

Disclaimer

This dissertation consists of a series of chapters that have been prepared as stand-alone manuscripts for subsequent submission for publication purposes. Consequently, unavoidable overlaps and/or repetitions may occur between chapters.

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Chapter 1

General introduction

In the past, management strategies, especially in conservation areas in southern Africa, have concentrated on managing large mammal communities and protecting vegetation communities. Management aims have included focusing on the improvement of grazing swards and control or reduction of woody biomass (Stander *et al.*, 1993; Parr, 2003). However, since the Convention of Biological Diversity as summarized by Glowka *et al.* (1994), the emphasis of conservation agencies has shifted from primarily conserving mammal diversity to determining and conserving the diversity of other groups, such as the invertebrates.

Importance of invertebrates

Invertebrates are widely regarded as powerful monitoring tools in environmental management because of their great abundance, diversity and functional importance, their sensitivity to perturbation, and the ease with which they can be sampled (Rosenberg *et al.*, 1986; Brown *et al.*, 1997; McGeoch, 1998). According to Underwood and Fisher (2006) invertebrate populations can register the short-term impact of land management and restoration efforts, as well as indicate long-term general ecosystem change, such as restoration of mine sites or climate change (e.g. McGeoch, 1998; Parmesan *et al.*, 1999; Bisevac & Majer, 1999; York, 2000). Invertebrates are most commonly used operational units for measuring biodiversity (Purvis & Hector, 2000) and thus no biodiversity monitoring program can be considered credible without their inclusion (Taylor & Doran, 2001). Insects constitute a substantial proportion of terrestrial species richness and biomass, and play a significant role in ecosystem functioning (McGeoch, 1998). Global

insect species richness is estimated to be about 3.5 million species (Gaston, 1991; Stork, 1993; May, 2000; Alroy, 2002; Parr, 2003).

Monitoring environmental change

In monitoring environmental change, taxa that are hypersensitive to perturbations (Kareiva *et al.*, 1993) are most often chosen. Agosti *et al.* (2000) indicated that ants' small size and reliance on relatively high temperatures make them especially sensitive to climate and micro-climate change. The point of baseline monitoring studies is to determine the degree to which ecosystem properties (e.g., productivity, biomass, species composition and richness) vary naturally. The cost and logistics of including ants in a monitoring program are vital considerations for land managers and conservation practitioners (Agosti *et al.*, 2000). In a restoration study, Andersen (1993) has shown that fire breaks the dominance of Acacia plants and allows a greater diversity of ants as a consequence of increased plant heterogeneity. Correlations between ant distributions, rainfall and temperatures (Farji-Brener & Ruggiero, 1994; Andersen, 1995) as well as activity patterns under changing conditions of temperature and humidity (Schumacher & Whitford, 1974; MacKay, 1981; Cerdá *et al.*, 1997), may allow researchers to predict which species can cope with changes in global temperatures and rainfall (Folgarait, 1998).

Effects of climate change on species distribution

The earth's climate has warmed by approximately 0.6°C over the past 100 years and organisms, populations and ecological communities do not respond to approximated global averages but rather regional changes are more relevant in the context of ecological response to climate change (Sakchoowong *et al.*, 2008). Climate change over the past ~30 years has produced numerous

shifts in the distributions and abundances of species (Parmesan & Yohe, 2003; Root *et al.*, 2003) and has been implicated in one species-level extinction (Pounds *et al.*, 1999; Thomas *et al.*, 2004). The presence of every plant and animal (and its conditions) is a measure of the conditions under which it is existing or existed previously.

All plants and animals have evolved to survive in different combinations of physical and chemical conditions, some species have narrow tolerances and some have wide tolerances. Organisms with narrow tolerances (or species which are sensitive to small changes in their environment) may be useful indicator species; because changes in distribution and abundance of these species may indicate environmental perturbations (Spellerberg, 1991). There can be differences in response to climate change between species at a particular time or in a particular season. Climatic regimes influence species' distributions, often through species-specific physiological thresholds of temperature and precipitation tolerance (Sakchoowong *et al.*, 2008). If higher temperatures increase the probability of fires or flooding, then the competitive interactions within ant communities might change the rules of coexistence leading to new assemblages and thus affecting biodiversity (Wiens, 1977; Folgarait *et al.*, 2007). Non-native species from adjacent areas may cross frontiers and become new elements of the biota. However, for species originating from habitats more suitable than the new location provides, a permanent establishment at the new locality may not be possible without changes in local conditions (Sakchoowong *et al.*, 2008).

Climate change along elevational gradients

Elevational range shifts in herbivorous insect species, can serve as a sensitive indicator of changing climate (Hodkinson & Bird, 1998) and climatically induced elevational range shifts can

sometimes produce unexpected consequences. According to Wilson *et al.* (2007), changes in species ranges can be detected more rapidly in mountainous regions than lowland because they often retain comparatively intact habitats and because the steep elevational gradients enable species to track climatic changes over short distances.

Elevational gradients are isolated, fragmented, spatially complex, comprise harsh environmental conditions and in certain areas subject to human disturbance through recreation or grazing. Thus they produce a mosaic of different habitat types and/or microclimate, serving as centres of micro-evolution and adaptation in insects (Haslett, 1997). Microclimatic variations in elevational gradients may have major modifying effects on the reproductive success and distribution of insects (Weiss *et al.*, 1988). Elevational gradients can also serve as major barriers to gene flow between populations of the same species and they may produce variation in the seasonal phenology of insect host plants such as leaf flushing, leaf maturity, leaf senescence and fall, flowering, seed maturity and dispersal (Watt & McFarlane, 1991; Hunter, 1992; Hill & Hodkinson, 1995; Hodkinson, 1997; Hill *et al.*, 1998; Virtanen & Neuvonen, 1999; Hodkinson *et al.*, 2001).

Temperature varies across elevational gradients and there may be significant differences from ambient air temperature within vegetation or the surface soil layers, this may be increasingly important for insects at higher elevations (Geiger *et al.*, 1995). Variation in rates of growth and development at different temperatures may lead to differences in the mean body size of an insect species along an elevational gradient (Hodkinson, 2005).

Species richness patterns along elevational gradients

Various studies have examined the pattern of species richness across elevational and latitudinal gradients. Numerous studies have demonstrated fewer species at higher elevations than at lower elevations, or no species above a certain elevation (e.g. Weber, 1943; Janzen, 1973; Janzen *et al.*, 1976; Collins, 1980; Atkin & Proctor, 1988). The number of species also declines with increasing latitudes, altitudes, and aridity (Kusnezov, 1957; Fowler & Claver, 1991; Farji-Brener & Ruggiero, 1994; Samson *et al.*, 1997). Mid-elevation peaks in species densities have been suggested to be most diverse at intermediate elevations because primary production is highest due to a favourable relation between rates of photosynthesis and respiration (Janzen, 1973; Janzen *et al.*, 1976; Terborgh, 1977; Brühl *et al.*, 1999). Rapoport's rule (Stevens, 1992) suggests that climates at higher elevations are more variable, so species at higher elevations can tolerate more variability and therefore have larger elevational ranges (Sanders, 2002), however McCain and Knight (2013) suggested that this pattern is not as common as previously thought to be the case and it can be misleading. A mid-domain peak in richness is generated when there is increasing overlap of species ranges toward the centre of the domain because the extents of the elevational range of species are bounded by the highest and lowest elevation possible in the region (Colwell & Hurtt, 1994). Temperature is a key environmental variable that decreases with increasing altitude and is known to influence a number of taxa such as birds (Rahbek, 1997) and especially invertebrates such as ants (Botes *et al.*, 2006).

Changes in body size with elevation

Body size of an animal can also be associated with range size and geographic patterns of distribution and diversity (Gaston & Blackburn, 2000; Gaston, 2003; Brown *et al.*, 2004). However currently there is no convincing general hypothesis available that explains insect body

size patterns across climatic gradients (Brehm & Fiedler, 2004). Bergmann's Rule predicts that body size increases with latitude and perhaps elevation (Mayr, 1956; McNab, 1971). Available literature on insect species, indicate that body size does not vary regularly with elevation and so far three different patterns have been observed. Body size of some species is larger at higher elevations (Stalker & Carson, 1948; Miller, 1991; Hawkins & Devries, 1996) some smaller (Hawkins & Devries, 1996; Sota, 1996; Blanckenhorn, 1997) and some show no change at all (Hawkins & Devries 1996; Krasnov *et al.*, 1996). According to Chown and Klok (2003) there have been only a few investigations of body size variation with altitude in insects (e.g. intraspecific: Arnett & Gotelli, 1999; interspecific: Hawkins & DeVries 1996), and none that have sought to compare intraspecific altitudinal size clines in closely related species at different latitudes.

Why ants?

Ant assemblages are important in terms of community ecology (Ipser *et al.*, 2004); they are valuable indicators for measuring environmental change and ecosystem functioning (Andersen & Majer, 2004; Underwood & Fisher, 2006; Fagan *et al.*, 2008; Mitrovich *et al.*, 2010). Ants are important in below ground processes through the alteration of the physical and chemical environment and through their effects on plants, microorganisms and other soil organisms (Folgarait, 1998). They perform a variety of ecological functions in terrestrial ecosystems, including keystone functions such as the cycling of nutrients and organic matter, turning over soil, seed dispersal, structuring invertebrate (Greenslade, 1976) and plant assemblages (Buckley, 1982; Huxley & Cutler, 1991) and predation and scavenging of small animals (e.g., Hölldobler & Wilson, 1990; Folgarait, 1998; MacMahon *et al.*, 2000; Mitrovich *et al.*, 2010).

Based on their total numbers and great diversity worldwide ants are significant ecological components of most terrestrial communities (Hölldobler & Wilson, 1990); they are easily sampled, with statistically representative samples possible within a week or less (Agosti *et al.*, 2000). Ant species diversity is manageable (they are not hyperdiverse) compared to many other insect groups (Agosti *et al.*, 2000); they have been shown to be sensitive and rapid responders to environmental variables (Campbell & Tanton, 1981; Majer, 1983; Andersen, 1990) and that supports their selection as useful indicators for measuring performance of regional habitat conservation plans in protecting biodiversity and ecosystem processes (Mitrovich *et al.*, 2010).

Several studies have been conducted on ants in various parts of South Africa for example: Parr *et al.* (2004) studied ant assemblages in the Kruger National Park and recently studies by Botes *et al.* (2006); Munyai & Foord (2012); Bishop *et al.* (2014) also investigated ant diversity across altitudinal and vegetation gradients. Botes *et al.* (2006) investigated ant assemblages within the main vegetation types in the Cederberg Mountains of the Western Cape and found that temperature explained significant proportions of the variation in species density and abundance. Munyai and Foord (2012) examined variation in epigeal ant diversity along a north-south elevational transect over the Soutpansberg Mountains and found that richness peaked at the lowest elevation on the southern aspect but had a hump-shaped pattern along the northern slope. Bishop *et al.* (2014) studied ant diversity patterns at the Maloti-Drakensberg Mountains (Sani Pass) in KwaZulu-Natal and found a hump-shaped pattern across the elevational gradient. They also found that species density patterns were largely influenced by elevational effects while abundance was mostly driven by mean temperature.

Objectives and structure of the dissertation

Mariepskop is part of the Drakensberg mountain range and represents an important altitudinal gradient on the boundary of Mpumalanga and Limpopo provinces. It extends from around 560 metres above sea level to 1940 m.a.s.l. and has recently been identified as a site for monitoring long-term changes in biodiversity. This study was conducted across an altitudinal gradient from 700 m a.s.l to 1900 m a.s.l at Mariepskop (Fig. 1).

The main objectives of this research are to investigate the ant diversity and species richness patterns across the altitudinal gradient at Mariepskop. The dissertation also intends to explore the role of various environmental factors (vegetation, altitude and substratum) in determining ant assemblage structure and to describe the ant body size patterns across species in relation to altitude. In doing so it also provides baseline information about ant diversity and assemblage structure at Mariepskop.

The dissertation has four chapters. Chapter 2 of the dissertation explores ant diversity across the altitudinal gradient, describes richness patterns and attempts to explore the role of environmental variables in order to explain ant assemblages. Chapter 3 investigates the relationship between ant body size and altitude. Chapter 4 is a general discussion of the findings of the study.

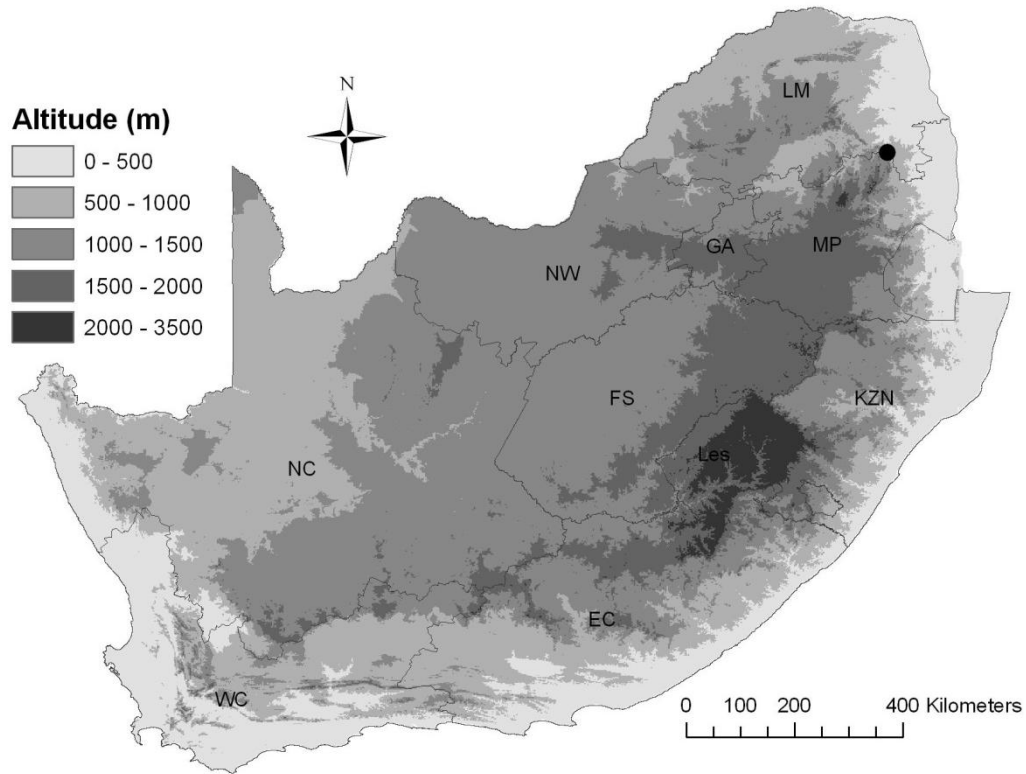


Figure 1. Map showing the location of Mariespok Mountain within South Africa. The dot indicates the approximate position of the sampling site at Mariespok. The letters represent the various provinces of South Africa and Lesotho. LM = Limpopo, MP = Mpumalanga, GA = Gauteng, KZN = KwaZulu-Natal, NW = North-West, FS = Free State, EC = Eastern Cape, NC = Northern Cape, WC = Western Cape and Les = Lesotho.

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Chapter 2

Ant diversity across an altitudinal gradient

Abstract

Ants are valuable indicators for measuring environmental change and ecosystem functioning. Elevational gradients are suitable areas to study ecosystem functioning and the effects of environmental change, because the components of climate and local environment vary in a non-random fashion along elevational gradients. This chapter examines the pattern of ant species richness across the elevational gradient and how it compares with other areas. It also explores the role that various environmental factors such as vegetation, altitude, area and substratum play in determining ant assemblage structure. Sampling was undertaken during March and November 2011 across an altitudinal gradient at Mariepskop in the northern Drakensberg Mountains, ranging from 700 m to 1900 m. Pitfall traps were used to sample ants at five elevational sites and environmental variables were also collected at each sampling site. A total of 19,109 ants comprising 92 morphospecies from 30 genera were caught. Ant species density decreased monotonically with an increase in altitude. Abundance also declined with increasing altitude. Altitude, vegetation complexity, height of grass, proportion of bare ground and clay in the soil were the environmental variables that contributed significantly to the variance explained in the ant assemblages. Twenty one ant species were characteristic of certain altitudinal sites. Different ant assemblages occupy different altitudinal sites and several species are characteristic of each of the altitudinal sites at Mariepskop. Species that are indicators for the highest elevation in this study could be susceptible to climate change because they have very narrow distributions.

The diversity of species across altitudinal gradients cannot be determined by only one factor but rather a combination of variables acting together

Key words: Ants, altitude, species richness, Mariepskop, elevational gradients.

Introduction

Insects are abundant, easy to sample and diverse; thus they are regarded as a powerful monitoring tool in environmental management (Rosenberg *et al.*, 1986; Brown *et al.*, 1997; McGeoch, 1998). Ants assemblages are important in terms of community ecology (Ipser *et al.*, 2004); they facilitate the development of other organisms in their mounds, including unique plants that otherwise would not exist (King, 1977; Folgarait *et al.*, 1996); they create and modify habitat for other organisms and modulate the availability of resources by creating the bioturbation (Johnson, 1990); they can disperse plant propagules (Wilson, 1992) and anthills facilitate the appearance of invasive plant species (Bucher, 1982; Folgarait *et al.*, 1996; Farji Brener & Margutti, 1997). Anthills may create patches of mycorrhizal enrichment (Friese & Allen, 1993) which can help the establishment of plants (Allen *et al.*, 1989) due to the dispersion of fungal spores (McIlveen & Cole, 1976); they help change the physical and chemical properties of the soil through construction of nests consequently increasing soil drainage and aeration through the formation of underground galleries and chambers, and transforming organic matter and incorporating nutrients by food storage; (Denning *et al.*, 1977; Gotwald, 1986; Majer *et al.*, 1987; Cherrett, 1989; Folgarait, 1998).

Ants are important in below ground processes through the alteration of the physical and chemical environment and through their effects on plants, microorganisms and other soil organisms (Folgarait, 1998). They perform a variety of ecological functions in terrestrial ecosystems, including keystone functions such as the cycling of nutrients and organic matter, turning over soil and seed dispersal. They are valuable indicators for measuring environmental change and ecosystem functioning (Andersen & Majer, 2004; Underwood & Fisher, 2006; Fagan *et al.*, 2008; Mitrovich *et al.*, 2010).

Altitudinal gradients are useful for studying the influence of environmental variables on biodiversity, as changes in environmental variables take place over short geographical distances (Lomolino, 2001). They create varied climates, along with resultant soil differentiation and promote the diversification of plant species (Brown, 2001; Lomolino, 2001). Hua (2004) suggested that mountains generally have a conical shape and thus as the elevation increases, the area of the elevation band with certain set of environmental and climatic conditions decrease. Lomolino (2001) stated that high elevation habitats are smaller and also more isolated from other mountains, other zonal communities within the same mountain, and from human populations. Mountains can be represented as islands due to their reduced connectivity to means of colonization by plants and animals (Hua, 2004). Components of climate and local environment (such as temperature, precipitation, seasonality, disturbance regimes and soil characteristics) vary in a non-random fashion along most elevational gradients (Lomolino, 2001).

Altitudinal gradients yield consistent ecological conditions and are linked to several environmental variables of interest to theoretical and applied research on biodiversity (Hu *et al.*,

2001). The altitudinal gradient of species richness may be intricately related to species-area relationships (Rahbek, 1997; Lomolino, 2001). The effect of area on species richness has been described as one of ecology's few laws (Lawton, 1999) and under the area hypothesis larger regions are expected to be more diverse than smaller regions (Rosenzweig, 1995; MacArthur & Wilson, 2001). Generally a greater area will provide greater habitat diversity which can harbor more species (Williams, 1964) and they are also accompanied by decreased rates of extinction and increased rates of speciation or colonization due to a greater number of barriers and the maintenance of larger population sizes (Preston, 1962; MacArthur & Wilson, 2001). Rapoport's rule states that there is a positive relationship between the latitudinal/altitudinal geographical range of an organism and latitude/altitude (Stevens, 1989; Stevens, 1992). This positive relationship could be explained by species at lower elevation approaching their upper elevation limits whereas those that occupy higher elevations have comparatively larger climatic tolerances and so can be found across a greater altitudinal range (Stevens, 1992).

The relationship between richness and elevation is an ecological pattern that has been frequently documented (Lawton *et al.*, 1987; Stevens, 1992; Rahbek, 1995; Lomolino, 2001; Chatzaki *et al.*, 2005; Botes *et al.*, 2006; Munyai & Foord, 2012). However the pattern is still controversial (Chatzaki *et al.*, 2005); certain researchers have reported a monotonic decrease in species richness with increasing elevation (Lawton *et al.*, 1987; Stevens, 1992), where species richness continuously declines as elevation increases; others favor a hump-shaped pattern, where the peak of species richness occurs at an intermediate elevation (McCoy, 1990; Colwell & Hurtt, 1994; Rahbek, 1997; Fleishman *et al.*, 1998; Sanders, 2002; Chatzaki *et al.*, 2005; Bishop *et al.*, 2014). Along altitudinal gradients, the species richness-altitude relationship generally follows a

decreasing or hump-shaped pattern, depending on the main attributes of scale (i.e. the unit of sampling and the geographical space covered (Rahbek, 2005)).

