sanders (2002) discussed a decline of species richness at higher elevation as a result of severe climatic conditions whereas few species can physiologically survive these conditions.

Fluctuating climatic conditions led to increased extinction rates. In contrast, stable climatic conditions allowed species to specialise (Klopfe, 1959; Pianka, 1966) and this increased speciation rate. Areas with stable climatic conditions had more species compared with areas with frequently fluctuating climates. According to this hypothesis temperate areas are expected to have fewer species due to fluctuating climatic conditions while areas towards the equator which have more stable climatic conditions, had high species richness. Pianka (1966) observed that this variation in climatic conditions between temperate regions and tropical regions are reflected by rainfall and temperature which varied less in the tropics than in temperate regions.

2.3.3 Historical Hypotheses

These hypotheses addressed species diversity patterns based on time as a limiting factor of species diversity along gradients. They suggested that temperate regions have not yet reached saturation in species richness due to recent disturbances and glaciations (Fischer, 1960; Pianka, 1966). They argued that there has been insufficient time for species to either colonise or evolve and increase their diversity in these areas (Pianka, 1966). Among these historical hypotheses are the evolutionary rate hypotheses stating that the tropics have a higher evolutionary rate (Gillman *et al.,* 2009), and as a result there is high species richness due to increased speciation (Rohde, 1992). The predictions by these hypotheses are considered to be mysterious and not based on widely tested patterns of diversity (Pimm & Brown, 2004).

2.3.4 Ecological Hypotheses

Predation, mutualism, competition and parasitism among species in the tropics have resulted in more species in these areas. At regional scales, species diversity is thought to be driven by these local biotic processes (Currie, 1991). Pianka (1966) urged that this was the case because competition played an important role in the tropics as it is a crucial component of evolution. This hypothesis insisted that increased specialisation in the tropics is the result of ecological interactions between species that had led to increased speciation, hence more species in the tropics (Pianka, 1966). High disturbance and increased predation rates at low elevation were hypothesised to be responsible for decreased species diversity at low elevations (Sanders, 2002).

2.4 Environmental Factors that Determine Species Diversity

2.4.1 Climatic Factors

2.4.1.1 Precipitation

Precipitation, which is the main driving force behind primary productivity, could affect species diversity directly or indirectly (Delsinne *et al.,* 2010). It can limit or hinder physiological tolerance directly or indirectly through control of productivity of the habitat (Hawkins *et al.,* 2003; Delsinne *et al.,* 2010). The availability of water in desert vegetation was described as an important limiting factor in this environment (Zemmrich *et al.,* 2010).

Studies have reported that precipitation was responsible for an average of over 60% of the variation in species richness of plants and animals (Hawkins *et al.,* 2003). Because plant species richness is limited by availability of water and solar energy, this also limited animal species richness as plants are the base of a food web (Wright, 1983; Hawkins *et al.,* 2003). In an analysis of 85 large scale studies, Hawkins *et al.* (2003) concluded that animal species richness was highly correlated with water availability in the tropical to warm temperate regions.

Joshi *et al.* (2008) found that sites with highest insect species diversity were sites with the longest rainy season. Furthermore, in the same study, a positive relationship between insects diversity and rainfall was shown. The availability of water was found to be the strongest predictor of animal species diversity in the tropics, subtropics and temperate zones (Hawkins *et al.,* 2003).

Some studies have found a positive correlation between ant species richness and rainfall (Parr *et al.,* 2004). However, Dunn *et al.* (2009) noted that species richness of ground foraging ants, in contrast with other taxa, was relatively higher in dry and hot regions of the world. A negative influence of rainfall on ant alpha-diversity has been suggested and it was concluded that rainfall seems to have no influence on diversity at both regional and geographic scales, except for areas where annual rainfall is less than 200 mm (Davidson, 1977b; Delsinne *et al.,* 2010; Segev, 2010).

Sanders *et al.* (2003) found that temperature combined with precipitation explained 80% of ant species variation along elevational gradients in the Springs Mountains of southern Nevada. Ant diversity was positively correlated with temperature and primary productivity on a continental scale (Kaspari *et al.,* 2003; Sanders *et al.,* 2007; Dunn *et al.,* 2009; Segev, 2010). As such, Segev (2010) suggested that studies covering relatively short distances should be conducted over a climatic gradient. Segev (2010) believed that if a short distance study was conducted to test climate effects on ant species over a climatic gradient, it would minimize the effects of other accompanying environmental variables.

2.4.1.2 Temperature and Humidity

Laucoul & Freedman's (2006) results suggested that climate-related influences are the key variables among environmental variables that structure species diversity. This suggestion is also supported by the results of Sanders *et al.* (2007) and McCain (2007b), where warm sites supported more species because they supported more individuals.

Temperature was correlated with net primary productivity, indirectly limiting physiological ranges of individuals and it also drove speciation (Kaspari *et al.,* 2000; Sanders *et al.,* 2007). Hawkins *et al.* (2003) found a correlation between animal species richness and temperature in temperate and polar regions. A positive correlation has also been found between aquatic plants and water temperature (Laucoul & Freedman, 2006).

Declines in temperature at high elevations have been reported to be a cause of linear decline in arthropod species richness with an increase in elevation (Röder, 2010). While in the arid environment, Sanders *et al.* (2007) hypothesised that higher mean and maximum temperature allows ants to forage and harvest more and thereby reducing extinction rates. Kaspari *et al.* (2003) called for a focus on temperature and area if gradients of species richness beyond spatial scale are to be understood because they are linked to the balance between extinction and speciation.

Wang *et al.* (2001) and Araújo & Fernandes (2003) have suggested that the decrease of ant diversity at high elevations was a result of low temperatures that delay the development of larvae and thus reduce survival and colonization rates while extinction rates increase. Furthermore, metabolic processes and pupal development were thought to be interrupted by low temperature at high elevation (Brühl *et al.,* 1999). Dunn *et al.* (2010) pointed out that depending on the importance of temperature and net primary productivity in a region, temperature is likely to limit ant fitness, foraging and abundance at lower temperatures more than it affects plants.

Dunn *et al.* (2009) reported the influence of temperature on ant diversity, stating that it influences rates of mortality and extinction. The shallow and humid soil at higher elevations in Serra do Cipò is thought to limit ant colony development (Araújo & Fernandes, 2003). Low temperatures and saturated wet soil were also mentioned as variables responsible for decreased species richness at high elevation of Mount Kinabalu (Brühl *et al.,* 1999).

The increased humidity of litter was hypothesised to reduce the foraging ability of smaller ants as they may be trapped in the water film caused by the increase in humidity (Brühl *et al.,* 1999). High humidity at high elevation in tropical areas was also thought to shorten foraging time. In the tropics high elevations have waterlogged conditions and these limited the availability of dry nesting sites for ants in the soil and around dead wood (Brühl *et al.,* 1999). In contrast the short season and increased humidity of the temperate regions does not apply and ants here also occur at high elevation (Brühl *et al.,* 1999).

2.4.1.3 Energy (Productivity)

The influence of energy is critical in species diversity patterns. However, energy availability depends on climate and the ideas about this relationship have been said to date back during the beginning of biogeography (Hawkins *et al.,* 2003). The relationship between energy and climate has been proposed as an explanation for species gradients (Hawkins *et al.,* 2003).

The availability of food resources influenced species diversity along environmental gradients (Ruano *et al.,* 2000). Ant genera have been studied and grouped in different functional groups e.g. specialists such as larger Ponerinae, generalists in subfamily Myrmicinae and opportunists in genus *Tetramorium* (Andersen, 1997a). Brühl *et al.* (1999) suggested these groups preferred different diets in the tropics, Brühl *et al.* (1999) observed different ant food resources were more abundant at low elevations. As a result, the distribution of ant species richness was also higher at lower elevation.

Sanders *et al.* (2003) provided evidence that suggested a peak in ant species richness at high elevations in arid ecosystems. On a larger scale, however, Kaspari *et al.* (2000) found that warmer habitats had more ant species and that there was a positive correlation between productivity and ant species richness. Insect diversity of the Pindari forests in the western Himalayas in India was significantly related to food resources, disturbances and elevation (Joshi *et al.,* 2008).

2.4.2 Ecological and Edaphic Factors

2.4.2.1 Competition, Predation, Mutualism and Parasitism

Biotic factors have been shown to influence ant communities (Cushman, 1993; Wang *et al.*, 2001). These are biotic processes such as predation, competition, parasitism and mutualism. These ecological species interactions have been thought to promote species coexistence that in turn increased speciation and thereby increased species diversity (Pianka, 1966). Rojas & Fragoso (2000) pointed out that competition, predation and parasitism are responsible for structuring ant communities in a North American desert.

Hadly & Maurer (2001) argued that species with improved ecological abilities e.g. dispersal and tolerance abilities, dominate the environment in high densities. This have been urged on the crucial factor that predation has in ecological systems, because it influenced the structure of assemblages as it involves the transfer of energy between species (Wilson, 1991; Thrush, 1999; Barros, 2005).

Pianka (1966) discussed the importance of predation and insisted that it reduced the level of competition and thereby allowed the existence of new predator species in an area. The influence of predation, however, has often been based on small scale studies and sessile organisms. Barros (2005) studied the importance of predation on benthic populations and revealed that factors other than predation e.g. disturbance caused by experimental design, gave rise to differences in assemblages. Hobaek *et al.* (2002) found zooplankton species richness was controlled by fish predation levels and other factors such as lake size, lake productivity and water quality.

Competition has been reported not only to constrained ant species distributions and morphology but also affected ant social characteristics (Davidson, 1977a). While Leavings (1983) and Wang *et al.* (2001) were more specific and suggested that predation by other ants influenced ant species distribution. In a study conducted along an elevation transect in Serra do Cipò in Brazil, the presence of aggressive ant species negatively influenced the presence of less aggressive species (Araújo & Fernandes, 2003).

Because different ant species tend to share similar resources e.g. nesting material and food, competition played a key role in structuring local ant assemblages (Parr & Gibb, 2010). This is mainly because ant colonies are generally long-lived and sessile. As a result, ant species are commonly observed interacting with each other aggressively and one species will dominate and increase its ability to access resources (Parr & Gibb 2010).

2.4.2.2 Soil parameters

Soil parameters have a particularly large influence on the composition and structure of terrestrial species, either directly or indirectly. These factors have significant effects on species distribution. Medinski *et al.* (2010) provided a list of studies that have reported a positive correlation between soil fertility and plant species. They also noted that plant species richness has particular soil resource requirements which therefore limit diversity. This has been reported to be more influenced by soil texture than rainfall. It was argued that soil texture was responsible for determining where water (rainfall) was stored, thus restricting movement of water in the soil, and also restricting seedlings development (Medinski *et al.*, 2010).

Delsinne *et al.* (2010) found that there was no relationship found between alpha diversity of ants, soil texture and chlorides in the Paraguayan dry Chaco. Excess salt in the soil have been thought to affect ant diversity indirectly e.g. through its negative effects on plant productivity (Delsinne *et al.*, 2010).

2.4.2.3 Elevation

Elevation was identified as a variable that was frequently related to change in assemblages (Escobar *et al.*, 2005). A negative correlation between ant species richness and elevation was reported by Wang *et al.* (2001) and Araújo & Fernandes (2003). The negative correlation, however, have been ascribed to reduced vegetation complexity, less habitat area and increases in harshness of habitat at high elevation (Araújo & Fernandes, 2003). Similarly, there was a significant influence of elevation on dung beetle species diversity (Escobar *et al.*, 2005).

Adverse conditions at high elevation, such as low temperature, were reported to reduce the availability of resources (Brown, 1973; Jansen, 1973; Araújo & Fernandes, 2003). At high elevations, the high air and soil humidity limited species development and led to reduced populations (Araújo & Fernandes, 2003). Habitat structure was very important in structuring ant assemblages because it played a major role in their interactions with the ecosystem.

2.4.2.4 Habitat Structure

The interrelationships of species and habitat structure, specifically vegetation cover, played a vital role in structuring species diversity. Shmida & Wilson (1985) pointed out that the distribution of species in a landscape was largely influenced by the difference in habitat conditions. While more species could be accommodated in communities with larger niche hyperspace, habitat diversity was the major determinant of this relationship (Shmida & Wilson, 1985). Vegetation cover was important for some taxa (small mammals where it provided protection from predators) and influenced micro-climate and behavioural stress, and indirectly controlled primary production and therefore food supply (Ferguson & Forsyth, 1980).

Characteristics of the habitat had a major influence on insect diversity and composition along gradients (Joshi *et al.*, 2008). Sfenthourakis *et al.* (2005) found that sites with sparse and open vegetation had higher insect species richness and diversity than forest sites (closed habitat). Gibb & Parr (2010) provides evidence that increased habitat structure (complex environment) caused ants to discover resources slower.

Abiotic and biotic variables restricted the ability of ants to access resources because they are small and also prone to desiccation (Kaspari, 2000). Araújo & Fernandes (2003) observed a decrease in number of ant species in xeric habitats and attribute this to a decrease in habitat complexity and severe climatic conditions. Microhabitat has been reported to have influenced a decline in leaf litter ant diversity on Mount Kinabalu in Malaysia because litter accumulation was rare above 2600 m (Brühl *et al.,* 1999). Gotelli & Ellison (2002) found species density of bog ants was marginally associated with vegetation composition. In the Australian canopy forest, arboreal ant species richness was highest in the wettest habitats while it was low in ground foraging ants (Majer *et al.,* 2001; Dunn *et al.,* 2009).

In Brazil, Araújo & Fernandes (2003) found greater diversity of ant species in a mesic habitat, indicating highly productive habitat (e.g. those along rivers) support more ant species. They believed that increased habitat complexity and availability of resources due to diverse woody plants in their study area, provided more diverse nesting sites and better foraging conditions (Araújo & Fernandes, 2003). Sanders *et al.* (2003) further discussed the indirect effects of climate on primary productivity's influence on species richness.

2.4.3 Area

Available area had a major influence on species diversity and larger areas had higher species diversity (MacArthur & Wilson, 1963). This was because larger areas encourage speciation if populations can be easily separated by geographic barriers (Kaspari *et al.,* 2003). In Colorado and Nevada, more than 90% of ant species richness was explained by area (Sanders, 2002).

2.5 Bioindicators

2.5.1 What are Bioindicators?

In ecological and biogeographical studies, identification of indicator or characteristic species was regularly done to define habitats (Dufrêne & Legendre, 1997). McGeoch (1998) provided a critical discussion of the definition of bioindicators. They were divided into three categories; ecological, environmental and biodiversity indicators.

