University of Venda

A functional and trait-based approach in understanding ant community assembly in the Soutpansberg Mountains, South Africa

by

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Declaration

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

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Abstract

The concept of taxonomic diversity has been widely used to investigate diversity patterns and the mechanism underlying community assembly. However, functional and trait diversity can further explain the factors driving community assembly because they capture different aspects of species ecological roles such as habitat requirements and resource use. To investigate the factors shaping community assembly along the elevational Soutpansberg transect, ants were used as a model study organism because they are widely distributed geographically, ubiquitous and play several important roles in ecosystems. Functional and taxonomic diversity patterns along the elevation, their drivers (seasonality, soil properties, temperature and habitat structure) were examined using a long-term dataset (8 years) collected seasonally. Morphological and physiological traits at a community level are quantified and their relationship to temperature, soil properties and habitat structure modelled. Traits were used to test the size-grain hypothesis, Janzen's rule and Brett's rule. Functional and taxonomic diversity had a humped-shaped pattern on the northern and a decreasing pattern on the southern aspect. However, taxonomic diversity did not decrease monotonically on the southern aspect. Functional diversity was mainly related to habitat structure and temperature while taxonomic diversity was explained by seasonality, soil properties and temperature. Functional and taxonomic diversity were positively related at a larger scale but habitat specific at a smaller scale. Taxonomic diversity explained more variation in functional diversity than habitat structure and their interactions. The results supported the size-grain hypothesis and Janzen's rule but not the Brett's rule. Patterns in taxonomic and functional diversity mirrored each other but were the result of different mechanisms. Temperature was however important for both measures. Incorporating functional diversity analysis into taxonomic diversity contributed significantly in understanding the different mechanisms underlying community assembly along the Soutpansberg transect. This together with trait responses to environmental variables such as a decrease in size with increased temperature could be used to model the responses of ant communities to global change drivers such as climate and land use change.

Acknowledgements

I thank God for giving me the strength, wisdom and ability to complete this research. I couldn't have made it this far without God. "Trust in the Lord with all your heart, and lean not on your own understanding, in all your ways acknowledge Him, and He shall direct your paths." Proverbs 3:5-6.

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Chapter 1

General introduction

Biodiversity in mountain ecosystems have long received interest from biogeographers and ecologists (Grytnes and Vetaas 2002). Mountains support endemic species that occur nowhere else on the planet and provide ecosystem services that are important for forestry, agriculture, cultural and recreational activities (Siniscalco and Barni 2018). They also support about one quarter of the terrestrial biodiversity and harbor nearly 50% of the world's biodiversity hotspots (Körner and Ohsawa 2005). Understanding patterns of mountainous biodiversity is important for biodiversity conservation, nature reserve area planning and management sustainability (Grytnes and Vetaas 2002). As a result, many studies have documented patterns of biodiversity in small mammals (Rowe 2009), birds (McCain 2009), plants (Acharya *et al*. 2011) and invertebrates (Gillette *et al.* 2015) along elevational gradient.

Biodiversity patterns can be investigated through taxonomic diversity (Sanders 2003), functional diversity (Reymond *et al.* 2013), trait- environment relationships (Blonder *et al.* 2017) and phylogenetic diversity (Dainese *et al.* 2015). Taxonomic diversity concerns the number and relative abundance of species in a community (Moore 2001). Functional diversity refers to "the value and range of species and organismal traits that influence ecosystem functioning" (Tilman 2001). It reflects the diversity of physiological, ecological and morphological traits found in a community (Petchey and Gaston 2006). These components are absent in measures of taxonomic diversity (Pavoine and Bonsall 2011). Trait-environment relationships describes the relationship or how well the traits are related to the environment (Schofield *et al*. 2016). Traits can reveal how communities are assembled through their associations with the environment (Yates *et al.* 2014). Phylogenetic diversity measures the features of biodiversity of different subsets of species from a phylogeny (Faith 2015). The use of phylogenetic diversity reflects the accumulation of genetic, phenotypic and phenological variations between evolutionary lineages (Harvey and Pagel 1991). Different diversity indices can improve the understanding of how communities are structured on spatial scales (Pavoine and Bonsall 2011).

Diversity patterns of taxonomic diversity have been studied along the elevational gradient of the Soutpansberg Mountains (Munyai and Foord 2015) using ants (Hymenoptera: Formicidae) because of their abundance and ecological importance within ecosystems (Ness and Morin 2008). The Soutpansberg transect is comprised of a mesic southern aspect characterized by Forest, Thicket, Sedgeland-herbland and Thicket/bush-land habitats and an arid northern aspect characterized by open dry savannah. This study showed that ant taxonomic diversity patterns are strongly determined by geometric constrains and temperature.

Literature review

Taxonomic diversity

Much of the current understanding of biodiversity patterns comes from analyses of taxonomic diversity, particularly species richness and turnover (Arnan *et al*. 2017). Patterns of species richness and their drivers have been the subject of debate for several decades in community ecology (Rohde 1999; Hodkinson 2005). There are three main types of species richness patterns in relation to increasing elevation: (1) a humped-shape pattern with high diversity at inter-mediate elevation, (2) a monotonic decrease and (3) a plateau at low elevations (McCain 2009). Among these patterns the most commonly reported pattern is the humped-shaped pattern but the mechanisms underlying these patterns are still a subject of debate (Lee *et al.* 2013). As a result, various hypotheses have been proposed to explain elevational patterns of species richness (Szewczyk and McCain 2016).

Hypotheses

Four main hypotheses have been developed and tested to explain patterns of taxonomic diversity along elevational gradients namely, the elevational climate model, thermal energy, area and mid-domain effect (Szewczyk and McCain 2016). The elevational climate model predicts that the combination of precipitation and temperature determines diversity, assuming highest diversity at warmer and wetter elevations (McCain 2007). The diversity pattern determined by the elevational climate model has been shown to rely on the local climate of the mountain (Szewczyk and McCain 2016). Arid mountains typically have highest water availability at middle elevations as a result of dry climate at lower elevations (Mollhagen and Bogan 1997, Brown 2001). The latter results in mid-elevation peak diversity as water limitation restricts diversity toward lower elevations while temperature restricts diversity toward the summit (Szewczyk and McCain 2016). On the other hand, mountains in wet climates have high availability of water and the diversity is driven by temperature. Thus, high diversity will be at lower elevations and decline towards the summit (McCain 2007).

The thermal energy hypothesis predicts a monotonic decrease in diversity with increasing elevations. This hypothesis has been shown to drive ant diversity (Sanders 2007; Malsch *et al*. 2008). This hypothesis is closely related to all temperature-based hypotheses that predicts a close relationship between diversity and temperature along elevational gradients (Pianka 1966; Kaspari *et al*. 2000; Allen *et al.* 2002). Hölldobler and Wilson (1990) showed that warmer temperatures can allow longer foraging periods. Warmer temperatures may also increase food resources through increased productivity (Kaspari *et al*. 2000). Temperature has also been shown to drive evolutionary and ecological processes because metabolic rates and chemical reactions increases with increasing temperature (Allen *et al.* 2002). These processes may also be linked the area along the elevational gradient (Rosenzweig 1992).

The area hypothesis proposes that diversity increases with an increase in area of elevational bands (Terborgh 1973; Rosenzweig 1992). This hypothesis argues that increases with area leads to reduced extinction rates resulting in high species richness because species populations have larger populations in larger areas (Gaston 2000). Larger areas are also likely to have more habitats, increasing the probability of having additional species from nearby habitats (Terborgh 1973; Rosenzweig 1992; Romdal and Grytnes 2007). Within these areas patterns of species richness may be caused by the geometric constrains (McCain 2009).

The mid-domain effect (MDE) or geometric constrains has been shown to be highly effective in explaining elevational patterns (Kluge *et al.* 2006; McCain 2009). The MDE postulates that patterns of biodiversity would be expected if geometric constrains are the only factor determining the distribution of species’ ranges (Szewczyk and McCain 2016). Thus, a hump-shaped pattern will emerge when species are randomly distributed within a geographically constrained domain (Colwell and Lees 2000).

In spite of the hypotheses proposed, studies have shown that a taxonomic approach could be incomplete surrogate for measuring biodiversity (e.g. Cadotte *et al.* 2011). Taillefer (2016) showed that it does not reflect ecological reality and that taxa are difficult to identify to species level due to taxonomic uncertainty. Thus, incorporating new biodiversity estimates that describe the functional (Petchey and Gaston 2006) characteristics of the community can improve understanding of biodiversity patterns.

Functional diversity

It is increasingly accepted that quantifying functional diversity can give more insight into temporal and spatial changes in community structure and composition (Pavoine and Bonsall 2011). Cadotte *et al* (2009) and Devictor *et al* (2010) showed that functional diversity can predict ecosystem productivity and stability better than taxonomic diversity. To identify areas with high functional diversity has broad conservation implications, as these areas can be preferentially selected for protection, thus conserving highly functioning ecosystems with the greatest amount of functional differences between species (Hector *et al.* 2001).

Elevational patterns of functional diversity

Although there have been many studies focusing on taxonomic diversity along elevational gradients (e.g. Bishop *et al*. 2014; Sander 2003), few studies have analyzed functional diversity patterns and their underlying mechanisms (e.g. Swenson *et al.* 2011). Duivenvoorden and Cuello (2012) and Lee *et al* (2013) showed that plant functional diversity decreases with elevation in the Andean forests of the Ramal de Guaramacal and Baekdudaegan in South Korea respectively. Reymond *et al* (2013) examined the effects of elevation on ant functional diversity using morphological, developmental, behavioural and ecological traits of ants on Mount la Schera in the Swiss National Park. They found that functional diversity decreased with increasing elevation and argued that lower temperatures act as a filter on ant assemblages. Using morphology as a direct measure of functional diversity, Warne (2013) found a mid-peak pattern of ant functional diversity along a Costa Rican volcano. This pattern may reflect community structuring via interspecific competition (Warne *et al*. 2013). Thus, examining traits may be one step further in predicting community responses to environmental changes (Yates *et al.* 2014).

Trait-environment relationships

An understanding of the relationship between traits and environmental variables is critical for predictions of functional and compositional changes of communities and their responses to climate change (Fortunel *et al.* 2014). Traits influence the fitness of organisms and functioning of the ecosystem (Petchy and Gaston 2006). Studies of morphological traits have revealed responses of assemblage structure to habitat structure (Montaña and Winemiller 2010), morphological disparity between assemblages (McClain *et al.* 2004) and divergent or convergent patterns of morphology among continents (Inward *et al.* 2011). While studies of physiological traits (thermal tolerance) have predicted how species will respond to climate change (Deutsch *et al.* 2008).

Significant differences in morphological traits of ants have been suggested to be influenced particularly by environmental conditions (Schofield *et al.* 2016). Habitat complexity and temperature play a major role in structuring variation among morphological traits of species (Reymond *et al.* 2013; Ossola *et al.* 2015). Therefore, quantifying the links between morphological traits of species and habitat conditions represents a necessary step in determining the processes governing species assemblages (Wiescher *et al.* 2012). Moreover, it enhances understanding of ecosystem functioning and may also enable predictions of how ongoing climate change can alter ant assemblages and diversity (Yates *et al.* 2014).

Changes in ambient conditions influence the conditions in which physiological processes are occurring and consequently changes the species fitness based on physiological constraints (Arnan and Blüthgen 2015). Therefore, a species' physiological niche can at that point be utilized to foresee how its spatial range will respond to climate change (Grant and Porter 1992). Physiological niche models can possibly characterize species niches by incorporating physiological data (Kearney and Porter 2004) and predict species spatial ranges.

Understanding species limitations is significant for understanding worldwide, regional and local patterns of biodiversity (Araújo *et al.* 2005). Physiological impediments are principal constrains acting upon the distribution and abundance of organisms (Kearney and Porter 2009), therefore analyzing species physiology is essential for understanding the distribution and diversity of organisms and, eventually, anticipating their response to climatic change (Buckley *et al.* 2012).

Physiological traits are linked with the two geographical patterns, Brett's rule (Brett 1956) and Janzen's rule, also known as the climatic variability hypothesis (Janzen 1967). Brett's rule states that there is less geographic variation in upper (CT_{max}) than in lower (CT_{min}) thermal tolerance (Brett 1956). According to Janzen's rule, there is greater thermal tolerance range where there is more variable environmental temperatures (Stevens 1989). Support for Brett's and Janzen's rule have been observed in terrestrial invertebrates (Hoffmann *et al.* 2013), vertebrates (McCain 2009). It is poorly understood whether broad spatial patterns of ant thermal tolerance are in line with those reported for other taxa (Bishop *et al*. 2017). However, evidence for Janzen's rule was observed in the northern Costa Rica for ants (Baudier 2017). The relationship between elevation and thermal tolerance has been shown to be complex and most studies focuses on non-tropical regions (Baudier 2017).

Temperature can influence organisms in many ways, their physiological performance, population growth rates and survival (Angilletta 2009). Thus, extreme temperatures may affect species performance and their existence in an environment (Bishop *et al*. 2017). A major factor determining their success in different environmental gradients is the development of different mechanisms to overcome the problems associated with extreme temperatures (Alford 2010). The temperature range in which an organism can survive is defined by its critical thermal maximum (CT_{max}) and critical thermal minimum (CT_{min}), outside of which the organisms loses its muscular control and its unable to function (Lington 2007).

Temperature has been identified as the major abiotic factor determining the distribution and structure of ant communities as it limits foraging time (Kaspari *et al*. 2015). The thermal tolerances of ants have been used to predict the impacts of climate change (Diamond *et al*. 2012), describe patterns of dominance (Parr *et al*. 2005) and the success of invasive species (Holway *et al*. 2002). Patterns of ants' thermal tolerance have only begun to be revealed (e.g. Hemmings and Andrew 2017) and can be fruitful in understanding how temperature changes may alter communities.

Thesis objectives

Long-term studies based on repeated measurements have been shown to be powerful in detecting changes in the environment (Warren and Chick 2013; Munyai and Foord 2015). Here, long-term (8 years) ant functional and taxonomic diversity is investigated by incorporating ant morphological traits data to provide valuable insight into how communities are assembled and compare elevational patterns of taxonomic and functional diversity, their response to environmental drivers (temperature, habitat structure, soil properties and seasonality) as well as exploring the relationship between taxonomic and functional diversity within habitats and across the transect (Chapter 2).

This study will examine how morphological traits respond to environmental variables (temperature, habitat structure, soil properties) and how physiological traits (thermal tolerance) of dominant ant species respond to environmental temperatures. We test if patterns of ant thermal tolerance conform to predictions of Janzen’s and Brett’s rule across the elevation (Chapter 3).

Chapter 2

Understanding community assembly along elevational gradients: taxonomic versus functional diversity and their drivers

Abstract

Understanding how taxonomic and functional diversity are related and their response to environmental variables can give insight into how communities are assembled. However, whether patterns in these two diversity indices differ along elevational gradients and what kind of environmental variables control or shape them are still poorly understood. This study compares functional and taxonomic diversity patterns of ants across an elevational transect in the Soutpansberg Mountains in South Africa. Epigaeic ants were collected using pitfall traps from 44 replicates across 11 elevational sites and related to soil temperature, habitat structure, soil properties and seasonality using GLMM with replicates as random factors. Functional and taxonomic diversity exhibited a humped-shaped pattern on the northern aspect and decreased with increasing elevation on the southern. Both diversity indices were positively related to temperature, taxonomic diversity was also related to soil properties and seasonality, while functional diversity was driven by habitat structure. Taxonomic diversity varied between seasons and was higher during the wet season while functional diversity did not vary seasonally. Taxonomic and functional diversity were positively correlated but at finer scales the relationship was habitat specific. The results suggest that taxonomic and functional diversity patterns may be predicted by different environmental variables and their relationship may be determined by spatial scale. In conclusion, examining both taxonomic and functional diversity and their drivers can reveal the mechanisms that structure ant communities along elevational gradients.

Introduction

Community assembly is the study of processes that shape the abundance and identity of species within their ecological communities (Kraft and Ackerly 2014). It is a complex phenomenon driven by an interplay between ecological interactions of species that shapes local communities and biogeographic and evolutionary processes that lead to variation in diversity and composition of species (Kraft and Ackerly 2014). For that reason, an understanding of what shapes community assembly remains elusive (Pavoine and Bonsall 2011).

Habitat filtering (Keddy 1992) and niche differentiation (Silvertown 2004) are among the dominant mechanisms structuring communities. Habitat filtering imposes ecological filters that select species from a regional pool given that their traits are suitable for that habitat (Keddy 1992). Species in a community therefore become functionally similar and those that are functionally dissimilar are filtered because they cannot compete and deal with local environmental stress (Mayfield and Levine 2010). Niche differentiation on the other hand suggests that coexisting species differ in their resource-acquisition traits, increasing complementarity of resource use (Silvertown 2004) while decreasing the intensity of inter-specific competition (Gross *et al.* 2007). Fitzgerald *et al* (2017) posit that less attention has been given to how assembly mechanisms differ at a temporal scale.

Knowledge about the factors controlling community assembly is important as it ultimately affects ecosystem function (Kraft and Ackerly 2014). For example, the role of the ongoing climate change in structuring communities is evident in modern shifts in species distribution that correlate with increasing temperatures (Woodall *et al.* 2009). Quantifying abiotic and biotic factors underlying spatial distribution is therefore important in ecology and can also give insights into the mechanism driving change in communities (Cavender-Bares *et al.* 2009).