Both patterns have been documented in a variety of habitats and taxa (e.g., Stevens, 1992; Brown, 1995; Rahbek, 1995; Brown & Lomolino, 1998; Sanders, 2002). Until recently, the most widely accepted pattern was a decline in species richness with increasing elevation (e.g. Brown, 1988; Stevens, 1992) but a growing body of evidence suggests that for a wide variety of taxa, mid-elevation peaks in species richness are perhaps more general (e.g. Rahbek, 1995, 1997; Lees *et al.*, 1999; Colwell & Lees, 2000; Bishop *et al.*, 2014).

A number of studies have examined the effects of elevation on ant species richness with differing conclusions (Sanders, 2002). Species richness of leaf litter ants in a Malaysian rainforest decreased exponentially with increasing elevation (Brühl *et al.*, 1999). In contrast, Fisher (1998), in a study in Madagascar, detected peaks in species richness at mid-elevations in leaf litter ants, Samson *et al.* (1997) reported a peak in species richness at mid-elevations in forests in the Philippines. In South Africa, Botes *et al.* (2006) found no clear patterns in their study on ants of the Cape Floristic Region. Recently Munyai & Foord (2012) recorded a hump-shaped pattern in ant species richness along the northern slopes of Soutpansberg Mountains in South Africa.

So far not enough is known about the factors that govern species richness, especially along environmental gradients such as elevational gradients (Sanders *et al.*, 2003). The general idea is that there is not a single overriding factor which defines the response of organisms to environmental gradients, but rather a combination of factors, the intensity of which depends largely on the local conditions and the history of a region, and on the special characteristics of each taxon (e.g. Brown & Lomolino, 1998; Chatzaki *et al.*, 2005). Even though one would not

expect a generalised pattern in terms of ant species richness responses, understanding factors that govern them, may be important for understanding the functioning of ecosystems. Habitat complexity and cover are important factors in determining the presence of invertebrate species and their richness. Lassau and Hochuli (2004) described habitat complexity as the heterogeneity in the arrangement of physical structure in the habitat survey. Various studies suggest that species richness of ants (Andersen, 1986) and a range of other arthropods (Uetz, 1979, Gardner *et al.*, 1995, Humphrey *et al.*, 1999, Hansen, 2000) are positively associated with habitat complexity. In their study on spiders Jiménez–Valverde and Lobo (2007) found that variation in species richness resulted from the joint effects of the three variables they considered and that around 30% of the total variability in species richness is not attributed to a single variable. Although vegetation structure is one of the main determinants of spider community composition, the exact mechanism of influence is unknown. Jiménez–Valverde and Lobo (2007) suggested availability of structures for attaching a web and of ambush and refuge sites as probably the most direct effects of vegetation complexity on the other hand microclimate, prey availability or reduced cannibalism may be indirectly related (Uetz, 1991; Marc *et al.*, 1999).

Mariepskop is part of the Drakensberg mountain range and represents an important altitudinal gradient on the boundary of Mpumalanga and Limpopo provinces. It extends from around 560 metres above sea level to 1940 m.a.s.l. and has recently been identified as a site for monitoring long-term changes in biodiversity. Other studies that have been done on insects have focused on monitoring the effects of climate change (Botes *et al.*, 2006), habitat fragmentation and habitat conservation (Mitrovich *et al.*, 2010). In South Africa studies by Botes *et al.* (2006) investigated how ant assemblage structure differs between the main vegetation types, how restricted ants are

to the major vegetation types and which environmental variables influence the observed assemblage structure. Munyai & Foord (2012) investigated spatial variation in ant diversity along an elevational transect over the Soutpansberg Mountain, how patterns can be related to environmental variables and how restricted taxa are to altitudinal zones and vegetation types. Bishop *et al.* (2014) focused on ant diversity across an altitudinal gradient and the role that temperature and seasonality plays in determining species density. The present study investigated ant species richness patterns across an elevational gradient and the environmental variables responsible for the observed pattern, thus this study on Mariepskop Mountain will further contribute to the growing body of knowledge. Based on available literature, the present study hypothesizes that species richness will follow a hump-shaped pattern where species richness is higher at intermediate altitude. Therefore this study aims to: a) describe the pattern of species richness across the altitudinal transect and how it compares with other areas and, b) explore the role of various environmental factors (vegetation, altitude, area and substratum) in determining ant assemblage structure.

Methods

Study area

The study took place at Mariepskop (24°53'S, 30°52'E) which is a part of the Mpumalanga Drakensberg mountain range of southern Africa, on the border between Limpopo and Mpumalanga provinces. Mariepskop lies on the eastern side of the Drakensberg escarpment facing to the west of the Blyde River Canyon and at 1945 m above sea level (m.a.s.l) it is the highest peak in the northern Drakensberg Escarpment. The study took place on the northern side of the mountain and the altitudinal transect ranged from the lowest altitude (700 m.a.s.l) at the

bottom of Moholoholo Nature Reserve (24°29'S, 30°53'E) up to the highest point (1900 m.a.s.l) at the top of Mariepskop (24°53'S, 30°52'E). Situated on the northern side of Mariepskop is the town of Kampersrus and the nearest large town is Hoedspruit which is about 30km straight line distance from Mariepskop. The climate is comprised of summer rainfall with dry winters; the mean annual precipitation is about 450 mm and the mean annual minimum and maximum temperature at Hoedspruit is 3.7°C & 38°C.

The top of the mountain was previously used by the military and so access is restricted which has resulted in limited development around the area. The site is relatively pristine and no formal studies have been conducted in the area, it is unique in its floral diversity with over 2000 plants species recorded (Mössmer & Willis, 2000). About 900 vertebrate species including the Samango monkeys, Mariepskop Dwarf chameleon and Three Rondawels Flat Gecko were also recorded in a report on biodiversity of Mpumalanga Province (2003).

The vegetation across the altitudinal gradient falls within Savanna (Granite Lowveld & Legogote Sour Bushveld) and Grassland (Northern Escarpment Quartzite Sourveld & Northern Escarpment Afromontane Fynbos) biomes. Granite Lowveld comprises of tall shrubland with few trees to moderately dense low woodland on the deep sandy uplands such as described by Mucina *et al.*, (2006) and this vegetation type was found at the lowest sampling site (about 700m.a.s.l) of the mountain. The subsequent site further up (about 1000 m.a.s.l) has the vegetation type of Legogote Sour Bushveld which is comprised of medium to large shrubs that form dense woodlands areas. Mucina *et al.* (2006) suggested that soils in these sites are shallow to deep, sandy or gravelly and well drained.

Further up the slopes (1300 & 1500 m.a.s.l.) vegetation is of Northern Escarpment Quartzite Sourveld type. The landscapes of this type are dominated by short, closed grassland rich in forb species with scattered trees (*Protea roupelliae*, tree fern, tall shrubs and herbs) (Mucina *et al.*, 2006). The highest site at the top of Mariepskop is of Northern Escarpment Afromontane Fynbos type and the dominating structural form is shrubland with ericoid growth form. The terrain is very rocky and fires are very rare. It has summer rainfall which is augmented by mist during large parts of the year. The temperature is cooler than the surrounding area with mean annual temperature of 15.6°C (Mucina *et al.*, 2006).

Ant sampling

Sampling was done at five altitudinal sites (700 m, 1000 m, 1300 m 1500 m & 1900 m) which were recorded on a GPS. The sites selected were in mixed grassland and savannah vegetation away from roads, forestry and other human disturbances. Ground dwelling ants were sampled at each site in March 2011 and November 2011 by means of pitfall traps. This is an efficient technique for sampling ant communities in open vegetation (Andersen, 1991; Gallé, 1991; De Bruyn, 1993). At each altitudinal site four replicates, consisting of 10 pitfall traps each were placed during each sampling event as in Botes *et al.* (2006). The replicates were separated by a minimum distance of 120 m from each other. The coordinates of the centre of each replicate were recorded for spatial analysis. For each replicate the 10 traps were laid out in a grid (2 x 5) with traps spaced at 10-m intervals. To reduce the possibility of the traps being flooded, round plastic bucket lids with a diameter of 220 mm were supported on wire legs approximately 100 mm above each trap. Pitfall traps (diameter 60 mm & volume 120 ml) containing 60 mL of a 50% propylene glycol solution as preservative, were placed at each site to capture ground dwelling ants. Propylene glycol does not significantly attract or repel ants (Adis, 1979; Botes *et*

al., 2006). Pitfalls were left open for three days after which they were exchanged for a further three days per sampling event. Ants collected were placed in 70% alcohol and identified to species where possible or assigned to morphospecies using the *Identification guide to the ant genera of the world* (Bolton, 1994). Voucher specimens have been kept in the ant collection in the Department of Zoology and Entomology at the University of Pretoria.

Vegetation sampling

Vegetation structure was recorded at each sampling site in December 2011 to determine the horizontal and vertical distribution of the vegetation. The horizontal distribution of vegetation was determined by estimating the basal coverage of grass, woody forbs, forbs, exposed rock and bare ground following the methods outlined by Rotenberry & Wiens (1980), Bestelmeyer & Wiens (1996), Parr *et al.* (2004) and Botes *et al.* (2006). A 1-m² grid was placed over each pitfall trap and the percentage of ground covered by the four categories (10 pitfalls) each within the grid was estimated. Maximum vegetation height at each replicate was recorded at 20 randomly selected points in the replicate.

To quantify vegetation complexity at different heights, a white square 10 cm x 12 cm with 20 black dots placed on the card in a grid was placed at 4 cm, 25 cm, 50 cm, 75 cm, 100 cm and 150 cm above ground level. The number of dots visible were then counted and recorded at each of the heights from one meter and two meters from the card through the undisturbed vegetation. The scale was then reversed in order to generate an index of complexity in which a higher number refers to higher complexity.

Soil sampling

Soil samples were collected from each altitudinal site (four samples per site) in April 2011. These soil samples were analysed in the laboratory at the Department of plant production and soils science, University of Pretoria for proportions (sand, silt and clay), pH (KCL), phosphorus, potassium, calcium, magnesium and organic carbon.

Analysis: Ant assemblages

Rarefaction curves for the ants collected across the full altitudinal gradient were compiled using the analytically calculated Sobs (Mao Tao) for the sites to compare species richness across the sites (Estimate SV8, Colwell, 2006, <http://viceroy.eeb.uconn.edu/estimates>; see also Gotelli & Colwell, 2001). Individual-based rarefaction curves were used to compare total species richness and abundance across all sites in the altitudinal study transects. The observed number of species (Sobs), non-parametric incidence-based coverage estimator (ICE) and Michaelis-Menten (MMM_{Mean}) richness estimates were computed using EstimateS (Colwell, 2006, see also Gotelli & Colwell, 2001). Species accumulation curves for all ants were produced in order to assess the completeness of sampling (Colwell & Coddington, 1994). The program randomized sample order 100 times, and averaged randomisations to produce smooth species accumulation curves. Although estimators are valuable tools, they should not be viewed uncritically, and should be considered as yielding minimum estimates of species richness (Longino *et al.*, 2002).

Analyses of similarity (ANOSIM) were used to find out if there were any significant differences between ant assemblages from sites at different altitude. The ANOSIM procedure of PRIMER (Clarke & Gorley, 2006) is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke & Warwick, 2001). ANOSIM

produces a global R-statistic, which is an absolute measure of distance between groups where an R-value approaching one indicates strongly distinct assemblages, whereas an R-value close to zero indicates that the assemblages are barely separable. Sometimes R-values may be very low indicating that assemblages are barely separable, but these values may also be significantly different from zero (Clarke & Warwick, 2001). Therefore the R-values obtained in the analysis were used to compare ant assemblages between altitudinal sites. Non-metric multi-dimensional scaling (MDS) ordinations were used to display the relationship between ant assemblages and altitude for both sampling periods. The Bray-Curtis similarity metric was used to determine whether ant assemblage structure varied between altitudinal sites in the MDS and ANOSIM. Data were fourth-root transformed prior to analyses to reduce the weight of common species.

Species density and relative abundance

One way Analysis of variance (ANOVA) was used to test the significances of the species density and abundance for all the altitudinal sites. Species density is the number of species collected in a particular total area and was calculated from the values obtained in EstimateS (Gotelli & Colwell, 2001) and for abundance the mean number of individuals recorded in the study was calculated.

Environmental variables

To calculate the available area for each altitudinal site across the band, the center of each band was represented by the respective altitudinal site (e.g. for 1900 m, the band width was between 1800 m and 2000 m). The collinearity in the abiotic variables (10 soil parameters, altitude and available area) and biotic variables (9 vegetation parameters) was determined using Pearson's product moment correlations. This was done in order to investigate the extent to which the

different predictor variables account for variation in ant diversity. When variables were significantly correlated (i.e. > 0.80), only the variables that were considered biologically relevant were retained in the subsequent analyses.

In the set of abiotic variables (10 soil parameters, altitude and available area) collinearity was removed by reducing them to six (P, K, Mg, altitude, proportion of clay and silt) variables that were used in all subsequent analyses (Table 1). There were five soil parameters that were selected for analyses of which three were chemical (P, K, Mg; Table 2) and two composition (proportion of clay and silt; Table 2). Available area was omitted from further analyses as it was highly correlated to silt and two other abiotic variables (C & pH) were correlated with altitude and thus not used in further analyses (Table 1).

In habitat structure variables (biotic) collinearity was removed by excluding four variables (proportion of ground covered by grass and woody forbs; height of trees and number of trees per quadrat). The vegetation variables that were used were therefore: proportion of ground covered by forbs, exposed rocks and bare ground; height of grass and vegetation complexity (V4, V25 & V50). The vegetation complexity values (V4, V25 & V50) indicate vegetation complexity scores at 4 cm, 25 cm and 50 cm above ground level (Table 1).

Table 1. Pearson's product moment correlations of the abiotic and biotic variables. Significant values are indicated in bold. V4 = vertical complexity of vegetation at a height of 4 cm, V25 = vertical complexity of vegetation at a height of 25 cm, V50 = vertical complexity of vegetation at a height of 50 cm G = proportion of grass, WF = proportion of woody forbs, F = proportion of forbs, ER = proportion of exposed rock, BG = proportion of bare ground, HG = height of grass, HT = height of trees, TQ = number of trees per quadrat.

	Altitude	Area	Sand	Silt	Clay	C	pH	P	Ca	K	Mg
Area	-0.62										
Sand	-0.02	-0.45									
Silt	-0.61	1.00	-0.52								
Clay	0.15	0.29	-0.98	0.37							
C	0.92	-0.52	0.02	-0.53	0.10						
pH	-0.93	0.81	-0.09	0.80	-0.05	-0.75					
P	0.18	-0.49	0.79	-0.55	-0.73	0.42	-0.15				
Ca	-0.34	0.74	-0.11	0.70	0.01	-0.02	0.66	0.16			
K	0.25	0.45	-0.84	0.49	0.84	0.36	0.03	-0.43	0.46		
Mg	-0.35	0.75	-0.14	0.72	0.03	-0.04	0.67	0.13	1.00	0.48	
Na	-0.65	0.83	-0.39	0.83	0.28	-0.38	0.86	-0.15	0.84	0.48	0.86
V4	-0.87	0.22	0.31	0.21	-0.38	-0.71	0.74	0.24	0.20	-0.47	0.21
V25	-0.93	0.81	-0.24	0.82	0.09	-0.92	0.91	-0.49	0.37	-0.02	0.39
V50	-0.78	0.61	0.37	0.56	-0.52	-0.75	0.78	0.01	0.44	-0.41	0.44
G	0.86	-0.32	-0.39	-0.29	0.47	0.66	-0.81	-0.33	-0.39	0.43	-0.39

WF	-0.05	0.39	-0.92	0.46	0.90	-0.23	0.04	-0.96	-0.16	0.60	-0.13
F	0.76	-0.19	-0.61	-0.14	0.69	0.59	-0.69	-0.47	-0.32	0.61	-0.31
ER	0.06	0.60	-0.02	0.55	-0.08	0.20	0.26	0.05	0.78	0.41	0.77
BG	-0.83	0.18	0.43	0.15	-0.49	-0.64	0.71	0.36	0.24	-0.53	0.24
HG	0.10	0.58	-0.11	0.53	0.03	0.32	0.26	0.13	0.87	0.56	0.86
HT	-0.81	0.56	0.15	0.53	-0.25	-0.52	0.90	0.26	0.70	-0.07	0.71
TQ	-0.87	0.45	0.22	0.42	-0.31	-0.61	0.87	0.26	0.53	-0.23	0.54

Table 1. (Continued)

	Na	V4	V25	V50	G	WF	F	ER	BG	HG	HT
V4	0.48										
V25	0.67	0.62									
V50	0.43	0.60	0.77								
G	-0.57	-0.97	-0.63	-0.71							
WF	0.17	-0.31	0.33	-0.26	0.42						
F	-0.38	-0.91	-0.51	-0.75	0.96	0.60					
ER	0.40	-0.31	0.11	0.37	0.09	-0.13	0.04				
BG	0.45	0.99	0.56	0.63	-0.99	-0.44	-0.96	-0.24			
HG	0.51	-0.28	0.04	0.23	0.06	-0.13	0.06	0.96	-0.22		
HT	0.83	0.84	0.65	0.65	-0.92	-0.30	-0.83	0.19	0.85	0.27	
TQ	0.72	0.94	0.66	0.66	-0.98	-0.32	-0.90	0.00	0.94	0.06	0.98

Table 2. Soil characteristics and ground cover of the sampling sites. Both were determined once in December 2011.

Site	Soil composition (%)			Soil variables							Ground cover (%)				
	Sand	Silt	Clay	C (%)	pH	P (mg/kg)	Ca (%)	K (%)	Mg (%)	Na (%)	G	WF	F	ER	BG
1900m	81.2	4.1	12.2	3.9	4.5	7.2	104.3	69.5	46.8	33	76.1	1.5	4.2	5.8	12.5
1500m	22.9	9.9	60.2	2.4	5.0	4.9	70.3	110.5	50.8	39.8	84.8	5.1	6.6	2.8	0.8
1300m	61.0	10.9	22.3	1.4	5.2	5.2	162.0	71.8	70.3	36.0	75.7	3.6	4.4	9.3	7.2
1000m	52.8	13.9	28.6	2.0	5.9	6.2	1302.5	102.5	374.8	48.5	42.1	2.7	2.2	13	40.2
700m	73.5	8.8	13.8	0.4	5.6	6.2	86.5	49.0	51.0	40.3	25.1	2.5	0.4	0.3	71.8

Redundancy Analysis (RDA) was used to examine the relationship between ant assemblage structure within the different altitudinal sites and environmental variables (Borcard *et al.*, 2011). The analysis was done for assemblages in all five altitudinal sites together and all species that had fewer than five individuals were removed from analysis and the remaining species data were log transformed prior to analysis (Lepš & Šmilauer, 2003). A forward selection procedure of environmental variables was used to determine which of the variables significantly explained ant assemblage structure. The significance of each variable was judged using a Monte-Carlo permutation test (ter Braak, 1994). The results were then displayed as biplots in which environmental variables are depicted as arrows and samples as symbols (Lepš & Šmilauer, 2003). Based on sample scaling, the length of the arrows indicates the relative importance of the environmental variables in explaining species composition of the samples and the arrows point in the expected direction of the steepest increase there of (Lepš & Šmilauer, 2003; Botes *et al.*, 2006). Species sample relationships were displayed as biplots to determine which species contribute to the differences between assemblages.

In order to identify characteristic ant species for each altitudinal site, the Indicator Value Method (Dufrene & Legendre, 1997) was used with the package `labsv` in R. In this method, measures of specificity (uniqueness to a particular site) and fidelity (frequency of occurrence within that site) are combined for each species independently. High indicator values (IndVal, expressed as %) show that a species has high fidelity and specificity to the site and it can be considered characteristic of a particular site. Indicator values for each species were calculated based on the species abundance matrix using a random reallocation of replicates among groups (Dufrene & Legendre, 1997). Species with significant IndVal greater than 70% were then

regarded as indicators of a particular site (McGeoch *et al.*, 2002; Van Rensburg *et al.*, 2002; Botes *et al.*, 2006; Munyai & Foord, 2012).

Results

Species composition

A total of 19,109 ant individuals, 92 (morpho) species from 30 genera were collected from five altitudinal sites (Appendix 1). Most species and genera belonged to the subfamily Myrmicinae (39 and 13 respectively), followed by the Formicinae (35 and 7 respectively). The most speciose genera were *Lepisiota* (17 species), *Tetramorium* (16 species) and *Camponotus* (11 species).