An ecological indicator was defined as "a characteristic taxon or assemblage that is sensitive to identified environmental stress factors, that demonstrates the effects of these stress factors on biota, and whose response is representative of the response of at least a subset of other taxa present in the habitat" (McGeoch, 1998; p. 183). Species that demonstrate a negative response to disturbance and were sensitive to disturbance were good examples of ecological indicators (Pearce & Venier, 2006).

An environmental indicator was defined as "a species or group of species that respond predictably, in ways that are readily observed and quantified, to environmental disturbance or to a change in environmental state" e.g. detectors, exploiters, sentinels, bioassay organisms and accumulators (McGeoch, 1998; p. 183).

Biodiversity indicators were defined as "a group of taxa (e.g. genus, tribe, family or order, or a selected group of species from a range of higher taxa), or functional group, the diversity of which reflects some measure of the diversity (e.g. character richness, species richness, level of endemism) of other higher taxa in a habitat or set of habitat" (McGeoch 1998; p. 184).

Dufrêne & Legendre (1997) proposed and developed a method to quantify bioindicator value which is called the Indicator Value Method (IndVal). Based on this method, indicator species were identified as those species which were characteristic of a particular habitat. This was determined by looking at the degree of specificity and fidelity of the identified species to the habitat (McGeoch *et al.,* 2002). Using this method, the assessment of the degree of fidelity (frequency of occurrence) and specificity (uniqueness to a particular site) between habitat types was quantified to identify indicator species (van Rensburg, 1999). Representative and reliable indicator (characteristic) species were considered to be those with high IndVal value (i.e. IndVal >70%) for the particular site (van Rensburg, 1999).

2.5.2 Ants and other Insects as Indicator Species

Insects played a significant role in ecosystem functioning and were therefore valuable ecological indicators because they were diverse and they played vital roles in the ecosystem (O'Neill *et al.,* 2010). Sawchik *et al.* (2005) provided evidence that butterflies were extremely sensitive to vegetation change and as the result they could be used to characterise different types of habitat.

Pearce & Venier (2006) recommended the use of invertebrates, especially beetles and spiders, as bioindicators. There is, however, a lack of taxonomic expertise, especially with spiders, which renders them problematic as bioindicators. Beetles are regarded as sensitive indicators of temperature and moisture gradient (Butterfield *et al.,* 1995).

Majer *et al.* (2007) maintained that ant ecology is well understood and therefore they had an advantage over other insect taxa. Ants are also regarded as terrestrial "engineers" because of their ability to modify and regulate the distribution of resources available to other living organisms (Jones *et al.,* 1994) thus they play a vital role in nutrient cycling (Hölldobler & Wilson, 1990). Hence, ants have been shown to be bioindicators of ecological processes (Andersen & Sparling, 1997), habitat regeneration (Silva *et al.,* 2007), forest clearing (Majer *et al.,* 1997) and soil quality (Lobry de Bruyn, 1999). Alonso & Agosti (2000) and Underwood & Fisher (2006) provide a critical discussion on the use of ants in biodiversity studies, conservation monitoring and management of ecosystem.

Andersen (1997a) grouped ants into different functional groups, some of which could assist in studies that aim to predict the response of indicator taxa to disturbance and environmental change. Ants and other soil micro-invertebrates could collectively be used to indicate the quality of soil as they played a significant role in regulating soil processes that led to soil formation (Lobry de Bruyn, 1999).

2.6 Conclusion

Species diversity patterns along both elevational and latitudinal gradients have been widely studied in an attempt to investigate the distribution of both animals and plants on Earth. Several hypotheses have been proposed to explain both gradients. Hawkins *et al.* (2003) admits that there is insufficient evidence to reach an agreement with regard to primary factors responsible for broad-scale richness gradient. However, for ants in particular, several studies suggested that further investigation to better understand the factors that drive species distribution, especially those concentrating more on the mechanisms that influence ants species success between habitats along elevational gradient are essential (Araújo & Fernandes, 2003).

Wang *et al.* (2001) mentioned the association of ants with many environmental factors and suggested that these factors might be correlated with each other. In their conclusion, they pointed out that it is vital to identify these factors and study their relationship with ant communities (Wang *et al.,* 2001).

What might be responsible for shaping patterns of ant species along elevational transect? This question has remains largely unanswered regardless of many studies on ants conducted before. There is a contrast between studies dealing with ant diversity at global and regional scale. Results obtained from these two yielded contradictory findings that confuse the factors that are responsible for driving ant diversity.

Emphasis has been placed on what the pattern of ant species richness along elevational transects is, while few studies have identified the mechanisms that underlie these assemblages of ant species. In addition, except for one study in South Africa (Botes *et al.,* 2006) there have been few studies that investigated elevational gradients in ant diversity and the environmental factors that underlie them.

CHAPTER THREE: ECOLOGICAL SETTING OF THE STUDY AREA

3.1 Introduction

The Soutpansberg is a major centre of plant endemism and biodiversity. It has the highest plant genus and family-level diversity among the 18 recognized Centres of Plant Endemism (CPE) for southern Africa (van Wyk & Smith, 2001; Hahn, 2002; 2006). It also has 33% of South African's reptiles, 116 species in total which is equal to the entire Kruger National Park. Sixty percent of South Africa's mammal species occur in the region which represents more mammal species per unit area than in seven of the eight most diverse biodiversity hotspots of the world (Berger *et al.*, 2003). The region has 75% of South Africa's avifauna (Berger *et al.*, 2003). Foord *et al.* (2008) recorded a total of 54 spider families, which translates into 82% of South Africa families. It also forms the focal point of the recently established Vhembe Biosphere Reserve[1].

3.2 Locality of the Study Area and Site Selection

The study area is located at Lajuma Research Centre, within the western part of the Soutpansberg mountains in the Limpopo province, near the north-eastern border of South Africa (Fig. 1). The western part of the Soutpansberg is situated along the R522 road that connects the towns of Makhado and Vivo. Lajuma is 46 km from Makhado and 26 km from Vivo. The transect is 16.3 km long with a north-south orientation, consisting of eleven elevational sites with 44 replicates ranging from 900m a.s.l (23 03.846° S, 29 29.400° E) on the farm Koedoesvlei in the south, ascending to 1700 m a.s.l (23.02408° S, 29.42908° E) at its highest, on the farm Lajuma and descending to 800 m a.s.l (22 56.683° S, 29 26.359° E) in the north on the farm Goro (see Fig. 3, Appendix A). The transect spans three biomes, namely: Forest, Grassland and Savanna (see Fig. 2).

[1]www.unesco.org

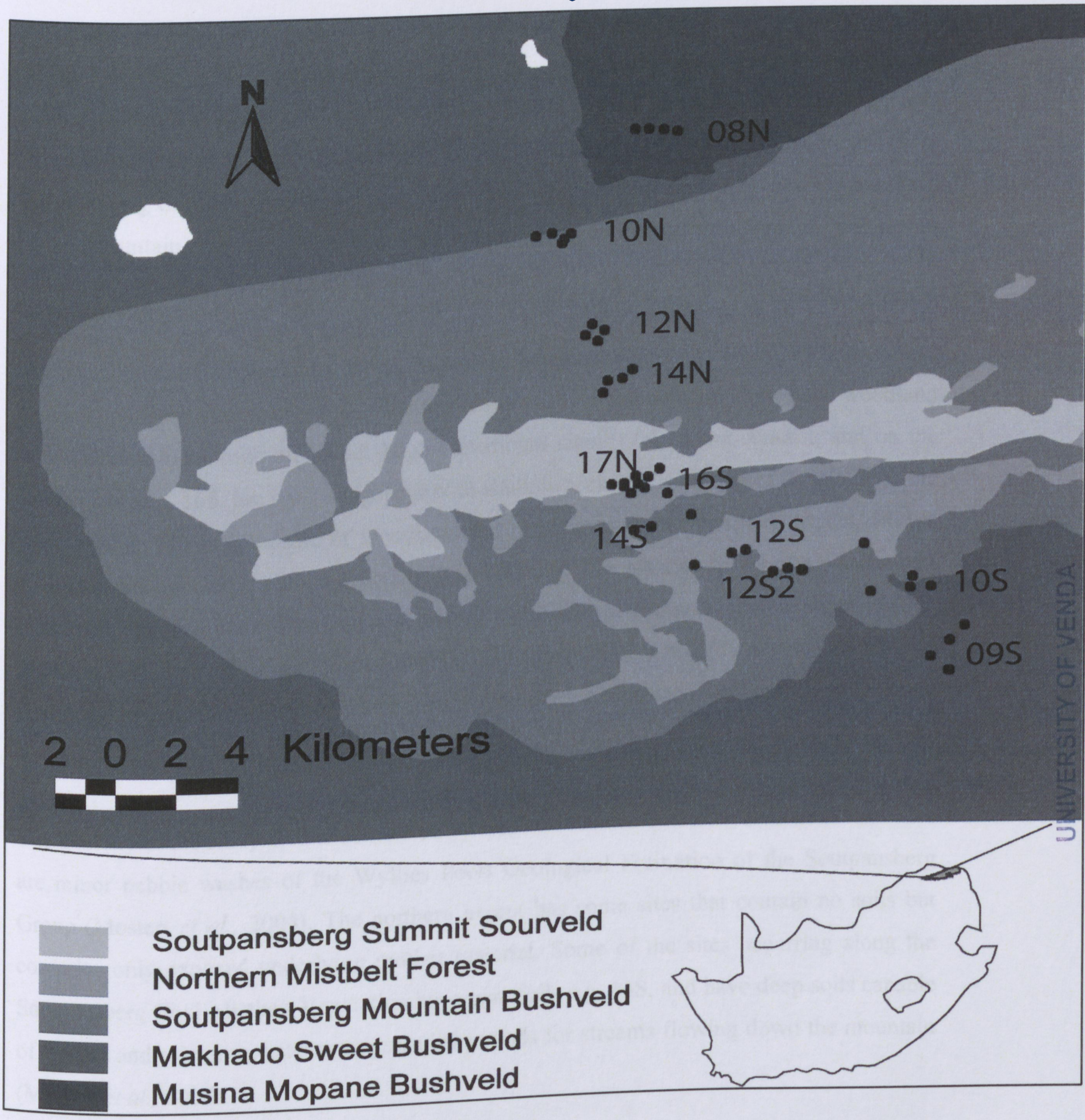


Figure 1 Location of the transectat Lajuma South Africa and the position of the 44 replicates along the elevational transect projected onto a vegetation map from Mucina & Rutherford (2006).

3.3 Vegetation, Geology, Soil and Other Landscape Features

Mostert *et al.* (2008) identified five vegetation types occurring along the transect, which are: Soutpansberg Arid North Bushveld (ANB), Soutpansberg Leached Sandveld (LS), Soutpansberg Cool Mistbelt Vegetation (CMV), Soutpansberg Forest (SF) and Soutpansberg Moist Mountain Thickets (SMMT). The different vegetation types where all the eleven elevational sites are occurring are shown in (Table 1).

The sites in the Soutpansberg Moist Mountain Thickets (12S2, 10S and 09S) are close bushland with red clay-loamy soils. The forest site (12S) is characterized by closed woodland with red clay-loam soils on basalt. High elevational sites, 17N on the summit, and on the southern aspect, 16S, are open sedgeland with shallow rocky soils on quartzite. While on the same aspect, 14S is a mosaic of woodland and grassland. On the northern aspect, 14N is characterized by rocky soils on quartzite. The 10N and 12N sites on the northern aspect are characterized by shrubland and open woodland with rocky screed and rocky shallow soils on quartzite. The low elevational site of the northern aspect 08N is mixed open woodland with deep sand on quartzite. The dominant woody plant species for each of the above vegetation types is shown in Table 1, based on Hahn (2006).

The geology of the study area is dominated by erosion-resistant quartzite, sandstone and there are minor pebble washes of the Wyllies Poort Geological Formation of the Soutpansberg Group (Mostert *et al.*, 2008). The northern aspect has some sites that contain no soils but comprise only exposed underlying mother material. Some of the sites occurring along the Soutpansberg Cool Mistbelt Vegetation have peat soils e.g. 14S, and have deep soils capable of storing and releasing water over extended periods for streams flowing down the mountain (Mostert *et al.*, 2008).

The study area has a wedge-shaped appearance with most northern sites having moderate slopes and southern sites with steep slopes (Mostert *et al.*, 2008).

3.3.1 Climate

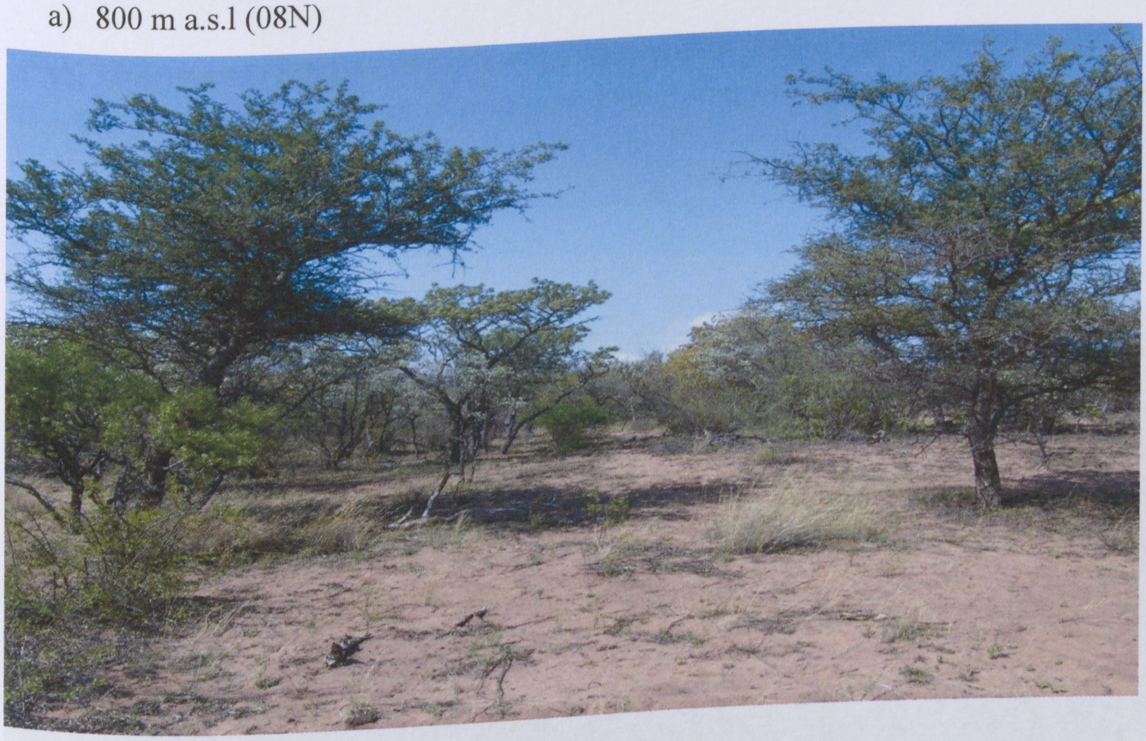
The Soutpansberg region experiences cool, dry, season temperatures during winter (May to August) that ranges from 12-22ºC (Kabanda, 2003) with warm, wet, summer (December to

February) temperatures ranging from 16-40°C. In addition, minimum winter temperatures seldom drop below freezing point (Mostert *et al.,* 2008). However, climate (especially precipitation and mist precipitation) differs dramatically because of the extreme topographic diversity and elevational changes over short distances (Mostert *et al.,* 2008). Some areas on the northern aspect of the Soutpansberg mountain receives less than 367 mm as opposed to some areas on the southern aspect, their precipitation may increase as high as 3 233 mm annually due to orographic mist (Mostert *et al.,* 2008).