The number of species and their relative abundance provides a starting point for describing communities (Pavoine and Bonsall 2011). Estimating the number of species (species richness) in a given area is a basic step in community ecology (Colwell and Coddington 1994) and is the most commonly used measure of biodiversity. Investigating species richness can reveal the impacts of climate change since it is expected to reduce (Thomas *et al.* 2004) or increase (Boutin *et al.* 2017) the number of species.

Although spatial patterns of species richness are well studied, there are several hypotheses that explain these patterns (Szewczyk and McCain 2016). The main hypotheses include (1) the ‘thermal energy hypothesis’, relating increased species richness to higher rates of biotic processes as well as interactions (Allen *et al*. 2002; Mittelbach *et al.* 2007); (2) the ‘area hypothesis’, assuming greater opportunities for maintaining speciation and richness in larger areas (Rosenzweig 1995; Romdal, and Grytnes 2007); (3) the ‘geometric constraint hypothesis’, postulating that geometric constrains are the only factor determining the distribution of species even in the absence of environmental drivers (Colwell *et al.* 2004; Brehm *et al.* 2007) and (4) the ‘climate model hypothesis’, predicting that the combination of precipitation and temperature determines diversity, predicting higher richness at warmer and wetter areas (McCain 2007).

Numerous studies (e.g. Colwell *et al.* 2002; Sanders *et al.* 2007) along different environmental gradients found support for one or the other of these hypotheses. However, recent studies have shown that species richness is not enough to infer a deeper mechanistic understanding of the underlying processes that influence communities (Lavergne *et al.* 2010). Incorporating functional diversity can improve our understanding of diversity patterns since they capture different aspects of species ecological roles, habitat requirements and resource use (Nunes *et al*. 2016). In general, taxonomic diversity does not represent the functional differences among species (Schmera *et al.* 2017). Functional diversity can be used to evaluate functional traits, examine species relationship with the environment, and can reveal principles elucidating the assembly of communities (Siefert *et al.* 2013).

Elevations are powerful natural experimental systems (Bässler *et al.* 2016). Studies of the distribution and diversity of species along these gradients have re-emerged because elevations are seen as a place to study the effects of global warming (Parmesan 2006). Environmental conditions along elevational gradients change rapidly going up a mountain, making it practical to perform evolutionary and ecological studies over short distances (Körner 2007). In this context, elevational gradients are good for testing how and which environmental factors affect the taxonomic and functional diversity of ant community assembly.

Ants (Hymenoptera: Formicidae) are well studied social insects, geographically widespread and important for ecosystem functioning (Ratchford *et al*. 2005). They play major roles in ecosystem functioning, soil movement and including seed dispersal (Hölldobler and Wilson 1990). Changes in ant abundance might have consequences for biodiversity and ecosystem processes (Oberg *et al*. 2012). Ants are used as indicators of land management practices and restorations efforts (Andersen 1990), making them an ideal model taxon to investigate factors determining community assembly.

This study aims to contribute to our understanding of functional diversity along environmental gradients by comparing the functional diversity patterns with that of taxonomic diversity for ants across an elevational transect in the north-eastern parts of South Africa based on data that have been collected seasonally from 2009 to 2016. More specifically we ask how functional diversity varies across the mountain, identify correlates and possible drivers of this diversity and test whether it is correlated with taxonomic diversity. This study predicts that diversity will increase with increasing temperature because of the thermophilic nature of ants (Hölldobler and Wilson 1990) and that diversity will increase in sites with more bare ground and decrease in complex habitats where foraging is difficult (Gibb and Parr 2010). Functional diversity will decrease with increasing elevation since traits may become less diverse following unfavorable conditions for ants at high elevations such as a decreased temperature (Reymond *et al.* 2013). We further predict that taxonomic and functional diversity patterns will change with seasons because ants are most active and abundant during hot summer rainfalls (Parr *et al.* 2004). Lastly, we predict that functional and taxonomic diversity will have a positive linear relationship.

Materials and methods

Study area

The study was carried out along an elevational gradient in the Soutpansberg Mountain, located in the north-eastern corner of South Africa. The Soutpansberg (Fig 2.1) forms part of the Vhembe Biosphere Reserve (VBR) which includes priority areas for biodiversity conservation namely, Mapungubwe National Park and Kruger National Park. The Soutpansberg Mountain is known for its remarkable biological diversity and it has been identified as the Centre of Endemism (Van Wyk and Smith 2001).

The western Soutpansberg (Fig 2.1a), where the transect is located, consists mainly of sandstone, erosion-resistant quartzite, conglomerate, basalt, and shale rocks (Mostert *et al.* 2008). The climate within the study area varies dramatically due to the topographic complexity and elevational changes over short distances with rainfall ranging from 367 mm annually in the north of 1874 mm in the south (Hahn 2002).

The transect has a north-south orientation that extends over the highest point of the Mountain (Fig 2.1b), Lajuma (1748 m), in the Luvhondo Nature Reserve. It spans an elevational range of 900 m in the north from 800 to 1.700 m a.s.l and descends another 800 m on the south to 900 m a.s.l (Fig 2.1) (Munyai and Foord 2012). There are five structurally distinct habitat types across the Mountain, namely sedgeland, forest, shrubland, thicket and woodland. The lowest site on the southern aspect (09S) is characterized by low, closed Shrubland (Fig 2.2a), site 10S is covered with short Thicket (Fig 2.2b), the mid-elevations are comprised of Tall (12S) (Fig 2.2c) and Short forest (12S2) (Fig 2.2d) (Edwards 1983). The higher elevational sites 14S (Fig. 2.2e), 16S (Fig 2.2f) and 17N (Fig 2.2g) on the southern aspect and summit consists of a Sedgeland-herbland matrix. All sites 08N (Fig 2.3a), 10N (Fig 2.3b), 12N (Fig 2.3c) and 14N (Fig 2.3d) on the northern aspect are dominated by short open Woodland (Fig 2.3) (Table 2.1) (Edwards 1983).

Table 2.1 Summary of 11 sites along the elevation with their habitats and aspects.

Habitat	Site	Aspect
Woodland	08N, 10N, 12N, 14N	North
Shrubland	09S	South
Thicket	10S	South
Tall forest	12S	South
Short forest	12S2	South
Sedgeland-herbland	14S,16S,17N	South/North

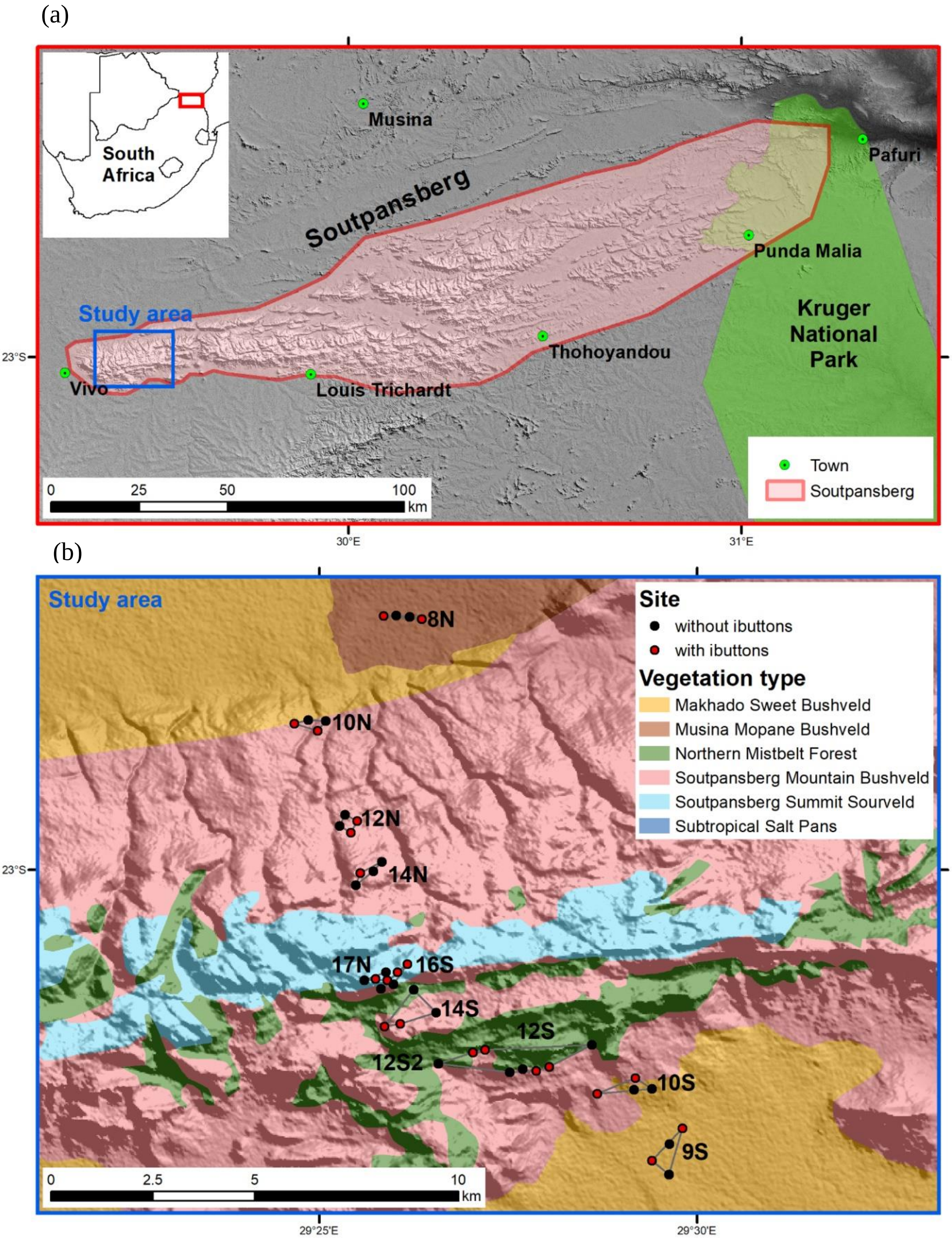

Figure 2.1 Map of the Soutpansberg and study area (a). The vegetation map (b) shows the study design including the 11 sites and 44 replicates (red symbols are replicates where soil temperature is recorded).

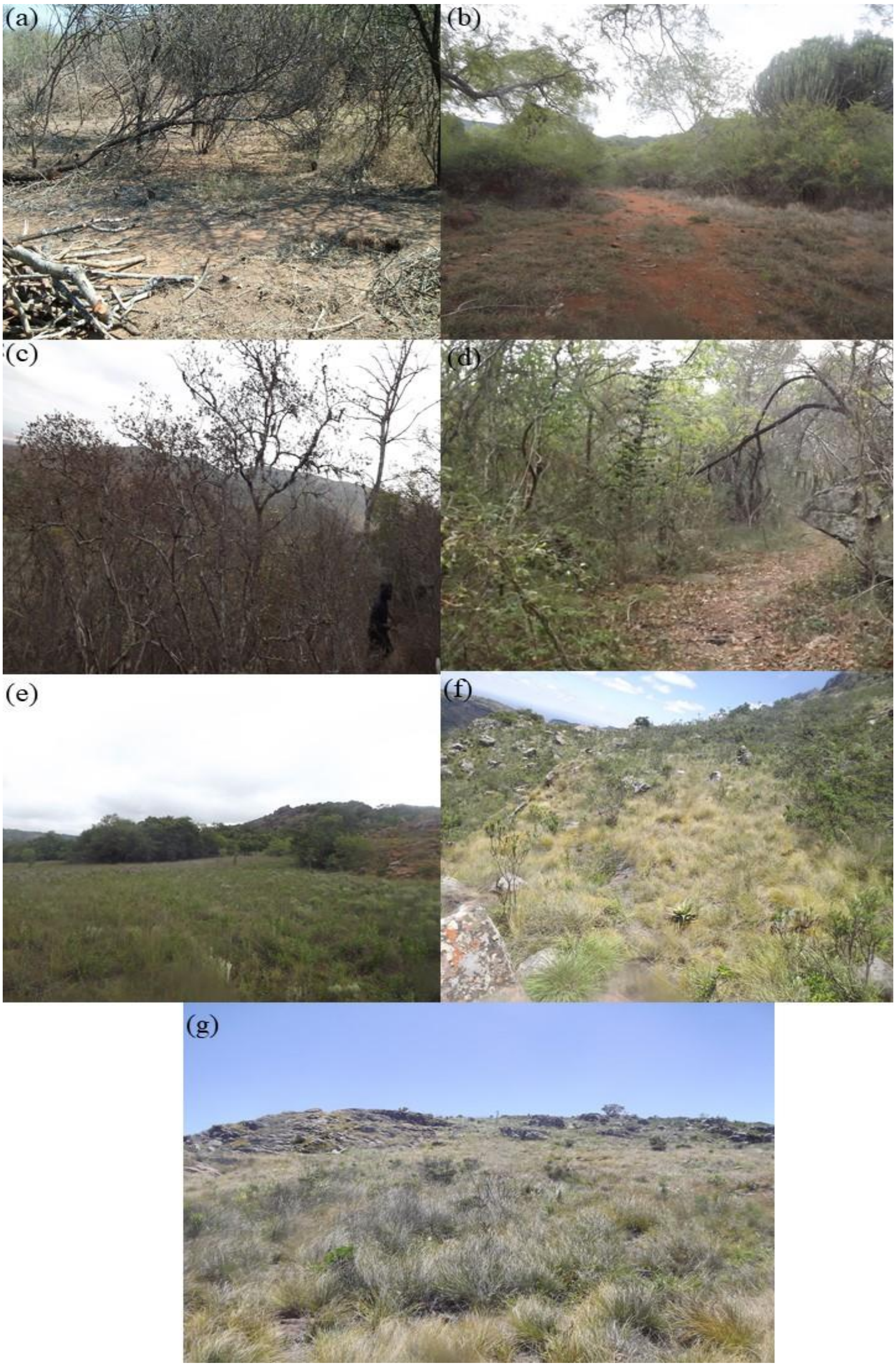

Figure 2.2 Habitat types on the southern aspect of the transect: (a) 09S (closed Shrubland), (b) 10S (low Thicket), (c) 12S (Tall forest), (d) 12S2 (Short forest), (e) 14S, (f) 16S and (g) 17N (Sedgeland-herbland).

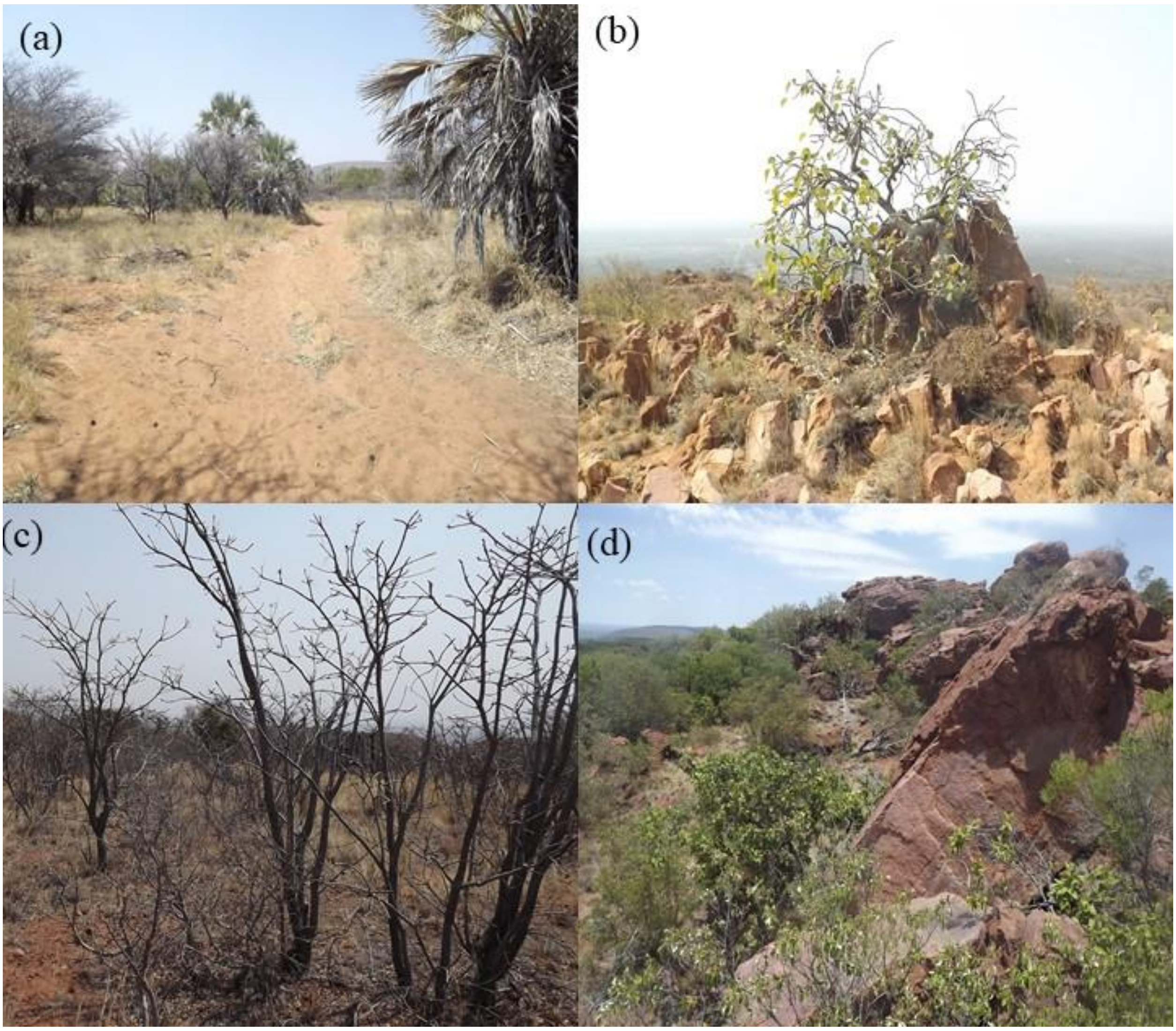

Figure 2.3 Open woodland habitat type on the northern aspect of the transect: (a) 08N, (b) 10N, (c) 12N and (d) 14N (Woodland).