Sampling completeness

Species accumulation curves show that the observed richness (Sobs) converged closely with the richness estimators (ICE and MMMean) for all the five sites combined (i.e. full altitudinal gradient) indicating that the overall sampling was fairly complete and that majority of ant species at each site were sampled (Fig. 1). Although no asymptote was reached, sampling was relatively complete and therefore unlikely to bias the overall analysis and results. Similar results were obtained when accumulation curves were plotted for each altitudinal site separately (Fig. 2).

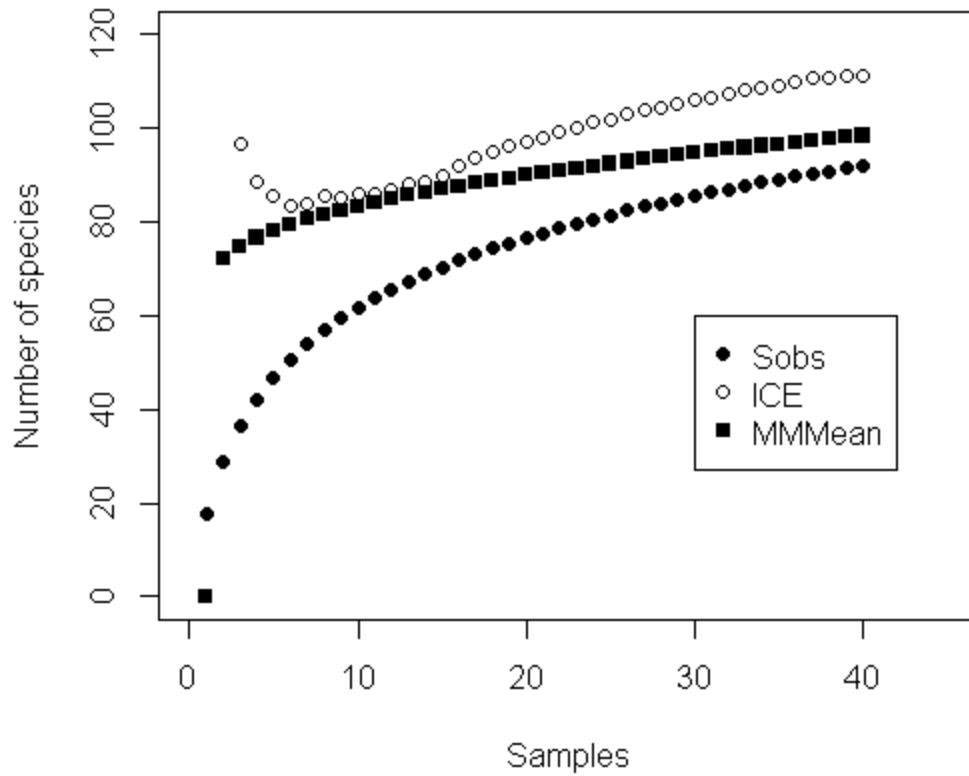


Figure 1. Species accumulation curve for ants sampled at Mariepskop indicating number of species richness and samples. The observed number of species (Sobs), non-parametric incidence-based coverage estimator (ICE) and Michaelis-Menten (MMMean) are the richness estimates.

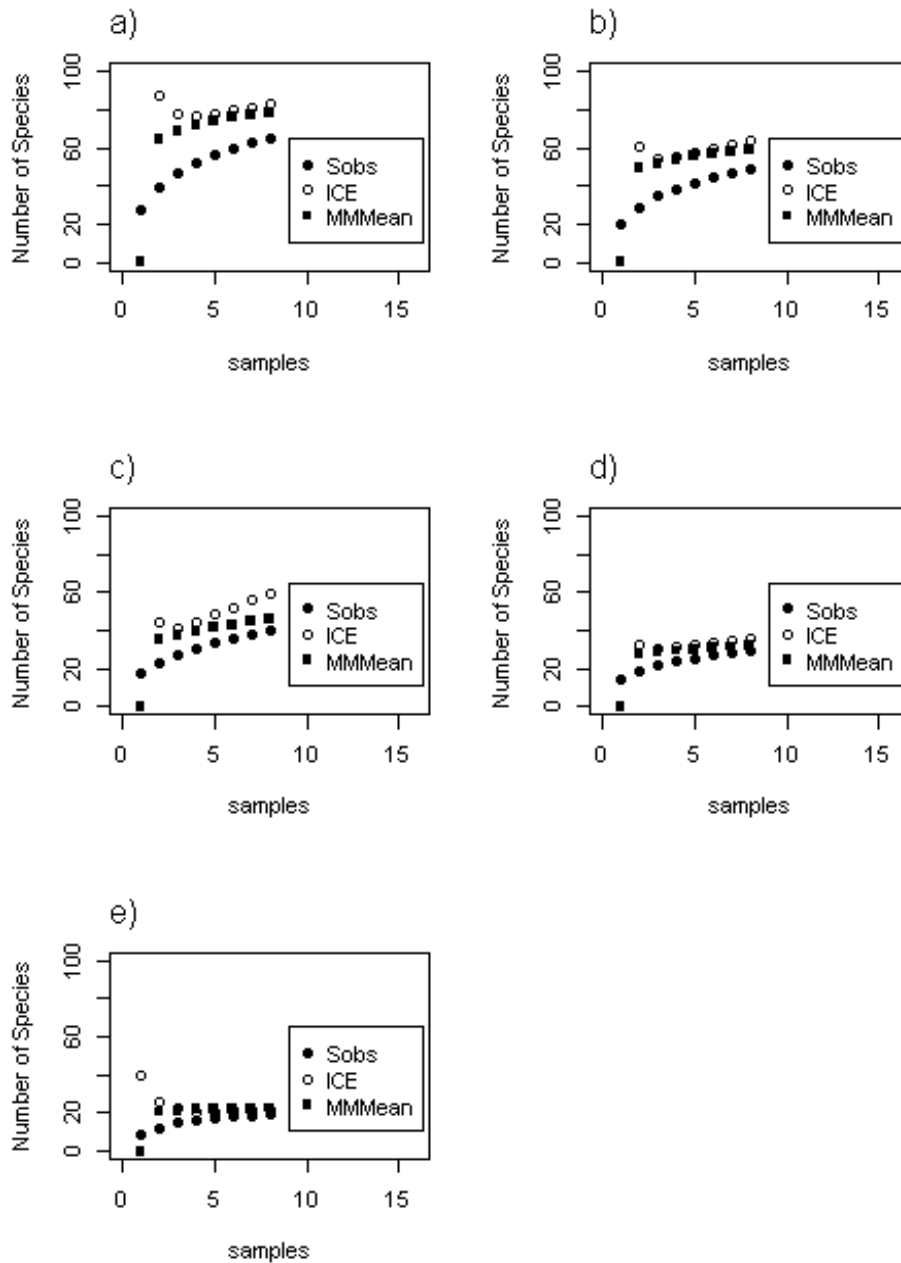


Figure 2. Species accumulation curves for each of the five altitudinal sites at Mariepskop indicating number of species richness and samples. The observed number of species (Sobs), non-parametric incidence-based coverage estimator (ICE) and Michaelis-Menten (MMMean) are the richness estimates. a) 700 m, b) 1000 m, c) 1300 m, d) 1500 m, e) 1900 m.

Species rarefaction curve show that species richness was higher at lower altitudinal sites (i.e. 65 at 700 m and 49 at 1000 m) and it was lower at the highest altitudinal site (i.e. 19 at 1900 m). Species richness across the whole altitudinal gradient decreased from lower altitudinal sites to the highest, regardless of the number of individuals collected. Even though the site at 1300 m had a high number of individuals, the number of species did not increase significantly (Fig. 3).

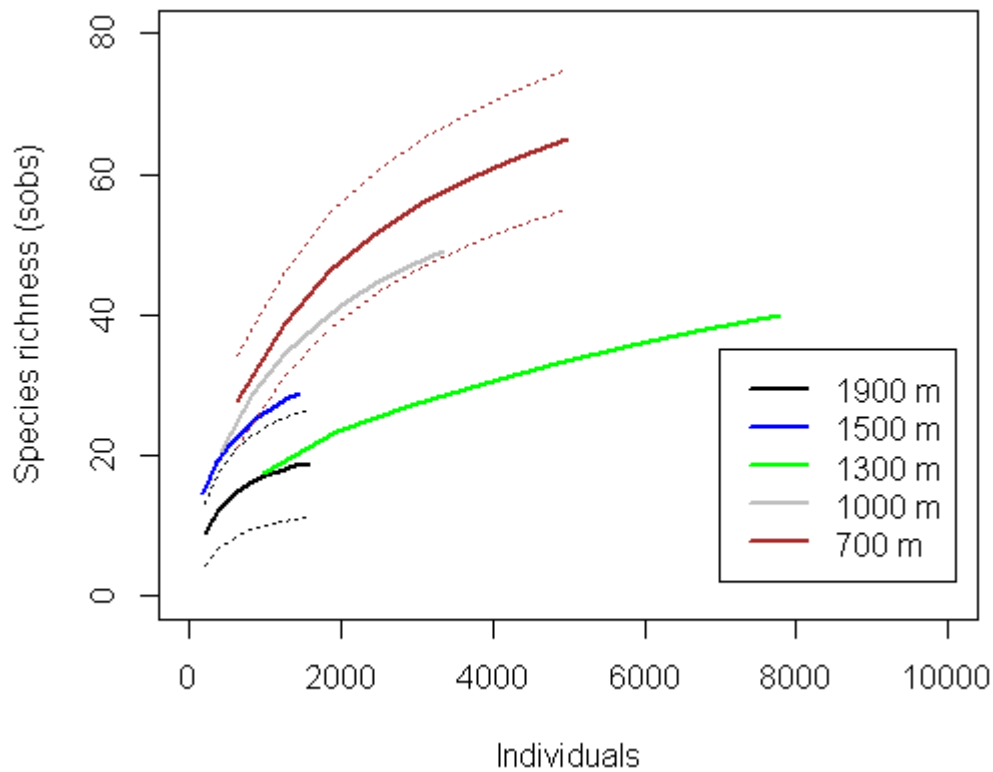


Figure 3. Species rarefaction curve for ants samples at Mariepskop indicating species richness. Broken lines indicate the lower and upper confidence intervals for the 700 m and 1900 m sites.

Community compositional changes

Results of the ANOSIM revealed that there were significant differences between the ant assemblages occupying the different altitudinal sites (Global $R = 0.762$, $p = 0.001$, Fig. 4). Ant assemblages between four sites showed R -values of one, indicating that they are strongly distinct assemblages (Table 3). The rest of the groups also showed significant differences with the exception of 1900 m vs. 1500 m ($R = -0.125$, $p = 0.743$). A negative R statistic value indicates that the two sites can barely be distinguished from one another and that there is more within-group variation than between-group variation (Table 3).

The non-metric multidimensional scaling (MDS) ordinations displayed that ant assemblages differ significantly across altitudinal sites (Fig. 4). The overlap between the two highest altitudinal sites (1900 m and 1500 m) shows that they are compositionally similar to one another (Fig. 4), which is supported by the negative R statistic value in ANOSIM pairwise tests (Table 3).

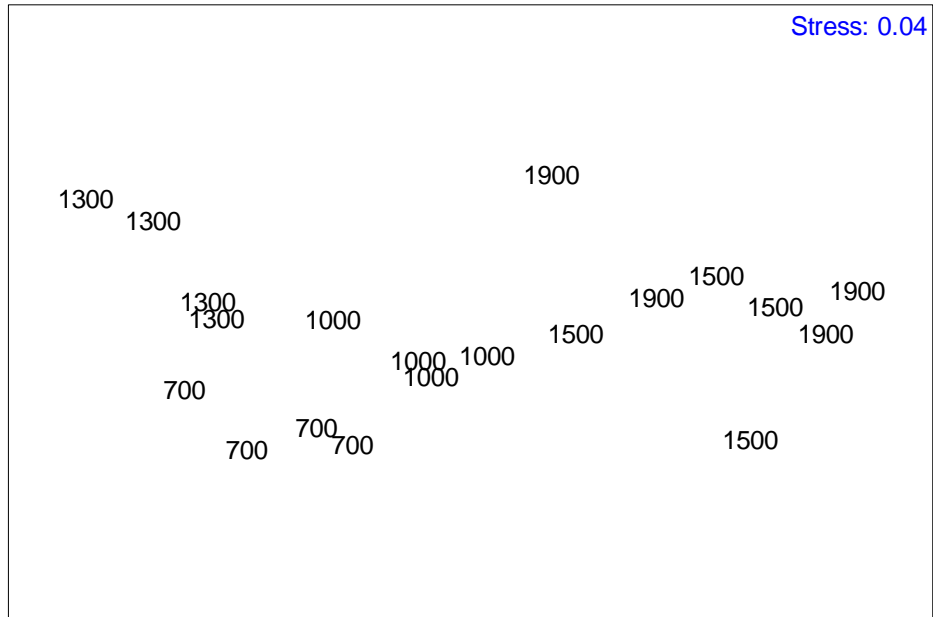


Figure 4. Non-metric multidimensional scaling (MDS) ordinations of abundance of ant species in each replicate of the five different altitudinal sites at Mariepskop based on a Bray-Curtis similarity matrix (stress = 0.04).

Table 3. Pairwise comparisons of ant assemblages between altitudinal sites using analysis of similarity. The *R* statistic is a measure of the similarity of assemblages. If *R* is significantly different from zero, then there are significant differences between assemblages. Significant values ($R > 0.7$) are in boldface.

Altitudinal sites	<i>R</i> statistic	<i>P</i> -value
1900 vs. 1500	-0.125	0.743
1900 vs. 1300	1	0.029
1900 vs. 1000	0.792	0.029
1900 vs. 700	1	0.029
1500 vs. 1300	1	0.029
1500 vs. 1000	0.833	0.029
1500 vs. 700	1	0.029
1300 vs. 1000	0.969	0.029
1300 vs. 700	0.719	0.029
1000 vs. 700	0.646	0.029

Species richness, relative abundance and altitude

The results indicated that there was a significant difference in species density (ANOVA, $F = 145.90$, $p < 0.001$) and abundance (ANOVA, $F = 4.71$, $p = 0.04$) across the altitudinal sites (Fig. 5). Ant species density decreased monotonically with an increase in altitude (from 700 m to 1900 m) (Fig. 5a). Overall there was a decline in abundance with increasing altitude, with the exception that the 1300 m site had a very high abundance (Fig. 5b) and that can be attributed to very high abundance of only three to four species (Appendix 1). Available area and species density decreased with an increase in altitude (Fig. 6); however area was smaller at the lowest altitudinal site where species density was highest.

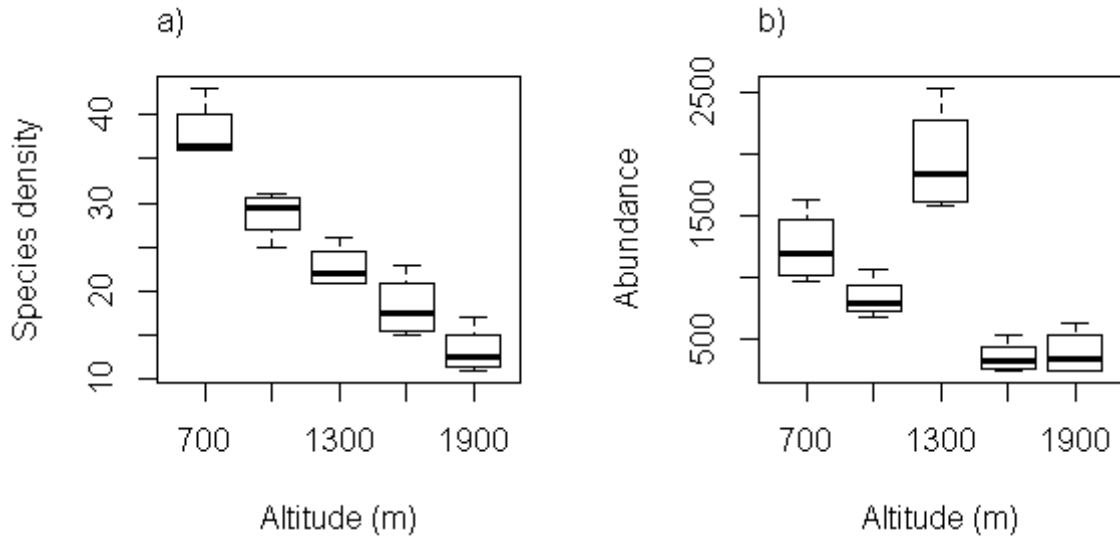


Figure 5. Boxplots of species density (a) and abundance (b) across the altitudinal gradient indicating the mean values.

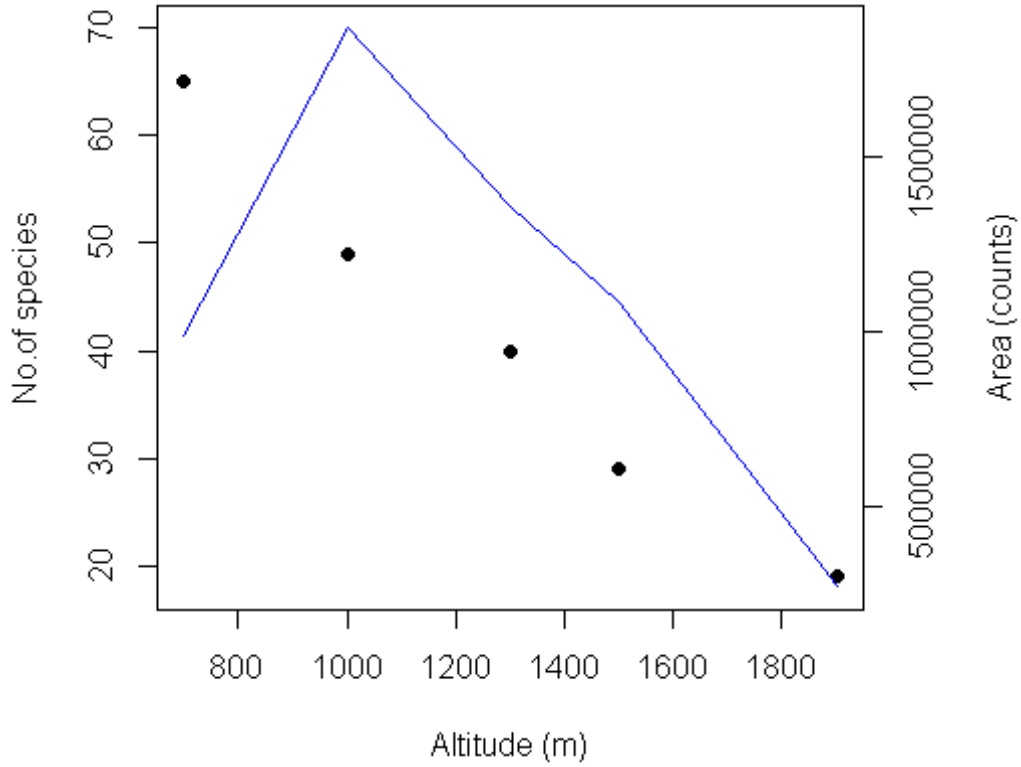


Figure 6. The relationship between available area, altitude and species density. The line represents the available area while the symbol represents species density at a particular altitudinal site.

Vegetation complexity

The vegetation of Mariepskop ranges from savanna at the bottom (700 m) to grassland at the top (1900 m). The index of complexity indicates that at Mariepskop, vegetation complexity increases with increasing altitude (Fig. 7). The lower numbers in the index indicate that vegetation at the lower sites (700 m & 1000 m) was more sparse whereas vegetation at higher altitudes was more dense, hence the high number. At heights of 50 cm and 75 cm above ground, vegetation complexity was very low at the three lowest sites (700 m, 1000 m & 1300 m) with a slightly higher index at 1500 m and 1900 m. At heights of 100 cm and 150 cm vegetation complexity index was very low for all the altitudinal sites even at a distance of 1 m. Apart from some minor differences especially at 50 cm and 75 cm, the pattern of vegetation complexity at a distance of 2 m was similar (Fig. 8).