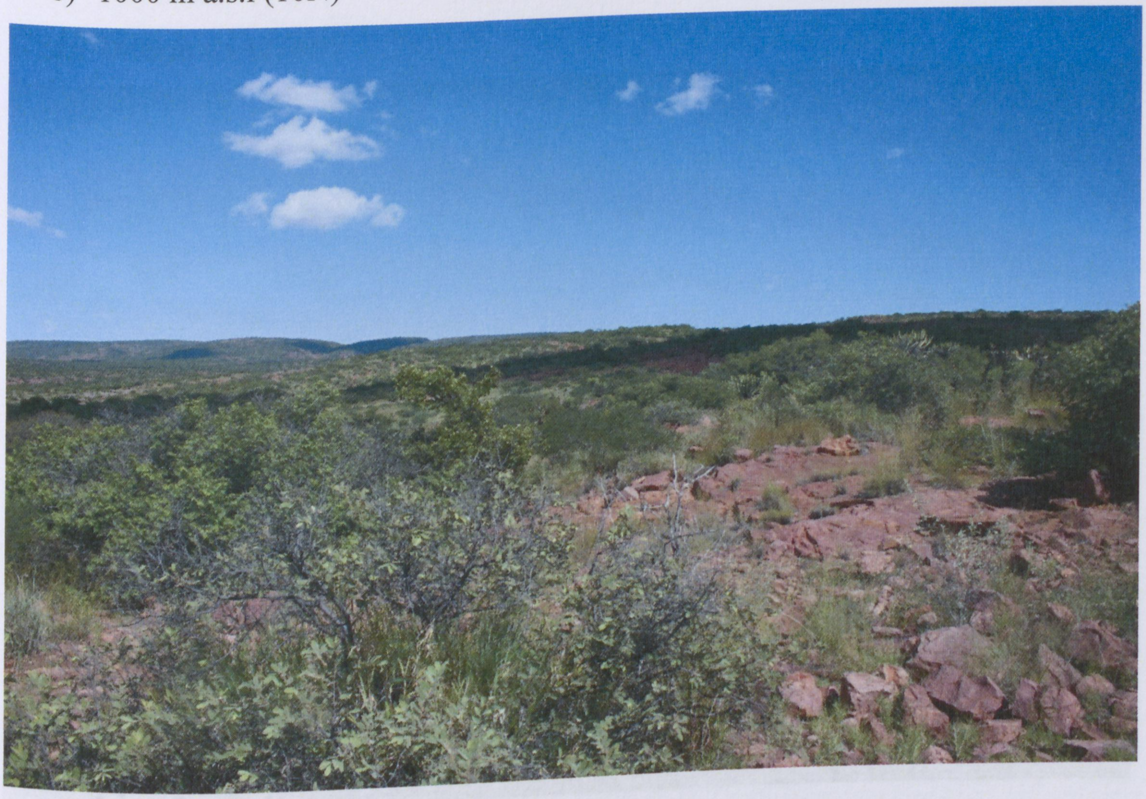
3.3.2 Important Plant Taxa along the transect

Some of the plant species that are endemic to the Soutpansberg, *viz*, *Aloe soutpansbergensis, Justicia montis-salinarum, Kalanchoe crundalli, Aloe vossi*and*Khadiaborealis L. Bol. Vangueria soutpansbergensis* (Hahn, 2002). Dominant woody plant species occurring at each elevational site and other plants form are listed in Table 1.

a) 800 m a.s.l (08N)



b) 1000 m a.s.l (10N)



c) 1200 m a.s.l (12N)

d) 1400 m a.s.l (14N)

e) 1700 m a.s.l (17N, Summit)

f) 1600 m a.s.l (16S)

g) 1400 m a.s.l (14S)

h) 1200 m a.s.l (12S2)

i) 1200 m a.s.l (12S)

j) 1000 m a.s.l (10S)

k) 900 m a.s.l (09S)

Figure 2a) – k) Images of representative sampling replicates at each of the 11 sites along the Soutpansberg elevational transect.

Table 1 Eleven elevational sites and dominant plant species occurring at different vegetation types along the transect, from Hahn (2006).

Elevational sites	Vegetation types	Dominant woody species
Northern Aspect		
800 m a.s.l (08N)	ANB	*Acacia tortilis, Grewia flava, Acacia nigrescens* and *Terminalia sericea*
1000 m a.s.l (10N)	LS	*Boscia albitrunca, Cammiphora apiculatum* and *Elephantorrhiza burkei*
1200 m a.s.l (12N)	LS	*Burkea africana, Ochna pulchra*
1400 m a.s.l (4N)	CMV	*Diospyros dichrophylla* and *Rhus magalismontanum*
1700 m a.s.l (17N)	CMV	*Coleochloa* species
Southern Aspect		
900 m a.s.l (09S)	SMMT	*Dichrostachys cinerea*
1000 m a.s.l (10S)	SMMT	*Acacia caffra* and *Olea europae*
1200 m a.s.l (12S)	SF	*Croton sylvaticus* and *Ekebergia capensis*
1200 m a.s.l (12S2)	SMMT	*Acacia caffra* and *Olea europae*
1400 m a.s.l (14S)	CMV	*Canthium inerme, Heteromorpha arborescens* and *Psydrax obovata*
1600 m a.s.l (16S)	CMV	*Coleochloa* species

3.3.3 Fauna Found along the Soutpansberg Transect

More than 45 mammals species, 40 reptiles and amphibians species; and also 128 bird species are found along the transect. One reptile species, the Soutpansberg flat lizard (*Platysaurus relictus*) is endemic to the region.

CHAPTER FOUR: RESEARCH METHODOLOGY

4.1 Introduction

This chapter provides information on how data were collected to determine the variation of patterns of ant abundance, species richness and assemblage structure across the transect and data on spatial and environmental variables that explain such variation in the study area. It provides the methodologies used in collecting data and statistical analyses involved in analysing it.

4.2 Epigaeic Ant Sampling

Ant sampling followed the protocols of Parr *et al.* (2004) and Botes *et al.* (2006). At each elevational site, four replicates consisting of 10 pitfall traps each (ø 62 mm) was laid out in a grid (2 x 5) with 10 m spacing between traps. Each replicate was spaced at least 300 m apart (Fig. 3), to avoid pseudoreplication (McKillup, 2006) (see Appendix A). Disturbance of the surface around the traps was avoided as far as possible and surface materials were returned to their original state (Agosti *et al.*, 2000). The effect of digging (Greenslade, 1973) was assumed to be negligible (Botes *et al.*, 2006) and traps were set immediately.

The traps were filled with a 50% solution of propylene glycol that neither attracted nor repelled ants (Adis, 1979; Abensperg-Traun & Steven, 1995). Sampling was carried out in September 2009 and January 2010. Traps were set and left open for five days during each sampling period. Ant samples were washed in the laboratory and stored in 70% ethanol.

The ants were identified up to species level where possible or otherwise assigned to morpho-species following Bolton (1994) and Taylor (2010), under a Leica EZ4 microscope. Ant reference collections at Skukuza, Kruger National Park and in the Imbovane ant collection at Stellenbosch University, were used to assist identification where necessary.

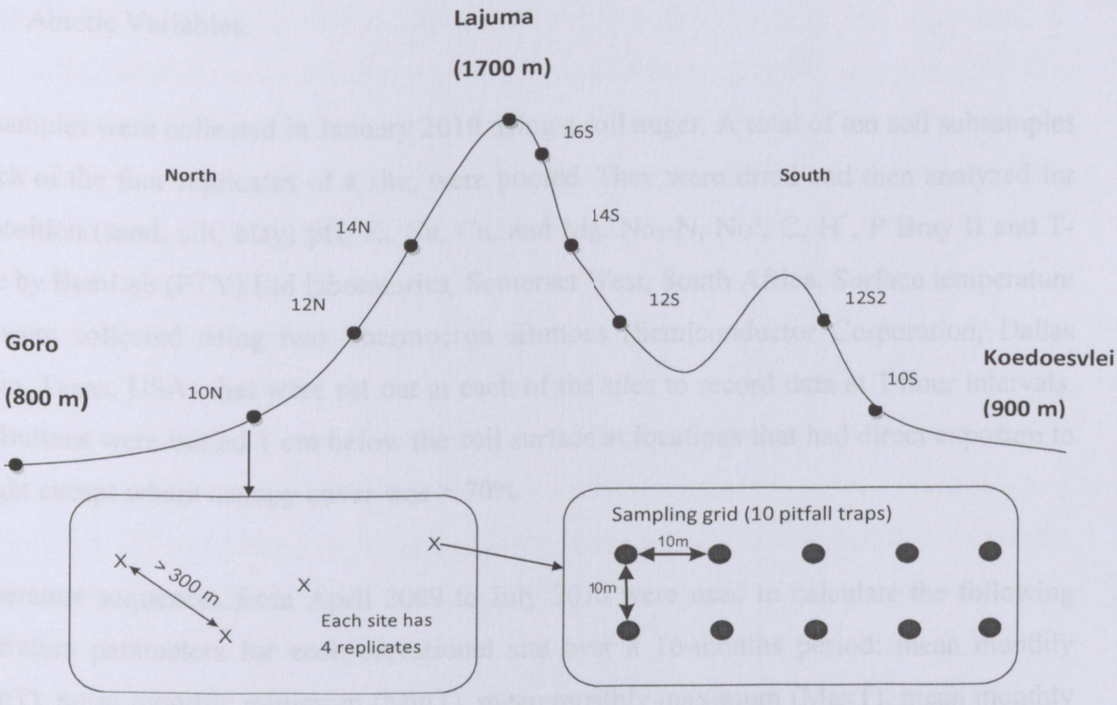


Figure 3 Sampling layout of the Soutpansberg elevational transect, with 11 sites ranging from Koedoesvlei at 900 m a.s.l centred over the Lajuma research station at 1700 m a.s.l to Goro Nature Reserve at 800 m a.s.l

4.3 Environmental Variables

4.3.1 Biotic Variables

The vegetation structure (vertical and horizontal) was determined in September 2009 and January 2010 following methods set forward by Rotenberry & Weins (1980) and Bestelmeyer & Weins (1996) with similar protocols employed by Parr *et al*. (2004), Botes *et al*. (2006) and Barrow *et al*. (2007). The horizontal structure was determined by placing a 1 m² grid over each pitfall trap (see Fig. 3) and the percentage area covered by vegetation, leaf litter, exposed rock and bare ground was visually estimated. Average ground cover was calculated for each replicate. The vertical distribution of vegetation was determined through foliage height profiles obtained by measuring vegetation height at four points located at 90° angels from a 1.5-m radius centred on each pitfall trap. At each sampling point, the number of hits on a 1.5m rod was recorded at 25cm intervals.

4.3.2 Abiotic Variables

Soil samples were collected in January 2010 using a soil auger. A total of ten soil subsamples in each of the four replicates of a site, were pooled. They were dried and then analyzed for composition (sand, silt, clay) pH, K, Na, Ca, and Mg, No_3-N, No^3, C, H^+, P Bray II and T-Value by BemLab (PTY) Ltd laboratories, Somerset West, South Africa. Surface temperature data were collected using two Thermocron iButtons (Semiconductor Corporation, Dallas /Maxin, Texas, USA) that were set out at each of the sites to record data at 1 hour intervals. The iButtons were buried 1 cm below the soil surface at locations that had direct exposure to sunlight except where canopy cover was > 70%.

Temperature sequences from April 2009 to July 2010 were used to calculate the following temperature parameters for each elevational site over a 16-months period: mean monthly (MeanT), mean monthly minimum (MinT), mean monthly maximum (MaxT), mean monthly temperature range (MRange), absolute maximum (AbsMaxT) and absolute minimum (AbsMinT) temperature for each elevational site.

The effect of area on ant species density and abundance was evaluated by calculating the area available at each of the elevational zones. This was calculated by creating a Minimum Convex Polygon of all replicate points with a 40 km buffer which encompassed the area under study. A 3 arc-seconds Shuttle Raster Topography Mission (SRTM) digital elevation model (DEM) was used to extrapolate 6 height classes (700-900 m, 900-1100 m, 1100-1300 m, 1300-1500 m, >1500). These were then split into north and south groups respectively. The north-south divide was extrapolated using watershed polygons generated through IDRISI using the same DEM as above. The Soutpansberg-Blouberg gap was bridged by a straight line rather than following ambiguous watersheds.

4.4 Statistical Analysis

EstimateS V8 (Colwell, 2000, http://vice-roy.eebuconn.edu/estimates) was used to compile species accumulation curves which determined whether the sampling was representative. Sample-based rarefaction curves for ants were compiled separately for each site (Gotelli & Colwell, 2001). The individual-based curves were rarefied to the lowest number of individuals recorded at a site to ensure valid comparisons of species richness between sites. The lowest number of individuals, 330 at 12S, was however considerably lower than that of highest, 7418 at 10S. The Coleman curve for these sites was therefore extrapolated to that of 16S, which had 671 individuals (Gotelli & Colwell, 2001).

This study distinguishes between species density, which is the total number of species caught in each sampling grid, and species richness which was calculated by Coleman rarefaction in EstimateS V8 (Cowell, 2000, http://vice-roy.eebuconn.edu/estimates), rarefying the number of individuals for each grid to that of the site where the lowest number of individuals were caught.