Sampling design

Epigaeic ants were sampled biannually from September 2009 to September 2016 (Appendix 2.A), during the wet (January) and dry (September) periods of the year. Sampling was done at eleven sites at approximately 200 m elevational distances (Fig 2.1b). Each site had four replicates that were at least 300 m apart to avoid pseudo-replication (McKillup 2011) (Fig 2.4). At each replicate, ten pitfall traps (each ø 62 mm) were laid out in a sampling grid (2 × 5) with 10 m spacing between traps (Fig 2.4). All traps contained 50% solution of propylene glycol and were left open for five days during each survey. Ants were washed and stored in 70%

ethanol in the laboratory and later identified to morphospecies or species level by TC Munyai, University of KwaZulu-Natal.

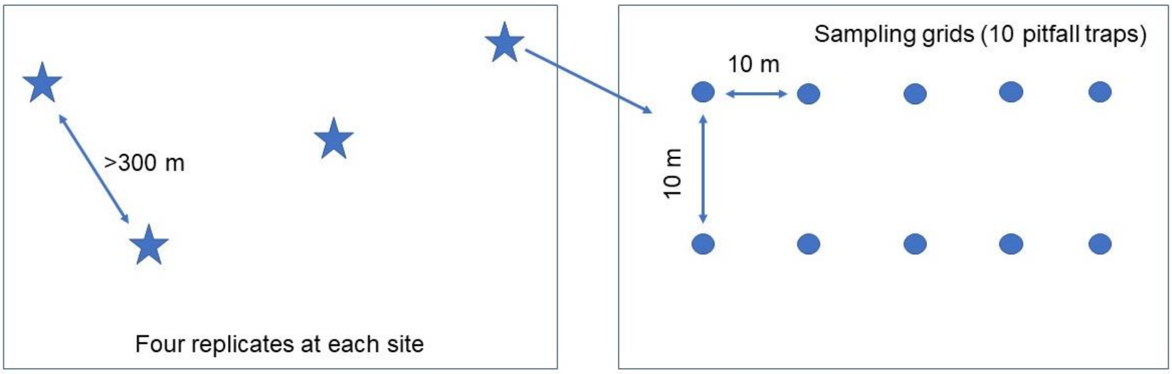

Figure 2.4 Sampling design showing the four replicates at each site and sampling grids.

Environmental variables

Temperature

Temperature was recorded in two replicates at each of the sites (Fig 2.1b). Within each replicate, one Thermocron iButton (Semiconductor Corporation, Dallas/Maxin TX and USA) was buried 1 cm below the soil to record the temperature at one-hour intervals.

Soil properties

In January 2010, ten random soil samples were taken from each replicate using a soil auger. Soil samples were dried and analyzed for composition (clay, sand, rock and silt), pH, conductivity, Carbon (C), Potassium (K), Sodium (Na), Calcium (Ca), Magnesium (Mg), Phosphorus (P), Nitrate (NO3) and T value (Munyai and Foord 2012), by BemLab (pty) Ltd laboratories, Somerset West, South Africa.

Habitat structure

During each survey, a 1 m^2 grid were placed over each pitfall trap and imaged (Fig 2.5) and used to quantify horizontal habitat structure by estimating the percentage area covered by either bare ground, vegetation, rock and leaf litter. A 1.5 m measuring rod was placed at four corners of the grid at a distance of 1.5 m from the pitfall trap. The number of hits (vegetation contacts) on the rod was recorded along 25 cm intervals of the rod (0 - 25 cm, 25 - 50 cm, 50 - 75 cm, 75 - 100 cm, 100 - 125 cm, 125 - 150 cm, 150+ cm).

Figure 2.5 An image of 1 m^2 grid placed over each pitfall trap

Morphological traits

Ten morphological traits that are ecologically related to resource use by ants were selected to describe species traits (Yates *et al.* 2014; Schofield *et al.* 2016) (Table 2.2). Standard linear measurements were taken in millimeters (mm) using a light microscope (Carl Zeiss Discovery V12, Jena, Germany) for each individual. From each site, a minimum of five individuals were measured for each species. A total of 485 individuals from 122 species were measured (Appendix 2.B).

Table 1.2 Ten examined morphological traits, their abbreviations, continuous measures and functional significance.

Morphological trait	Abbreviation	Continuous measures of traits (mm)	Hypothesized functional significance
Mandible length	ML	From the mandibular apex to the anterior clypeal margin (Fig 2.6).	Indicative of diet; longer mandibles could allow predation of larger prey (Fowler *et al.* 1991).
Clypeus length	CL	Maximum length of the clypeus (Fig 2.6).	Well-developed clypeus relate to liquid feeding behavior (Davidson *et al.* 2004).
Head width	HW	Maximum width of the head across the eyes (Fig 2.6).	Size of spaces through which ant can pass (Sarty *et al.* 2006); mandibular musculature (Kaspari 1993).
Head length	HL	Mid-point of the anterior clypeal margin to the midpoint of the posterior margin (Fig 2.6).	May be indicative of diet; longer head length may indicate herbivory (Yates *et al.* 2014).
Eye length	EL	Maximum diameter of the compound eye (Fig 2.7).	Indicates feeding behavior, predatory ants have larger eyes (Weiser and Kaspari 2006).
Eye width	EW	Maximum eye width (Fig 2.7).	Ability to see laterally (Baker *et al.* 2007).
Scape length	SL	Maximum straight-line length of the scape (Fig 2.7).	Related to perception; length size correlates to simplified environments (Weiser and Kaspari 2006).
Weber's length	Weber's	The diagonal length of the mesosomal in profile from the point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron (Fig 2.7).	Indicative of the body size (Weber 1938), also correlates to habitat complexity and metabolic function (Yates *et al.* 2014).
Hind femur length	HFL	Maximum length of the hind femur (Fig 2.7).	Related to increased foraging speed in simple habitats, smaller leg length allows exploitation of crevices in complex habitats (Sarty *et al.* 2006; Gibb and Parr 2013).
Hind tibia length	HTL	Maximum length of the hind tibia excluding the proximal part of the articulation which is received into the distal end of the hind femur (Fig 2.7).	

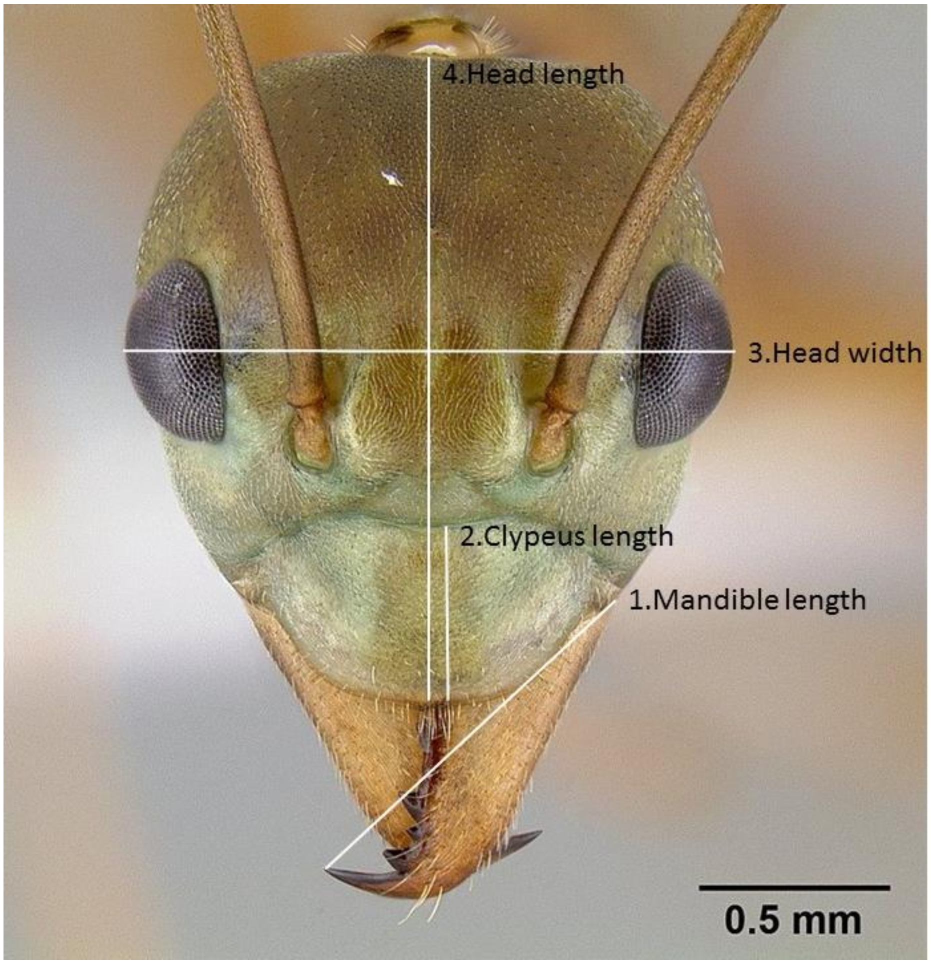

Figure 2.6 A visual representation of the head continuous morphological measurements taken from each specimen in millimeters (mm). Image ©AntWeb.

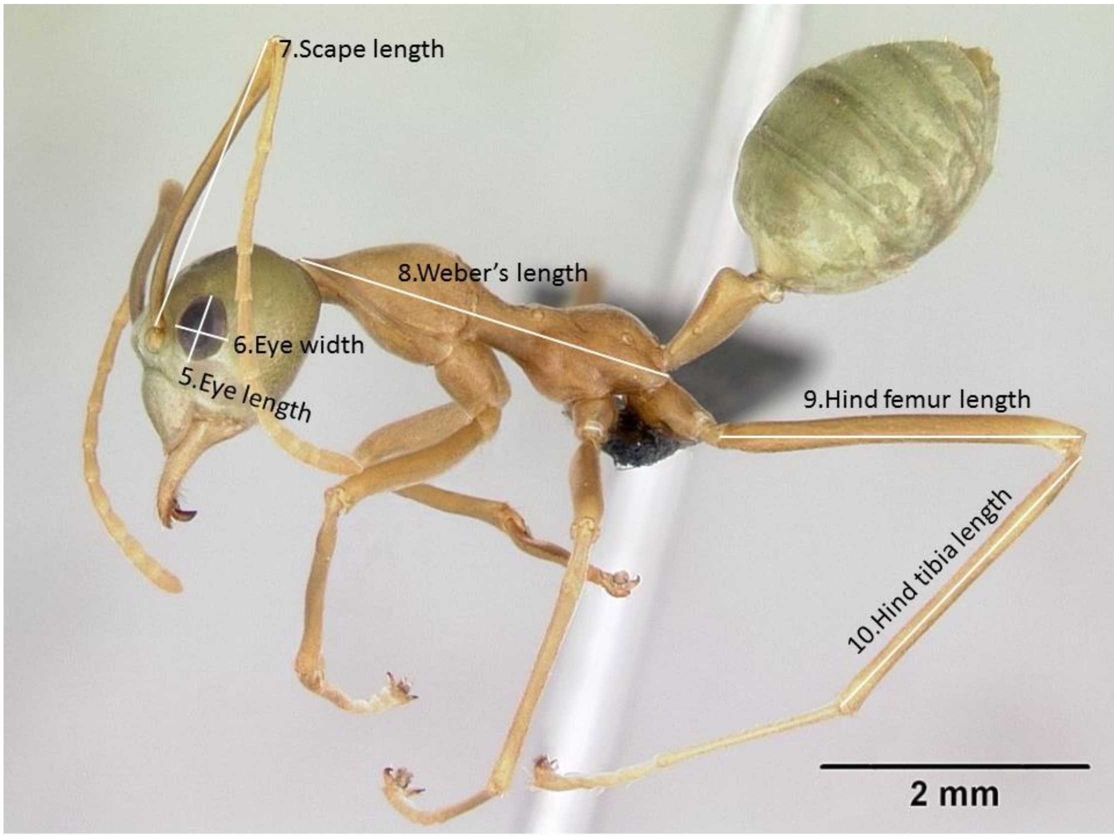

Figure 2.7 A visual representation of the lateral continuous morphological measurements taken from each specimen in millimeters (mm). Image ©AntWeb.

Statistical analysis

All analyses were conducted using the R programming environment version 3.4.1 (R Core Team, 2017).

Principal component analysis (PCA)

Principal component analysis (PCA) was performed to summarize the variation for vertical and horizontal habitat structure respectively. The first two principal coordinates explained 37% and 24% of variation for vertical (cumulative variation=61%) and 41% and 30% (cumulative variation=71%) for horizontal habitat structure.

The first principal component axis for vertical habitat structure (vertPC1) was negatively correlated with habitats that had very little vertical structure and positively correlated with sites that are more complex at intermediate levels above the ground (50 - 75 cm, 75 - 100 cm, 100 - 125 cm) (Appendix 2.C). The second principal component (vertPC2) was positively correlated with canopy cover (125 - 150 cm, 150+) and negatively related to sites that had a large number of hits below 25 cm and no canopy cover (Appendix 2.C).

The first principal component axis for horizontal habitat structure (horPC1) was positively correlated with bare ground and negatively correlated with vegetation cover (Appendix 2.D). The second principal component (horPC2) was positively correlated with leaf litter cover and negatively related to rock cover (Appendix 2.D).

PCA was also used to summarize variation in soil characteristics and the first two axes explained 46% and 15% of the variation. The first principal component axis (soilPC1) was positively correlated with acidic soil and negatively related to basic soils (Appendix 2.E). The second principal component axis (soilPC2) was positively related with sites that had sandy soil and negatively associated with clay soil (Appendix 2.E).

Taxonomic diversity

Taxonomic diversity was determined by calculating the total number of species caught in each replicate for each survey. After accounting for correlation between independent variables, the response of taxonomic diversity to mean and minimum monthly temperature, horizontal (horPC1 and horPC2) and vertical (vertPC1 and vertPC2) habitat structure, soil properties (soilPC1 and soilPC2), elevation and season was modelled using Generalized Linear Mixed Effects Models (GLMMs) with a log link function, Poisson error distribution and replicates as random factors to account for temporal pseudo-replication. The best models were identified using the “dredge” function in the R package MuMIn (Barton 2015). This function generates models using all combinations of the terms in the global model and weights each model according to its importance. Model residuals were inspected for normality, homogeneity and independence. To determine variable importance, we summed the AICc weights for each variable in a model. Models were evaluated using Akaike information criterion (AIC). Marginal R^2_m (fixed effects only) and conditional R^2_c (fixed and random effects) were calculated for the best model to determine the variation explained by fixed and random effects (Nakagawa and Schielzeth 2013).

Functional diversity

Functional dispersion (FDis) was used as an estimator of functional diversity. FDis is the mean distance of individual species to the centroid of all species in the community *(*Laliberté and Shipley 2011). The mean values of morphological traits were computed for each species while the relative abundance for each species were accounted for by computing the weighted centroid of the X = $[x_{ij}]$ (species x trait) matrix as follows:

$$\boldsymbol{c} = [c_i] = \frac{\sum a_j x_i}{\sum a_j} \qquad \text{Equation (1)}$$

where **c** represents the weighted centroid in the *i*-dimensional space, a_j is the abundance of species *j* and lastly x_{ij} the attribute of species *i* for species *j*. To quantify functional diversity for each replicate and season, the unweighted pairwise mean distance *z* to the weighted centroid was computed as follows:

$$FD = \frac{\sum a_j z_j}{\sum a_j} \qquad \text{Equation (2)}$$

Where a_j represents the abundance of species j and z_j is the distance of species j to the weighted centroid $\boldsymbol{c}$.

The response of functional diversity to environmental variables (same variables as for taxonomic diversity) was modelled using Linear Mixed-Effects Models with a Gaussian distribution and replicates specified as random factors to account for temporal pseudo-replication while all predictor variables were included as fixed effects. The selection of the best models and determining the variation explained by fixed and random effects followed the same procedure as that for taxonomic diversity.

Relationship between functional and taxonomic diversity

The relationship between functional and taxonomic diversity was modelled using Linear Mixed-Effects Models with species richness and habitats as predictor variables and replicates as random factors.