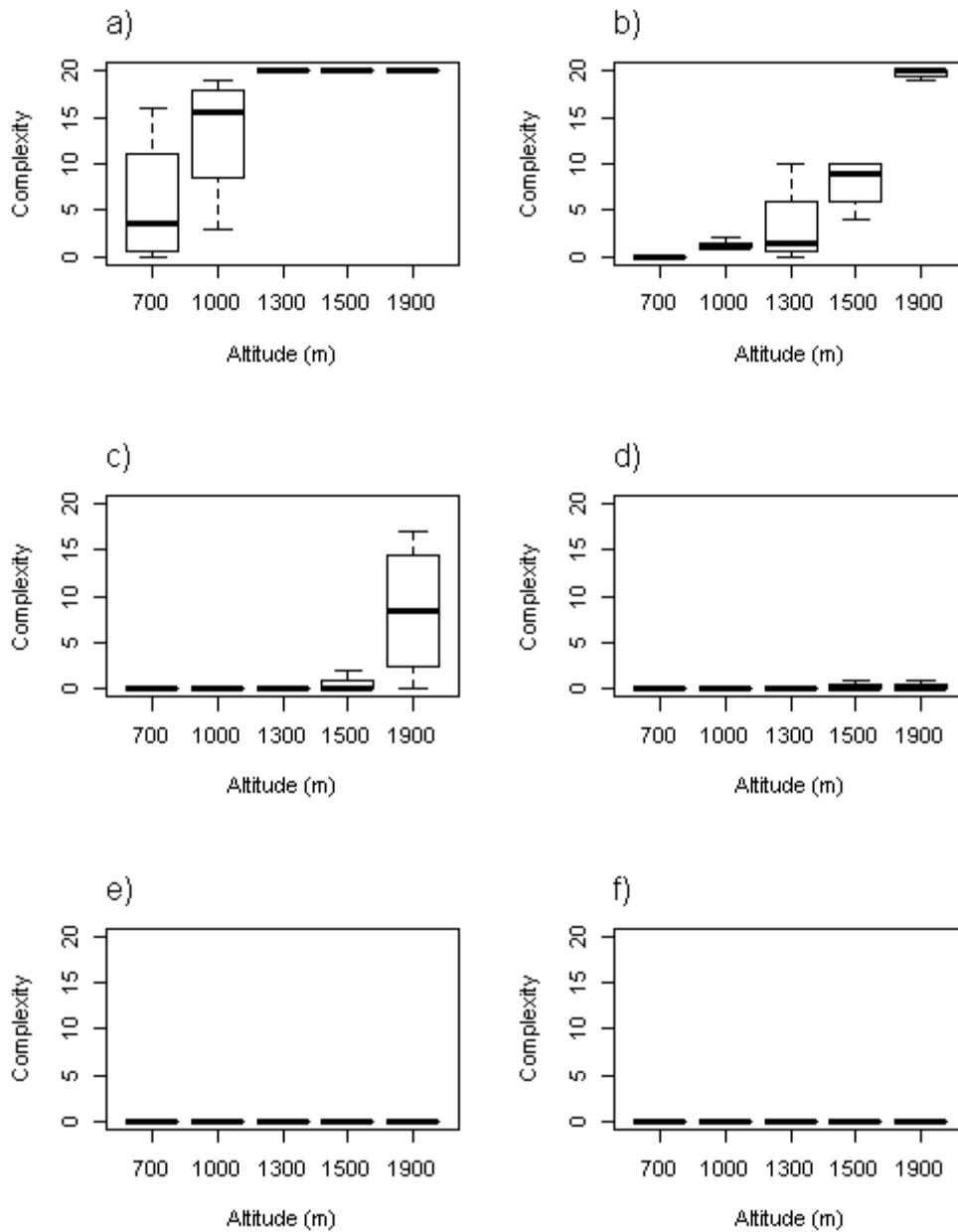


Figure 7. Boxplots displaying the index of vegetation complexity across all the altitudinal sites. Low number indicates low complexity (sparse vegetation) while a higher number indicates higher complexity (dense vegetation) recorded at a distance of 1m. Vegetation complexity measured at: a) 4 cm, b) 25 cm, c) 50 cm, d) 75cm, e) 100 cm and f) 150 cm.

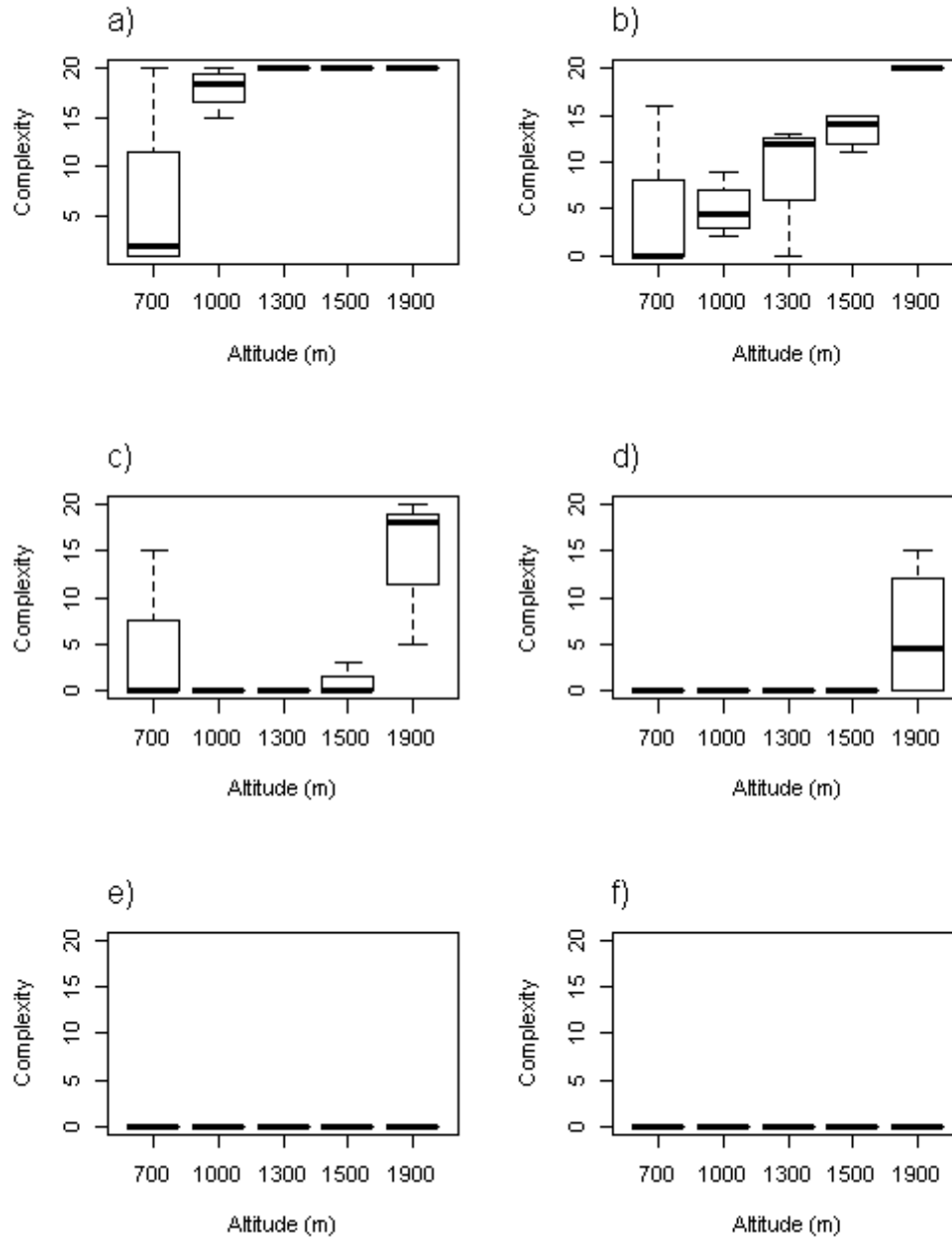


Figure 8. Boxplots displaying the index of vegetation complexity across all the altitudinal sites. Low number indicates low complexity (sparse vegetation) while a higher number indicates higher complexity (dense vegetation) recorded at a distance of 2 m. Vegetation complexity measured at: a) 4 cm, b) 25 cm, c) 50 cm, d) 75cm, e) 100 cm and f) 150 cm.

For horizontal distribution of vegetation, the results indicate that the proportion of ground covered by grass increased with increasing altitude, whereas the proportion of bare ground decreased with an increase in altitude (Fig. 9a & e). Even though the proportion of grass increased with altitude, there were no significant changes in grass height across the altitudinal gradient (Fig. 9f). There were no substantial differences in the proportion of ground covered by forbs, woody forbs and exposed rocks across the entire altitudinal gradient (Fig. 9b-d).

Altitudinal ranges of ants

The total percentages of ant species that occur only at low (700 m, 18.5%) or mid-elevations (up to 1000 m, 45.6%) make up more than half (64%) of the species collected across the entire altitudinal gradient (Fig. 10). There were 36 (41%) species that were found at a single altitudinal site and only six species were found in all five altitudinal sites. Of the 19 species found at the highest altitudinal site (1900 m), only one was unique to that site. Most species that were found at the two highest sites occurred across the entire gradient. Four species were only found at the highest altitudinal sites (1900 m and 1500 m) two of which were found only at 1500 m and the other two in both sites.

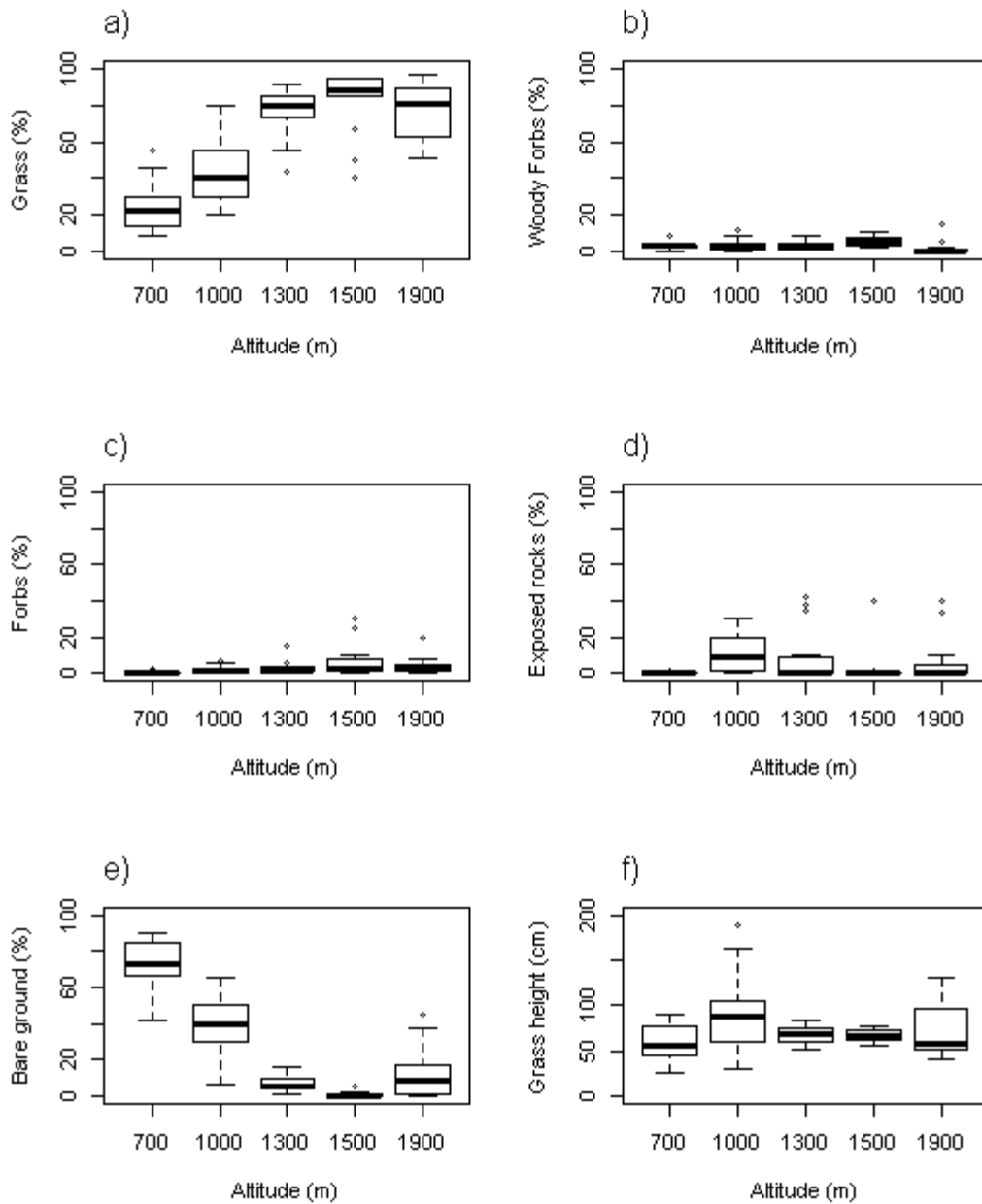


Figure 9. Horizontal distribution of vegetation across the altitudinal gradient. Percentage of ground covered by : a) grass, b) woody forbs, c) forbs, d) exposed rocks, e) bare ground and f) height of grass.

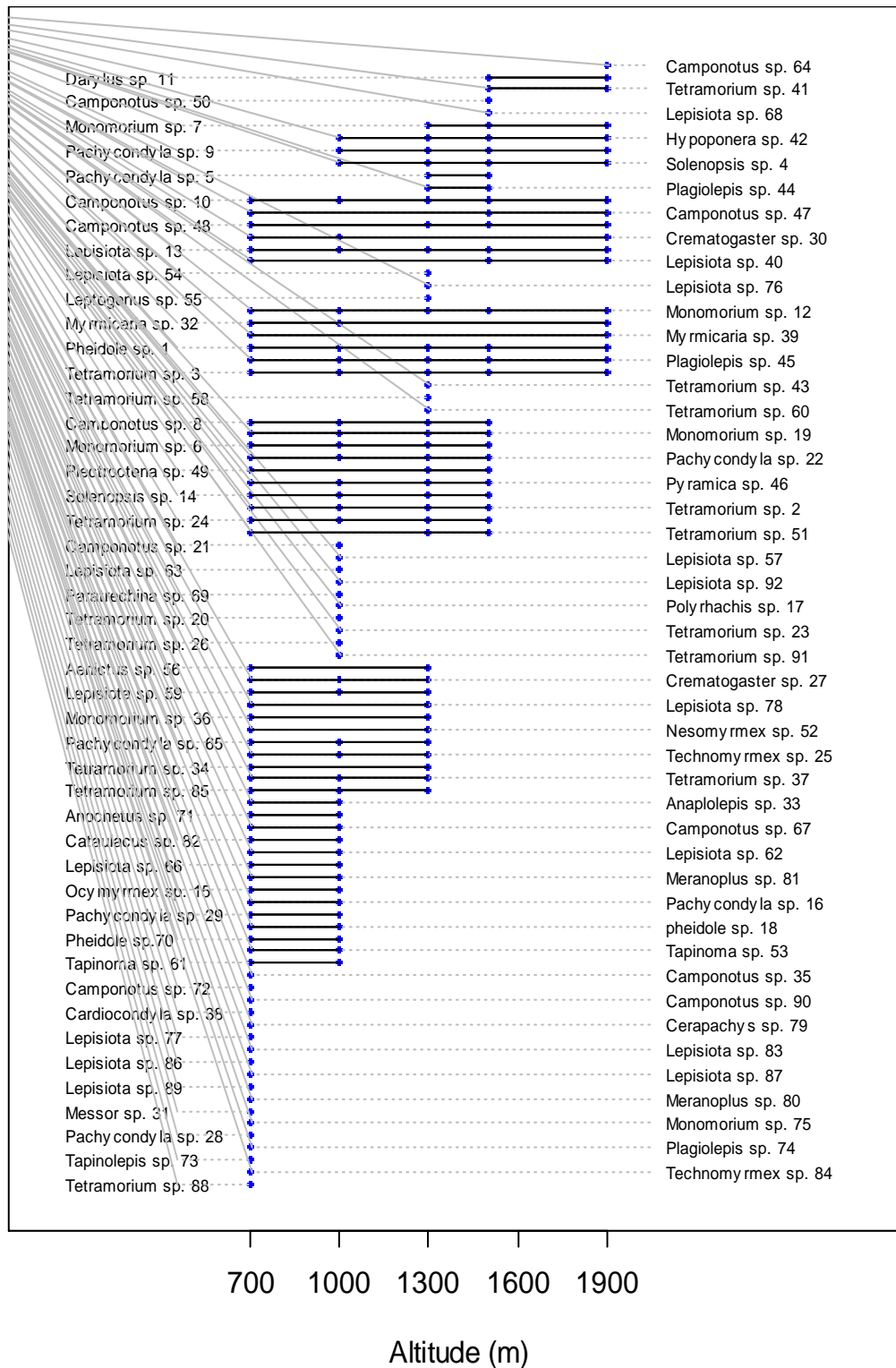


Figure 10. Altitudinal range of the different ant species along the altitudinal gradient of Mariepskop Mountain.

The IndVal analyses revealed that 21 species were characteristic of certain altitudinal sites, of which 12 were indicators only for the lowest site (700 m) (Table 4). There were three species each for altitudinal sites at 1000 m and 1300 m whereas the site at 1500 m had only one species that fulfilled the criteria for indicator species (*Plagiolepis* sp. 44, IndVal = 78%, P = 0.004). *Crematogaster* sp. 30 (IndVal = 85%, P = 0.004) and *Myrmicaria* sp. 39 (IndVal = 98%, P = 0.001) were the only two ant species which were characteristic of the highest altitudinal site (1900 m) (Table 4). No species were indicators of more than one altitudinal site.

Table 4. List of indicator species according to the Indicator method. Highlighted values are for species that are indicators for a particular altitudinal site.

Species	Altitudinal site	%IndVal	p-value
<i>Anaplolepis</i> sp. 33	700 m	100.00	0.002
<i>Camponotus</i> sp. 72	700 m	75.00	0.016
<i>Crematogaster</i> sp. 27	1000 m	85.00	0.001
<i>Crematogaster</i> sp. 30	1900 m	85.00	0.004
<i>Meranoplus</i> sp. 81	700 m	76.00	0.004
<i>Monomorium</i> sp. 19	700 m	73.00	0.002
<i>Monomorium</i> sp. 75	700 m	100.00	0.001
<i>Myrmicaria</i> sp. 32	700 m	92.00	0.003
<i>Myrmicaria</i> sp. 39	1900 m	98.00	0.001
<i>Ocymyrmex</i> sp. 15	700 m	84.00	0.003
<i>Pachycondyla</i> sp. 9	1300 m	73.00	0.002
<i>Pheidole</i> sp. 18	1000 m	79.00	0.003
<i>Pheidole</i> sp.70	700 m	95.00	0.005
<i>Plagiolepis</i> sp. 44	1500 m	78.00	0.004
<i>Solenopsis</i> sp. 14	1300 m	99.00	0.003
<i>Solenopsis</i> sp. 4	1300 m	92.00	0.002
<i>Tapinoma</i> sp. 53	700 m	70.00	0.044
<i>Tapinoma</i> sp. 61	700 m	92.00	0.002
<i>Tetramorium</i> sp. 20	1000 m	75.00	0.015
<i>Tetramorium</i> sp. 34	700 m	97.00	0.002
<i>Tetramorium</i> sp. 37	700 m	96.00	0.002

Redundancy analyses

Five of the environmental variables contributed significantly to the variance explained in the ant assemblages (Table 5). The first axis represents an environmental gradient of increasing altitude and decreasing magnesium content. The second axis represents increasing percentage of bare ground and decreasing percentage of clay in the soil (Fig. 11). Although altitude was the most important variable in the first axis, it was the percentage of clay in the soil that explained the overall highest variance in assemblage structure.

Table 5. The environmental variables that explained significant amount of variation in species composition (R -values, ter Braak & Šmilauer, 2002) from redundancy analysis (RDA). The significance of the R -values was determined using Monte Carlo permutation tests (P = significance and F = test statistic). Eigenvalues indicate the additional variance explained by each variable. Axes 1 and 2 are the first two ordination axes of the biplots of samples and environmental variables. A negative R -value reflects gradient direction in the RDA ordination. Sum of all canonical eigenvalues: 0.62; Alt: altitude; BG: proportion of bare ground; HG: height of grass. Significant R -values are highlighted.