The inventory completeness was calculated as the ratio of observed species (S_{obs}) to six species estimates, namely: Chao 1 Mean, Chao 2 Mean, Jack 1 Mean, Jack 2 Mean, Bootstrap Mean and MMmeans (1 run).

Pearson's product moment correlations were conducted in R to avoid collinearity among biotic and abiotic variables (two abiotic: percentage bare ground, percentage exposed rock and two biotic: leaf litter and percentage vegetation cover) and (28 abiotic variables: elevation, available area, 6 temperature and 20 soil parameters). When variables were significantly collinear (r >0.5), only the variables that were considered biologically relevant were retained. The collinearity of the 28 abiotic variables resulted in a reduced number of 15 variables that were used in further analyses (Appendix B).

The six temperature variables were reduced to two: mean monthly temperature and absolute minimum temperature. Seven soil parameters were chosen for the analysis of which five were chemical (pH, K, Na, C, PBrayll) and two structural (proportion of sand and stone) components (see Appendix D). Elevation correlated with available area, proportion of rock cover correlated with absolute minimum temperature and was therefore excluded. The remaining four vegetation variables were therefore retained (average total number of hits per sampling point, the proportion of ground covered by vegetation, bare ground and leaf litter) (see Appendix D).

The environmental variables that best explained variation in species density and total abundance of ants were analyzed using generalized linear models (GLM) with a log link function and Poisson error distribution in R (R Development Core Team 2010) including only significant variables, following the method used by McGeoch & Price (2004). If the data were overdispersed, a quasi-likelihood approach that allowed parameter estimation without knowing the error distribution of the response variable was used by defining the error distribution as "quasipoisson" (McCullagh & Nelder, 1989).

The role played by environmental variables is important and so is the effect of spatial heterogeneity in determining species assemblages (Borcard *et al.,* 1992). Although some species may share a common spatial structuring, mainly as the result of spatially structured environmental variables, thus allowing this common spatial structure to show up in both dependent and independent biotic variables (Borcard *et al.,* 1992).

It is important to have a final model that is able to partition the total variation of species data (e.g. environmental, spatially structured, unexplained and non-spatial environmental variables) (Borcard *et al.,* 1992). Therefore, trend surface analysis and partial linear regression approaches were used here to quantify the variation explained in total species density and abundance by environmental variables (biotic and abiotic) and spatial position (Legendre & Legendre, 1998; Botes *et al.,* 2006).

Trend surface analysis was used to identify the combination of spatial variables that explained significant amounts of variation in dependent variables (Legendre and Legendre 1998). The effect of linear and more complex spatial structures on dependent variables were extracted using a third order polynomial (Borcard *et al.,* 1992; Botes *et al.,* 2006):

$$f(x,y) = b_0 + b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$$

where x and y were longitude and latitude respectively.

Partial linear regression was then conducted where the best-fit trend surface and environmental models were combined. The final model had both spatial and environmental terms and was used to partition explained variance in species richness and abundance into four components (van Rensburg *et al.,* 2002; Botes *et al.,* 2006): (1) non-environmental spatial (variance explained by space alone); (2) spatially structured environmental (2) non-spatial environmental (variance explained by environmental variables alone); and (4) unexplained or residual variation (Borcard *et al.,* 1992; Legendre & Legendre 1998).

The species response models were determined based on gradient length (beta diversity in community structure) of a Detrended Correspondence Analysis (DCA) in CANOCO 4.54 (ter Braak & Šmilauer, 2008) and the use of either linear or unimodal species responses. If the length of the longest axis was less than three, a linear species response was assumed and redundancy analysis (RDA) was used (Lepš & Šmilauer, 2003). All species with less than five individuals in the entire dataset were removed for this analysis.

To identify environmental variables that explained most of the variation in species composition, a forward selection of environmental variables (a multivariate equivalent of stepwise regression) (Borcard *et al.,* 1992), was used and their significance tested with a Monte-Carlo permutation test. The results were shown as a biplot in which the environmental variables were depicted as arrows and samples as symbols (Lepš & Šmilauer, 2003). Species sample relationships were also displayed to determine which species contributed to differences between assemblages. Only species with more than 70% of their variability explained by the biplot were included. As with species density and abundance, partial constrained analysis was done to partition out the effect of space in species matrices (Borcard *et al.,* 1992). Partial canonical ordination of the species and spatial matrices, while controlling for the effect of environmental descriptors, enabled the partial removal of the spatial component.

The IndVal method was used to identify indicator species for each vegetation type and aspect along the transect (Dufrěne & Legendre, 1997). Groups of ant assemblages were first identified using group average linking hierarchical clustering in Primer v.6.1.6 (PRIMER-E Ltd, Clarke & Gorley, 2006) to aid the identification of groups of ant assemblages across the transect.

When using the indicator value methods, the degree of specificity (uniqueness to a particular site) and fidelity (frequency within the vegetation type/aspect) was assessed (van Rensburg *et al.*, 2002) and the species with highest indicator value (IndVal) were identified as reliable and representative indicators of the site/slope within which they occur. Only species with significant IndVal greater than 70% were selected (for further discussion, see van Rensburg *et al.,* 1999; McGeoch *et al.,* 2002; Botes *et al.,* 2006).

CHAPTER FIVE: RESULTS

5.1 Introduction

This chapter provides summarized data, results and analysis of the research.

5.2 Research Findings

5.2.1 Analysis of Patterns of Ant Species Richness, Density and Abundance along the Transect.

A total of 75 ant species representing 27 genera in seven subfamilies (20,051 individuals) were collected during the two sampling events (Appendix C). The subfamily Myrmicinae, with 35 species and 10 genera, had the greatest representation followed by the subfamily Formicinae (20 species and 5 genera). The subfamily Ponerinae had more genera (7) than the Formicinae (5 genera), but fewer species (15 vs 20) (see Appendix C). The most speciose genera were *Camponotus* (13 species), *Pheidole* (9 species) and *Pachycondyla* (6 species) while three others (*Tetramorium, Meranoplus and Monomorium*) had 5 species each.

The site 09S had the highest number of observed species followed by 12N, while 17N had the lowest observed species followed by 12S (Table 3). Sample-based species rarefaction curves for the transect as a whole approximated asymptotes for the two sampling periods indicating that most of the species were collected (see Fig. 4). Although six of the 11 sites in the inventory completeness, namely: 12N, 14N, 14S, 16S, 12S and 12S2 (See Table 2) had rarefaction curves and estimators which did not converge closely to the highest observed species density for these sites, the rest did (including for the whole transect) (see Table 2, Table 3, Appendix D). Similarly to what has been reported in Botes *et al.* (2006), the 9% of singletons and 8% doubletons were the reasons for the difference between observed and other species richness estimators.

Table 2 Inventory completion based on six species richness estimators: Chao 1, Chao 2, Jack 1, Jack 2, Bootstrap and MMmeans (1 run) for ant assemblages along the Soutpansberg elevational transect for the 2009/10 season.

Sites	Minimum	Maximum
08N	81%	98%
10N	64%	97%
12N	51%	82%
14N	54%	87%
17N	70%	93%
16S	56%	84%
14S	44%	83%
12S	35%	91%
12S2	48%	82%
10S	67%	91%
09S	66%	87%
Whole transect	81%	91%

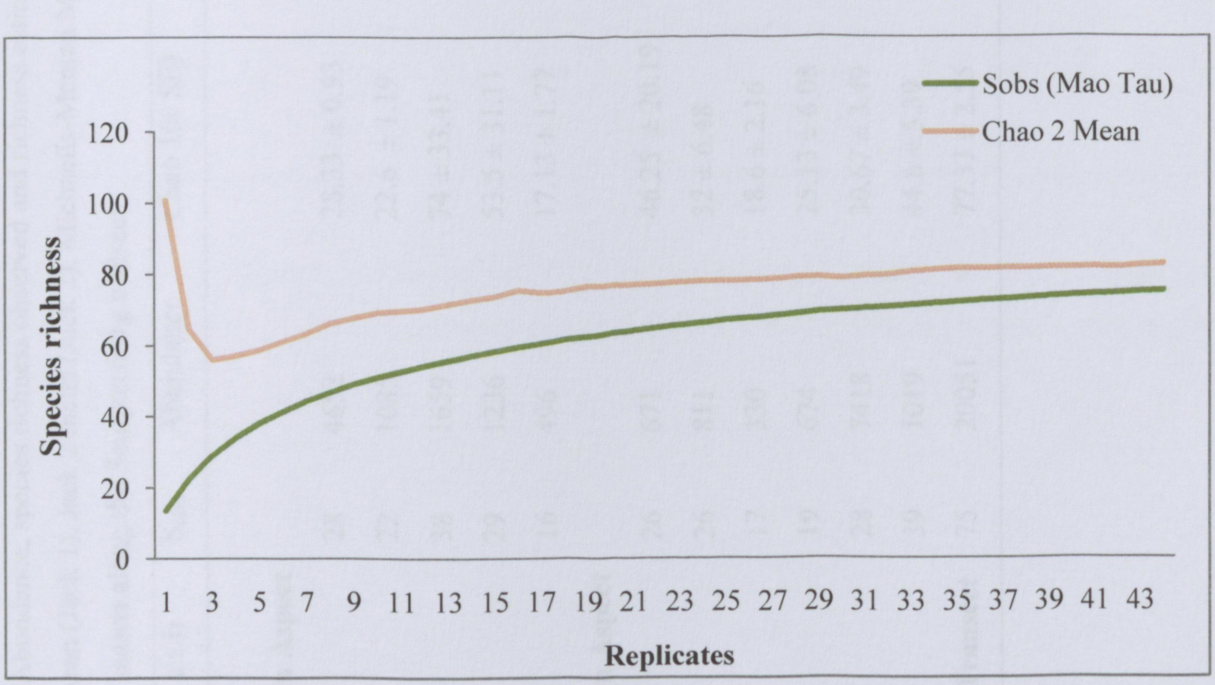


Figure 4 Sample based species rarefaction curves of ant assemblages for the whole transect.

Table 3 Abundance, species richness observed and richness estimates based on six estimators: Chao 1 mean (Chao 1), Chao 2 Mean (Chao 2), Jack 1 mean (Jack 1), Jack 2 mean (Jack 2), Michaelis-Menten Mean richness estimator (MM_{mean}) and Bootstrap mean (Bootstrap) for the 2009/10 season along the Soutpansberg transect.

Sites (m a.s.l)	S_{obs}	Abundance	Chao 1(± SE)	Chao 2 (± SE)	Jack 1	Jack 2	MM_{mean}	Bootstrap
Northern Aspect								
08N	28	4652	28.33 ± 0.93	30.19 ± 2.59	33.25	34.54	34.54	30.72
10N	22	1085	22.6 ± 1.19	24.72 ± 2.78	29	29.86	29.86	25.27
12N	38	1659	74 ± 33.41	78.33 ± 24.64	57.25	69.89	69.89	46.27
14N	29	1236	53.5 ± 31.11	36.14 ± 5.9	37.75	40.75	40.75	33.28
17N	16	496	17.13 ± 1.77	19.6 ± 3.85	21.25	22.54	22.24	18.57
Southern Aspect								
16S	26	671	46.25 ± 20.19	38 ± 9.19	36.5	41.64	43.63	30.84
14S	26	811	32 ± 6.48	58.67 ± 26.33	38.25	46.82	36.57	31.17
12S	17	330	18.6 ± 2.16	47.25 ± 28.68	26.63	33.59	30.7	21.01
12S2	19	674	25.13 ± 6.08	39.17 ± 17.42	66.36	34.95	29.95	23.13
10S	28	7418	30.67 ± 3.49	33.06 ± 4.43	35.88	37.48	41.63	32
09S	39	1019	44.6 ± 5.39	48.55 ± 6.43	53	58.57	58.73	45.64
Whole Transect	75	20051	77.33 ± 2.55	82.62 ± 5.68	87.7	91.72	82.17	81.33

According to individual-based rarefaction (Coleman, 1981)to330 individuals, 09S was the most species-rich with 29 species, followed by 12N (24 species). The least species-rich sites were the summit (17N) and 10S, both with 14 species (Fig. 5). Species density correlated with species richness at all sites except for 12N and also at 10S, where it was considerably greater because *Pheidole megacephala* (Fabricius, 1793) was particularly abundant (Fig. 6, Appendix C). There was a peak in species richness at mid-elevations of the northern aspect and species richness was highest at 09S at the southern aspect(Fig. 5).

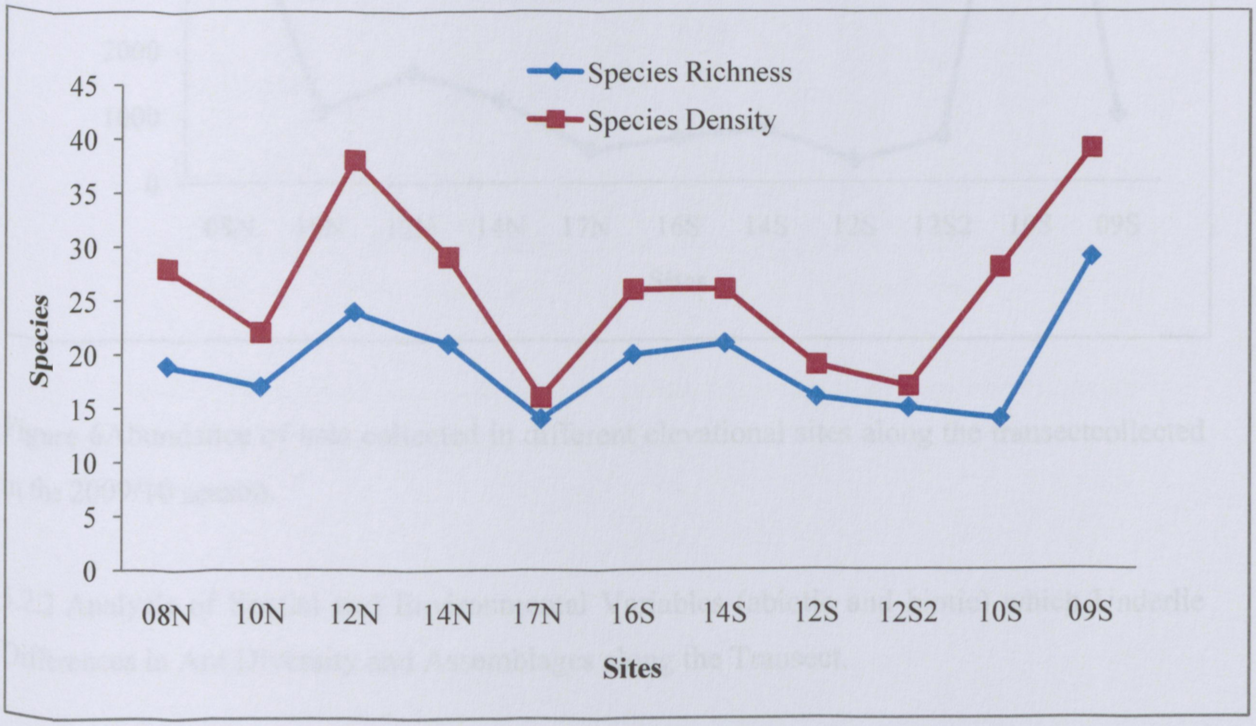


Figure 5 Species richness values derived from individual-based species accumulation curves and species density of ant assemblages across the different elevational sites collected in the 2009/10 season.