Results

Taxonomic diversity patterns and environmental correlates

Taxonomic diversity had a hump-shaped pattern on the northern aspect and a more complex pattern on the southern aspect, though generally decreasing with elevation (Fig 2.8). On the northern aspect, the highest taxonomic diversity was observed at 14N, 08N and 12N in the low open Woodland habitats on the northern aspect. On the southern aspect taxonomic diversity peaked at 09S, 10S and 14S while 12S and 12S2 (Forest habitats) had the lowest diversity (Fig 2.8), even lower than the summit (17N). Monthly mean temperature, soilPC1, soilPC2 and seasonality were included in the best models (Table 3). Mean temperature and soilPC2 estimates were positive and highly significant (Table 2.3), implying that taxonomic diversity increases with increasing temperature (Appendix F) and sites with sandy soil had more species than areas with clayey soils (soilPC2) ($P < 0.001$) (Appendix 2.G). Taxonomic diversity also increased significantly in the wet season ($P < 0.01$) (Table 2.3, Fig 2.9) and were negatively associated with soilPC1, this implies that species richness was higher in more basic soils than in acidic soils ($P < 0.05$) (Table 2.3,

Appendix 2.H). The best model for taxonomic diversity had a marginal of R^2_m of 0.26 (the variance explained by fixed factors) and R^2_c of 0.39 (variance explained by both fixed and random factors).

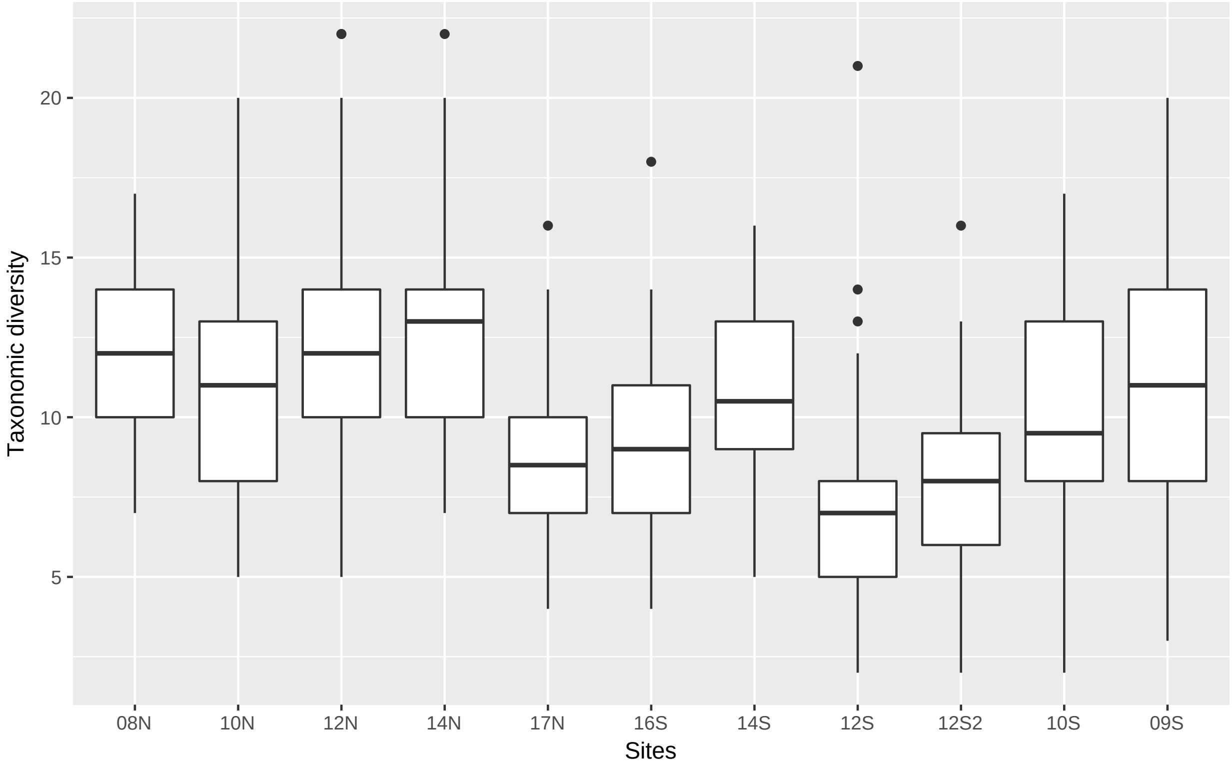

Figure 2.8 Box plot of ant taxonomic diversity patterns across the Soutpansberg elevational gradient starting on the northern aspect at the base of the mountain (800 m a.s.l) peaking on the summit (1700 m a.s.l.) and descending on the southern aspect for 15 surveys (2009 - 2016).

Table 2.3 Summary of the models for the response of ant taxonomic diversity to environmental variables: mean and minimum temperature, horPC1 (bare ground+, increased vegetation cover-), horPC2 (leaf litter cover+, rock cover-), vertPC1 (very little vertical structure-, more complex structure linked to increased vegetation+), vertPC2 (canopy cover+, low vegetation and no canopy cover-), soilPC1 (acidic soils+, basic soils-) and soilPC2 (sandy soil+, clay soil-). The variable importance indicates the number of times the variable was included in all the candidate models, variables a value of one were included in all models that had a weighting > 0.

Taxonomic diversity	Variable											Model weight	df	AIC	Δ AIC
	HorPC2	VertPC1	Mean temp	SoilPC2	HorPC1	Elevation	SoilPC1	Season wet	VertPC2	Year	Min temp				
Model 1			***	***			*	**			ns	0.18	8	3106.24	0.00
Model 2			***	***			*	**				0.15	7	3106.55	0.30
Model 3		ns	***	***			*	***				0.07	8	3108.09	1.85
Model 4			***	***	ns		*	**			ns	0.05	9	3108.71	2.74
Model 5			***	***			*	**				0.05	8	3108.71	2.55
Variable importance	0.2	0.26	1.00	1.00	0.2	<0.01	0.97	1.00	0.2	0.07	0.49				

Best model: TD ~ $e^{0.1\ (\pm 0.02)\ \text{mean temp}\ -\ 0.2(\pm 0.02)\ \text{min temp}\ +\ 0.1\ (\pm 0.01)\ \text{season wet}\ -\ 0.3\ (\pm 0.01)\ \text{soilPC1}\ +\ 0.5\ (\pm 0.01)\ \text{soilPC2}}$

*, < 0.05; **, <0. 01, ***<0.001, ns but included in the model

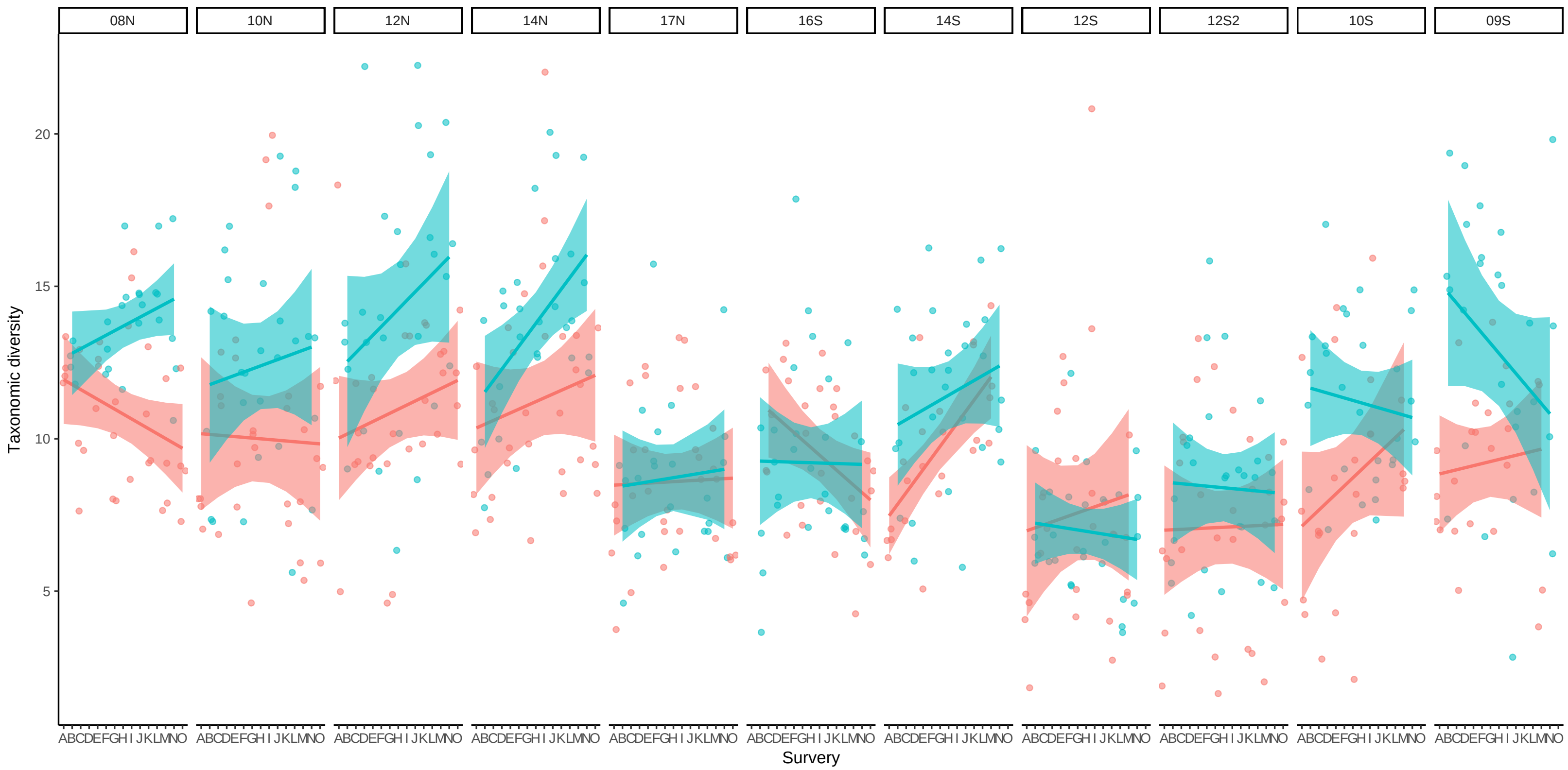

Figure 2.9 Seasonal trends of ant taxonomic diversity in dry (red) and wet (blue) season for all 15 sampling surveys (A to O represents number of surveys) from 2009 to 2016 across the Soutpansberg elevational gradient starting on the northern aspect at the base of the mountain (800 m a.s.l.) peaking on the summit (1700 m a.s.l.) and descending to the southern aspect.

Functional diversity patterns and response to environmental correlates

Functional diversity had a hump-shaped pattern on the northern aspect and decreased with elevation on the southern aspect (Fig 2.10). The highest functional diversity was observed at a mid-elevational site (10N) on the northern aspect followed by 12N (Fig 2.10). Lowest functional diversity was observed at 14S on the southern aspect and at the summit, 17N (Fig 2.11), with a clear decrease in diversity with elevation. Functional diversity was best predicted by horizontal habitat structure (horPC2), vertical habitat structure (vertPC1), and mean temperature (Table 2.4). Functional diversity was negatively associated with horPC2 ($P < 0.001$), suggesting that functional diversity increases in rocky habitats and decreases in habitats dominated by leaf litter (Appendix 2.I). Functional diversity was also positively associated with mean temperature ($P < 0.01$) (Appendix 2.I) and vertPC1 ($P < 0.01$) (Appendix 2.K), decreasing in habitats with very little vertical structure. No seasonal effect was observed (Table 2.4, Fig 2.11). The best model had a R^2_m of 0.32 (the variance explained by fixed factors) and R^2_c of 0.5 (variance explained by both fixed and random factors).

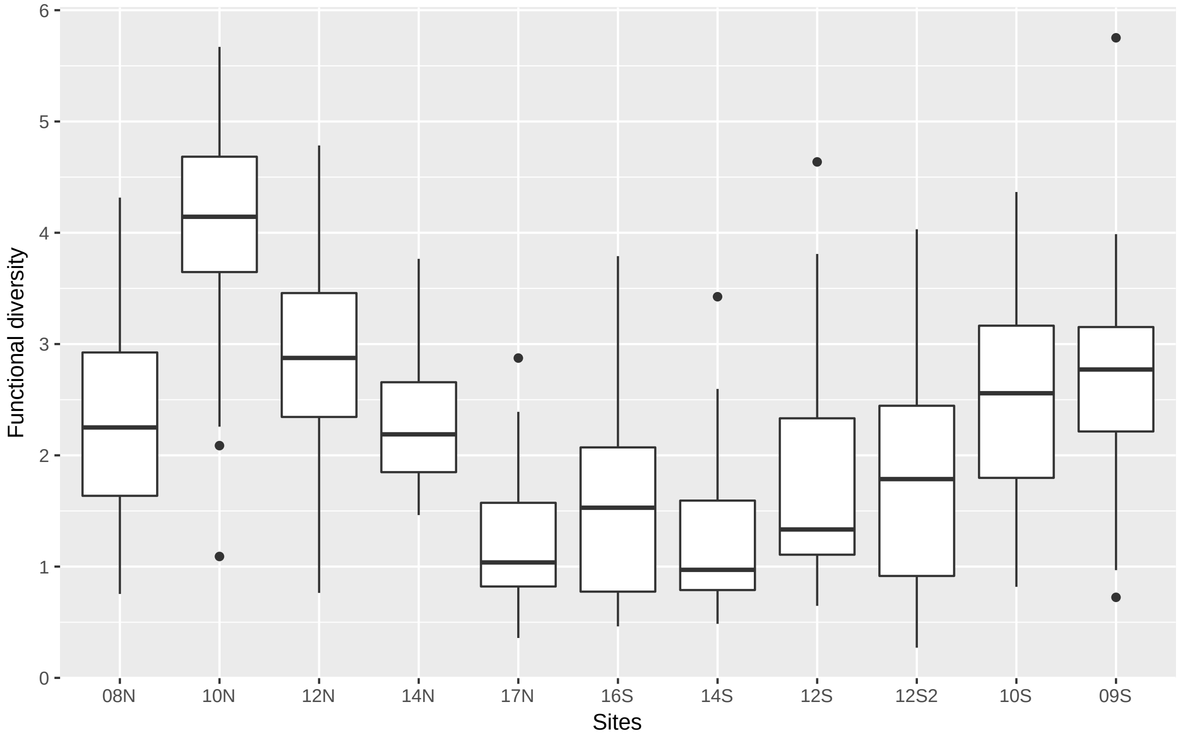

Figure 2.10 Box plot of ant functional diversity patterns across the Soutpansberg elevational gradient starting on the northern aspect at the base of the mountain (800 m a.s.l.) peaking on the summit (1700 m a.s.l.) and descending to the southern aspect for 15 surveys (2009 - 2016).

Table 2.2 Summary of the models for the response of ant functional diversity to environmental variables: mean and minimum temperature, horPC1 (bare ground+, increased vegetation cover-), horPC2 (leaf litter cover+, rock cover-), vertPC1 (very little vertical structure-, more complex structure linked to increased vegetation+), vertPC2 (canopy cover+, low vegetation and no canopy cover-), soilPC1 (acidic soils+, basic soils-) and soilPC2 (sandy soil+, clay soil-). The variable importance indicates the number of times the variable was included in all the candidate models, variables a value of one were included in all models that had a weighting > 0.