Variable	Eigenvalues	P	F	R	
				Axis 1	Axis2
Alt	0.268	0.005	6.575	0.904	□ 0.186
BG	0.133	0.005	3.763	□ 0.536	0.665
Clay	0.105	0.005	3.381	0.089	□ 0.920
HG	0.059	0.010	2.024	□ 0.081	0.096
Mg	0.053	0.010	1.938	□ 0.461	0.059

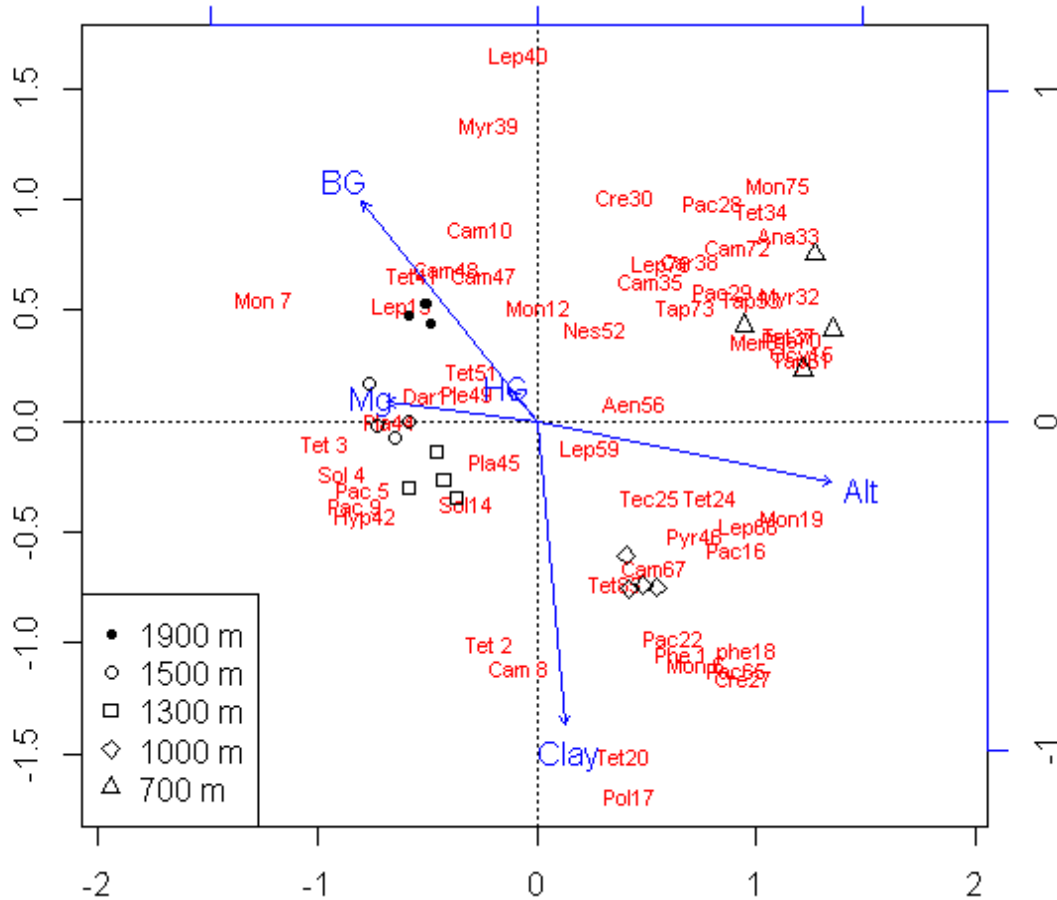


Figure 11. RDA ordination (biplot, sample scaling) of the ant assemblages occurring in the different altitudinal sites across the whole transect in relation to environmental variables. The text in red refers to the species and the abbreviations used are based on the first three letters of the genus and a number (full details of names in Appendix 1 & Fig. 10).

Discussion

Species richness

The ant species richness of Mariepskop compares favourably with other areas in South Africa. Botes *et al.* (2006) used a sampling protocol similar to the current study and they recorded 85 species, 24 genera and 72,379 individuals in the Cederberg (Cape Floristic Region). They sampled a larger area and had 17 altitudinal sites ranging from sea level to 1926 m. Another study which was comparable with this study was conducted recently in the Soutpansberg and they recorded 78 species, 28 genera and 40,294 individuals (Munyai & Foord, 2012) while the present study recorded 19,109 individuals, 92 morphospecies from 30 genera. They sampled in 11 altitudinal sites which ranged from 800 m to 1700 m and just like Botes *et al.* (2006) they also observed fewer species and genera with double the number of ants that I collected at the five altitudinal sites. Bishop *et al.* (2014) sampled over a period of six years (2006–2012) from 900 m to 3000 m at Sani Pass and collected 92 ant species in 28 genera and 60,236 individuals.

Species richness pattern

For this study ant species density decreased monotonically with an increase in elevation. Lomolino (2001) suggested that if a much broader perspective on elevational gradients which includes the full range in elevation of a particular region is considered, intermediate peaks in species density may be a common, and perhaps the general pattern. However many other studies including the present one did not extend their elevational surveys from summit to sea level due to practical or logistical reasons and it is possible that a mid-altitude peak in species richness exists. Notably, Munyai & Foord (2012) and Bishop *et al.* (2014) both recorded hump-shaped patterns without sampling from sea level whereas Botes *et al.* (2006) could not establish such a pattern

despite sampling from sea level. For this study at Mariepskop, all the altitudinal sites except for the two highest sites had 40 or more observed species compared to Cederberg and Soutpansberg that had below 30 for most of their sites. The results suggest that species richness at Mariepskop is intermediate between that of a higher energy savanna environment (Samways, 1983, 1990; Swart *et al.*, 1999; Lindsey & Skinner, 2001; Munyai & Foord, 2012) and grassland ecosystems in southern Africa.

In Madagascar Fisher (2002) also did not record a peak of species richness at mid-altitude which he stated was consistent with other studies on ants in that area. Brühl *et al.* (1999) observed a decrease in species richness with an increase in altitude, at Mount Kinabalu in tropical Borneo and they suggested that constant low temperature at higher altitudes throughout the year and the high humidity may pose problems for ants to forage by critically shortening foraging time. In contrast, Ward (2000) found that species richness peaked at mid-elevations in the tropics, but decreased continuously with elevation in temperate regions. Fisher (2004) sampled a gradient ranging from 110 m to 640 m of Monts Doudou in the Congo Basin, which is not a particularly long altitudinal gradient. He used seven principal sampling methods and recorded 310 species in 56 genera and although it was the most thorough inventory conducted in Africa at the time, they found that species richness was relatively constant along the elevational gradient. His results showed that elevation had no measurable effect on species richness and composition in that area. In the western Himalayas, ant species richness increased with an initial increase in elevation, peaked at mid-elevation and thereafter decreased, thus forming a mid-elevation peak (Bharti *et al.*, 2013), they attributed the pattern observed to adverse environmental conditions such as the decrease in temperature, food stress, other altitude-related stress, lack of trees, scarcity of litter, or nesting stress coupled with foraging difficulty.

The five altitudinal sites had distinct ant assemblages i.e. altitude explained significant amounts of the variation in ant assemblages. The largest proportion of indicator taxa was restricted to the lower altitudinal sites (12 species). This suggests that several of the lower altitude taxa could be defined as specialists, whereas others are more generalist. The specialist taxa might therefore also be more sensitive to environmental change.

Role of environmental variables

Several variables have been associated with the decrease in arthropod species diversity across altitudinal gradients such as reduction in the availability of resources at high altitude (MacArthur & Wilson, 1967), available area (Rosenzweig, 1995; Botes *et al.*, 2006), temperature and humidity (Lassau & Hochuli, 2004; Botes *et al.*, 2006; Malsch *et al.*, 2008; Munyai & Foord, 2012). Lower temperatures at high altitudes prolong larval development and reduce survival, thereby further decreasing colonisation and increasing extinction rates (Brown, 1973; Torres, 1984; Lawton *et al.*, 1987; Malsch *et al.*, 2008) and air humidity is high at high altitudes resulting in high soil humidity which may limit establishment of colonies (Wilson, 1971; Brown, 1973).

Lassau and Hochuli (2004) investigated habitat complexity on ant assemblages in three National Parks in Australia and found that low habitat complexity sites supported a much greater species richness of ants. An interesting pattern they detected was that species composition of ants differed between habitat complexity treatments with high complexity sites generally more similar to each other than to low complexity sites. This was the case with the present study results were in the highest sites (1500 m and 1900 m) with the highest vegetation complexity close to the ground had assemblages that were barely separable, however the middle site (1300

m) which was also very complex showed significantly different assemblages compared with the other two. Also for the present study, vegetation complexity was negatively correlated with altitude which was the reason why effects of vegetation complexity are not displayed in the RDA. Thus the lower species richness probably has more to do with a harsher environment at higher altitude than vegetation complexity alone. Lassau and Hochuli (2004) found that species richness of ants was greater in areas with low habitat complexity in the Sydney woodlands. My results are consistent with what they found and suggest that higher levels of complexity may not be preferred environments to the majority of ant species within a savanna. Differences in the complexity for our study reflect the change from savanna to dense grassland at Mariepskop.

Reasons why low complexity could be favourable for ants is that ant movement may be more energy efficient in less complex areas where ground cover is more negotiable at the scale of a foraging ant (Kaspari & Weiser, 1999; Lassau & Hochuli, 2004) and it could be easier for ants to follow chemical cues excreted for trails by other individuals in a colony (Lassau & Hochuli, 2004). However in their studies on wasps and on beetles Lassau and Hochuli, (2005; 2005b) found that high complexity habitats supported greater abundance and species richness when using pitfall traps. Other reasons suggested were that low complexity areas may be simpler construction and guarding of nests or lower soil moisture, and shadow levels, leading to greater light and heat intensities for energy requirements since the vast majority of ants are strongly thermophilic (Hölldobler & Wilson, 1990). One thing that should be noted is the point that the low complexity sites are also potentially the warmest because they are at lower altitude and the problem with this study is that I could not separate the effects associated with altitude and the effects associated with vegetation complexity.

The results for this study were consistent with Munyai and Foord (2012) who also recorded highest ant richness and diversity in warm and open habitats that were characterized by high proportions of bare ground. In the present study, bare ground was positively correlated with vegetation complexity and negatively correlated with altitude, grass and forbs. Ant assemblages associated with these habitats were characterized by high ant species richness; however abundance did not change much with changes in vegetation complexity or habitat cover although it first decreased with altitude then peaks at mid-altitude before dropping once again at higher altitudes.

Clay was positively correlated with K and proportion of woody forbs (WF), but negatively correlated with sand (Table 1). Percentage of both clay and sand was not correlated with altitude but seem to affect the abundance of ant species and only proportion of clay explained some of the variation in ant species richness. Other soil components were either negatively correlated or not correlated at all with altitude except for Carbon which was positively correlated with altitude. Soil Carbon decreases rapidly with an increase in temperature or altitude (Smith *et al.*, 2002; Link *et al.*, 2003) and that can affect chemical, physical and biological properties of soil, which in turn contributes to ecosystem function and stability (Link *et al.*, 2003). According to Botes *et al.* (2006) such changes will ultimately affect plant distributions, which in turn will affect the ant assemblages.

Sanders (2002) found a humped-shaped pattern of species richness and available area explained more variation in species richness and for Botes *et al.* (2006) area together with several temperature and vegetation variables, contributed significantly to the separation of the assemblages in the major vegetation types and biomes. In this study, area decreased with altitude and it was correlated with altitude and was not used in further analyses.

Ant abundance and diversity have been shown to vary considerably with temperature (Andersen, 1995; Parr *et al.*, 2005; Botes *et al.*, 2006; Munyai & Foord, 2012). Botes *et al.* (2006) found that ant species density increased with mean monthly temperature and that along with variables such as area and vegetation variables, temperature significantly contributed to the separation of the assemblages in the major vegetation types and biomes which was in line with other studies (Andersen, 1986; Parr *et al.*, 2005). According to Munyai and Foord (2012) differences in temperature gradients over their 900 m altitudinal range between the northern and southern aspect could explain the contrasting responses of ants on the two aspects. Ants are thermophilic and relatively higher species richness of ground foraging ants are found at hot dry regions (Brown, 1973; Hölldobler & Wilson, 1990; Kaspari *et al.*, 2000; Dunn *et al.*, 2009). However for this study I was unable to test for the effects of temperature on ant assemblages, which suggests that future research at Mariepskop should include temperature as one of the environmental variables in order to better understand the variables responsible for the observed pattern. Habitat quality is often associated with increasing temperature; species richness and abundance increase with improvement in habitat quality (Andersen, 1995; Cerdá *et al.*, 1998; Bestelmeyer *et al.*, 2000).

Lomolino (2001) indicated that the pattern that could be observed in a study is actually a spurious outcome of biases in the sampling regime. Sampling regime plays an important role determining the pattern of species richness thus Wolda (1987) and McCoy (1990) suggested that continuous sampling over long periods of time may be necessary and could lead to a monotonic pattern of species decline in their studies, while short-term sampling may lead to mid-elevational peaks. They both examined the distribution of insects along elevational gradients and Wolda (1987) concluded that species richness declines with increasing elevation whereas McCoy (1990)

recorded hump-shaped patterns in some of the insects. For this study, sampling was done in two different seasons for six days each using pitfall traps, although it is still a snapshot it is probably sufficient for this investigation. Even though pitfall traps are known to be biased they are often the most practical approach. In their studies on spiders (Chatzaki *et al.*, 2005) also used pitfall traps and they maintain that even if long term sampling were to be done their results would not change.

The present study at Mariepskop is the first effort to describe the elevational gradient in the ant fauna of the region and will serve as baseline study for the area. With a total of 92 species recorded for this study, Mariepskop can be considered as highly diverse. There was also a significant difference between the ant assemblages occupying different altitudinal sites. Several species are characteristic to each of the altitudinal sites at Mariepskop, and the species that were indicators for the highest elevation in this study could be susceptible to climate change because they have very narrow distributions. Vegetation complexity correlates negatively with altitude and together with the percentage of bare ground and clay in the soil, explained overall highest variance in assemblage structure. This further strengthens what other studies in South Africa have observed that not a single factor alone determines the diversity of species across altitudinal gradients but rather a combination of variables acting together.

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Appendix 1

Ant species collected with pitfall trapping at Mariepskop for 2011 for March and December 2011 combined. Data are number of ants per species for each altitudinal site. Species codes only apply for this study.

Subfamilies and species	Altitudinal sites				
	700m	1000m	1300m	1500m	1900m
Aenictinae					
<i>Aenictus</i> sp. 56	105	0	7	0	0
Cerapachyinae					
<i>Cerapachys</i> sp. 79	2	0	0	0	0
Dolichoderinae					
<i>Tapinoma</i> sp. 53	58	4	0	0	0
<i>Tapinoma</i> sp. 61	234	21	0	0	0
<i>Technomyrmex</i> sp. 25	11	4	11	0	0
<i>Technomyrmex</i> sp. 84	1	0	0	0	0
Dorylinae					
<i>Dorylus</i> sp. 11	0	0	0	27	4
Formicinae					
<i>Anaplolepis</i> sp. 33	708	1	0	0	0
<i>Camponotus</i> sp. 10	8	2	8	10	8
<i>Camponotus</i> sp. 21	0	1	0	0	0
<i>Camponotus</i> sp. 35	124	0	0	0	0
<i>Camponotus</i> sp. 47	2	0	0	1	4
<i>Camponotus</i> sp. 48	1	0	8	2	4
<i>Camponotus</i> sp. 50	0	0	0	1	0
<i>Camponotus</i> sp. 64	0	0	0	0	1
<i>Camponotus</i> sp. 67	3	4	0	0	0
<i>Camponotus</i> sp. 72	9	0	0	0	0
<i>Camponotus</i> sp. 8	8	22	159	59	0
<i>Camponotus</i> sp. 90	1	0	0	0	0
<i>Lepisiota</i> sp. 13	10	2	24	53	13

<i>Lepisiota</i> sp. 40	6	0	0	7	17
<i>Lepisiota</i> sp. 54	0	0	1	0	0
<i>Lepisiota</i> sp. 57	0	1	0	0	0
<i>Lepisiota</i> sp. 59	1	1	4	0	0
<i>Lepisiota</i> sp. 62	1	2	0	0	0
<i>Lepisiota</i> sp. 63	0	1	0	0	0
<i>Lepisiota</i> sp. 66	16	19	0	0	0
<i>Lepisiota</i> sp. 68	0	0	0	2	0
<i>Lepisiota</i> sp. 76	0	0	1	0	0
<i>Lepisiota</i> sp. 77	2	0	0	0	0
<i>Lepisiota</i> sp. 78	79	0	3	0	0
<i>Lepisiota</i> sp. 83	1	0	0	0	0
<i>Lepisiota</i> sp. 86	2	0	0	0	0
<i>Lepisiota</i> sp. 87	2	0	0	0	0
<i>Lepisiota</i> sp. 89	1	0	0	0	0
<i>Lepisiota</i> sp. 92	0	1	0	0	0
<i>Paratrechina</i> sp. 69	0	2	0	0	0
<i>Plagiolepis</i> sp. 44	0	0	10	36	0
<i>Plagiolepis</i> sp. 45	3	7	13	7	5
<i>Plagiolepis</i> sp. 74	2	0	0	0	0
<i>Polyrhachis</i> sp. 17	0	16	0	0	0
<i>Tapinolepis</i> sp. 73	19	0	0	0	0

Myrmicinae

<i>Cardiocondyla</i> sp. 38	8	0	0	0	0
<i>Cataulacus</i> sp. 82	1	1	0	0	0
<i>Crematogaster</i> sp. 27	82	477	1	0	0
<i>Crematogaster</i> sp. 30	29	8	0	0	205
<i>Meranoplus</i> sp. 80	3	0	0	0	0
<i>Meranoplus</i> sp. 81	29	9	0	0	0
<i>Messor</i> sp. 31	4	0	0	0	0
<i>Monomorium</i> sp. 12	384	155	1590	118	468
<i>Monomorium</i> sp. 19	443	153	3	5	0
<i>Monomorium</i> sp. 36	1	0	1	0	0
<i>Monomorium</i> sp. 6	309	339	576	148	0

<i>Monomorium</i> sp. 7	0	0	35	143	38
<i>Monomorium</i> sp. 75	245	0	0	0	0
<i>Myrmicaria</i> sp. 32	109	4	0	0	6
<i>Myrmicaria</i> sp. 39	5	0	0	0	318
<i>Nesomyrmex</i> sp. 52	4	0	3	0	0
<i>Ocymyrmex</i> sp. 15	31	6	0	0	0
<i>Pheidole</i> sp. 1	1003	1573	874	543	271
<i>Pheidole</i> sp. 18	33	126	0	0	0
<i>Pheidole</i> sp.70	181	10	0	0	0
<i>Pyramica</i> sp. 46	20	4	2	1	0
<i>Solenopsis</i> sp. 14	1	1	517	1	0
<i>Solenopsis</i> sp. 4	0	7	2458	55	143
<i>Tetramorium</i> sp. 2	16	16	1158	18	0
<i>Tetramorium</i> sp. 20	0	121	0	0	0
<i>Tetramorium</i> sp. 23	0	3	0	0	0
<i>Tetramorium</i> sp. 24	83	36	57	5	0
<i>Tetramorium</i> sp. 26	0	1	0	0	0
<i>Tetramorium</i> sp. 3	8	15	37	44	47
<i>Tetramorium</i> sp. 34	92	0	3	0	0
<i>Tetramorium</i> sp. 37	351	10	4	0	0
<i>Tetramorium</i> sp. 41	0	0	0	9	18
<i>Tetramorium</i> sp. 43	0	0	1	0	0
<i>Tetramorium</i> sp. 51	3	0	2	67	0
<i>Tetramorium</i> sp. 58	0	0	4	0	0
<i>Tetramorium</i> sp. 60	0	0	1	0	0
<i>Tetramorium</i> sp. 85	3	14	7	0	0
<i>Tetramorium</i> sp. 88	2	0	0	0	0
<i>Tetramorium</i> sp. 91	0	2	0	0	0
Ponerinae					
<i>Anochetus</i> sp. 71	1	1	0	0	0
<i>Hypoponera</i> sp. 42	0	1	16	11	1
<i>Leptogenys</i> sp. 55	0	0	1	0	0
<i>Pachycondyla</i> sp. 16	43	105	0	0	0
<i>Pachycondyla</i> sp. 22	8	9	8	1	0

<i>Pachycondyla</i> sp. 28	9	0	0	0	0
<i>Pachycondyla</i> sp. 29	5	1	0	0	0
<i>Pachycondyla</i> sp. 5	0	0	93	44	0
<i>Pachycondyla</i> sp. 65	9	20	4	0	0
<i>Pachycondyla</i> sp. 9	0	2	66	18	4
<i>Plectroctena</i> sp. 49	1	0	4	3	0
Total	4979	3341	7775	1439	1575

Chapter 3

Ant body size patterns across an altitudinal gradient

Abstract

Body size is one of the most fundamental traits of an animal. It can be associated with patterns of distribution and it influences how an organism interacts with the environment as well as other organisms. Bergmann's rule predicts that body size of organisms increase with latitude and it was extended to altitude and thus ant body size is also expected to increase with altitude. However other patterns have also been documented and they have suggested mechanisms such as temperature, resource availability and starvation resistance as some of the factors that contribute to observed patterns. Consequently, this study investigates ant body size patterns across altitudinal gradients and compares them with patterns of other arthropod taxa; it also explores potential mechanisms for generating body size variations in ant assemblages. To achieve this, ant species were measured and used to test for the presence of intraspecific and interspecific altitudinal body size patterns. Simple regression models were applied to investigate the associations between body size and elevation and two methods; Stevens' method and the across-species method were used for interspecific investigations. Intraspecific investigations indicate a significant increase in body size with increasing altitude for the species *Pheidole* sp. 1, *Monomorium* sp. 12, *Tetramorium* sp. 3 and *Plagiolepis* sp. 45. Interspecific investigations displayed a decrease in ant body size with increasing altitude for the Stevens' method whereas the across-species method did not show any significant relationship between altitude and ant body size. Ant body size partially conforms to Bergmann's rule for the intraspecific investigation but not for the interspecific investigations. Availability of resources and starvation resistance

might be associated with a positive relationship between body size and altitude, while a negative relationship may be attributed to mechanisms such as desiccation resistance. Future studies may provide further information about the effects of the various mechanisms involved in structuring ant body size patterns.