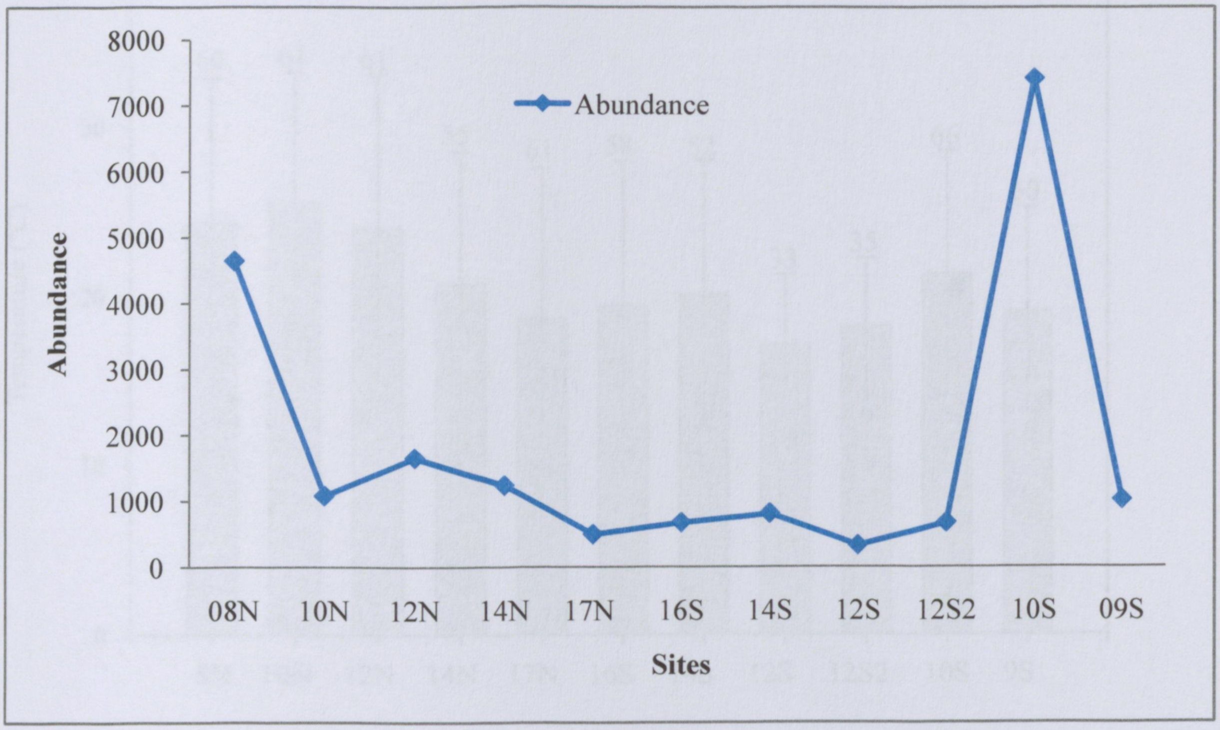


Figure 6 Abundance of ants collected in different elevational sites along the transectcollected in the 2009/10 season.

5.2.2 Analysis of Spatial and Environmental Variables (abiotic and biotic) which Underlie Differences in Ant Diversity and Assemblages along the Transect.

The highest mean temperature was found at 10N (rocky screed site with open shrubland) and the lowest at 12S (red clay-loam soil site with closed woodland) (Fig. 7). The lowest absolute minimum temperature was recorded at the summit and the highest at 10N. The highest absolute maximum temperature was found at 10S and the lowest at 12S (Fig. 7). Mean monthly temperature range was the highest at the summit and the lowest in the forest (Fig. 8).

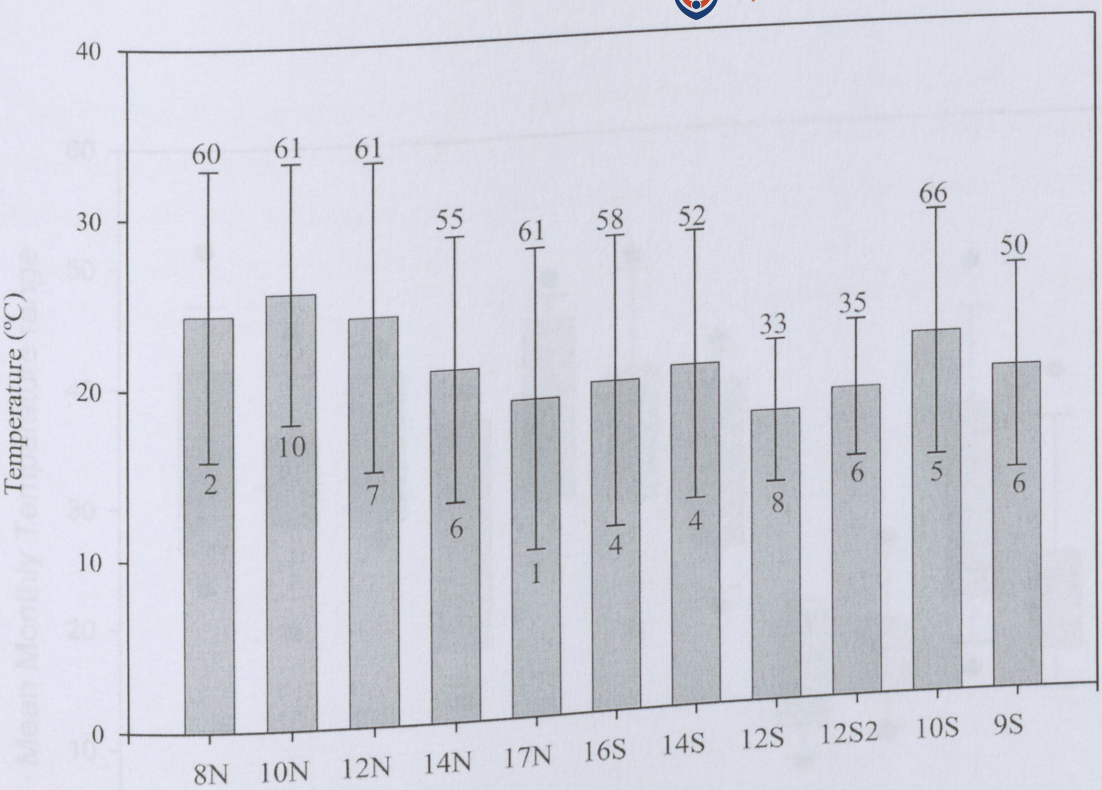


Figure 7 Mean monthly temperature, absolute maximum temperature and absolute minimum temperature for the transect between April 2009 – June 2010.

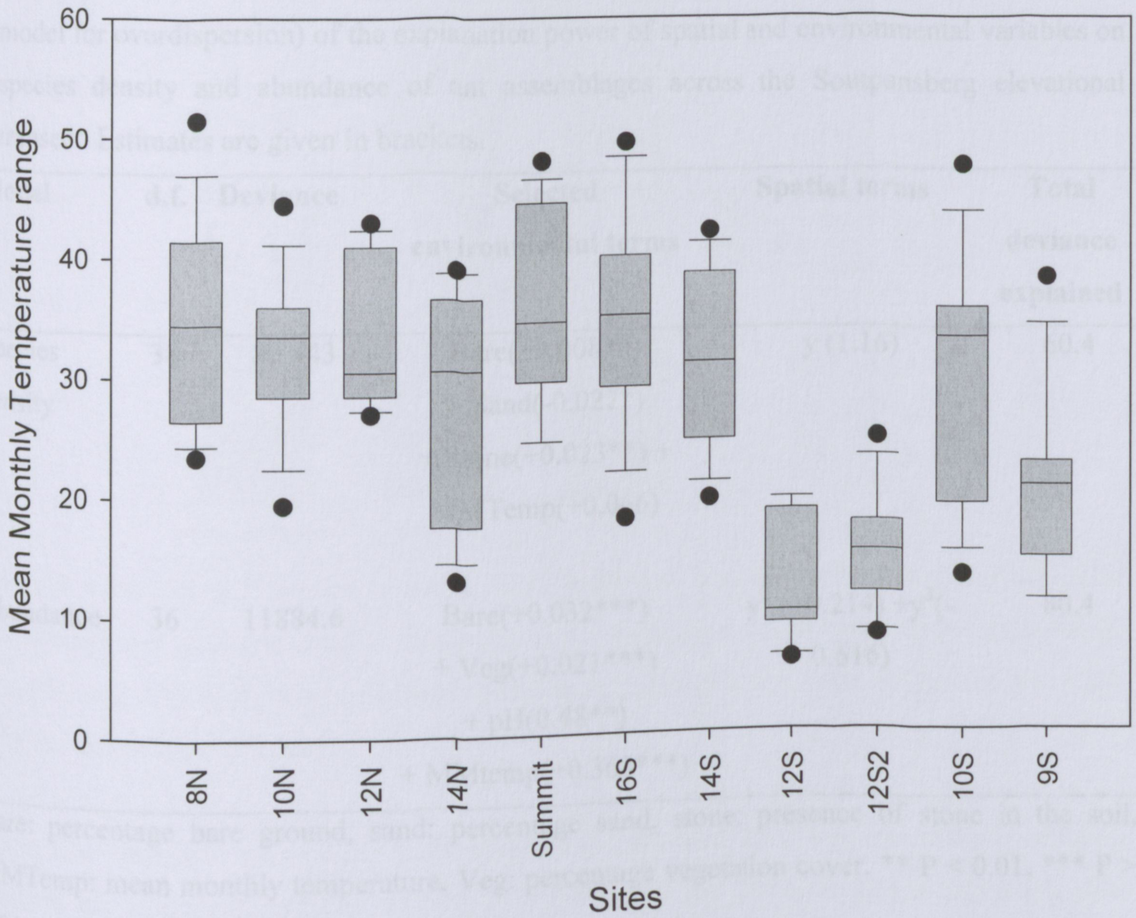


Figure 8 Mean monthly temperature range for different elevational sites along the transect between April 2009 – June 2010.

The significant terms in the Generalized Linear Model (GLM) fitted to the species density of ants per site across the mountain were related to three environmental variables, which were percentage sand, presence of stone in the soil and percentage bare ground (Table 4). Percentage sand was the only variable that was negatively correlated with species density whereas mean monthly temperature was positively related but was not significant in the final model. There were four environmental variables across the transect that were significantly related to species abundance, namely; mean monthly temperature, pH, percentage bare ground and percentage vegetation cover (Table 4).

Table 4 Generalized linear model (Poisson error distribution, log link function, quasi-poisson model for overdispersion) of the explanation power of spatial and environmental variables on species density and abundance of ant assemblages across the Soutpansberg elevational transect. Estimates are given in brackets.

Model	d.f.	Deviance	Selected environmental terms	Spatial terms	Total deviance explained
Species density	38	80.443	Bare(+0.008**) + Sand(-0.022*) + Stone(+0.023**) + MMTemp(+0.066)	y (1.16)	60.4
Abundance	36	11884.6	Bare(+0.032***) + Veg(+0.021***) + pH(0.48**) + MMtemp(+0.363***)	y^2 (+0.214) +y^3(-0.616)	80.4

Bare: percentage bare ground, sand: percentage sand, stone: presence of stone in the soil, MMTemp: mean monthly temperature, Veg: percentage vegetation cover. ** $P < 0.01$, *** $P > 0.01$.

Environmental variables explained almost 61% of the variation in ant species density, only 5% of this could be ascribed to the geographical position of the sites whereas space alone explained only 1 % (Fig. 9). Almost 80% of the variation in ant abundance along the transect was the result of environmental variables. Local effects of environmental variables accounted for 32% of the total variation whereas the major cause of the spatial pattern in species variation was the result of spatially structured environmental descriptors (Fig. 9). The unexplained variation was fairly low and might be attributed to stochastic error.

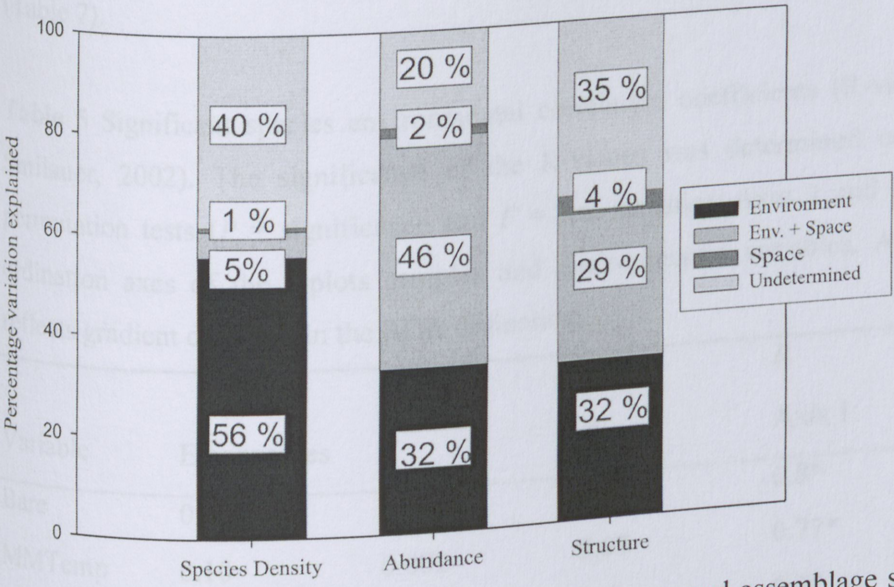


Figure 9 Percentage variation in ant density, abundance and assemblage structure explained by spatial and environmental variables along the Soutpansberg transect based on variation partitioning with Generalized Linear Modelling for species density and abundance and RDA for ant assemblage structure.