Functional diversity	Variable											Model weight	df	AIC	Δ AIC
	HorPC2	VertPC1	Mean temp	SoilPC2	HorPC1	Elevation	SoilPC1	Season	VertPC2	Year	Min temp				
Model 1	***	**	**	ns	ns		ns					0.17	9	1520.46	0.00
Model 2	***	***	***	ns	***							0.15	8	1520.64	0.17
Model 3	***	***	***	ns	ns	ns						0.08	9	1521.96	1.50
Model 4	***	***	***	ns		***						0.07	8	1522.26	1.80
Model 5	***	***	***	ns		***	ns					0.06	9	1522.47	2.01
Variable importance	1.00	0.98	0.93	0.76	0.67	0.56	0.51	0.12	0.07	0.03	0.02				

Best model: FD ~ 0.1 (±0.10) horPC1 - 0.4 (±0.08) horPC2 + 0.05 (±0.02) mean temp - 0.04 (±0.66) soilPC1 + 0.8 (±0.69) soilPC2 + 0.2 (±0.05) vertPC1

*, < 0.05; **, <0. 01, ***<0.001, ns but included in the model

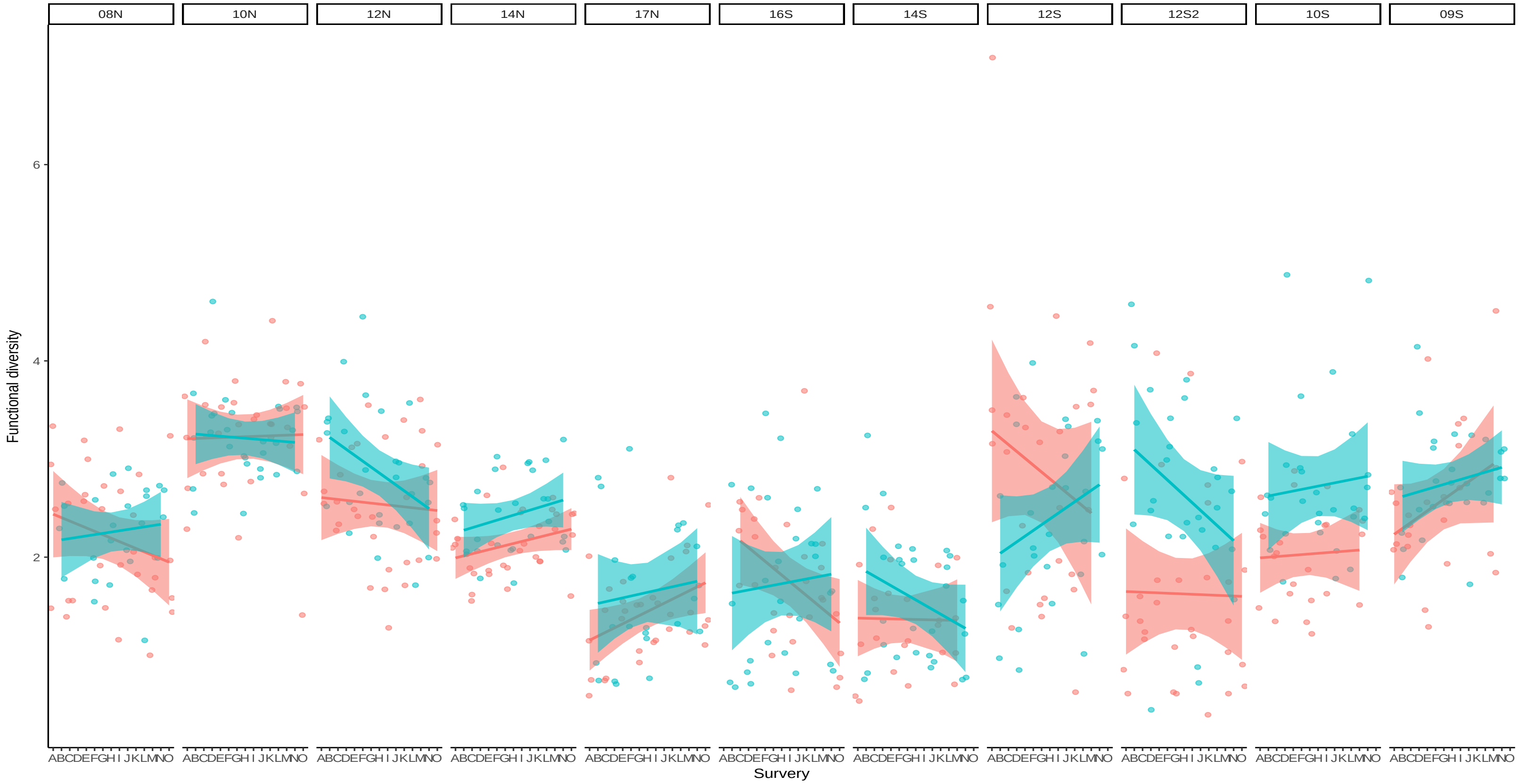

Figure 2.11 Seasonal trends of ant taxonomic diversity in dry (red) and wet (blue) season for all 15 sampling surveys (A to O represents number of surveys) from 2009 to 2016 across the Soutpansberg elevational gradient starting on the northern aspect at the base of the mountain (800 m a.s.l.) peaking on the summit (1700 m a.s.l.) and descending to the southern aspect.

Relationship between taxonomic and functional diversity

In general, functional diversity was positively related to taxonomic diversity (Fig 2.12) but the sign of the relationship was affected by habitat (Table 2.5, Fig 2.13). Increasing in the Sedgeland-herbland (T = 0.55), Thicket (T = 1.20) and decreasing in the Tall forest (T = -1.93), Short forest (T = -0.4) and Woodland (T= -0.59). Taxonomic diversity, habitat and their interactions explained F = 19.9, F = 14.1 and F = 1.77 respectively of variation in functional diversity.

Table 2.3 Summary of the Linear Mixed Models for the relationship of taxonomic diversity in different habitats to functional diversity.

Habitat structure and taxonomic diversity	Estimate	Standard error	T value
Taxonomic diversity	0.005	0.003	1.567
Short forest	0.129	0.086	1.491
Sedgeland-herbland	0.155	0.086	1.799
Tall forest	0.185	0.080	2.320
Thicket	0.091	0.092	0.984
Woodland	0.303	0.061	4.931
Taxonomic diversity × Short forest	-0.003	0.007	-0.407
Taxonomic diversity × Sedgeland-herbland	0.003	0.005	0.554
Taxonomic diversity × Tall forest	-0.013	0.006	-1.939
Taxonomic diversity × Thicket	0.008	0.006	1.203
Taxonomic diversity × Woodland	-0.002	0.004	-0.599
Model: Functional diversity ~ taxonomic diversity * habitat + (1| Replicate)			

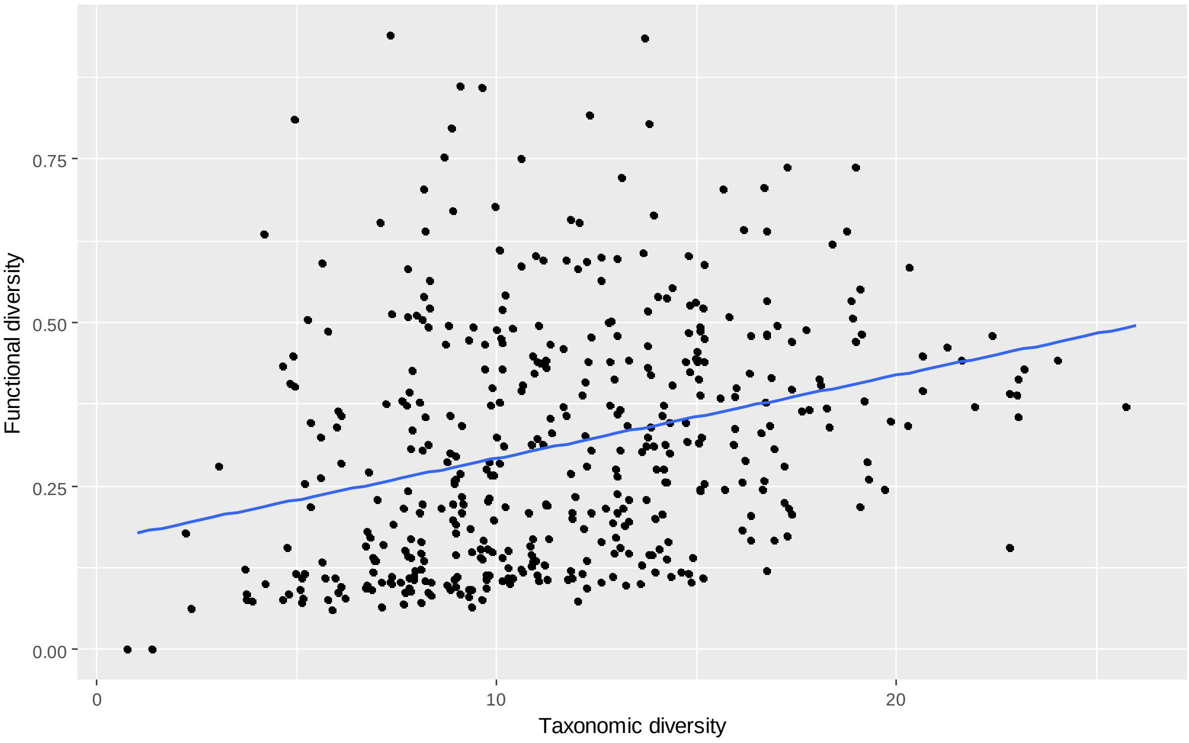

Figure 2.12 Relationship between taxonomic and functional diversity across the Soutpansberg transect.

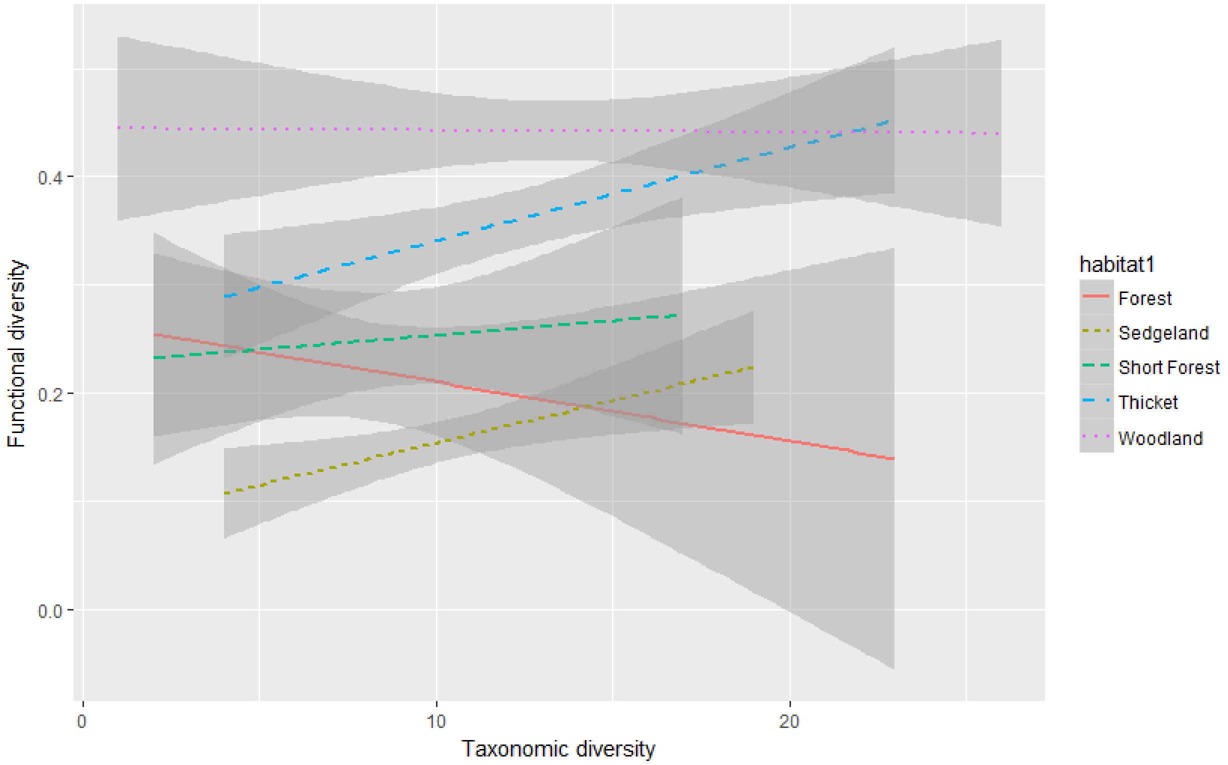

Figure 2.13 Habitat-specific relationship between taxonomic and functional diversity across the Soutpansberg transect. Shaded areas represent different habitat types.

Discussion

In general, taxonomic and functional diversity patterns seem similar across the Soutpansberg Mountain, and only differ between the elevations at which they peak (northern aspect) or the form of the decreasing trend in diversity on the southern aspect (more complex for taxonomic diversity). Both taxonomic and functional diversity were positively related to temperature, while taxonomic diversity was also related to soil properties and seasonality, functional diversity was largely driven by habitat structure. There was a positive linear relationship between taxonomic and functional diversity at a broader scale, but these relationships were habitat-specific at smaller scale, increasing, decreasing or staying the same depending on the habitat considered.

The hump-shaped pattern of taxonomic diversity is consistent with the commonly reported mid-elevation peak found in several studies (e.g. Bishop 2017; Venter *et al.* 2017). The fact that this pattern is consistent and endures over time provides further support for the reality of the pattern. These patterns can be explained by the mid-domain effect or geometric constraints hypothesis

(Szewczyk and McCain 2016), and the area hypothesis (Sanders *et al.* 2003). A previous long-term study along the Soutpansberg Mountain found evidence for the mid-domain effect in shaping ant diversity (Munyai and Foord 2015).

A decrease in ant functional diversity with elevation is similar to findings of Reymond *et al* (2013) on Mount la Schera in the Swiss National Park. A mid-elevational peak pattern was also observed in ants at Volcan Cacao (Warne 2013) and epiphytic ferns at Costa Rica (Kluge and Kessler 2011). Lee *et al* (2013) showed that climatic variables (temperature and precipitation) were better predictors of plant functional diversity. This may imply that a limited number of strategies may allow species to survive in colder habitats (high elevations) (Machac *et al.* 2011). This is particularly true for ants since low temperatures provide inhospitable and stressful conditions for metabolic processes of insects (Dreiss *et al.* 2015). Therefore, ant traits will become more similar and less diverse with increasing elevations and decreased temperatures. Surprisingly, functional diversity on the northern aspect peaked at 10N where taxonomic diversity was lowest for northern aspect, implying that functional diversity may increase with decreasing taxonomic diversity. Similarly, functional diversity was lowest at site 14S where taxonomic diversity peaked on the southern aspect. This pattern points the presence of functionally generalized species found at this site, because 14S is located on an ecotone between two habitats (Forest and Sedgeland).

Temperature was a good explanatory variable for both taxonomic and functional diversity. Increased richness might be related to the fact that ants are highly thermophilic (Hölldobler and Wilson 1990) and that open habitats tend to have higher temperatures as compared to closed or complex and cooler sites (Lassau *et al.* 2005) (i.e. richness declined in more complex habitats, 12S and 12S2 and increased in open sites, woodland, 08N - 14N, sedgeland/shrubland, 14S and thicket, 09S) (Fig. 8). High richness in warmer sites may be expected since lower temperatures limit ant foraging activity (Bernadou *et al.* 2015). Thus, habitat structure might have indirect effect on richness through changes in temperature along the Soutpansberg Mountain.

Habitat structure is one of the most important determinants of structure and diversity of ant assemblages (Ossola *et al.* 2015). However, habitat structure was not related to taxonomic diversity but a good predictor of functional diversity. Similarly, Amazonian ant taxonomic diversity was also invariant between savanna and forest habitats (Vasconcelos and Vilhena 2006). High functional diversity in rocky sites (10N) may be indicating more variation in ant morphological traits as a result of resource partitioning. Cadotte *et al* (2011) showed that functional diversity increases with increased partitioning of available resources. Increased rock cover may provide more opportunities for different species to make their nests (Robinson 2008: McCaffrey and Galen 2011). Rock cover nesting preference was found to be the mechanism for behavioral thermoregulation for an Alpine ant, *Formica neorufibarbis* (McCaffrey and Galen 2011). Comparing ant functional diversity in the woodlands and grasslands, Cross *et al* (2016) observed high functional diversity in woodlands and grasslands in the northern Kimberley region of Australia's seasonal tropics. The mechanism underlying this pattern lies in more energy efficient ant movement in less complex habitats where the ground cover is more navigable (Lassau and Hochuli 2004). A positive association between functional diversity and complex structure linked to increased vertical habitat structure is in line with the findings of Pacheco and Vasconcelos (2012), where these habitats appear to facilitate higher biodiversity by providing a greater variety of resources.

Decreasing functional diversity in leaf litter and very little vertical structure may be broadly due to canopy cover (i.e. Forest sites 12S and 12S2). Denmead (2016) also observed a decrease in functional diversity for leaf litter invertebrates in lowland rainforest while de Souza *et al* (2012) showed that many ant nests found in leaf litter can be characterized as temporary because most of them consists of workers and immature stages without the presence of queens. This suggest that leaf litter may not be conducive to habitat stratification because they do not offer greater opportunities for nesting and partitioning resources (McGlynn 2006). These findings indicate that at local scales ant assemblages are strongly influenced by habitat structure (Cross *et al*. 2016).

Soil attributes are important in explaining ant diversity because most ant species nest in the soil (Wang *et al*. 2001). A strong positive relationship between taxonomic diversity with sandy, basic soils is similar to what Boulton *et al* (2005) found. Factors such as ease of tunneling and chamber construction would account for larger diversity in sandy soils tied with the ability to maintain low temperatures inside nests (Dugas 2001). Andersen (1995) also observed high ant species richness on sandy soils reflecting their preference for open habitats.

A decrease in species richness with clayey, acidic soils is consistent with Boulton *et al* (2005). A negative correlation between ant taxonomic diversity and clay soils suggest that ants may experience difficulties in nesting in clay rich soils (Boulton *et al.* 2005). Clay soils may also affect ant taxonomic diversity through their indirect effects on plant distribution as plant community attributes are cited as the best predictors ant diversity (Torres and Snelling 1997). Clayey soils in this study are associated with thickets and forests, which indirectly resulted in more canopy cover and leaf litter ultimately affecting ant richness. In contrast, Andersen *et al* (2015) posits that clay soils typically support different ant communities due to their poor drainage and propensity for waterlogging. A recent study reported high ant diversity and abundance of generalized Myrmicinae and subordinate Camponotini on clay soils (Oliveira *et al.* 2017). The latter argued that clay soils have higher fertility compared to sandy soils and are more likely to be selected for use by ants.

Higher taxonomic diversity during the wet season is consistent with the findings of Bishop *et al* (2014) in the Maloti-Drakensberg mountains. Parr *et al* (2004) showed that during wet seasons ants are most active and abundant. Therefore, seasonal variations in abundance, activity and species richness in ants is not unexpected (Castro *et al.* 2011). High species richness pattern was also observed in dung beetles in the Brazilian tropical dry forest (de Siqueira Neves *et al.* 2010). Although most studies report high richness during wet season, Marques *et al* (2017) showed that ant species richness was high during the dry season. The latter argued that availability of resources decreases during dry season therefore ants may forage longer periods and thereby increasing the chances that they would fall into the traps.