Key words: Mariepskop, altitude, ants, body size, Bergmann's rule.

Introduction

Body size is possibly the most fundamental trait of an animal (McMahon & Banner, 1983; Peters, 1983; Calder, 1984; Schmidt-Neilsen, 1984; Gouws *et al.*, 2011). According to Wilson (1975) animals can coexist based on the differences in their body sizes and this can be due to the fact that different sized animals tend to eat different sized foods or otherwise utilize different resources, until a point is reached where there is too much overlap to allow coexistence. Cushman *et al.* (1993) stated that body size influences every aspect of an animal's life, including interactions with the environment, rates of its physiological processes as well as the outcomes of its interactions with other organisms. Even when many other environmental factors are taken into consideration, food quality and temperature are very important and low temperature and better diets are linked to larger adults in ectotherms (Atkinson, 1994).

Nylin and Svård (1991) stated that as a first step to understanding how life-histories evolve it is necessary to understand the selection pressures that contribute to body size. Body size can be related to a number of physiological and ecological features such as metabolic rate, production rate, survival probability and likelihood of dispersal (Peters, 1983; Brown *et al.*, 2004). Body size can be associated with range size and geographic patterns of distribution and

diversity (Gaston & Blackburn, 2000; Gaston, 2003; Brown *et al.*, 2004) and this supports Lawton (1990) in the notion that body size could possibly influence the organization of ecological communities.

The components of climate and local environment (such as temperature, precipitation, seasonality, disturbance regimes and soil characteristics) vary in a non-random fashion along most elevational gradients (Sparks *et al.*, 1995; Lomolino, 2001). These variations can influence life-history strategies, including reproduction, larval growth and development (Sparks *et al.*, 1995). High elevation habitats are smaller and more isolated from other mountains, other zonal communities within the same mountain, and from human populations (Lomolino, 2001).

Bergmann's Rule predicts that body size in endotherms (within species or among closely related species) varies inversely with ambient temperature and thus increases with latitude (Mayr, 1956; McNab, 1971). This rule is highly prevalent in the literature (Van Voorhies, 1996, 1997; Mousseau, 1997; Partridge & Coyne, 1997), however some researchers have criticized it, including Scholander (1955, 1956) and Geist (1987), who concluded that it has no basis in fact or theory. According to Meiri (2011) the rule implies a tendency of organisms to be smaller at high temperatures and low latitudes and larger at low temperatures and high latitudes. Owing to this reason, Bergmann's latitudinal rule was extended to altitude and body size is also expected to increase with altitude because temperature decreases with altitude (Zhang *et al.*, 2012). The existence of relationships between body size and altitude among insects has remained largely unexplored until recently (Hawkins & Lawton, 1995).

There are only a few investigations of body size variation with altitude in arthropods (Cushman *et al.*, 1993; Hawkins & DeVries, 1996; Arnett & Gotelli, 1999; Chown & Klok, 2003; Heinze *et*

al., 2003; Entling *et al.*, 2010; Gouws *et al.*, 2011; Meiri, 2011) (Table 1). Body size studies can include intraspecific or interspecific investigations. For intraspecific investigations, body size clines are studied within species (Arnett & Gotelli, 1999; Heinze *et al.*, 2003; Gouws *et al.*, 2011; Meiri, 2011) and for interspecific investigations, they are studied across species or at the assemblage level (Cushman *et al.*, 1993; Hawkins & DeVries, 1996; Entling *et al.*, 2010). Studies including Arnett & Gotelli, (1999) and Chown & Klok, (2003) conclude that larger body sizes are more prevalent at higher latitudes.

In a study on Geometrid moths in southern Ecuador, Brehm and Fiedler (2004) found an overall decrease in body size with increasing altitude. A study by Vamosi *et al.* (2007) in Canada on diving beetles indicated a decrease in body size with an increase in altitude. For their investigations on body size-climate relationships of European spiders, Entling *et al.* (2010) found inconsistent relationships within spider families. However, the mean body size of spider assemblages increased from cool/moist to warm/dry environments in all three datasets evaluated. They suggested that this increase could be accounted for by turnover from small-bodied to large-bodied spider families.

When Hausdorf (2003) did an interspecific study on land snails of Europe he found no relationship between their body size and altitude, even though there was a marginally significant decrease with increasing latitude. He suggested that high altitude species may have evolved adaptations to the cooler climate or adaptations that enabled them to use resources that are available only at higher altitudes and cannot be used efficiently by more wide-ranging species. With regard to other groups, Lindsey (1966) demonstrated that amphibian and reptilian faunas increase in body size with latitude. In a study on spiny frogs Hu *et al.* (2011) found that the body size did not increase with altitude.

The negative relationship between body size and altitude has been attributed to various mechanisms including desiccation resistance, metabolic rate, competition and predation (Mousseau, 1997; Blackburn *et al.*, 1999; Entling *et al.*, 2010). Warmer temperatures during development of an organism lead to a smaller size due to higher metabolic costs, warm temperatures after maturity may allow such individuals to forage more and lay in more reserves for survival and/or reproduction (Kaspari, 2005). Desiccation resistance increases with body size due to stronger cuticle and smaller surface area to volume ratio (Remmert, 1981; Entling *et al.*, 2010). Other hypotheses suggested for body size variations along latitudinal and/or altitudinal gradients are resource availability, starvation resistance and heat conservation (Cushman *et al.*, 1993; Vamosi *et al.*, 2007). If resources are scarcer at higher elevations, and competition for them is greater, then there may be greater selection for larger body size (Smith *et al.*, 2000). Larger body mass increases starvation resistance (Calder, 1984; Lindstedt & Boyce, 1985) and this may be an advantage at high latitudes where resources are often seasonally scarce (Blackburn *et al.*, 1999).

Bergmann's rule suggested heat conservation as a mechanism to explain larger body size at higher altitudes/latitudes or cooler climates and this is because larger bodied species have lower surface to volume ratios, which allows them to conserve heat better in cooler climates. However Blackburn *et al.* (1999) proposed that although body size may be related to climate the reason should not be surface to area to volume ratios at least in endotherms since larger-bodied mammals and birds can have thicker and heavier layers of fur and feathers (Scholander *et al.*, 1950; Herreid & Kessel, 1967; Calder, 1984) which may result in better heat conservation. Cushman *et al.* (1993) also argued that the heat conservation mechanism is unlikely to explain

Bergmann's rule in insects and other ectotherms since large body mass may be a disadvantage because it should slow heat gain.

High elevations are also associated with reduced oxygen availability (Chappelle & Peck, 1999) or partial pressure of oxygen, which may limit the distribution of larger organisms more so than smaller organisms (Vamosi *et al.*, 2007). The largest individuals within a species or the largest species have higher oxygen requirements. Body size in amphipod communities displays a negative relationship with elevation which has been attributed to the declining partial pressure of oxygen at high elevations (Chappelle & Peck, 2003). Vamosi *et al.* (2007) examined diving beetles in Alberta and found that their body size decrease with elevation, thus their results were consistent with a role for oxygen availability but not for temperature which is lower at higher altitudes (Cushman *et al.*, 1993; Atkinson, 1995; Kaspari, 2005). They therefore concluded that species richness and probability of occupancy based on body size varied along latitudinal and elevational gradients. The contrasting patterns for species richness and body size along the latitudinal and elevational gradients suggest differential influence of correlated environmental variables, such as temperature (Spicer & Gaston, 1999).

Studies measuring body size, life-history characters, development, and population dynamics over a temperature gradient will assist in distinguishing the factors responsible for clinal variation among populations (Smith *et al.*, 2000). Extensive theoretical work on the evolutionary trade off between offspring size and number predicts that more competitive environments or shorter seasons (such as may occur at higher elevations) will favour fewer, larger offspring (Parker & Begon, 1986; Lloyd, 1987). It is predicted that large species would play critical roles in ecosystems even though they typically occur at low densities and this may be due to genetic differences between individuals contributing to differences in body size or that

size is a trait subject to non-heritable, environmentally induced variation (Brown *et al.*, 2004; Woodward *et al.*, 2005).

For insect species, size does not vary regularly with elevation and so far three different patterns have been observed from literature (Table 1). Some species are larger at higher elevations (Stalker & Carson, 1948; Miller, 1991; Krasnov *et al.*, 1996) some smaller (Sota, 1996; Blanckenhorn, 1997) and some show no change at all across elevational gradients (Hawkins & Lawton, 1995; Hawkins & Devries 1996).

Ants differ from the vast majority of insects because of their social life style and so it is unclear whether other non-social, non-terricolous groups are subjected to the same environmental stress as ants (Hawkins & Lawton, 1995). This study focused on ants because they are dominant members of terrestrial communities and their distributions are comparatively well known. The aim of the study is to investigate altitudinal patterns of body size variations in ants and to compare them with patterns of other arthropods taxa as well as exploring potential mechanisms for generating body size variations in ant assemblages. To accomplish this I asked two questions: i) whether ants of the same species have different body sizes across an altitudinal gradient (Intraspecific) and ii) if ant assemblages have different body size across an altitudinal gradient. Based on patterns typically observed for other taxa and the fact that environmental parameters such temperature decreases with altitude and they have been implicated as one of the factors that affects body size, I predict that larger species will be more prevalent at higher elevations.

Table 1. Examples of studies done on body size (BS) distributions of various taxa across altitudinal and latitudinal gradients. The methods of analyses they used as well as their results are also presented.

Taxon	Author	Lat/Alt	Midpoint Method	Stevens' Method	Across Species	Other	Results
Beetles	Vamosi <i>et al.</i> , 2007	Altitude				GLM	BS decrease with altitude
Ants	Geraghty <i>et al.</i> , 2007	Both	X	X			No relationship with altitude
Land snails	Hausdorf, 2003	Altitude	X	X	X		No significant relationship
Spiny frogs	Hu <i>et al.</i> , 2011	Altitude			X		BS decrease with altitude
Spiders	Entling <i>et al.</i> , 2010	Latitude		X			BS decrease with latitude
Butterflies	Hawkins & Lawton, 1995	Latitude	X	X	X		Inconsistent patterns
Beetles (weevils)	Chown & Klok, 2003	Altitude				GLM	BS decrease with altitude
Butterflies	Barlow, 1994	Latitude	X				BS decrease with latitude
Ants	Cushman <i>et al.</i> , 1993	Latitude	X			X	BS increase with latitude

Methods

Study area

The study took place at Mariepskop (24°53 'S, 30°52 'E) which is a part of the Drakensberg mountain range of southern Africa on the border between Limpopo and Mpumalanga provinces. Mariepskop lies on the eastern side of the Drakensberg escarpment facing to the west of the Blyde River Canyon and at 1945 m above sea level (m.a.s.l) it is the highest peak in the northern Drakensberg Escarpment. The study took place on the northern side of the mountain and the altitudinal transect ranged from the lowest altitude (700 m.a.s.l) at the bottom of Moholoholo Nature Reserve (24°29'S, 30°53'E) up to the highest point (1900 m.a.s.l) at the top of Mariepskop (24°29'S, 30°53'E). Situated on the northern side of Mariepskop is the town of Kamperus and the nearest large town is Hoedspruit which is about 30 km straight line distance from Mariepskop. The climate is comprised of summer rainfall with dry winters; the mean annual precipitation is about 450 mm and the mean annual minimum and maximum temperature at Hoedspruit is 3.7°C & 38°C.

The top of the mountain was previously used by the military and so access is restricted which has resulted in limited development around the area. The site is relatively pristine and no formal studies have been conducted in the area, it is unique in its floral diversity with over 2000 plant species recorded (Mössmer & Willis, 2000). About 900 vertebrate species including the Samango monkeys, Mariepskop Dwarf chameleon and Three Rondawels Flat Gecko were also recorded in a report on biodiversity of Mpumalanga Province (2003).

The vegetation across the altitudinal gradient falls within Savanna (Granite Lowveld & Legogote Sour Bushveld) and Grassland (Northern Escarpment Quartzite Sourveld & Northern

Escarpment Afromontane Fynbos) biomes. Granite Lowveld comprises of tall shrubland with few trees to moderately dense low woodland on the deep sandy uplands such as described by Mucina *et al.* (2006) and this vegetation type was found at the lowest sampling site (about 700m.a.s.l) of the mountain. The subsequent site further up (about 1000 m.a.s.l) has the vegetation type of Legogote Sour Bushveld which is comprised of medium to large shrubs that form dense woodlands areas. Mucina *et al.* (2006) suggested that soils in these sites are shallow to deep, sandy or gravelly and well drained.

Further up the slopes (1300 & 1500 m.a.s.l.) vegetation is of Northern Escarpment Quartzite Sourveld type. The landscapes of this type are dominated by short, closed grassland rich in forb species with scattered trees (*Protea roupelliae*, tree fern, tall shrubs and herbs) (Mucina *et al.*, 2006). The highest site at the top of Mariepskop is of Northern Escarpment Afromontane Fynbos type and the dominating structural form is shrubland with ericoid growth form. The terrain is very rocky and fires are very rare. It has summer rainfall which is augmented by mist during large parts of the year. The temperature is cooler than the surrounding area with mean annual temperature of 15.6°C (Mucina *et al.*, 2006).

Ant sampling

Sampling was done at five altitudinal sites (700 m, 1000 m, 1300 m 1500 m & 1900 m). The sites selected were in mixed grassland and savannah vegetation away from roads, forestry and other human disturbances. Ground dwelling ants were sampled at each site in March 2011 and November 2011 by means of pitfall traps. This is an efficient technique for sampling ant communities in open vegetation (Andersen, 1991; Gallé, 1991; de Bruyn, 1993). At each altitudinal site four replicates, consisting of 10 pitfall traps each were placed during each

sampling event as in Botes *et al.* (2006). The replicates were separated by a minimum distance of 120 m from each other. The coordinates of the centre of each replicate were recorded for spatial analysis. For each replicate the 10 traps were laid out in a grid (2 x 5) with traps spaced at 10-m intervals. To reduce the possibility of the traps being flooded, round plastic bucket lids with a diameter of 220 mm were supported on wire legs approximately 100 mm above each trap. Pitfall traps (diameter 60 mm & volume 120 ml) containing 60 mL of a 50% propylene glycol solution as preservative, were placed at each site to capture ground dwelling ants. Propylene glycol does not significantly attract or repel ants (Adis, 1979; Botes *et al.*, 2006). Pitfalls were left open for three days after which they were exchanged for a further three days per sampling event. Ants collected were placed in 70% alcohol and identified to species where possible or assigned to morphospecies. Ant specimens were identified using the *Identification guide to the ant genera of the world* (Bolton, 1994).

Ant body size measurements

For the study, the maximum length of the alitrunk (referred to as Weber's Length of the thorax) was measured. Weber's Length is the distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum (Brown, 1953) and is a commonly used metric in studies of ant body size (Gotelli & Ellison, 2002; Nipperess & Beattie, 2004; Weiser & Kaspari, 2006; Sanders *et al.*, 2007). For the interspecific investigations eight individuals (or as many specimens available where fewer than eight were captured) from each species were randomly selected from all the five sites across the gradient and measured using a dissecting microscope (Zeiss Stem Dv4-Oberkochen, Germany) fitted with an ocular micrometer (Appendix 1). For the intraspecific investigation, only those species that occurred across the entire gradient (i.e. at all five altitudinal sites) were measured. There were only six species that occurred at all sites (i.e.

Pheidole sp. 1, *Monomorium* sp. 12, *Tetramorium* sp. 3, *Lepisiota* sp. 13, *Camponotus* sp. 10, *Plagiolepis* sp. 45). One of these species was omitted as it is known to be polymorphic (*Camponotus* sp.10). For each species, eight individuals were measured per site (or as many specimens available where fewer than eight were captured).

Data analysis

To test for accuracy of measurements, two morphospecies (*Pheidole* sp. 1 & *Tetramorium* sp. 3) that were recorded in all the five altitudinal sites were selected. For each of these species, eight individuals from all five altitudinal sites were randomly selected and measured five times each and then the mean and standard deviations were calculated for each individual.

For the intraspecific investigation, eight individuals were randomly picked from each species and measured as in the methods above. The values of body size of all the species measured were then plotted against each altitudinal site. Simple regressions were plotted to show relationship between altitude and body size.

For the interspecific approach, eight individuals were randomly selected from each species and measured as above. To investigate the associations between body size and elevation, simple regression models were applied using two methods. For the first method, mean body size of each species was calculated and plotted against the midpoint of its altitudinal range and all species were used as separate data points (*Across-species method*; Letcher & Harvey, 1994). The midpoint is the middle point of the altitudinal range at which each species occurs. For the second method, the means of body sizes of all species occurring at the same altitude were plotted against altitude using simple regressions (*Stevens method*; Steven, 1989).

Results

In total 92 (morpho) species were collected from five altitudinal sites (Appendix 1). When testing the accuracy of the measurements for both *Pheidole* sp. 1 and *Tetramorium* sp. 3, the standard deviations of all individuals measured show that the measurement process was precise (Table 2). The mean for *Pheidole* sp. 1 was 0.86, minimum standard deviation 0.00 and the maximum 0.0179. For *Tetramorium* sp. 3, mean was 0.85, minimum standard deviation 0.00 and the maximum 0.0141.

Table 2. Ant species used to test for accuracy of measurements indicating the mean and standard deviations (SD) of the body size. ID refers to the identity of the individual ant specimen that was measured repeatedly (five times).

<i>Pheidole</i> sp. 1		<i>Pheidole</i> sp. 1		<i>Tetramorium</i> sp. 2		<i>Tetramorium</i> sp. 2	
ID	Mean ± SD	ID	Mean ± SD	ID	Mean ± SD	ID	Mean ± SD
1	0.62 ± 0.0167	21	0.80 ± 0.0000	1	0.72 ± 0.0089	21	0.80 ± 0.0089
2	0.66 ± 0.0089	22	0.82 ± 0.0089	2	0.80 ± 0.0089	22	0.78 ± 0.0000
3	0.75 ± 0.0111	23	0.85 ± 0.0110	3	0.80 ± 0.0141	23	0.82 ± 0.0000
4	0.89 ± 0.0179	24	0.86 ± 0.0089	4	0.79 ± 0.0110	24	0.80 ± 0.0000
5	0.83 ± 0.0110	25	0.91 ± 0.0110	5	0.81 ± 0.0110	25	0.86 ± 0.0089
6	0.93 ± 0.0110	26	0.89 ± 0.0110	6	0.88 ± 0.0089	26	0.78 ± 0.0141
7	0.74 ± 0.0000	27	0.86 ± 0.0089	7	0.73 ± 0.0110	27	0.99 ± 0.0110
8	0.60 ± 0.0890	28	0.86 ± 0.0089	8	0.80 ± 0.0089	28	0.84 ± 0.0089
9	0.66 ± 0.0089	29	0.84 ± 0.0089	9	0.88 ± 0.0000	29	0.96 ± 0.0089
10	0.90 ± 0.0000	30	0.87 ± 0.0110	10	0.84 ± 0.0000	30	0.86 ± 0.0089
11	0.96 ± 0.0141	31	0.87 ± 0.0110	11	0.84 ± 0.0000	31	0.87 ± 0.0110
12	0.91 ± 0.0110	32	0.87 ± 0.0110	12	0.84 ± 0.0089	32	0.90 ± 0.0000
13	0.68 ± 0.0167	33	0.97 ± 0.0110	13	0.91 ± 0.0110	33	0.90 ± 0.0000
14	0.95 ± 0.0179	34	0.94 ± 0.0089	14	0.94 ± 0.0141	34	0.96 ± 0.0000
15	1.00 ± 0.0089	35	1.04 ± 0.0089	15	0.81 ± 0.0110	35	0.97 ± 0.0089
16	0.96 ± 0.0089	36	0.99 ± 0.0110	16	0.76 ± 0.0089	36	0.97 ± 0.0110
17	0.89 ± 0.0110	37	0.91 ± 0.0110	17	0.78 ± 0.0000	37	0.88 ± 0.0000
18	0.87 ± 0.0110	38	0.96 ± 0.0089	18	0.86 ± 0.0089	38	1.06 ± 0.0000
19	0.82 ± 0.0089	39	1.13 ± 0.0179	19	0.79 ± 0.0110	39	1.08 ± 0.0000
20	0.79 ± 0.0110	40	1.13 ± 0.0110	20	0.82 ± 0.0089	40	0.86 ± 0.0089

Intraspecific investigations

For the intraspecific investigation, the species *Pheidole* sp. 1 ($R^2 = 0.42$; $P < 0.001$; Fig. 1a), *Monomorium* sp. 12 ($R^2 = 0.40$; $P < 0.001$; Fig. 1b) and *Tetramorium* sp. 3 ($R^2 = 0.40$; $P < 0.001$; Fig. 1c) showed a significant increase in body size with increasing altitude. The regression for *Lepisiota* sp. 13 did not show a significant relationship with altitude ($R^2 = 0.0036$; $P > 0.05$; Fig. 1d). Four out of the five species investigated had significant positive relationships between body size and altitude. Although there were six species occurring in all five sites only four species were presented as part of the results and they are: *Pheidole* sp. 1, *Monomorium* sp. 12, *Tetramorium* sp. 3 and *Lepisiota* sp. 13 (Fig. 1). One of the species not displayed in the results was *Plagiolepis* sp. 45 ($R^2 = 0.49$; $r = 0.72$; $P < 0.001$) because it showed similar results to *Pheidole* sp. 1, *Monomorium* sp. 12 and *Tetramorium* sp. 3.