The first canonical axis in the RDA (Fig. 10b) explained 25.7% of the sample variation across the whole transect (F = 8.440, P = 0.04) and the first and second canonical axes together explained 34.3 % (F = 1.9, P = 0.01). Seven environmental variables contributed significantly to the variance explained in ant assemblages (Table 5). The first axis represented an environmental gradient of increasing bare ground, mean monthly temperature, percentage sand and sodium in the soil, decreasing leaf litter and area (Fig. 10b, Table 5). The second axis represented an environmental gradient of decreasing absolute minimum monthly temperature (Fig. 10b, Table 5).

Percentage bare ground and mean monthly temperature were the most important environmental variables followed by percentage sand in the soil, absolute minimum monthly temperature, area, percentage leaf litter, available area and sodium (Table 5, Fig. 10b). Sixteen species had more than 30% of their variability explained by the ordination subspace across the transect (Fig. 10a). Three of these species were identified as associated with Arid North Bushveld (*Meranoplus* sp.05, *Tapinoma* sp.01 and *Pheidole* sp.04) and one species was associated with Soutpansberg Leached Sandveld (*Camponotus fulvopilosus* group) (Table 7).

Table 5 Significant species environmental correlation coefficients (R-values, ter Braak & Šmilauer, 2002). The significance of the R-values was determined using Monte Carlo permutation tests (P = significance and F = test statistic). Axes 1 and 2 are the first two ordination axes of the biplots samples and environmental variables. A negative R-value reflects gradient direction in the RDA ordination.

				R	
Variable	Eigenvalues	*P*	*F*	Axis 1	Axis 2
Bare	0.19	0.002	9.32	0.8*	-0.27
MMTemp	0.10	0.002	5.07	0.77*	0.38
Sand	0.07	0.002	4.35	0.3*	0.35
AMin	0.05	0.002	2.96	-0.17	-0.89*
Leaf	0.03	0.004	2.33	-0.41*	-0.24
Area	0.03	0.03	1.86	-0.05	-0.22
Na	0.03	0.008	2.03	0.54*	0.06

Sum of all canonical eigenvalues: 0.628

AMin, Absolute minimum monthly temperature; Bare, percentage bare ground; MMtemp, mean monthly temperature.

Analysis of similarity had indicated no significant differences between ant assemblage structure among the following elevational sites: 09S = 10S, 09S = 14S 10N = 12N, 12S = 12S2, 14S = 16S and 16S = 17N (Table 6).

Table 6 List of pair-wise comparisons of elevational sites that were not significantly different in one-way ANOSIM in Primer v.6.1 for the 2009/10 season

Elevational sites	*R (P)*
09S vs 10S	0.026 (0.057)
09S vs 14S	0.051 (0.057)
12S vs 12S2	0.208 (0.114)
14S vs 16S	0.104 (0.829)
16S vs 17N	0.052 (0.371)
10N vs 12N	0.188 (0.0143)

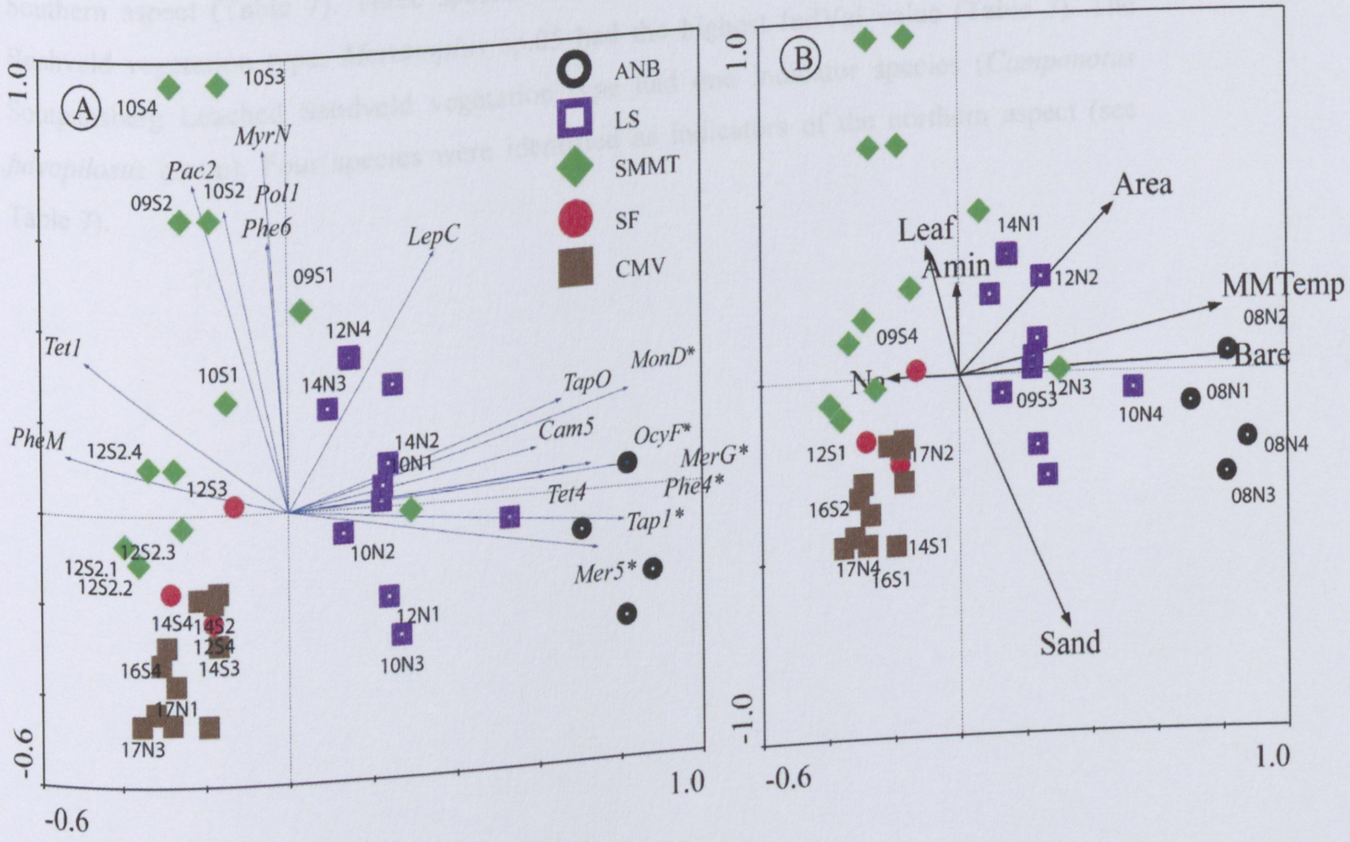


Figure 10a)RDA ordination (biplot, sample scaling) of (A) ant assemblages and species with more than 30% of their variability explained by the ordination subspace and (B) of environmental variables that explained significant amounts of variation in the different vegetation types and elevational sites. ANB = Arid North Bushveld, LS = Soutpansberg Leached Sandveld, CMV = Soutpansberg Cool Mistbelt Vegetation, MSB = Makhado Sweet Bushveld, SMMT = Soutpansberg Moist Mountain Thicket, SF = Soutpansberg Forest.

Cam5, *Camponotus* sp05, *LepC* = *Lepisiota capensis*, *Mer5** = *Meranoplus* sp.05, *MerG** = *Meranoplus gabler*, *MonD** = *Monomorium damarense*, *MyrN* = *Myrmicaria natalensis*, *OcyF** = *Ocymyrmex fortier*, *Pac2* = *Pachycondyla* sp.02, *Phe4** = *Pheidole* sp.04, *Phe6* = *Pheidole sp06*, *PheM* = *Pheidole megacephala*, *Pol1* = *Polyrhachis schistacea*, *TapO* = *Tapinoma* sp.01, *Tap1** = *Tapinolepsis* sp.01, *Tet1* = *Tetramorium* sp.01, *Tet4* = *Tetramorium* sp.04.

5.2.3 Analysis of data on Indicator Species along the Transect

The IndVal analyses showed that eleven species had significant IndVal values higher than 70% along the transect (Table 7). There were no indicator species for Soutpansberg Cool Mistbelt, Soutpansberg Moist Mountain Thicket and Soutpansberg Forest, and also the Southern aspect (Table 7). Three species were identified as indicators of the Arid North Bushveld vegetation type, *Meranoplus* sp.05 had the highest IndVal value (Table 7). The Soutpansberg Leached Sandveld vegetation type had one indicator species (*Camponotus fulvopilosus* group). Four species were identified as indicators of the northern aspect (see Table 7).

Table 7 List of species that had significant indicator values (IndVal) larger than 70% for one of the two aspects and two of the five vegetation types along the Soutpansberg elevational transect for the 2009/10 season.

Aspect and Vegetation types	Species	%IndVal
Aspect		
Northern	*Ocymyrmex fortior*	99.31*
	Pheidole sp.04	71.43*
	Meranoplus gabler	71.43*
	Monomorium damarense	75.96*
Vegetation Types		
ANB	*Tapinolepsis Sp.01*	98.21*
	Pheidole Sp.04	96.24*
	Meranoplus Sp.05	100*
LS	*Camponotus fulvopilosus* group	89.09*

ANB; Arid North Vegetation, LS; Leached Sandveld

CHAPTER SIX: DISCUSSION, CONCLUSION AND RECOMMENDATION

6.1 Introduction

This chapter first provides the discussion of the findings in this study. It also draws conclusions and provides recommendations to address potential future problems.

6.2 Discussion

6.2.1 Ant diversity and Species Richness

A study in the Greater Cederberg Biodiversity Corridor collected 72 379 individuals in 85 ant species belonging to 24 genera along a 162 km transect with 17 elevational sites (Botes *et al.*, 2006). The Soutpansberg transect was ten times shorter, only contains 11 sites and although the current study collected fewer individuals (20 051) and marginally fewer species, it recorded more genera (24 vs 27). Parr *et al.*'s (2004) study of the impacts of fire on ant assemblages in the savanna of the Kruger National Park, using a comparable methodology, recorded 160 species in 37 genera but with a spatial extent 20 times that of the current study.

These findings were in accordance with evidence provided by Hahn (2002) (plants) and Foord *et al.* (2008) (spiders) for high diversity at higher taxonomic levels (genera, families) in the region.

The high diversity of ants found in the subfamilies Myrmicinae and Formicinae is a commonly recorded diversity pattern in South Africa (Samways, 1983, 1990; Swart, 1999; Lindsey & Skinner, 2001; Botes *et al.*, 2006).

6.2.2 Patterns of ant Species Richness, Density and Abundance

There was no clear species richness pattern of ants over the whole transect. The northern aspect, however, showed a peak at mid-elevation sites. This pattern was similar to that in several other studies of ants (Samson *et al.*, 1997; Fisher, 1998, 2004). This appeared to be true, particularly in arid regions (Sanders *et al.*, 2002, 2003). The southern aspect, in contrast, showed a peak at lowest elevation, a decline in mid-elevation while species richness increased towards the higher elevation but quickly declined at the highest elevation. This pattern was unusual but not totally unexpected as there were three biomes on the southern aspect and only one on the northern aspect.

The current study observed high species richness at sites with high percentage of bare ground. In contrast, Araújo & Fernandes (2003) suggested that the decline of ant species richness in their study might be because of reduced habitat complexity. The highest richness reported at mid-elevation and low elevation sites (12N & 09S) of this transect was similar in ant diversity patterns across other elevational transects in other regions (*inter alia* Samson *et al.,* 1997).

Sites with highest ant abundance did not have the highest species richness (see Fig.5, Fig. 6). Botes *et al.* (2006) and Parr *et al.* (2005) argued that species richness can be low where there is high abundance, as well as low abundance and they further suggested that this was a result of competition and environmental stress respectively. Site 10S had the highest abundance because of the high numbers of *Pheidole megacephala* (Fabricius, 1973) but together with 17N it had the lowest species richness (see Fig. 5, Fig. 6).

6.2.3 Ant Species Richness and Community Structure

The results from RDA suggested that the percentage bare ground, percentage sand in the soil and mean monthly temperature explained some of the differences in ant assemblages found along the transect (Table 5 and Fig. 10b). Bare ground and high temperature provided good foraging conditions for a larger number of ant species because many preferred open and hot habitat as these conditions improve the efficiency of locating, retrieving and defending food (Andersen, 2000).

The highest species richness at 09S, one of the sites with the highest available area, was in accordance with the geographical area hypothesis (Dunn *et al.,* 2010), although in the current study, area did not have significant terms in the GLM for species density, it was significant in explaining ant assemblage structure along the transect. Site 09S was also a heavily overgrazed and bush-encroached, predominantly by *Dichrostachys cinerea*. Similarly, a disturbed site on an elevational gradient in the Philippines (Samson *et al.,* 1997) also had a high peak value for species richness. Kumar & Mishra (2008) have pointed out that ants are efficient invaders of new habitats and this attribute could act to increase species richness.

A decrease in ant assemblage structure was correlated with an increase in leaf litter and high vertical complexity of the vegetation in the Soutpansberg Forest and Soutpansberg Moist Mountain Thicket (except at 09S) (see Fig. 10b). While the size of these forests might have played a role in this as they occupy the smallest area on the transect, Andersen (2000) observed that structural complexity reduced the ability of epigaeic ants to exploit food resources as a result of extensive leaf litter and Brühll *et al.* (1999) made the same observation. In the woodland of Australia, Lassau & Hochuli (2004) observed a negative correlation between ant richness and habitat complexity.

Relatively diverse ant assemblage structure on the North Arid Bushveld and Leached Sandveld vegetation type appeared to be related to low percentage leaf litter and increased percentage bare ground (see Fig. 10a; b). These two vegetation types (but not all sites of the Leached Sandveld, specifically 12N) were dominated by sandy and heavily textured soils. Andersen (2000) has pointed out that these kind of soils are preferred by ground-dwelling ant species. There was also a strong positive correlation between % sand and assemblage structure (Fig. 10b).

6.2.4 Ant Assemblage, Environmental and Spatial Variables

The significant relationship between species density and three environmental variables (percentage bare ground, percentage sand in the soil, and stone) showed that ants prefer open and hot habitat (Table 4). Also the significant contribution of variance explained by mean monthly temperature (Table 5) in ant assemblages across the transect probably reflected the occurrence of thermophilic species at sites with high species richness, especially the lower elevational sites of both southern and northern aspect. High temperatures allow ants, which are typically thermophilic, to forage more and harvest more energy (Dunn *et al.*, 2009). This includes most species in the subfamilies Myrmicinae and Formicinae, which are diverse (see Hölldobler & Wilson, 1990).