Functional diversity did not differ significantly between dry and wet seasons. The lack of seasonal variation in functional diversity was also observed for poneromorph ants (de Carvalho Pereira *et al.* 2016). Ramírez *et al* (2015) also showed functional diversity of bees in the tropical rainforest of the Magdalena Valley of Colombia remained constant during all seasons in all communities. The results may be implying that although there is loss of species during the dry season, there is no systematic loss of certain functional groups. However, Bishop *et al* (2015) observed high functional beta diversity of ants in dry than season. The latter predicted that dry seasons species may ranges may go back to their optimal elevational ranges and thereby increasing differences between elevations.

A positive linear relationship between taxonomic and functional diversity observed in this study have been observed in both animals and plants (birds: Devictor et al. 2010; pteridophytes: Kluge and Kessler 2011; ants: Arnan *et al.* 2017). This linear relationship is expected since the presence of more species in a community may reflect more functional traits (Losos 2008). Petchey and

Gaston (2002) also showed that taxonomic diversity (richness) is strongly related to functional diversity when traits are equally complementary. This may be particularly true for this study because taxonomic diversity explained a larger amount of variation in functional diversity than habitat.

The relationship between taxonomic and functional diversity seem to be scale dependent as suggested by Bernard-Verdier *et al* (2013) due to different processes that shape biodiversity at different scales. According to Mayfield *et al* (2010), it is theoretically possible to have a decrease in functional diversity with increased taxonomic diversity and vice versa. Linear relationships of taxonomic and functional diversity at a smaller scale (Fig 2.13) suggests that abundance of species with certain traits increases while those with other traits decreases, thus any new species gets filtered. This was particularly true for the Forest habitats. An increase of taxonomic diversity with functional diversity (i.e. in the Thickets) (Fig 2.13) may be reflecting niche partitioning among communities.

Understanding the environmental variables shaping taxonomic and functional diversity through time helps explain the patterns of ant communities along the elevation. Although taxonomic and functional diversity are predicted by different environmental variables their positive relationship suggests that changes in climatic patterns may have impacts on communities along the elevational gradient. Climate change will increase soil temperatures and indirectly altering habitat structures, implying richness may increase in elevations were species are able to cope and decrease in elevations were the conditions are too harsh. Such changes may put endemic species at risk and changes in an ecosystem as a whole because their ecological roles will be lost.

Chapter 3:

Ant (Hymenoptera: Formicidae) community morphology and physiology in relation to their environment.

Abstract

Species can only persist in their communities if their traits are compatible with their environmental characteristics. Trait-based approaches have become important tools for understanding the mechanisms underlying community assembly. The relationship between traits (morphological and physiological) and environmental variables was investigated using epigaeic ants in the western part of the Soutpansberg Mountains. Ten morphological traits were measured from a minimum of five individuals for each species at each elevation from ants collected using pitfall traps seasonally from 2013 to 2009 along the Soutpansberg Mountain transect. Physiological traits were measured *in situ* as CT_{max} and CT_{min} of dominant ant species along the elevation between January and February 2017 from ants collected using baits and active searching. Based on the Brett's and Janzen's rule, we predict that there is more variation in CT_{min} than CT_{max} along the elevational gradient and that greater variation in environmental temperatures is matched by a greater range in species thermal tolerances. A Generalized Linear Model (GLM) was used to test the relationship between morphological traits and environmental variables. Brett's and Janzen's rule were tested through Linear Mixed-Effects Models with species as random factors. Results support the size-grain hypothesis and Janzen's rule, but no evidence exists for Brett's rule. Environmental conditions showed to filter species well adapted to habitat characteristics (i.e. longer legs in hot environments and smaller bodies in more complex habitats). The relationship between thermal tolerance and elevation provides evidence for the vulnerability of ants to changes in temperature and can give insight into current and future distributions of ants along the elevation in the face of climate change.

Introduction

How is it that species persist in the places that they do? This question forms the basis of community assembly theory (Weiher *et al*. 2011). Species can only persist in their communities if their functional traits are compatible with habitat characteristics (Wiescher *et al.* 2012). Thus, a given habitat should compel species to converge on similar adaptive strategies through their traits while different habitats will cause species to display divergent adaptive traits (Schofield *et al*. 2016). Traits are characteristics (i.e. morphological, physiological, life history) that influence the fitness of an organism and functioning of the ecosystem (Petchey and Gaston 2006).

Morphological traits are the most accessible and functionally essential (Yates *et al*. 2014). They have been used to explore the relationships of species and their environmental variables (Salas-López 2017). Among all morphological traits, body size is probably the most studied trait, with evidence that it responds strongly to external change (Chown and Gaston 2010). Every aspect of an organism is influenced by its body size, including its interaction with abiotic conditions, its physiological processes and lastly the consequences of its interaction with other organisms (Lawton, 1990). According to the size-grain hypothesis, the size of an organisms depends on the environment where it lives. It states that terrestrial walking organisms becomes smaller as their environment becomes more planar and rugose (Kaspari and Weiser 1999). Thus, organisms living in complex habitats would be smaller and those living in less complex habitats could be larger without increasing cost of movement (Kaspari and Weiser 1999).

There is evidence for the relationship between other morphological traits and the use of food resources as well as the survival in different habitat conditions (Chapter 2.2, Table 2.2). Traits have been used to understand the structure of microbial communities (Green *et al.* 2008), plant (Grime 1977) and vertebrate (Ricklefs *et al.* 1981). The trait-approach can allow an improved understanding of broad-scale patterns and examine impacts of environmental change (Andrew *et al.* 2013).

Physiological traits (thermal tolerance) on the other hand are frequently used to evaluate fitness costs to climate variations and have been successful in predicting how ectotherms will respond to climate change (Deutsch *et al.* 2008; Diamond *et al.* 2012). Predicting how species will respond to changing ambient temperatures is complicated by the array of thermal microhabitats at a given site (Baudier 2017). Examples of microhabitat-driven thermal niches include those from canopy to forest floor (Kaspari *et al.* 2015), the effect of soil thermal buffering relative to surface conditions (Kumar and O'Donnell 2009) and sun versus patches of shades (McGlynn *et al.* 2010), especially for the ground-dwelling ectotherms. Most of the climate models rely on temperature data from weather stations placed 1-2 meters above the ground in the open (e.g. Strauss *et al.* 2013). However, standard weather data collection can be considered insufficient for examining the diversity of thermal environments that species experience within sites (McGlynn *et al.* 2010). Specific microhabitat thermal tolerance data may be vital for underpinning how species are limited or adapted to temperature, and their response to directional temperature change (Huey *et al.* 2012).

Individuals and species differ in their thermal sensitivity (Sunday *et al.* 2011), thus thermally distinct microhabitats might select for different thermal physiologies within a taxon and among species (Baudier 2017). This is true of ectotherms along elevational gradients as the temperature changes dramatically moving up a mountain (García-Robledo *et al.* 2016). Different thermal physiologies have been observed in both upper thermal limits across elevations, CT_{max} (beetles: García-Robledo *et al.* 2016) and lower thermal limits, CT_{min} (ants: Bishop *et al.* 2017).

Due to the thermophilic character of ants, ecological roles and their meaning in the context of climate change, the majority of studies have focused on their upper thermal limit, CT_{min} (e.g. Diamond *et al.* 2012). CT_{max} of ants have been tested in different microhabitats in the same ecosystem (Kaspari *et al.* 2015), under heating regimes (Stuble *et al*. 2013) and in different daily activity patterns of ant species (Fitzpatrick *et al.* 2014). However, Bishop *et al* (2017) showed that it is still poorly understood how cold temperatures (CT_{min}) affect species over environmental gradients. The latter argued that CT_{min} should constrain ant performance and activity. Warren and Chick (2013) showed that CT_{min} was critical in determining the migration of the montane ant *Aphaenogaster rudis* to higher elevations. As the warmth-loving ant *Aphaenogaster rudis* migrated, they displaced the cold tolerant ant *Aphaenogaster picea*, implying that as temperature rises warmth-adapted species may outcompete cold-adapted species (Warren and Chick 2013).

Based on the size-grain hypothesis, we ask if ant body size changes in more complex habitats will be smaller than those in open or less complex habitats. This study further explores the relationship between all morphological traits and environmental variables (temperature, habitat structure and soil). Using physiological traits, we test if thermal tolerances of dominant ant species are predicted by environmental temperatures (Janzen’s rule) and if there is more variation in CT_{min} than in CT_{max} across the elevation (Brett’s rule). We predict that ants will be smaller in complex habitats and larger in open or less complex habitats. Morphological traits will be related to environmental variables reflecting their adaptations to their habitats. We further predict that thermal tolerance will confirm both Janzen’s and Brett’s rule.

Materials and methods

Study site

The study area is centred on Lajuma Research Centre, within the western part of the Soutpansberg Mountains in the Limpopo province (Fig 3.1). The western part of the Soutpansberg is situated along the R522 road that connects Makhado and Vivo towns. The transect has a north-south orientation with four sites on the northern aspect and six sites on the southern aspect, each site consisting of four replicates. The transect forms part of a long-term monitoring project of ant and spider diversity (Munyai and Foord 2015). Detailed habitat descriptions are provided in Chapter 2.

Morphological traits

Ten morphological traits were measured (Chapter 2, Fig 2.6 & 2.7) from a minimum of five ants from each site. Standard linear measurements were taken in millimeters (mm) using a light microscope (Carl Zeiss Discovery V12, Jena, Germany). Traits were chosen based on their hypothesized functional significance (Schofield *et al.* 2016) (Chapter 2, Table 2.2).

Environmental variables

Environmental Temperature data was obtained in two replicates at each site along the elevation represented by red dots on the map in Fig 3.1. One Thermocron iButton (Semiconductor Corporation, Dallas/Maxin TX and USA) was buried 1 cm below the soil to record the temperature at one-hour intervals within each replicate. Soil samples were taken once in January 2010. Ten soil properties were sampled from each replicate and were analyzed for composition (clay, sand, rock and silt), pH, conductivity, Carbon (C), Potassium (K), Sodium (Na), Calcium (Ca), Magnesium

(Mg), Phosphorus (P), Nitrate (NO3) and T value (Munyai and Foord 2012). Habitat structure was quantified by estimating percentage area covered by bare ground, vegetation, leaf litter and exposed rock (horizontal structure) and vegetation contacts on the rod along 25 cm intervals of the rod (vertical structure) (Chapter 2). Temperature and habitat structure were quantified during each of the 15 surveys (2009 - 2016).

Live ant sampling

Live ant sampling and experimental work were undertaken from January to early February 2017 across the Soutpansberg transect (Fig 3.1). Live ant species (workers) were collected from twenty-one replicates with Thermocron iButtons to monitor the temperature (Fig 3.1). Ten baited (a mixture of jam and peanut butter) traps (50 ml plastic centrifuge tube vial) (Fig 3.2) were placed out at each of the twenty-one replicates in Fig 3.1 indicated by red dots and ants were also actively searched for. All sites were surveyed twice collecting species that were not collected during the first survey. Ants were transported back to base camp and thermal tolerances were tested immediately to reduce the impact of stress and resource depletion (Santos *et al.* 2011).

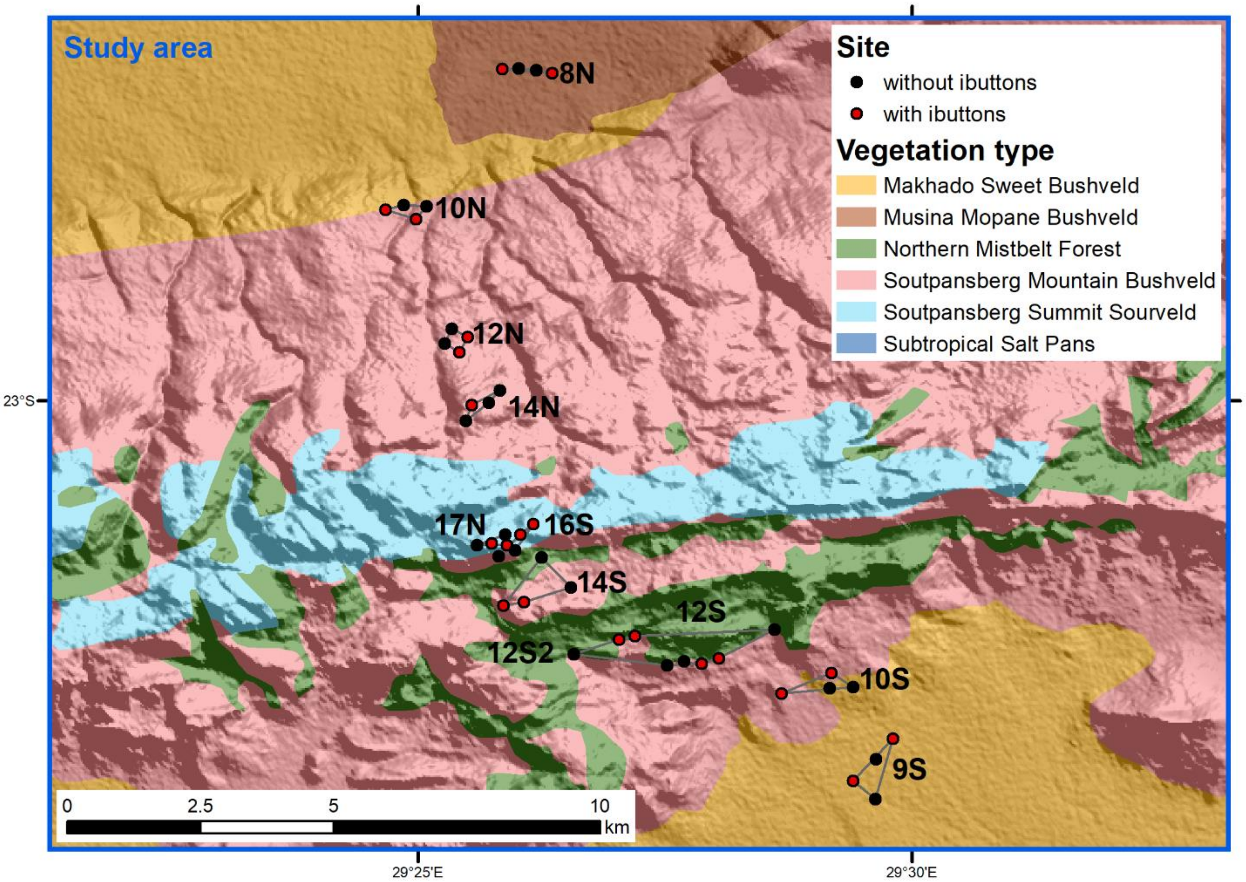

Figure 3.1 Map of the Soutpansberg transect showing sites (indicated by red dots) where iButtons were buried and live ants sampled.

Figure 3.2 Baited trap with a mixture of jam and peanut butter inside.

Thermal tolerance assays (Physiological traits)

A water bath (Grant, SG8 6GB; Grant Instruments, Cambridge Ltd, UK) filled with 1:1 water: propylene glycol to allow sub-zero temperatures was used to test the thermal tolerance of individuals. Critical thermal limits were determined by assigning 10 individuals (N = 10), one individual per chamber into a double-jacketed air filled insulated chamber coupled to a programmable water bath. A total of 45 species were tested CT_{min} and 43 for CT_{max} (Appendix 3.A). The fluid circulated around 11 chambers with ten ants of the same species per assay. Two Thermocron iButton loggers were assigned to one chamber to monitor temperature fluctuation inside the chambers and ensure an accurate temperature reading at which individuals reach their critical thermal limits. Temperature was ramped up at a constant rate of 0.5 °C (Diamond et al. 2012) per minute from 25 °C to 65 °C for CT_{max} and ramped down at the same rate from 20 °C to -10 °C for CT_{min}. CT_{max}/ CT_{min} was defined by the temperature at which an individual loses coordinated function, typically accompanied by loss of movement or neuromuscular control (Diamond *et al*. 2012). To identify the endpoints of the assays, ants were prodded gently with a soft paintbrush. All the ants used in the assays were preserved in 2.0 ml vials containing 95% ethanol for species level identification or identification to genus level then morpho-species level for species which could not be identified to species level. These were compared with reference collections housed in the Zoology Department, University of Venda in South Africa (Munyai and Foord 2015). Updated ant genera names were confirmed using Fisher and Bolton (2016).

Statistical analysis

Morphological trait-environment relationships

The fourth corner problem was proposed with the aim of associating species traits and environmental variables using species abundance data to understand how traits are related to the environment (Brown *et al.* 2014). It is a matrix algebra problem which determines the trait-environment relationship (**D**) by combining species abundance (**L**), trait (**Q**) and the environment (**R**) (Legendre *et al*. 1997) (Fig 3.3a). The fourth corner modelling approach was used to determine the relationship between ant morphological traits and four environmental variables: temperature, soil, vertical and horizontal habitat structure. The ten morphological traits measured were reduced to a list of seven because they were highly correlated (Appendix 3.B). Traits that were more functionally meaningful of the pair were retained, namely head width, mandible length, clypeus length, scape length, eye length, hind femur length and weber's length. The matrix was constructed from ant morphological traits for each species (**Q**), species abundance at each replicate (**L**) and environmental variables at each replicate (**R**). The three tables (**RLQ**) were combined to identify the main relationship between environmental variables and traits mediated by species abundances. The **RLQ** results were combined with fourth corner model that allows for the evaluation of the significance between one single traits and one single environmental variable at a time (Dray *et al*. 2014) (Fig 3.3b). A generalized linear model (GLM) was used by applying the "traitglm" function of the mvabund-package (Wang *et al*. 2012). This function constructs a regression model for abundance (**L**) as a function of additive terms for each variable in (**R**) and (**Q**). GLM was fitted using a LASSO penalty that automatically does the model selection by setting to zero any interaction coefficient between the trait and environmental values that does not help reduce the Bayesian information criterion (BIC).