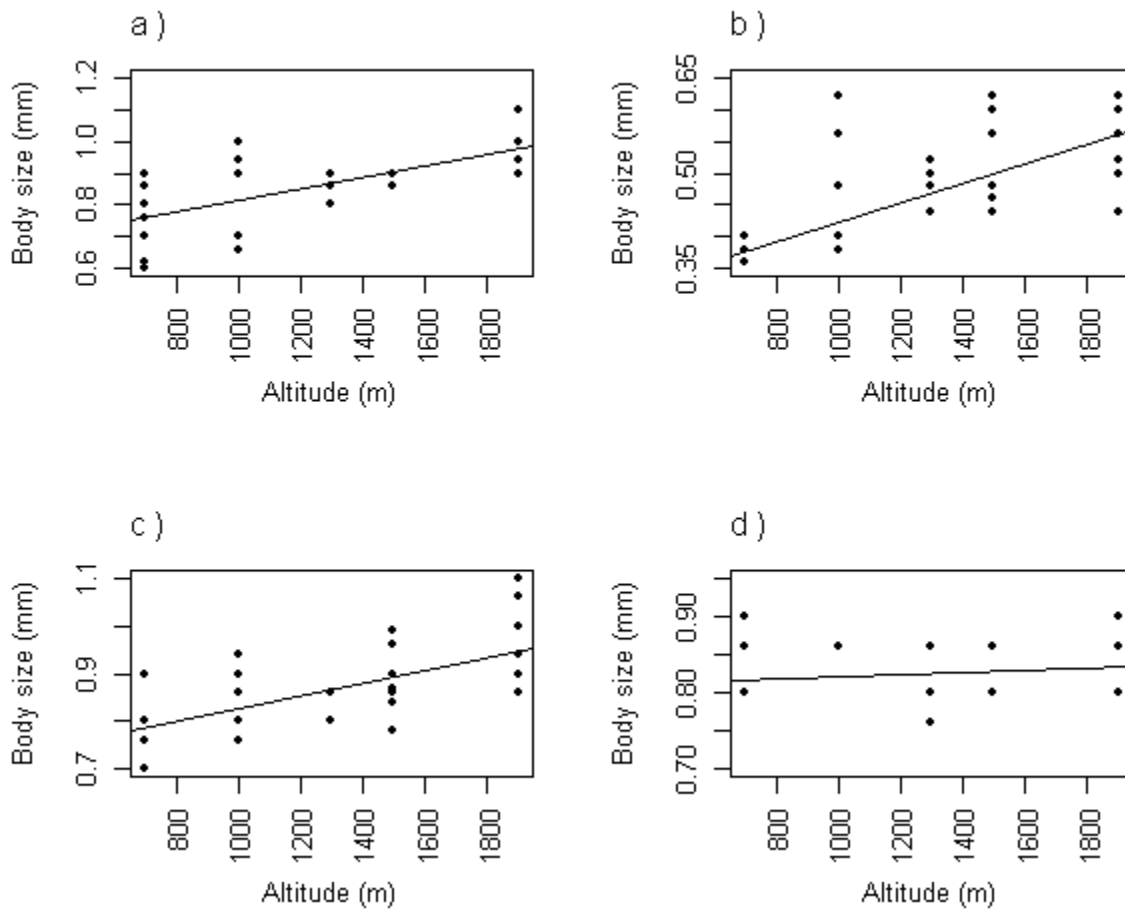


Figure 1. The relationship between ant body size and altitude within species; a) is *Pheidole* sp. 1 b) is *Monomorium* sp. 12 c) is *Tetramorium* sp. 3 and d) is *Lepisiota* sp. 13. Each symbol represents the body size of each individual per altitudinal site and the line is the best fit regression line.

Interspecific investigations

For the interspecific investigations the results display a significant relationship between ant body size and altitude for the *Stevens* method ($R^2 = 0.7192$; $P < 0.05$; Fig. 2) whereas the *across-species* method did not show a significant relationship between altitude and ant body size ($R^2 = 0.000066$; $P > 0.05$; Fig. 3).

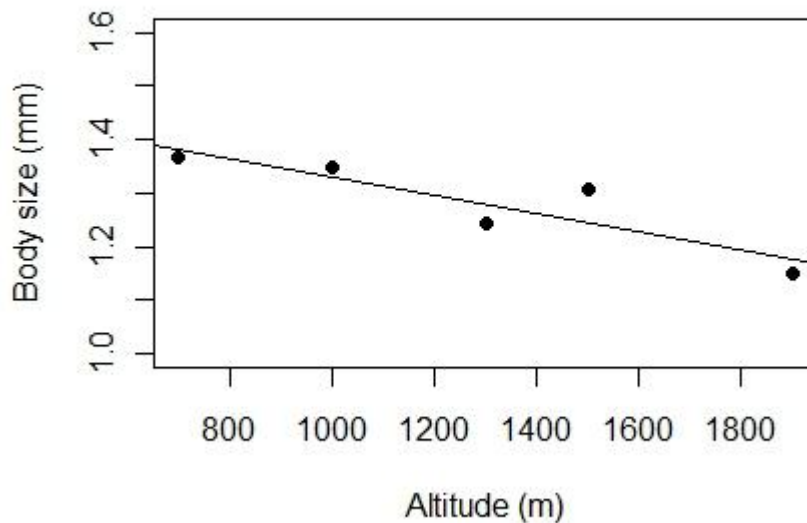


Figure 2. The relationship between body size and altitude for 92 ant species at Mariepskop using *Steven's* method. Maximum length of alitrunk (Weber's length of thorax) is used as an estimate of body size. Each symbol represents the mean body size of all species occurring at each altitudinal site, and the line is the best fit regression line ($R^2 = 0.7192$; $P < 0.05$).

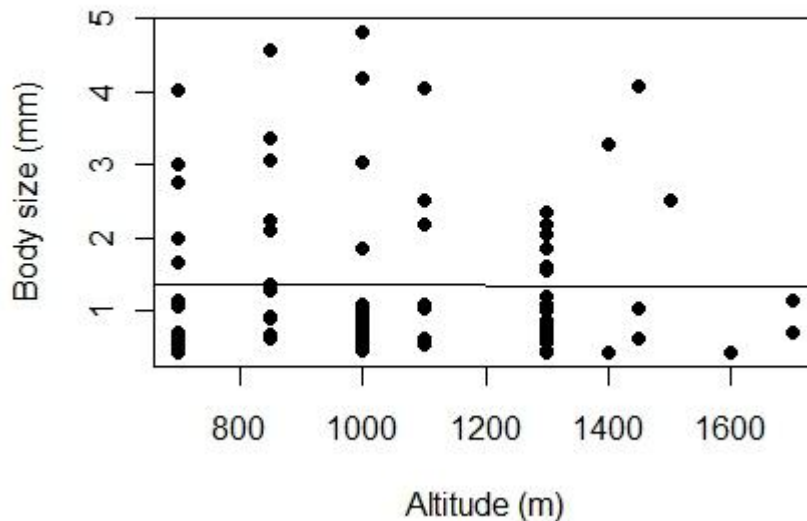


Figure 3. The relationship between body size and altitudinal midpoints of 92 ant species using *across-species* method. Maximum length of alitrunk (Weber's length of thorax) is used as an estimate of body size. Each symbol represents the mean body size of a single species, and the line is the best fit regression line ($R^2 = 0.00006657$; $P > 0.05$).

Considering the frequency of species across body size classes, it is evident that most of the species had small body sizes and very few species had large body sizes (Fig. 4). A similar pattern was observed when comparing the number of species per body size class at each of the altitudinal sites (Fig. 5). However, the total number of species decreased with increasing altitude. Species were characterised by a majority (ca. 50%) of ant individuals of the smallest size class (0 – 1 mm) and only three altitudinal sites (700 m, 1000 m & 1500 m) out of the five had species that fall under the largest size class (4 – 5 mm).

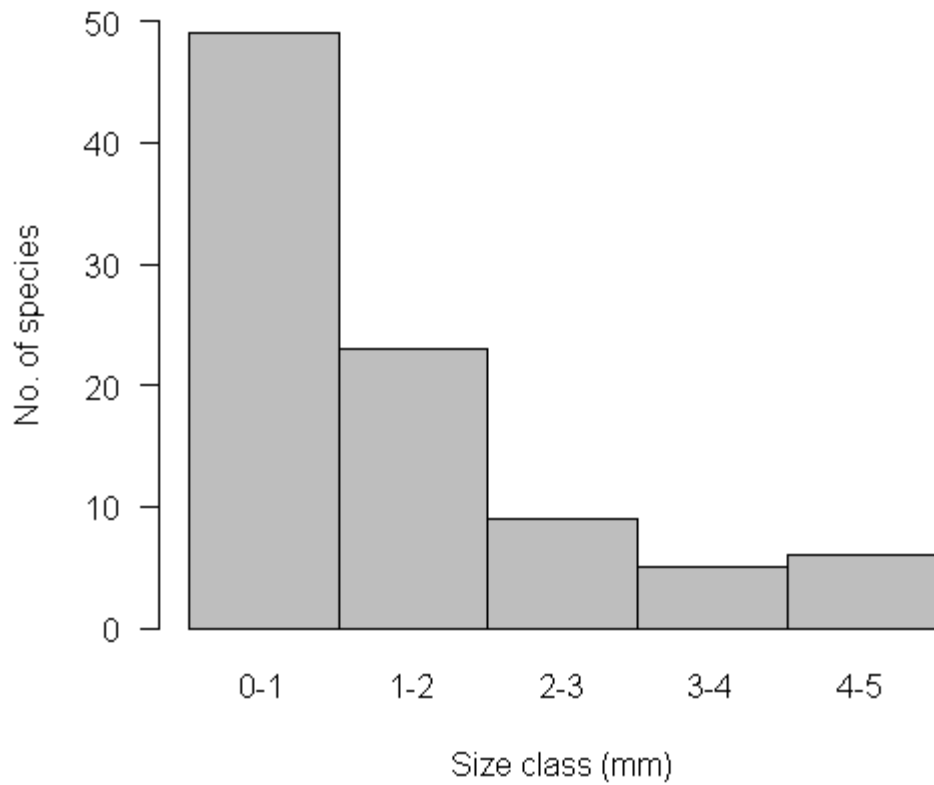


Figure 4. The number of species per body size class for all species across the entire altitudinal gradient.

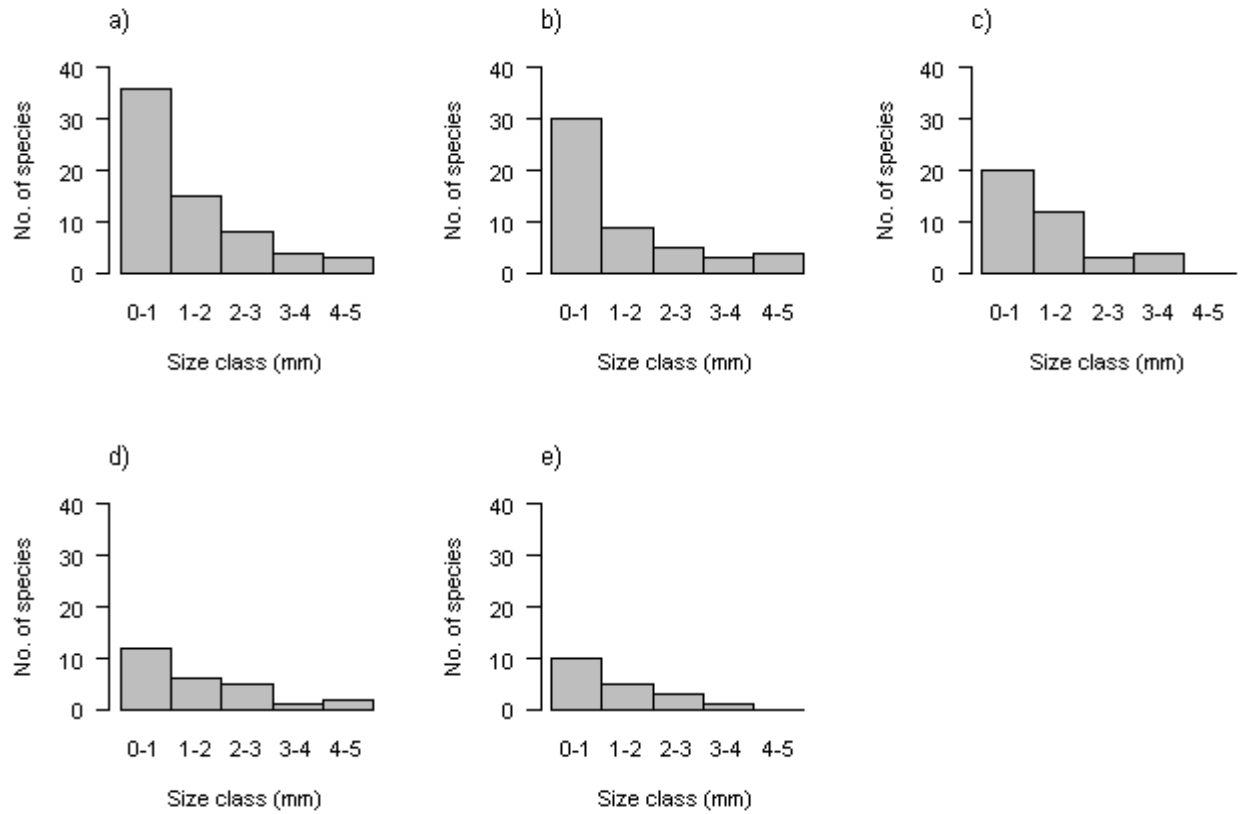


Figure 5. The number of species per body size class at each at each altitudinal site. a) 700 m, b) 1000 m, c) 1300 m, d) 1500 m, e) 1900 m.

Discussion

There is no convincing general hypothesis that explains the patterns of insect body size across climatic gradients (Brehm & Fiedler, 2004). Basset and Kitching (1991) proposed a theory, which states that the more complex the habitat structure (fractal dimension), the smaller the body size of insects living there. However for body size relationships empirical investigation is required in order to qualify such theories. To date only a few studies have investigated body size variation in ants (interspecific: Cushman *et al.*, 1993, Geraghty *et al.*, 2007; intraspecific: Heinze *et al.*, 2003).

Intraspecific body size patterns

Heinze *et al.* (2003) did an intraspecific study on the ants of the species *Leptothorax acervorum* from 16 localities throughout Europe and found that ant body size increased with latitude. The results for intraspecific investigations provided only partial support for Bergmann's rule across altitudinal gradients. They showed a significant increase in body size with an increase in altitude for four of the five species measured (Fig. 1).

Very few studies have tried to compare intraspecific altitudinal size clines in closely related species at different altitudes (Smith *et al.*, 2000; Chown & Klok, 2003; Lee *et al.*, 2012). Smith *et al.* (2000) investigated body size on the beetle (*Nicrophorus investigator*) at three sites over an elevational gradient in the southern Rocky Mountains of Colorado and found that beetles of this species had a larger body size at higher elevations. They suggested the pattern established may be due to the theory that tradeoffs between offspring size and number predicts that more competitive environment or shorter seasons such as may be found at higher elevations will favour large offspring which was initially proposed by Parker and Begon (1987). Lee *et al.*

(2012) investigated a spider species (*Myro kerguelenensis*) across an altitudinal gradient on Marion Island (50 to 600 m.a.s.l) and they found that despite high levels of variation within sites, there was little directional variation in size over the altitudinal gradient. They argued that the pattern observed probably has to do with interactions between the environment and altitudinal variation in resource availability, sex ratio and predation pressure. Their results therefore were inconsistent with either Bergmann's rule (as applied at the intraspecific level) or the converse Bergmann size trend. Chown and Klok (2003) examined intraspecific altitudinal body size clines in a monophyletic group of weevils from two regions (Marion Island & Heard Island) that differ considerably in seasonality. Body size increased with altitude on Marion Island but decreased with altitude on Heard Island. They suggested that body size increased on Marion Island due to year-round availability of resources, which may have been limited on Heard Island, where discrete generations indicate winter cessation of growth and development and hence the small body size.

Joyce *et al.* (2004) found that in their studies on the mountain stone weta *Hemideina maori* (Orthoptera: Anostostomatidae) in New Zealand, the body size increased with increasing altitude and decreasing temperature. However they established that little is known about how these variations in body size and environmental temperature influences survival probability. They also did a study which used a model to obtain estimates for survival and recapture probability and found that body size varies with elevation, but survival is similar between sites (Joyce *et al.*, 2004). Thus they suggested that body size at each altitude might be adapted to the local environment.

Interspecific body size patterns

Interspecific investigations did not show a significant relationship with altitude in the first method (*across-species*) even though a significant decrease with altitude in the second method was detected. The first method, the mean body size of each species was plotted against the midpoint of its altitudinal range, is probably more reliable than the second method (*Steven's*) which does a regression on average body size values and the same species can contribute values to several data points. This violates the assumption of independence required for regressions.

The results for the first method match that of Geraghty *et al.* (2007) whose studies did not support Bergmann's rule. They did their studies on ants in eastern North America and they were testing whether ant body size is related to latitude and elevation. They found no relationship between body size and elevational or latitudinal maxima when they did regressions for each species. They obtained similar results when they used the *mid-point* method thus did not report it.

Cushman *et al.* (1993) examined body sizes patterns across latitudinal gradients of 65 species of European ants. For the first analyses each species was treated as a single observation, thus to relate body size to latitude they determined the slope of the least square regression and performed randomisations tests and for the second analyses they used the midpoint of the range in body size. Using both these methods, Cushman *et al.* (1993) found that the body size of the ant species increased in higher latitudes. The other pattern they detected was that regional ant assemblages became increasingly dominated by species with large-bodied workers at higher latitudes. In contrast, results for the present study indicated that species in the largest body size class were absent at the middle and highest sites (1300 m & 1900 m) and the majority of species

were small across all the altitudinal sites. Even though results for the current study are consistent with Geraghty *et al.* (2007) who used similar methods to the *across-species* method, they contrast with those of Cushman *et al.* (1993) whose results support Bergmann's rule.

Mechanisms responsible for body size patterns

Animals of different sizes differ in many ways such as mobility, predation risk and metabolic requirements (Peters, 1983; West *et al.*, 1997) and these can affect their likelihood of colonising or persisting in a given local habit (Siemann *et al.*, 1999). Local patterns may at least partly be the result of local interspecific interactions such as competition, predation and/or parasitism (Brown & Nicoletto, 1991; Siemann *et al.*, 1999). Competition and predation pressure are higher in warm environments and they favour large bodied organisms because their size renders them less susceptible to natural enemies such as spiders and lizards (Entling *et al.*, 2010) and they are better migrants that can avoid the harshest extremes by moving elsewhere (Blackburn *et al.*, 1999). Entling *et al.* (2010) found this mechanism consistent with their interspecific studies on spiders. However intraspecific investigation for the present study as well as Heinze *et al.* (2003) was inconsistent with competition and predation pressure mechanism. Body size increased with altitude therefore I assume it increased with a decrease in temperature which is inconsistent with the competition and predation pressure mechanism.

Just a few species are able to exploit strongly seasonal environments (such as higher altitudes) and as a result can acquire more of the available resources, consequently growing into larger body size (Zaveloff & Boyce, 1988). Blackburn *et al.* (1999) further suggested that the idea could be applied at an intraspecific level where variation in body size might arise to allow individuals of a species to survive on a set of resources that are scarcer in cooler or more

seasonal climates. Starvation resistance and accelerated maturation have also been associated with an increase in body size with altitude/latitude (Cushman *et al.*, 1993; Atkinson, 1995; Kaspari, 2005). Cushman *et al.* (1993) proposed the reason why ant assemblages became increasingly dominated by species with large-bodied workers at higher latitudes was due to smaller ant species dropping out of assemblages at higher latitudes and that the mechanism most likely to explain this trend was starvation resistance. However due to insufficient data on ants Cushman *et al.* (1993) found it impossible to thoroughly assess the validity of the hypothesis. They assumed that it may be because of harsh climates at higher altitudes that lead to starvation of small-bodied workers and thus favouring species with large bodied workers. Results for the current study show a single pattern across the altitudinal gradient with smaller bodied ants dominating in each of the altitudes (Fig. 4 & 5). Two of the altitudinal sites did not even contain species falling under the largest size class category (i.e. 4–5 mm; Fig. 5c & e). Therefore I am unable to support the hypotheses suggested by Cushman *et al.* (1993) above and the proposed mechanism. Larger ant species are better able to resist starvation when conditions are unfavourable for longer periods, as they generally will be in more northern latitudes (Hawkins & Lawton, 1995). On the level of the individual, Cushman *et al.* (1993) observed that the dominance of ant species with large-bodied workers increases with latitude in northern Europe and the British Isles.