Generally, hot and open habitats support hot climate specialist ant species (Lassau & Hochuli, 2004). Sites 08N, 10N, 12N, 14N and 09S were regarded as hot and open, and the observed genera (e.g. *Meranoplus* and *Monomorium*) have been identified to belong to this functional group before by Andersen (1997a; 2000) and these genera were most common at these habitat (open and hot habitat). Most of these open and hot sites (e.g. 10N and 09S) also supported larger Ponerinae (e.g. *Pachycondyla, Platythyrea* and *Leptogenys*, see Appendix C) which were identified to belong to the specialist predators functional group by Andersen (1997a).

In this study, 60% of variation (environmental, spatially structured environmental variables and space) was explained by the GLM predicted species density. Energy could potentially explain the remaining residuals. Although this study observed few productive sites of the northern aspect, with rainfall ~200 mm/year (an indirect measure of productivity) were very species-rich, thus contradicting what was predicted by the species energy theory (Rosenzweig, 1995; Hawkins *et al.*, 2003). The highly disturbed site in the southern aspect, 09S and the northern aspect sites (dry and hot surfaces) supported more species than other southern aspect sites (~700 mm/year) with closed habitat, and moist soil surface.

Delsinne *et al.* (2010) argued that ant species richness was not correlated with precipitation because they are social organisms. Sociality enables them to exploit and recover food even in habitats which were less productive. Furthermore it has been argued that the effects of aridity on ants through physiological stress were maybe less pronounced for ground foraging species because they were adapted to hot environments (Hölldobler & Wilson, 1990; Delsinne *et al.*, 2010).

Recent climate change predictions for the Limpopo Province suggested that there will be an increase in temperature and rainfall in this Province (Davies *et al.*, 2010) and CO_2. The latter is believed to increase woody recruitment in arid areas (Bond & Midgeley, 2000). In the low elevational sites of the southern aspect of this study, such changes would thus increase woody plant species resulting in more shading and increased leaf litter.

These changes will affect the current ant assemblages (e.g. *Polyrhachis schistacea* (Gerstaecker, 1859) and *Myrmicaria natalensis* (Smith, 1858) as they are adapted to the present habitat (Bushveld on the southern aspect, see Fig. 10a), and they might shift to similar habitat on the northern aspect, or disappear totally. The changing environment, however, would probably benefit a few species e.g. *Dorylus helvolus* which appear to prefer closed woodland habitat with high leaf litter content. In addition, such changes in climate would affect the chemical, physical and biological properties of the soil, as it has been reported that change as the result of an increase in temperature may have negative effects on some of the soil elements such as organic soil carbon and nitrogen (Link *et al.,* 2003). This would probably affect plant distributions and thereby also affect ant assemblages.

Studies have shown that temperature, leaf litter, area, percentage sand in the soil and several vegetation variables, including percentage bare ground, had significant influence on ant assemblages along elevational transects (Botes *et al.,* 2006). A study in the woodland and adjacent heath of southern-eastern Australia by Andersen (1986) and another one in a regional scale using pitfall traps in the New England bogs and forest, reported ant species density to be higher in more complex habitats (Gotelli & Ellison, 2002). In contrast, the present study found that sites with a high percentage of bare ground and reduced complexity had higher ant diversity and assemblages. A recent study by Gibb & Parr (2010) provides evidence that complex habitat made ants to recover resources slower.

The small amount of variation accounted for by space suggested that no spatially structured process had been left out of the analysis. Species density and abundance of ants were largely under environmental control or that of environmental variables that are spatially structured. This also pointed to local processes (e.g. competition) that explained very little variation and might be caused by the large climatic and topographic variability across the mountain (Andersen, 1997b).

This trend contrasted with that found for ants of the Cederberg where environmental variables explained 38% in ant species density and 64% in ant abundance (Botes *et al.,* 2006), while for this study it was 60% and 80% respectively. This further suggested a limited role for dominance in the Soutpansberg ants that could be largely under the control of environmental stress or limited habitat suitability.

Parr *et al.* (2005), however, pointed to the importance of regional processes as well as habitat heterogeneity. Patch dynamics might be important in the Soutpansberg, with its varied topography and rapidly changing landscapes. Heterogeneity and patchiness in communities has received considerable attention in the Savanna biome in particular (van Coller *et al.,*

2005) and has been identified as a possible explanation for scatter around the dominant species relation in ants (Parr *et al.*, 2005).

6.2.5 Indicator Species of Vegetation Types and Aspect

The Arid North Bushveld had an ant assemblage distinct from other vegetation types. Variation in the ant assemblages of the northern and southern aspect have reflected influence of habitat structure on the distribution of ants along the transect. Similar results were reported by Lassau & Hochuli (2004) about the influence of habitat structure on ant diversity.

Distinct differences were evident in the ant assemblages found along the northern aspect but there was considerable overlap between the assemblages of the southern aspect evidenced by the absence of any indicator taxa for the vegetation types and aspect (Table 7). The lack of distinctive taxa associated with the southern aspect and its vegetation types, except maybe *Dorylus helvolus* (Emery, 1895) which was found only in the forest, could be the result of the recent (<100 years) loss of grasslands on the Soutpansberg because of extensive bush encroachment (Hahn, 2006) partly explained by elevated CO_2 levels (Bond & Midgeley, 2000; Bond, 2008).

6.3 Conclusion

This study determined the pattern of ant species richness, density, abundance and assemblage structure along the Soutpansberg elevational transect. There was no clear pattern of species richness or density along the whole transect, but the northern aspect had a peak in species richness/density at mid-elevation. The highest species richness and density was observed at low and mid-elevational sites (i.e. 09S & 12N) and those with highest species richness were ones with low ant abundance. Only the Arid North Bushveld vegetation type had an ant assemblage distinct from the other vegetation types.

Environmental variables (non-spatial and spatial) explained considerably more variation of ant diversity than space alone and local processes, e.g. competition, explained very little. The significant environmental variables in the GLM fitted to species density across the transect, were percentage sand in the soil, bare ground and stone volume. The significant environmental variables for abundance were bare ground, vegetation, pH and mean monthly temperature.

The significant environmental variables that explained variation in ant assemblages were bare ground, mean monthly temperature, percentage sand in the soil, absolute minimum temperature, leaf litter, area and sodium. The predicted changes in temperature and rainfall due to climate change (Davies *et al.,* 2010) could shift the assemblages from the southern to the northern aspect following the direct effects of such changes on environmental variables that have explained significant variation in ant assemblages in the current study.

The rate of these changes would depend on how close individual species were to their thermal tolerances based on current temperature regimes and predicted increases of temperature in future. Increased rainfall and CO_2 levels would certainly result in increasing density of thickets on the southern aspect. This would cause a reduction in ground vegetation cover and temperatures (reduced light availability) and bare ground (increased leaf litter) which could translate into lower ant abundance and diversity. Species associated with these thickets are expected to increase. In addition, indicator taxa identified at the lower elevations of the northern aspect could be expected to move uphill depending on their current thermal tolerances following a regional increase in temperature due to a steeper adiabatic lapse rate.

6.4 Recommendation

Ongoing monitoring of this transect would test predictions that have been suggested in this study. Recent predictions that there will be an increase in temperature and rainfall in the Limpopo Province, make it imperative that there is ongoing monitoring of the transect which is highly diverse at high taxonomic levels and it is obviously important to conserve this.

Studies dealing with the functioning of the ecosystem are vital in understanding and explaining any changes. The latter would also help in developing strategies for mitigating the impact of climate change on the fauna.

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Appendix A: Geographical co-ordinates of the 44 replicates from 11 elevational sites and their elevational ranges.

Sites	Replicates	Elevation	Coordinates
Southern Aspect			
800 m (08N)	8N1	811 m a.s.l.	22 56.683º S, 29 26.359º E
	8N2	808 m a.s.l.	22 56.649º S, 29 26.195º E
	8N3	808 m a.s.l.	22 56.633º S, 29 26.015º E
	8N4	813 m a.s.l.	22 56.641º S, 29 25.852º E
1000 m (10N)	10N1	1022 m a.s.l.	22 58.157º S, 29 24.979º E
	10N2	980 m a.s.l.	22 58.028º S, 29 25.086º E
	10N3	984 m a.s.l.	22 58.016º S, 29 24.856º E
	10N4	1013 m a.s.l.	22 58.062º S, 29 24.668º E
1200 m (12N)	12N1	1215 m a.s.l.	22 59.504º S, 29 25.421º E
	12N2	1199 m a.s.l.	22 59.418º S, 29 25.269º E
	12N3	1198 m a.s.l.	22 59.269º S, 29 25.342º E
	12N4	1189 m a.s.l.	22 59.351º S, 29 25.500º E
1400 M (14N)	14N1	1419 m a.s.l.	23 00.018º S, 29 25.545º E
	14N2	1412 m a.s.l.	23 00.018º S, 29 25.715º E
	14N3	1370 m a.s.l.	22 59.893º S, 29 25.831º E
	14N4	1433 m a.s.l.	23 00.202º S, 29 25.482º E
1700 m (17N)	17N1	1731 m a.s.l.	23 01.445º S, 29 25.745º E
	17N2	1695 m a.s.l.	23 01.458º S, 29 25.594º E
	17N3	1675 m a.s.l.	23 01.358º S, 29 25.883º E
	17N4	1693 m a.s.l.	23 01.460º S, 29 25.901º E
Southern Aspect			
900 m (09S)	9S1	903 m a.s.l.	23 03.846º S, 29 29.400º E
	9S2	900 m a.s.l.	23 04.030º S, 29 29.628º E
	9S3	904 m a.s.l.	23 03.629º S, 29 29.634º E
	9S4	907 m a.s.l.	23 03.420º S, 29 29.808º E
1000 m (10S)	10S1	1032 m a.s.l.	23 02.961º S, 29 28.680º E
	10S2	998 m a.s.l.	23 02.897º S, 29 29.400º E

	10S3	1000 m a.s.l.	23 02.908° S, 29 29.162° E
	10S4	1028 m a.s.l.	23 02.753° S, 29 29.185° E
1200 m (12S)	12S1	1206 m a.s.l.	23 02.417° S, 29 27.033° E
	12S2	1203 m a.s.l.	23 02.562° S, 29 26.577° E
	12S3	1221 m a.s.l.	23 02.378° S, 29 27.195° E
	12S4	1207 m a.s.l.	23 02.313° S, 29 28.608° E
1200 m (12S2)	12S2.1	1028 m a.s.l.	23 02.661° S, 29 27.869° E
	12S2.2	1206 m a.s.l.	23 02.638° S, 29 27.691° E
	12S2.3	1203 m a.s.l.	23 02.679° S, 29 27.518° E
	12S2.4	1221 m a.s.l.	23 04.035° S, 29 29.631° E
1400 m (14S)	14S1	1407 m a.s.l.	23 02.071° S, 29 25.863° E
	14S2	1419 m a.s.l.	23 01.583° S, 29 26.251° E
	14S3	1405 m a.s.l.	23 01.885° S, 29 26.549° E
	14S4	1427 m a.s.l.	23 02.033° S, 29 26.073° E
1600 m (16S)	16S1	1591 m a.s.l.	23 01.355° S, 29 26.033° E
	16S2	1623 m a.s.l.	23 01.513° S, 29 25.981° E
	16S3	1523 m a.s.l.	23 01.575° S, 29 25.818° E
	16S4	1587 m a.s.l.	23 01.249° S, 29 26.168° E

Appendix B: Pearson's product moment correlations done in R to avoid collinearity among 15 biotic and abiotic variables.

Appendix C: Subfamilies and ant species collected during September 2009 and January 2010 in different vegetation types. The abundance of the species collected during each sampling period is given. LS = Leached Sandveld, SMMT = Soutpansberg Moist Mountain Thickets, ANB = Arid North Busheveld, CMV = Cool Mistbelt Vegetation, SF = Soutpansberg Forest.

Subfamily and species	Sep-2009	Jan-2010	Vegetation type
Aenictinae			
Aenictus rotundatus (mayr, 1901)	75	29	LS; SMMT
Dorylinae			
Dorylus helvolus (Emery, 1985j)	1	20	LS; SMMT
Dolichoderinae			
Tapinoma sp.01	32	12	ANB; CMV; LS; SMMT
Technomyrmex sp.01	140	48	ANB; CMV; LS; SMMT
Formicinae			
Anoplolepsis (Zealleylla) refuscens (Santschi, 1917)	0	2	CMV
Camponotus fulvopilosus group (Emery, 1920)	12	48	ANB; CMV; LS
Camponotus sp.02	7	32	CMV; SMMT
Camponotus sp.03	2	0	CMV
Camponotus sp.04	4	26	ANB; CMV; LS; SF, SMMT
Camponotus sp.05	31	0	ANB; CMV; LS; SMMT
Camponotus maculatus	2	3	ANB; CMV; LS

(Fabricius, 1782)			
Camponotus sp.7	1	6	LS
			LS; SMMT
Camponotus sp.09	0	31	
Camponotus tanaemyrmex group (Ashmead, 1905b)	1	0	SMMT
Camponotus sp.11	0	19	LS; SMMT
Camponotus sp.12	0	8	SMMT
Camponotus cf. Mayr (Forel, 1916)	0	1	LS
Camponotus dofleini (Forel, 1911)	0	1	LS
Lepisiota capensis (Mayr, 1862)	63	113	ANB; CMV; LS; SF, SMMT
Lepisiota sp.04	2	5	CMV
Lepisiota sp.05	0	1	SMMT
Lepisiota sp.06	3	25	CMV; LS
Polyrhachis schistacea (Gerstaecker, 1859)	2	5	LS; SMMT
Tapinolepsis sp.01	165	743	ANB; CMV; LS; SMMT
Myrmicinae			
Crematogaster Sp.01	3	8	CMV; LS; SMMT
Crematogaster Sp.02	20	2	CMV; SF; SMMT
Crematogaster Sp.03	12	2	CMV; LS; SMMT
Crematogaster Sp.5	1	51	ANB; CMV; LS
Nesomyrmex Sp.01	9	20	ANB; CMV; LS; SF; SMMT
Nesomyrmex Sp.02	1	11	LS; SMMT
Meranoplus sp.01	17	8	CMV; LS; SF
Meranoplus glaber (Arnold,	1	33	ANB; CMV; LS