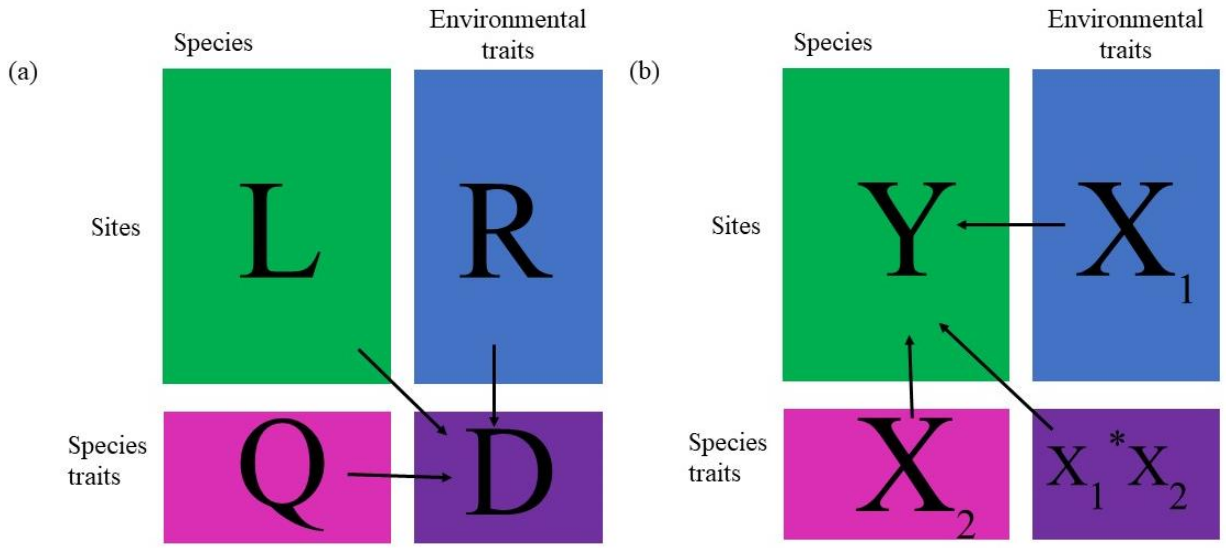

Figure 3.3 A graphical representation of the forth corner problem (a), which combines abundance (**L**), trait (**Q**) and environment (**R**) data to describe trait-environment relationship (Legendre *et al*. 1997). (b) represents the model-based solution of the forth corner problem, which predicts abundance (**Y**) as a function of predictor environment (**X_1**), species (X_2) and their interaction (**X_1*X_2**). The interaction between **X_1** and **X_2** is the forth corner (from Brown *et al*. 2014).

Thermal tolerance (Physiological traits)

Average thermal tolerances (CT_{max} and CT_{min}) for each species in each site across different elevations were calculated. Difference between CT_{max} and CT_{min} (CT_{range}) was also calculated for each species in each site. The relationship between thermal tolerance (CT_{max}, CT_{min} and CT_{range}) and environmental temperatures (maximum, minimum and range) were tested using Linear Mixed-Effects Models in the lme4 package (Bates *et al*. 2014) including species as random factor. Models were tested for CT_{max}, CT_{min} and CT_{range} separately. To test the variation between sites for CT_{max} and CT_{min} along the elevation Linear Mixed-Effects Models were used and species were included as random a factor. Tukey's honest significance difference (HSD) tests were applied to show how elevations differed from each other in terms of CT_{max} and CT_{min} respectively. Tukey's tests were performed with the 'glht' function in the package multicomp (Hothorn *et al.* 2008). All analyses were conducted using the R programming environment version 3.4.1 (R Core Team, 2017).

Results

Morphological trait-environment relationship

Morphological traits had a significant association with environmental variables ($P < 0.001$) (Fig 3.4), but only three traits (hind femur length, Weber's length and scape length) had strong associations while others showed weak associations. Femurs length increased with both mean and minimum temperatures, but the association was weak for minimum temperature (Fig 3.4). Longer femurs were also related to sandy soils, while ants in clay soils tended to have shorter femurs. Ants were smaller in hotter environments, and in sites with increased canopy cover and increased vegetation cover while larger ants were related to low vegetation cover and bare ground. Ants had wider eyes in hot and sandy environments and narrower in clay soils (Fig 3.4). Scapes were longer in sandy soils with rock cover and shorter in more complex habitats with canopy cover, clay soils, leaf litter, low vegetation cover and very little vertical structure. Clypeal lengths increased with minimum temperatures and ants in areas with more leaf litter and canopy cover also had longer clypei. Longer mandibles were only associated with increased canopy cover. Heads were narrower as vegetation and leaf litter cover increased (Fig 3.4).

Thermal tolerance (physiological traits)

CT_{max} was significantly related to maximum soil temperatures ($P < 0.001$) (Table 3.1) (Fig 3.5a & Fig 3.6a). CT_{min} was not related to environmental minimum soil temperatures ($P < 0.2$) (Table 3.1) (Fig 3.5b & Fig 3.6b). CT_{range} was also significantly related to soil temperature variance ($P < 0.001$) (Table 3.1) (Fig 3.5c & Fig 3.6c). CT_{max} had more variation ($P < 0.001$) at 17N than CT_{min} on the northern aspect ($P < 0.05$) at 12N and 17N (Table 3.2). There was no significant difference between sites for CT_{max} and CT_{min} on the southern aspect (Table 3.2). Tukey HDS tests showed that difference for CT_{max} were between 17N and 08N ($P < 0.01$), 17N and 10N ($P < 0.001$), 17N and 12N ($P < 0.01$) and 17N and 14N ($P < 0.01$). No significant difference between elevations were revealed for $CT_{min.}$ CT_{min} declined with elevation in both aspects while CT_{max} declined only in certain sites on both aspects.

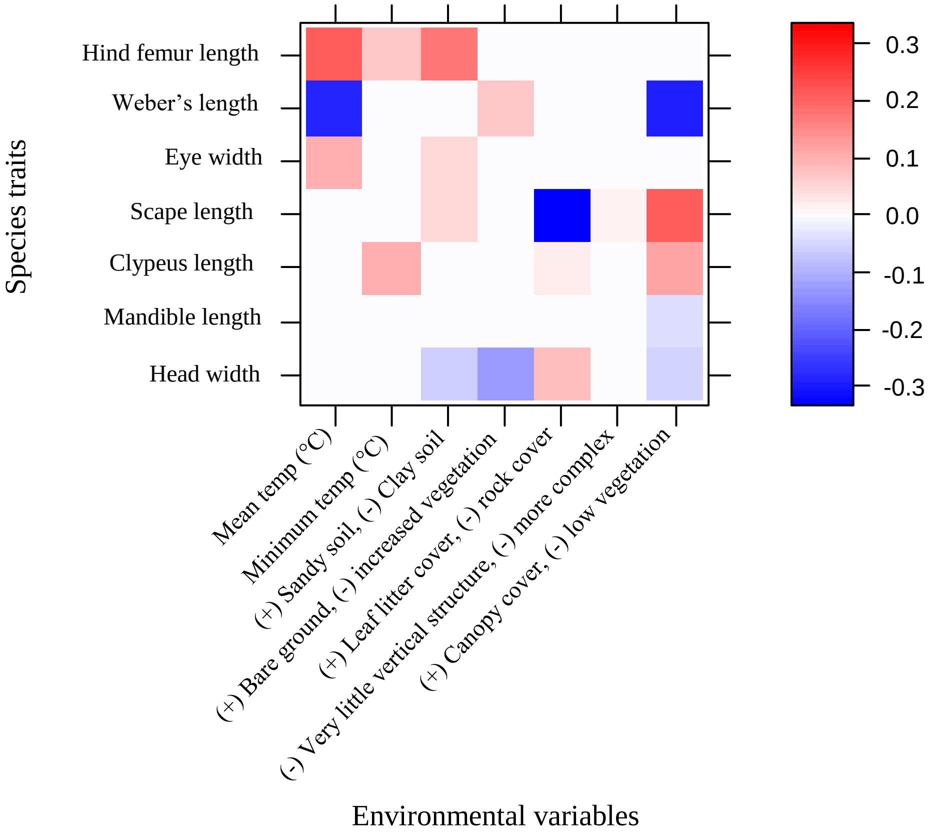

Figure 3.4 A graphical representation of the fourth corner model. Significant relationship between environmental variable and traits are represented in blue and red, the relative tone of the color shows the strength of relationship. Positive relationship is represented by the red color and negative relationship by blue color.

Table 3.1 Summary results of the Linear Mixed-Effects Models of the relationship between of thermal tolerance and to environmental temperatures where they were collected.

Thermal tolerance	Environmental temperature	P value
CT_{max}	Maximum temperature	***
Model: CT_{max} ~ 0.01 (0.1) maximum temperature + (1|species)		
CT_{min}	Minimum temperature	.
Model: CT_{min} ~ 0.01 (0.01) minimum temperature + (1|species)		
CT_{range}	Temperature variance	***
Model: CT_{range} ~ 0.01 (0.08) temperature variance + (1|species)		

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table 3.2 Summary results of the Linear Mixed-Effects Models of the relationship between elevation and thermal tolerance. Significant values are highlighted in bold.

		CT_{max}		CT_{min}	
Site	Aspect	P value	Estimate	P value	Estimate
Intercept	South	0.001	43.0	0.001	9.13
10S	South	0.19	3.01	0.28	-1.36
12S	South	0.69	-0.10	0.79	-0.38
12S2	South	0.66	-1.00	0.37	-1.19
14S	South	0.21	3.13	0.41	-1.03
16S	South	0.43	2.02	0.32	-1.30
		Model: CT_{max} ~ site + (1|species)		Model: CT_{min} ~ site + (1|species)	
Intercept	North	0.001	49.4	0.001	9.07
10N	North	0.34	0.94	0.80	-0.13
12N	North	0.26	-1.08	**0.05**	-1.09
14N	North	0.36	-1.06	0.44	-0.51
17N	North	**0.0004**	-7.75	**0.05**	-1.68
		Model: CT_{max} ~ site + (1|species)		Model: CT_{min} ~ site + (1|species)	

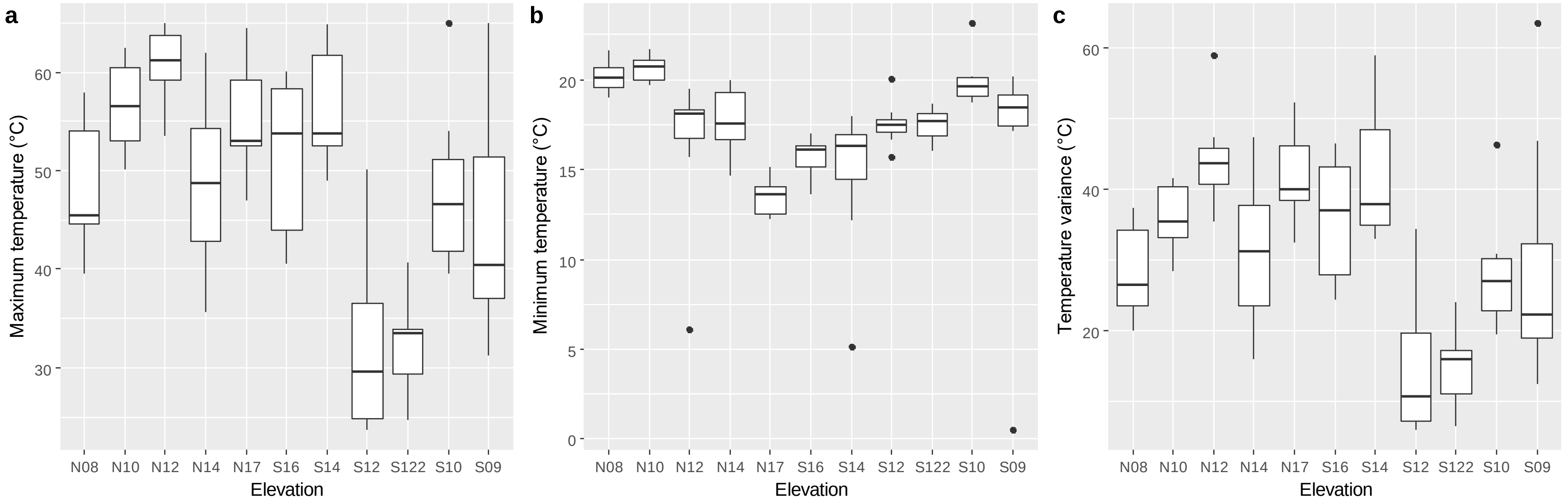

Figure 3.5 Box plots of maximum (a), minimum (b) and variance (c) in soil temperature recorded with Thermocron iButtons in January from 2009 to 2016 across the Soutpansberg elevational gradient starting on the northern aspect at the base of the mountain (800 m a.s.l.) peaking on the summit (1700 m a.s.l.) and descending to the southern aspect.

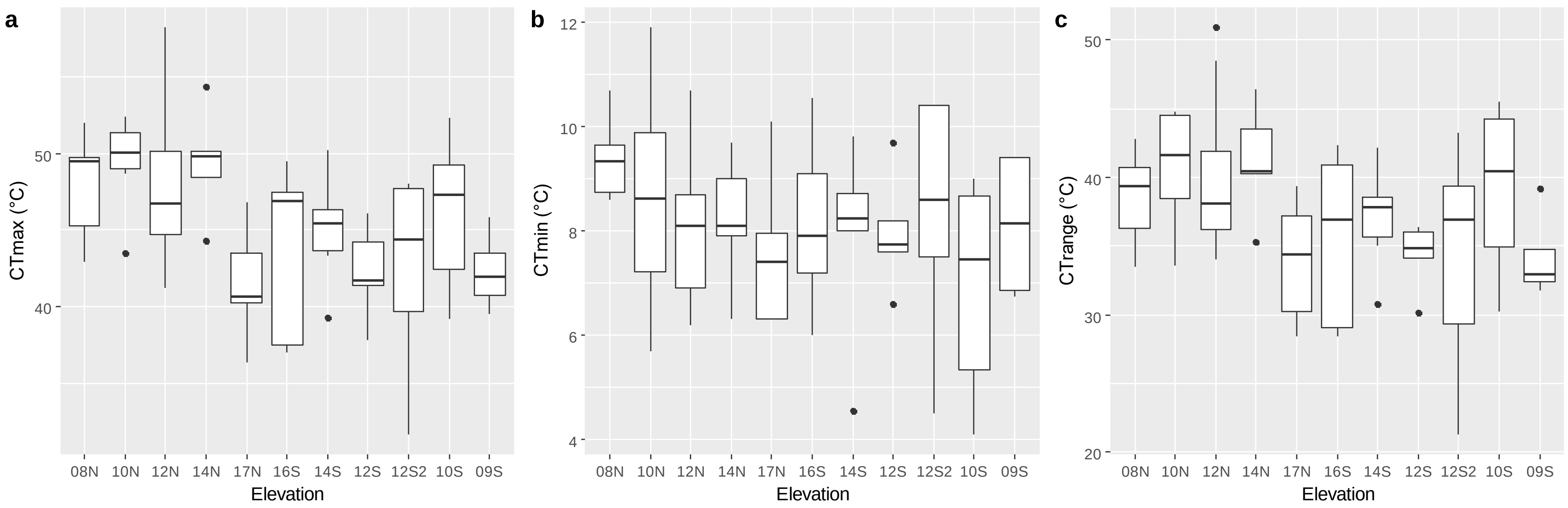

Figure 3.6 Box plots of the response of CT_{max} (a), CT_{min} (b) and CT_{range} (c) to elevation in January and February 2016 across the Soutpansberg elevational gradient starting on the northern aspect at the base of the mountain (800 m a.s.l.) peaking on the summit (1700 m a.s.l.) and descending to the southern aspect.

Discussion

We found support for the size-grain hypothesis, ants were smaller in complex habitats and larger in open habitats. Three morphological traits had strong associations with environmental variables (Hind femur length with mean temperature, Weber's length with mean temperature, increased canopy cover and low vegetation and scape length with increased leaf litter, canopy cover and low vegetation and rock cover). Thermal tolerance results support Janzen's rule but not Brett's rule, CT_{range} of ants was significantly related to environmental temperature variance. There was more variation between sites in CT_{max} than CT_{min} on the northern aspect and there was no difference between sites on the southern aspect, but both tended to decrease with elevation.

There were clear relationships between ant traits and their environment, including relatively longer femurs, an adaptive trait that enables ants to forage during the hottest time of the day (Wehner and Wehner 2011). Longer legs (femurs) are advantageous for ants that carry their bodies up from the hot surface and run faster than ants with short legs (Hurlbert *et al.* 2008). Additionally, running faster may shorten foraging time per unit distance covered thereby, reducing time exposed to heat and desiccation stress (Wehner *et al*. 1992). This adaptation is true for ants in hotter areas, especially middle to lower elevations on the northern aspect characterized by sandy soils.