Heinze *et al.* (2003) did a fasting endurance test and found that larger worker ants had more fats and when they are kept in isolation under cold temperatures, they survived significantly longer than smaller individuals. They argued that variation in ectothermic animals might be an adaptive consequence of the dynamics of cell growth based on the test they did which indicated that larger body size could be a result of fasting endurance. Interspecific

patterns observed may be due to changes in proportions across altitudes of different subfamilies which have different average body sizes and not to differences in the body size of species within ant subfamilies (Heinze *et al.*, 2003). In the intraspecific investigations I also found larger individuals of the same species of ants at higher altitudes. Thus results for the present study suggests that at individual level such a mechanism could be operating and therefore influencing the distribution of ants based on body size; however I did not test this idea. When considering the whole assemblage, I found a decrease in body size with altitude and a large percentage (53%) is comprised of small bodied species across the whole altitudinal gradient.

In a study of butterfly body sizes in the Afrotropics and Australasia, Barlow (1994) found that body size decreased with an increase in altitude. There is evidence that intraspecific variation in body size is related to latitude in at least some butterfly species (Hawkins & Lawton, 1995). Hawkins and Lawton (1995) concluded from their results as well as those of Cushman *et al.* (1993) that latitudinal gradients in insect body sizes are not identical across all taxonomic groups (e.g. butterflies and ants) and thus even within relatively narrow groups patterns may vary in different parts of the world. Nylin and Svård (1991) also found a decreasing butterfly body size with increasing latitude for nine out of the 16 species investigated, hence supporting a pattern previously detected by Barlow (1994). However butterflies differ from ants in a number of important biological and ecological characteristics, so it remains unknown if these differences account for the lack of congruence in the patterns found in the two groups.

In the present study, ant body size conforms to Bergmann's rule for the intraspecific investigation. The species that I investigated displayed significant positive relationships between body size and altitude but for the interspecific investigation, I did not establish any significant relationship between altitude and ant body size when using the *across-species* approach.

Availability of resources, starvation resistance, accelerated maturation and adaptation to local environment are some of the mechanisms expected to generate positive relationships between body size and altitude, while a negative relationship has been attributed to mechanisms such as desiccation resistance, metabolic rate, competition and predation. Body size relationships vary even across a variety of arthropods such as ants, spiders, butterflies and beetles and studies on geographic body size patterns across a variety of taxa would be useful. Patterns within species do not resemble the overall pattern across the assemblage and trends within species are not consistent thus suggesting that multiple factors affect body size relationships. Results for the present study and future studies may provide further information into basic body size distributions and processes that underlie the observed patterns.

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Appendix 1

Ant species collected with pitfall trapping for both sampling periods (April & December 2011) ordered according to the number of individuals measured per species (n), ns is the number of altitudinal sites at which each of the species was collected, ni is the number of individuals per species collected in all altitudinal sites. Body size is the mean (mm) of all the individuals per species and the standard deviations.

Species	n	ns	ni	Body size
<i>Pheidole</i> sp. 1	40	5	4264	0.87 ± 0.11
<i>Monomorium</i> sp. 12	40	5	2715	0.47 ± 0.10
<i>Solenopsis</i> sp. 4	31	4	2663	0.62 ± 0.12
<i>Monomorium</i> sp. 6	32	4	1372	1.07 ± 0.07
<i>Tetramorium</i> sp. 2	32	4	1208	1.05 ± 0.06
<i>Anaplolepis</i> sp. 33	8	2	709	2.24 ± 0.73
<i>Monomorium</i> sp. 19	23	4	604	0.63 ± 0.11
<i>Crematogaster</i> sp. 27	17	3	560	0.47 ± 0.02
<i>Solenopsis</i> sp. 14	10	4	520	0.77 ± 0.11
<i>Tetramorium</i> sp. 37	20	3	465	0.81 ± 0.12
<i>Myrmicaria</i> sp. 39	13	2	323	1.62 ± 0.16
<i>Tapinoma</i> sp. 61	16	2	255	0.63 ± 0.02
<i>Camponotus</i> sp. 8	32	4	248	2.18 ± 0.32
<i>Monomorium</i> sp. 75	8	1	245	0.63 ± 0.06
<i>Crematogaster</i> sp. 30	24	3	242	1.09 ± 0.13
<i>Monomorium</i> sp. 7	24	3	216	0.43 ± 0.01
<i>Pheidole</i> sp. 70	16	2	191	0.92 ± 0.04

<i>Tetramorium</i> sp. 24	29	4	181	1.08 ± 0.05
<i>Pheidole</i> sp. 18	16	2	159	1.37 ± 0.08
<i>Tetramorium</i> sp. 3	40	5	151	0.86 ± 0.09
<i>Pachycondyla</i> sp. 16	16	2	148	4.57 ± 0.43
<i>Pachycondyla</i> sp. 5	16	2	137	3.27 ± 0.13
<i>Tetramorium</i> sp. 20	8	1	121	0.95 ± 0.08
<i>Myrmicaria</i> sp. 32	20	3	119	1.85 ± 0.31
<i>Aenictus</i> sp. 56	16	2	112	1.01 ± 0.19
<i>Lepisiota</i> sp. 13	34	5	102	0.83 ± 0.04
<i>Tetramorium</i> sp. 34	11	2	95	1.09 ± 0.10
<i>Pachycondyla</i> sp. 9	22	4	90	4.08 ± 0.41
<i>Lepisiota</i> sp. 78	7	2	82	0.81 ± 0.07
<i>Tetramorium</i> sp. 51	13	3	72	0.64 ± 0.03
<i>Tapinoma</i> sp. 53	12	2	62	0.69 ± 0.02
<i>Plagiolepis</i> sp. 44	16	2	46	0.43 ± 0.04
<i>Meranoplus</i> sp. 81	16	2	38	0.65 ± 0.06
<i>Ocymyrmex</i> sp. 15	14	2	37	2.12 ± 0.12
<i>Camponotus</i> sp. 10	34	5	36	2.36 ± 0.61
<i>Plagiolepis</i> sp. 45	29	5	35	0.44 ± 0.05
<i>Lepisiota</i> sp. 66	16	2	35	0.62 ± 0.04
<i>Pachycondyla</i> sp. 65	20	3	33	1.85 ± 0.50
<i>Dorylus</i> sp. 11	12	2	31	1.13 ± 0.16
<i>Lepisiota</i> sp. 40	21	3	30	0.73 ± 0.08
<i>Hypoponera</i> sp. 42	18	4	29	1.03 ± 0.11
<i>Pyramica</i> sp. 46	15	4	27	0.53 ± 0.10

<i>Tetramorium</i> sp. 41	16	2	27	0.69 ± 0.04
<i>Pachycondyla</i> sp. 22	25	4	26	2.53 ± 0.27
<i>Technomyrmex</i> sp. 25	20	3	26	0.72 ± 0.11
<i>Tetramorium</i> sp. 85	18	3	24	0.64 ± 0.04
<i>Tapinolepis</i> sp. 73	8	1	19	0.68 ± 0.05
<i>Polyrhachis</i> sp. 17	8	1	16	3.04 ± 0.29
<i>Camponotus</i> sp. 48	15	4	15	2.19 ± 0.10
<i>Camponotus</i> sp. 72	8	1	9	3.02 ± 0.15
<i>Pachycondyla</i> sp. 28	8	1	9	4.03 ± 0.13
<i>Plectroctena</i> sp. 49	8	3	8	4.06 ± 0.62
<i>Cardiocondyla</i> sp. 38	8	1	8	0.51 ± 0.02
<i>Camponotus</i> sp. 47	7	3	7	2.05 ± 0.13
<i>Camponotus</i> sp. 67	7	2	7	3.05 ± 0.45
<i>Nesomyrmex</i> sp. 52	7	2	7	0.58 ± 0.06
<i>Lepisiota</i> sp. 59	6	3	6	1.05 ± 0.19
<i>Pachycondyla</i> sp. 29	4	2	6	3.38 ± 0.08
<i>Messor</i> sp. 31	3	1	4	1.67 ± 0.06
<i>Tetramorium</i> sp. 58	3	1	4	0.57 ± 0.05
<i>Lepisiota</i> sp. 62	3	2	3	0.89 ± 0.06
<i>Meranoplus</i> sp. 80	3	1	3	0.65 ± 0.06
<i>Tetramorium</i> sp. 23	3	1	3	1.06 ± 0.00
<i>Anochetus</i> sp. 71	3	2	2	1.34 ± 0.22
<i>Cataulacus</i> sp. 82	2	2	2	1.28 ± 0.28
<i>Monomorium</i> sp. 36	2	2	2	0.89 ± 0.16
<i>Cerapachys</i> sp. 79	2	1	2	0.62 ± 0.08

<i>Tetramorium</i> sp. 68	2	1	2	1.02 ± 0.08
<i>Lepisiota</i> sp. 77	2	1	2	0.59 ± 0.01
<i>Lepisiota</i> sp. 86	2	1	2	0.71 ± 0.01
<i>Lepisiota</i> sp. 87	2	1	2	0.72 ± 0.00
<i>Paratrechina</i> sp. 69	2	1	2	0.51 ± 0.16
<i>Plagiolepis</i> sp. 74	2	1	2	0.43 ± 0.01
<i>Tetramorium</i> sp. 88	2	1	2	0.67 ± 0.04
<i>Tetramorium</i> sp. 91	2	1	2	0.92 ± 0.08
<i>Camponotus</i> sp. 35	8	1	1	2.76 ± 0.14
<i>Camponotus</i> sp. 21	1	1	1	4.20 ± 0.00
<i>Camponotus</i> sp. 50	1	1	1	2.51 ± 0.00
<i>Camponotus</i> sp. 64	1	1	1	4.83 ± 0.00
<i>Camponotus</i> sp. 90	1	1	1	1.99 ± 0.00
<i>Lepisiota</i> sp. 54	1	1	1	1.20 ± 0.00
<i>Lepisiota</i> sp. 57	1	1	1	0.88 ± 0.00
<i>Lepisiota</i> sp. 63	1	1	1	0.88 ± 0.00
<i>Lepisiota</i> sp. 76	1	1	1	0.78 ± 0.00
<i>Lepisiota</i> sp. 83	1	1	1	0.72 ± 0.00
<i>Lepisiota</i> sp. 89	1	1	1	0.64 ± 0.00
<i>Lepisiota</i> sp. 92	1	1	1	0.68 ± 0.00
<i>Leptogenus</i> sp. 55	1	1	1	1.56 ± 0.00
<i>Technomyrmex</i> sp. 84	1	1	1	1.14 ± 0.00
<i>Tetramorium</i> sp. 26	1	1	1	0.84 ± 0.00
<i>Tetramorium</i> sp. 43	1	1	1	1.00 ± 0.00
<i>Tetramorium</i> sp. 60	1	1	1	0.82 ± 0.00

Chapter 4

General discussion and conclusion

The dissertation has examined ant assemblages and body size patterns across an altitudinal gradient at Mariepskop. No formal invertebrate surveys have been done across the altitudinal gradient at Mariepskop so this dissertation provides important baseline information. The analyses of species richness and body size patterns along the elevational gradient revealed several findings. Species density decreased monotonically with an increase in altitude with 92 ant species sampled from five altitudinal sites at Mariepskop. Vegetation complexity increased with altitude and available area decreased with increasing altitude. In terms of body size, the intraspecific investigation indicated that ant body size increased with increasing altitude while interspecific investigations showed a decrease in ant body size with increasing altitude using Stevens' method and no significant relationship when using the across-species method.

Species richness and body size pattern

The results for the present study indicate a monotonic decrease of species richness with an increase in elevation. This pattern is not uncommon in the literature as it was supported by other studies (Olson, 1994; Fisher, 1996; Brühl *et al.*, 1999). Various studies that have investigated invertebrate species richness across altitudinal gradients and some have recorded a hump-shaped pattern (Sanders, 2002; Vamosi, 2007; Wilson, 2007). Some studies recorded an increase in species richness at high elevations (Grabherr *et al.*, 1994; Klanderud & Birks, 2003; Walther *et al.*, 2005) while other studies reported a decrease in species richness with altitude (Fleishman *et al.*, 1998).

With regard to body size pattern, the interspecific investigations for the present study found no support for Bergmann's rule across elevational gradients. To date most of the other studies on arthropods (Hawkins & Devries, 1996; Blackburn & Ruggiero, 2001; Hausdorf, 2003; Brehm & Fiedler, 2004; Geraghty *et al.*, 2007) do not support the rule either. The intraspecific investigations have shown support for Bergmann's rule for this study. Many other intraspecific studies (Smith *et al.*, 2000; Chown & Klok, 2003; Heinze *et al.*, 2003; Joyce *et al.*, 2004; Lee *et al.*, 2012) were comparable with the findings for the present study. However in their studies on antlions, Arnett & Gotelli (1999) only found support for Bergmann's rule when they investigated body size with latitude and not with elevation. Studies in the literature indicate that positive intraspecific relationships with elevation are perhaps more common, at least with regards to invertebrates such as ants.

Ant assemblages and associated environmental variables

A number of biotic and abiotic factors are associated with the ant assemblages. For the present study variables that were most important in structuring ant assemblages were altitude, vegetation complexity, percentage of bare ground and clay in the soil. Vegetation structure changes across the gradient and it is known as one of the variables responsible for the pattern of distribution and abundance of ant species. Vegetation complexity is negatively correlated with altitude and for this study species density was higher in areas where vegetation was less complex. That observation however, may have nothing to do with vegetation structure but perhaps be driven by other factors such as environmental energy since high levels of environmental energy promote higher species richness (Wright, 1983; Rohde, 1992; Allen *et al.*, 2002). Several studies (Turner *et al.*, 1988; Currie, 1991; Roy *et al.*, 1998; Francis & Currie, 2003) have previously observed that energy-rich regions tend to support more species than energy-poor regions and that energy

rich environments support more species rather than simply more individuals per species (Davies *et al.*, 2004).

The proportion of bare ground in these areas also seemed to have an effect on species richness. It would be useful in future studies to explore those variables further in order to determine the extent to which they can affect species distributions. At Mariepskop, the type of vegetation changes with altitude, it starts as a savannah at the bottom and subsequently becomes grassland from 1300 m all the way to the top (1900 m). Thus further studies could be done to investigate variables responsible for the pattern of species richness and the distribution range.

Various other studies such as Botes *et al.* (2006) and Munyai & Foord (2012) investigated temperature as one of the variables that may determine the distribution and richness of species along altitudinal gradients in other areas and found it to be one of the most important explanatory variables. In another study on ants, Bishop *et al.* (2014) found temperature to be important in predicting species density from their investigations at Sani Pass and they suspected that it could be driving the decrease in density that they observed from the mid-elevational peak to the summit. The current study did not investigate the effects of temperature, therefore further studies in Mariepskop could include temperature as one of the explanatory variables. Temperature can also affect the body size of insects which is another aspect investigated in chapter 3 of the present study.

Body size patterns and associated mechanisms

Although the body size of insects is said to be bigger at higher altitudes (Stalker & Carson, 1948; Miller, 1991; Krasnov *et al.*, 1996), where temperatures are low, the results for the present study showed no pattern for the interspecific investigation. For investigations of individuals of the

same species (intraspecific), ant body size increased significantly with altitude. The fact that these investigations present conflicting results indicate that elevation and other potential environmental factors affects species and individuals within species differently and they need to be studied more extensively as they may reveal further insight. It is also not clear whether other species besides those examined for intraspecific studies will also assume the same pattern as those observed in this study, therefore future studies should perhaps include more species.

Besides temperature, other mechanisms have been associated with variations in body size with elevation. Desiccation resistance, metabolic rate, competition and predation (Blackburn *et al.*, 1999; Mousseau, 1997; Entling *et al.*, 2010) have been linked to a negative relationship between body size and elevation. Mechanisms such as availability of resources, starvation resistance, accelerated maturation and adaptation to local environment are considered to generate positive relationships between body size and altitude (Atkinson, 1995; Cushman *et al.*, 1993; Kaspari, 2005; Vamosi *et al.*, 2007). However for the present study, I can only speculate as to what mechanisms could have been responsible for the pattern observed, since none of those mechanisms were tested. In South Africa, at present little is known about the mechanisms associated with insect body size across elevational gradients and therefore results for the current study suggests a need for future research in that area.

Sampling regime

There is a need to conserve biodiversity; therefore it is important to undertake inventories and surveys that will help conservation organisations to understand the patterns of insect diversity in areas such as mountains that can be affected by climate change. Exhaustive inventories on broad geographical scales are probably impossible (Folgarait, 1998) therefore several studies (Romero

& Jaffe, 1989; Majer & Delabie, 1994; Majer, 1997) have suggested that it might be valuable to use more than one method of sampling.

Majer and Delabie (1994) suggested that a combination of pitfalls and other methods such as litter sifting and hand sorting increase the efficiency of species captures in comparison to any single method on its own. Longino and Colwell (1997) also supported that several methods should be used to efficiently capture additional species since they were unable to capture the number of species they expected even after a year of intensive sampling was employed. Parr and Chown (2001) investigated pitfall and Winkler methods with ants in a South African savanna and found that pitfalls captured more species than Winkler which renders them a good method to use.

However for the present study it would have been challenging to employ methods such as Winkler, litter sifting and hand sorting given the nature of the habitat sampled. The vegetation at Mariepskop changes from a savanna from the bottom with a sparse grass layer to dense grassland at the top. This renders it almost impossible to use other methods alone or together with pitfall trapping and hence the motivation to use only pitfall trapping as it is considered to be repeatable and consume less time than other methods. It would have been possible to use alternative methods at the two lowest altitudinal sites (700 m & 1000 m) which were savanna but not at the subsequent grasslands towards the top, which were not easily accessible. The two higher sites (1300 m & 1500 m) had to be accessed by helicopter, which meant that pitfall trapping was the most practical method to use as it only required limited time in the field.

The ant sampling for this study was the first quantitative, repeatable and complete survey done across this gradient. Human population, loss of habitat, disturbance and changes in land

use may all be implicated in the decline of populations but cause and effect cannot easily be demonstrated without data from monitoring and surveillance studies (Spellerberg, 1991). Baseline studies are important because identifying natural changes in the absence of long-term data is difficult, therefore ants for this study will be further identified to species level by experienced taxonomist. The ecology and population dynamics of many species remain unstudied and therefore makes it hard to assess the extent and nature of the effects of pollution and physical disturbance assessed (Spellerberg, 1991).

Components of climate and local environment (such as temperature, precipitation, seasonality, disturbance regimes and soil characteristics) vary in a non-random fashion along most elevational gradients (Lomolino, 2001). Therefore studies like the present one across elevational gradients are ideal to quantify climate change impacts.

Recommendations based on this study

Based on the findings of this study, several recommendations can be made for further research. Mariepskop is also known for its endemics including some butterflies, although the ants for present study are not yet identified to species level they may reveal some endemics associated with the mountain. First, to obtain a better understanding of the species richness patterns, sampling has to be done over long periods in order to establish trends and perhaps were possible, employ the use of more than one sampling method in order to collect other ants and not just ground-dwelling ants. However because methods differ in their efficiency and repeatability, the best possible method for the current study is pitfall traps given the nature of the elevational gradient.

Second, because this study examined how ant assemblages change in relation to area, vegetation complexity, soil composition and habitat cover of the study site; it would be advisable for future studies to investigate further how and to what extent these variables affect species richness, composition and abundance. This is important because general patterns suggest that species richness of a range of arthropods (Uetz, 1979; Andersen, 1986; Gardner *et al.*, 1995; Humphrey *et al.*, 1999; Hansen, 2000) is positively associated with habitat complexity. Habitat complexity can also influence the composition of arthropod assemblages such as ants (Gardner *et al.*, 1995; Lassau & Hochuli, 2004).

Third, future studies could also examine if different taxonomic groups such as arachnids and amphibians respond in the same way to the environmental variables above. Fourth, rainfall should also be included as one of the environmental variables examined because it affects humidity and temperature to dictate local environment. Rainfall patterns can influence long-term abundance of insect populations. Finally, further studies should investigate body size patterns across altitudinal gradients in relation to Bergman's Rule and explore the various mechanisms responsible for the patterns that have been documented in the available literature on invertebrates

Conclusion

The present study at Mariepskop recorded 92 species at only five altitudinal sites, thus illustrating the important role that mountains play as centres of biodiversity. Species richness decreased significantly with an increase in elevation and followed a monotonic pattern. A combination of variables acting together determines the diversity of species across the elevational gradient rather a single factor. For the present study, intraspecific investigation of ant

body size conforms to Bergmann's rule while interspecific shows no relationship. Ant body size patterns across species differ from patterns within species thus it would be valuable for body size studies to consider both intraspecific and interspecific investigations.

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