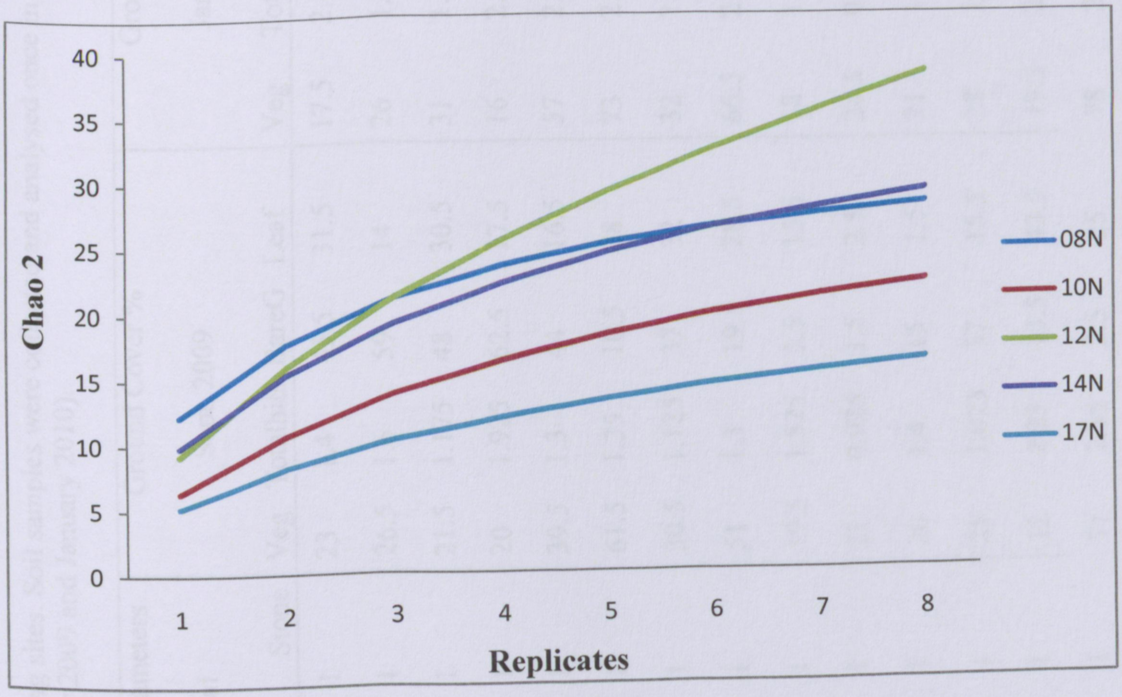
1926)			
Meranoplus sp.03	0	2	CMV; SMMT
Meranoplus sp.04	0	11	CMV; LS; SMMT
Meranoplus sp.05	0	8	ANB
Monomorium damarense (Forel, 1910f)	1462	1221	ANB, CMV; LS; SF; SMMT
Monomorium sp.02	226	552	CMV; LS; SMMT
Monomorium sp.03	4	67	ANB; CMV; LS; SMMT
Monomorium sp.04	66	0	ANB
Monomorium sp.05	30	26	LS; SF; SMMT
Pheidole sp.01	748	329	ANB; CMV; LS; SF; SMMT
Pheidole rugaticeps group (Emery, 1877)	19	2	CMV; LS; SMMT
Pheidole sp.03	298	183	ANB; CMV; LS; SMMT
Pheidole sp.04	181	1270	ANB; CMV; LS; SMMT
Pheidole sp.05	200	10	ANB; CMV; SF; SMMT
Pheidole sp.06	98	85	CMV; LS; SMMT
Pheidole sp.07	185	95	ANB; CMV; LS
Pheidole megacephala (Fabricius, 1793)	820	7015	CMV; LS; SF; SMMT
Pheidole sp.09	240	0	LS
Pyramica sp.01	1	0	LS
Myrmicaria natalensis (Smith, 1858)	93	275	CMV; LS; SF; SMMT
Ocymyrmex fortior (Santschi, 1911g)	73	649	ANB; CMV; LS; SMMT
Solenopsis sp.01	13	106	ANB; LS; SF; SMMT

Solenopsis sp.02	0	28	SMMT
Tetramorium sp.01	322	367	ANB; CMV; LS; SF; SMMT
Tetramorium sp.02	65	46	ANB; CMV; LS; SF; SMMT
Tetramorium setuliferum (Emery, 1895)	39	36	ANB; CMV; LS
Tetramorium sp.04	8	159	ANB; CMV; LS; SMMT
Tetramorium quadrispinosum (Emery, 1886)	92	192	ANB; CMV; LS; SMMT
Ponerinae			
Anochectus traegaordhi (Mayr, 1940b)	2	0	LS; SMMT
Hypoponera sp.01	0	1	SMMT
Hypoponera sp.02	0	2	CMV
Hypoponera Hlavac (Santschi, 1935b)	0	2	SMMT
Odontomachus troglodytes (Santschi, 1914)	1	6	ANB; LS
Pachycondyla sp.01	1	1	LS
Pachycondyla sp.02	8	25	SMMT
Pachycondyla sp.03	0	12	SMMT
Pachycondyla sp.04	1	2	SMMT
Pachycondyla sp.05	0	5	SF; SMMT
Pachycondyla sp.06	0	2	SF
Platythyrea sp.01	3	5	LS
Plectroctena mandibularis (Smith, 1858)	0	3	LS; SMMT
Leptogenys sp.01	0	6	SMMT
Leptogenys sp.02	0	33	CMV

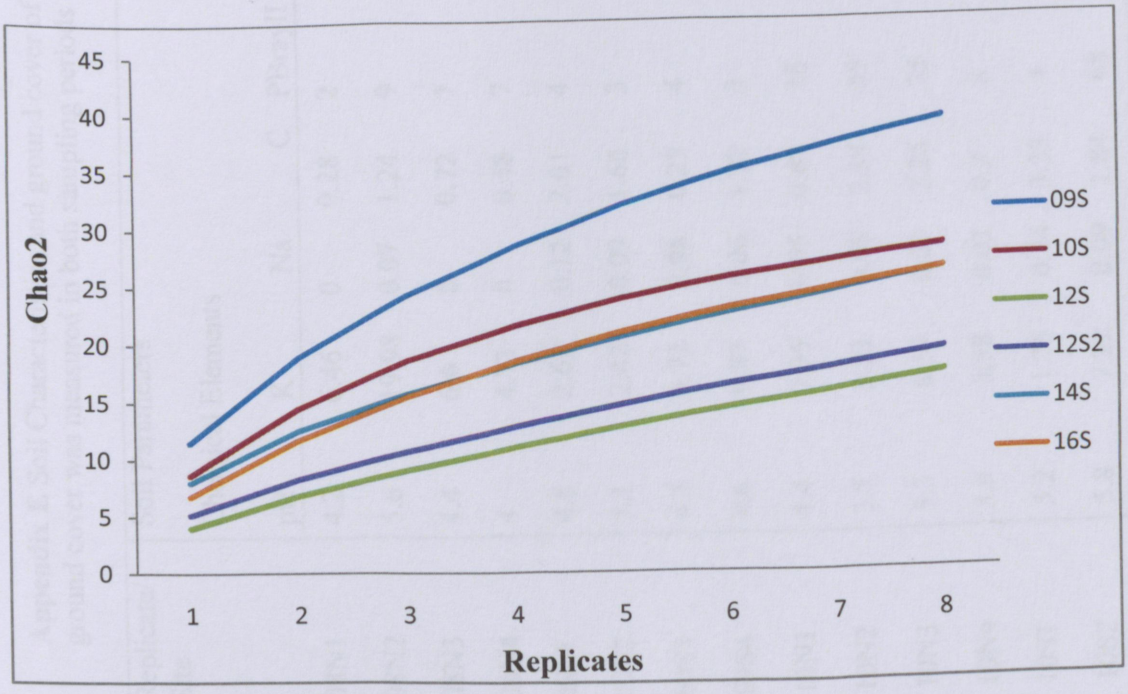
Psedomyrmecinae			
Tetraponera sp.01	0	1	ANB

Appendix D: Sample-based species rarefaction curves of ant assemblages,a) northern aspect Site: 08N, 10N, 12N, 14N, 17N, and b) southern aspect site 09S, 10S, 12S, 12S2, 14S and 16S.

a) Northern Aspect



b) Southern Aspect



Appendix E *Soil Characteristics and ground cover of the sampling sites. Soil samples were collected and analysed once in January 2010 and ground cover was measured in both sampling periods (September 2009 and January 2010).*

Replicate/ Site	Soil Parameters					Soil Parameters		Ground Cover %				Ground Cover %			
	Chemical Elements					Structural		Sept. 2009				Jan. 2010			
	pH	K	Na	C	PBrayII	Sand	Stone	Veg	Totalhits	BareG	Leaf	Veg	Totalhits	BareG	Leaf
08N1	4.2	6.46	0	0.28	2	99	1	23	1.4	45.5	31.5	17.5	2.425	53.5	29
08N2	5.6	19.98	0.07	1.24	9	98.6	1	26.5	1.6	59	14	26	1.875	46.5	27.5
08N3	4.4	6.6	0	0.72	7	99	1	21.5	1.175	48	30.5	31	1.55	59	10
08N4	4	4.73	0	0.48	7	98.6	1	20	1.925	62.5	17.5	16	2.45	66.5	17.5
09S1	4.8	2.61	0.12	2.01	4	73	1	39.5	1.3	44	16.5	57	2.675	36	7
09S2	5.1	2.42	0.09	1.66	3	68.8	1	61.5	1.35	10.5	28	73	2.95	15	12
09S3	4.5	5.72	0.08	0.25	4	84.6	1	30.5	1.125	37	32	32	1.725	50	18
09S4	4.6	9.87	0.06	1.72	3	88.6	1	51	1.3	19.5	28.5	66.5	2.075	12	21.5
10N1	4.4	7.95	0.05	0.62	18	97.6	1	19.5	1.525	5.5	15.5	18	1.425	2.5	11
10N2	3.5	3.53	0.08	2.34	55	98.6	1	21	0.925	1.5	2.5	24.5	0.975	0.5	0
10N3	5.3	8.37	0.09	2.26	25	98.6	1	20	1.4	15	1.5	21	1.975	4	0.5
10N4	3.9	3.58	0.01	0.3	8	98.6	1	21	1.075	37	15.5	28	1.975	31	9
10S1	5.2	1.75	0.14	3.33	4	90.6	1	12	2.25	13.5	43.5	19.5	2.75	9	39.5
10S2	5.8	7.22	0.09	1.84	68	78.6	1	71	2.35	2.5	25	78	2.475	2.5	18.5

10S3	5.1	1.78	0.15	2.31	3	78.8	1	41.5	2.4	9.5	45	49	2.675	8	39
10S4	5.1	2.17	0.1	1.61	3	76	1	43	2.8	3	45.5	52.5	2.875	2.5	36
12N1	3.7	3.59	0	0.99	6	98.6	1	29	2	24.5	20.5	42.5	2.975	16	13
12N2	3.8	4	0	0.94	4	99	27	55.5	2.625	1.5	30.5	68.5	2.775	1	14
12N3	3.1	1.69	0.03	3.98	8	98.6	1	36.5	3.125	9.5	27.5	51	3.075	18.5	5
12N4	3.6	2.79	0	1.59	6	98.6	1	26.5	2.225	15.5	50.5	46	2.7	10	42
12S1	6	5.9	0.04	2.53	56	96	1	54.5	2.475	4.5	39.5	38	2.9	0	60
12S2	5.1	3.87	0.16	5.06	16	96.6	1	19	2.275	5	66	22	2.8	1	67.5
12S2.1	4.5	9.18	0.04	0.69	4	93	1	79.5	2.225	5.5	15	73	4.025	2.5	24.5
12S2.2	4.5	7.95	0.08	2.42	7	96	1	50	4.45	2.5	37.5	64	5.625	3.5	30
12S2.3	5.4	2.26	0.13	5.14	5	94	1	50.5	3.225	18.5	31	57.5	4.9	6	34
12S2.4	5	6.39	0.12	2.3	6	91	1	48.5	2.675	0.5	48	50	3.875	1	47.5
12S3	6.4	4.02	0.14	5.11	42	94	1	26	3.3	1	69.5	24.5	4.05	0.5	69.5
12S4	6.2	11.7	0.11	2.34	4	93	1	46.5	1.475	2	44	54	2.525	1.5	38.5
14N1	3.9	3.81	0.03	0.95	11	96.2	8	38.5	2.3	28	22.5	58.5	3.075	12.5	19
14N2	3.9	5.45	0.02	0.73	9	95	1	56.5	1.9	24	15.5	61	1.925	23.5	10
14N3	3.8	3.38	0.02	0.88	9	98.6	1	32.5	2.224	19.5	30.5	53.5	1.8	13	18.5
14N4	4	3.22	0	0.5	6	98.6	1	64	2.4	13.5	20	73	2.475	10.5	14

14S1	4.1	5.8	0.01	1.33	12	96.6	4	44	2.9	2	23.5	48	3.05	0.5	19
14S2	4.2	3.53	0.02	0.71	8	96.6	1	71.5	2.875	1	22	84.5	2.75	1.5	9.5
14S3	3.9	2.32	0	1.16	32	95	1	66.5	2.75	6	25.5	77.5	3.35	5	15.5
14S4	3.9	21.26	0.03	1.15	53	94.6	1	95.5	3.525	0	3	96	2.55	0.5	1.5
16S1	3.9	2.33	0.03	4.98	14	96.4	1	90	1.925	2	1	93	1.625	1	0
16S2	4	2.26	0.05	3.6	12	96.4	4	78	2.725	0	12	85.5	2.45	0	3
16S3	3.9	3.2	0.11	4.47	26	96.4	16	85.5	3.025	2.5	0	88	2.775	0.5	0
16S4	4.1	3.28	0.04	1.82	11	96.4	1	76	1.975	8	9	87.5	1.55	3	1
17N1	4.2	4.8	0.04	1.79	10	96.2	1	92.5	2	4	0	90.5	2.025	2.5	2.5
17N2	4	4.9	0.04	3.44	13	96.4	19	89.5	2.125	1	1	90	1.925	0.5	1
17N3	3.7	7.39	0.07	4.4	46	96.2	1	81	1.425	0	2	85.5	1.575	0	0
17N4	4	3.64	0.04	3.71	21	95.2	1	85.5	1.775	2.5	0	86.5	1.55	1.5	0