Smaller ants in complex habitats with more leaf litter (i.e. 10S, 12S and 12S2) and larger ants in open habitats (i.e. 08N) support the size-grain hypothesis (Kaspari and Weiser 1999). Smaller bodies in complex environments should allow ants to move around efficiently (Schofield *et al.* 2016) as compared larger ants found in open habitats. This adaptation physically allows easy access to resources within complex environments (Gibb and Parr 2010). However, some findings do not support the size-grain hypothesis (e.g. Parr *et al*. 2003; Teuscher *et al.* 2009). The inconsistency between studies have been shown to be determined by factors such as, the variety of traits and habitat measured, as well as factors shaping habitat complexity (Ossola *et al.* 2015), spatial and temporal scales where habitat factors filter morphological traits (Yates *et al.* 2014; Gibb *et al.* 2015) and characteristics that affect species movements between habitats (Parr *et al.* 2003).

Larger ants in cold environments conforms to what Bishop *et al* (2016) observed in three continents (Africa, Australia and South America). This adaptive trait is useful for ants occupying high elevations because larger bodies lose heat slower than smaller bodies (Stevenson 1985). Therefore, larger bodies can be advantageous for heat conservation in cold environments (Bishop *et al.* 2016). Smaller ants at warmer temperatures confirm recent observations that under warmer temperature, colonies produce smaller workers (Molet *et al.* 2017). Smaller ants can therefore survive high temperatures because they can get rid of heat faster than larger ants.

Scape length facilitate following of pheromone trails (Weiser and Kaspari 2006). Hölldobler and Wilson (1990) showed that ants use scapes to communicate using pheromones when defending and relocating colonies. Longer scapes have been shown to be more sensitive to pheromone trails (Weiser and Kaspari 2006). In complex habitats longer scapes may be relatively important for locating food sources and colony communication. Ant's pheromones are hydrocarbons and fatty acids and they are volatile components depending on temperature (Morgan, 1984). Thus, their duration is crucial for its effectiveness as a signal (Hölldobler and Wilson 1990). Longer scapes in open rocky sites on sandy soil suggest enhanced communication as a result of high temperatures (i.e. northern aspect). Shorter scapes in sites with low vegetation, very little vertical structure, leaf litter and clay soil may be an indicative of species with small colonies. Shorter scapes in cooler environments (i.e. leaf litter) may be a result of less demanding facilitation of pheromones because they can stay out for a longer period.

Physiological traits were also related to environmental temperatures along the elevation. Support for the Janzen's rule appear to corroborate Bishop *et al* (2017) for ants and Gaston and Chown (1999) for dung beetles. According to the Janzen' rule more variability in environmental temperatures is matched by a greater range of species thermal tolerance. Temperatures changes dramatically along elevational gradients which could allow species to physiologically tolerate wider ranges of temperatures. Thus, temperature variation across elevation can shape patterns of thermal tolerance and reflect the magnitude of temperature experienced by organisms at a given site (Shah *et al.* 2017).

Although Brett's rule suggests that CT_{max} is less geographically variable than CT_{min} along a geographic gradient, this study observed more variation in between sites in CT_{max} than CT_{min} on the northern aspect. When tested along to elevational gradients, Brett's rule has contradictions (e.g. Oyen *et al.* 2016) and mixed empirical support (e.g. Bishop *et al.* 2016). It is unlikely that CT_{min} varied less because most studies have reported more variation in CT_{min} than CT_{max} (e.g. Gaston and Chown, 1999; Nyamukondiwa and Terblanche 2010). This may be due the methodology employed in this study because temperature was ramped at 0.5°C per minute for both CT_{max} and $CT_{min.}$ Ramping rates of 0.5 and greater per minute are considered faster rates (Hemmings and Andrew 2017) and they do not allow thermal equilibration between the ant and the ambient temperature (Lighton and Turner 2004). Thus, the methodology can drastically alter the results and biological interpretations of thermal stress on species (Terblanche *et al.* 2011; Castaneda *et al.* 2012).

A decreasing trend in CT_{max} with elevation conforms with the thermal limitation hypothesis (Kaspari *et al.* 2015), which predicts that species with higher CT_{max} are found in warmer elevational gradients and CT_{max} should decrease with increasing elevation. Thus, CT_{max} may be correlated with or reflect high maximum environmental temperatures (Kaspari *et al.* 2015). This is true for ants on the northern aspect because it experiences more higher temperatures than the southern aspect. These results suggest that ants may vary in their physiological sensitivity to variation of maximum temperatures along the elevational gradient. However, other studies of terrestrial ectotherms have generally found CT_{max} to be largely invariant across elevation and latitude (e.g. Addo-Bediako *et al.* 2000; Ghalambor et al. 2006; Hoffmann *et al*. 2013).

Species with lower CT_{max} are regarded to be more sensitive to abiotic changes than other members of the community (Wittman *et al.* 2010). Species with lower CT_{max} may face decreases in activity windows related to changes in environmental temperatures (Verble-Pearson *et al.* 2015). According to Bishop *et al* (2017), differences in ant foraging times may also be determined by differences in ant physiology. Thus, the ability to tolerate high temperatures may determine the survival of species under projected climate warming (García-Robledo *et al.* 2016).

Species from different elevations may differ widely in both CT_{max} and CT_{min}, with species from high elevations showing lower tolerance to high temperatures but able to tolerate colder temperatures than lowland species (Sunday *et al.* 2011, García- Robledo *et al.* 2016). CT_{min} is known to track lower temperatures in terrestrial environments (Sunday *et al.* 2012). Similar to this study Shah *et al* (2017), observed a decrease in CT_{min} with elevation in tropical stream insects and Baudier (2017) in subterranean and aboveground ant species. High cold tolerance may be reflecting persistence in cold temperatures at high elevations (Shah *et al.* 2017).

Variations in environmental soil temperatures may be a strong selective force on thermal tolerance of ants along the elevational gradient of the Soutpansberg Mountain. CT_{min} was not related to soil temperature and varied less than did CT_{max}, this implies that high temperatures play an important role in shaping ant distribution along this elevational transect. Elevational effects in CT_{max} being more pronounced on the northern aspect may be due to the fact that this aspect is hotter than the southern aspect, therefore species can have broader thermal tolerances to high temperatures. Ant species from the northern and southern aspect might therefore respond differently to the ongoing climate change. Suggesting that species on the southern aspect may be affected more as a result of their lower tolerance to high temperature extremes than those on the northern aspect. Environmental conditions may alter species traits through time, for example bush encroachment in simplex habitats where species have larger bodies may lead to smaller bodies. Bush encroachment may also lead to canopy cover, more leaf litter and reduced temperatures which may lead to loss of trait diversity because these sites are not species rich as compared to warmer and open sites. These changes may affect the functioning on an ecosystem since ants are play various ecological processes within ecosystems.

Chapter 4

Conclusions and recommendations

The focus of this study has been on a trait-based approach to better understand ant communities along an elevational gradient. Specifically, the investigation has dealt with two interconnected topics: (i) understanding community assembly along elevational gradients: taxonomic versus functional diversity and their diversity and (ii) Ant (Hymenoptera: Formicidae) community morphology and physiology in relation to their environment.

As expected, taxonomic and functional diversity increased with temperature, while taxonomic diversity is driven by soil properties and functional diversity by habitat structure. In the context of climate change, both taxonomic and functional diversity may increase as temperature increases because high temperatures seem to result in higher richness and functionally diversity. However, these increases may not occur at all sites along the elevation as it was observed that taxonomic diversity may increase with a decreasing functional diversity and vice versa. This suggest that there is a strong filtering that can be explained with reference to a relationship between taxonomic and functional diversity that was habitat specific at a smaller scale. For example, site 10N on the northern aspect has relatively low taxonomic diversity compared to other sites on the northern aspect with a clear increase in functional diversity. This site may have sufficient additional niches dimensions for any new traits to be added from other elevations. In sites where, taxonomic diversity increased with low functional diversity may be linked to environment that filters specific traits (e.g. generalist species that are found in an ecotone where several of them dispense in from different habitats).

A decrease in functional diversity (i.e. Sedgeland-herbland on the southern aspect) may be due to the three-dimensional complexity near the ground where ants forage. The complexity of the habitat near the ground may be particularly important because in the Thickets where the ground is less complex, functional diversity increased implying that these sites can have more functional traits. Thus, changes in these sites (i.e. bush encroachment) may lead to loss of functional traits.

The effect of habitat structure on traits is confirmed by the size grain hypothesis and the relationship of other morphological traits and environmental variables. It appears that changes not only in habitat structure but also in soil temperatures have impacts on traits along the elevational gradient. For example, long legs associated with higher temperatures may become longer when temperature increases as a result of increased running speed. Body sizes may decrease if simple habitats become complex or may cause species to dispense to simpler habitats where they might be out competed. Species with larger body sizes may be more affected and might disappear with implications for ecosystem functioning. These changes may lead to shifts in ant communities if environmental temperatures become more unstable as a result of climate change.

Physiological intolerance to temperature on the southern aspect may reflect that major changes in temperature can cause species to move to higher elevations. However, narrower thermal tolerance on the southern aspect may be a result of habitat such as the Forest where there are less variable temperatures. Implying that increased temperatures in the Forest and higher elevations may put species at risk because they will dispense to more suitable thermal niches. Thus, populations will get smaller as species dispense up the mountain species are more diverse at lower elevations. On the northern aspect it appears that climate change may affect species less given their broader thermal tolerance to higher temperatures. This aspect receives relatively high temperatures compared to the southern aspect, thus species traits may be enhanced, and few shifts may be observed on this aspect. Thermal tolerance results suggest that species on the southern aspect may be more vulnerable to impacts of climate change while species on the northern aspect might become more diverse. Low temperatures along the Soutpansberg transect do not seems to affect species as much as high temperatures, but a decreasing pattern with elevation shows that as moving up the mountain species are adapted to lower temperature and suggest that species at high elevations maybe at risk of climate change than lowland species.

Further studies investigating thermal tolerance along elevational gradients are important in assessing the vulnerability of ectotherms to climate change. Artificial warming experiments along the elevation can test predictions of the responses to climate change by manipulating species thermal niches. Further studies investigating functional and trait diversity can manipulate habitat structure (i.e. decrease structural complexity) and see how these changes affect community functional diversity and species traits. By quantifying only taxonomic diversity habitat structure has little impact on ant communities along the elevation, therefore different diversity indices may contribute significantly in understanding different mechanisms underlying community assembly along elevational gradients. Thus, taxonomic and functional diversity can be used simultaneously since these two indices can respond to different environmental conditions.

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Appendices

Appendix 2.A Sampling dates for 15 surveys from September 2009 to September 2016.

Date	Survey	Season
09/1/2009	September	Dry
01/01/2010	January	Wet
09/09/2010	September	Dry
01/10/2011	January	Wet
09/10/2011	September	Dry
01/09/2012	January	Wet
09/12/2012	September	Dry
01/09/2013	January	Wet
10/02/2013	September	Dry
02/11/2014	January	Wet
09/09/2014	September	Dry
01/10/2015	January	Wet
09/24/2015	September	Dry
01/14/2016	January	Wet
09/26/2016	September	Dry

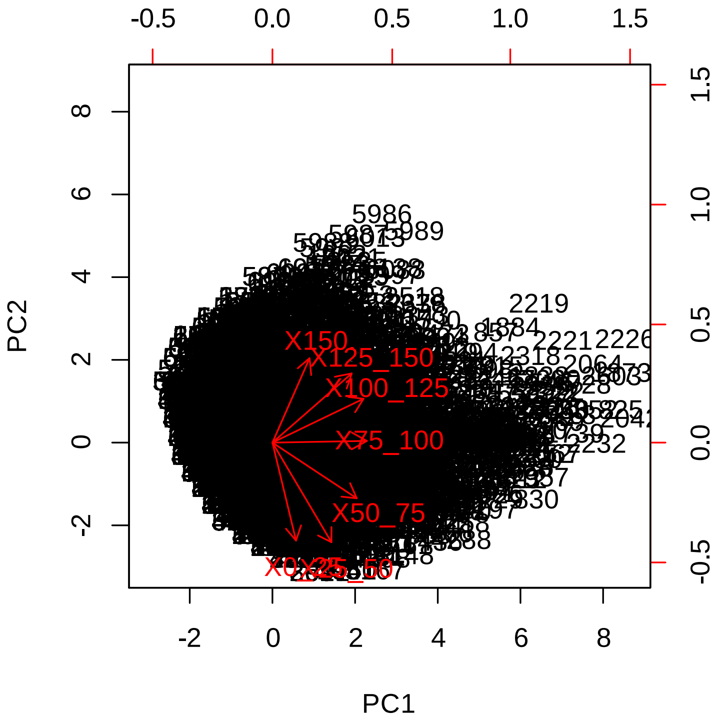
Appendix 2.B A list of species that 485 individuals were measured from along the elevation.

Species
Aenictus rotundatus Mayr
Anoplolepis cf custodiens
Bothroponera ? strigulosa
Bothroponera sp.02
Bothroponera sp.03
Camponotus cf niveosetosus
Camponotus dofleini
Camponotus fulvopilosus
Camponotus mayri forel
Camponotus sp.02 (rufoglaucus gp.)
Camponotus sp. 03 (niveosetosus gp.)
Camponotus sp. 04 (etiolipes gp.)
Camponotus sp. 05
Camponotus sp. 06 (maculatus gp.)
Camponotus sp.07 (empedocles gp.)
Camponotus sp. 11 (cinctellus gp.)
Camponotus sp.12 (cinctellus gp.)
Camponotus sp.17
Camponotus sp. 18 (maculatus gp.)
Camponotus sp.20 (niveosetosus gp.)
Camponotus sp.21 (cuniscupus gp.)
Cardiocondyla sp. 01
Cardiocondyla sp.02
Carebara sp. 01
Cerapachys sp. 01
Cataulacus sp. 01
Crematogaster sp. 01 subgenus sphaerocrema
Crematogaster sp. 02 (rufigena gp.)
Crematogaster sp. 03 (rufigena gp.)
Crematogaster sp. 04 subgenus sphaerocrema
Crematogaster sp. 06 (custanea complex)
Dorylus helvolus Linnaeus
Dorylus sp. 02
Lepisiota cf.longinoda Arnold
Lepisiota crinite mayr
Lepisiota sp. 01 (capensis gp.)
Lepisiota sp. 02 (spinosior gp.)
Lepisiota sp.08 (capensis gp.)
Lepisiota sp.09 (capensis gp.)
Lepisiota sp. 10 (capensis gp.)
Leptogenys intermedia Emery
Leptogenys schwabi Forel
Meranoplus cf glaber Arnold
Meranoplus inermis Emery
Meranoplus magretti

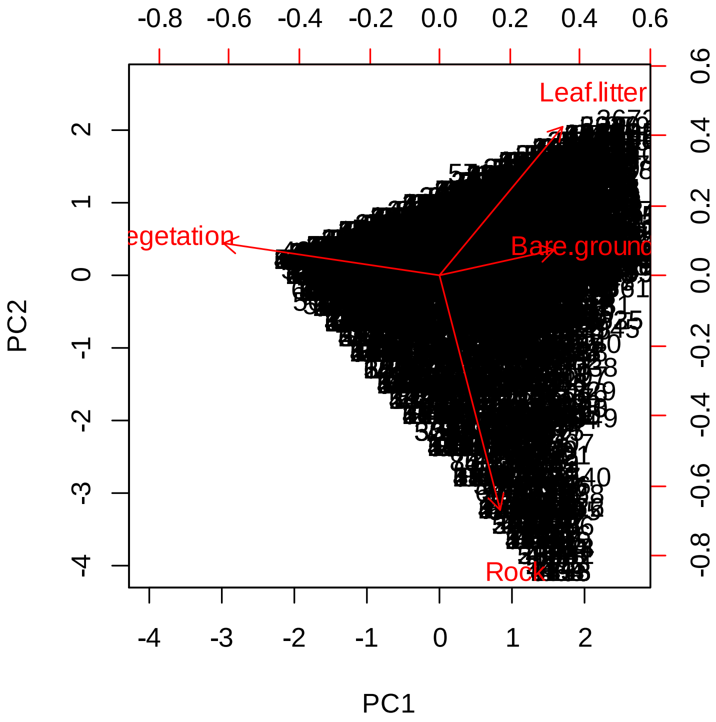
Meranoplus sp. 01
Mesoponera caffraria
Monomorium caffraria
Monomorium? Fastidium
Monomorium? Notulum Forel
Monomorium albopilosum Emery
Monomorium cf. drapenum Bolton
Monomorium cf. junodi Forel
Monomorium damarense Forel
Monomorium emeryi mayr
Monomorium sp. 01
Monomorium sp. 07
Monomorium sp.08 (monomorium gp.)
Monomorium sp.10 (salamonis gp.)
Monomorium sp. 12 (monomorium gp.)
Monomorium sp. 13
Myrmicaria natalensis
Ocymyrmex flaviventris Santschi
Ocymyrmex fortior
Ocymyrmex sp. 03
Odontomachus trolodytes
Pheidole sp. 01 (megacephala gp.)
Pheidole sp. 02 (liengmei gp.)
Pheidole sp. 03 (megacephala gp.)
Pheidole sp. 05 (megacephala gp.)
Pheidole sp. 06 (crassinoda gp.)
Pheidole sp. 07
Pheidole sp. 09 (crassinoda gp.)
Pheidole sp. 10 (megacephala gp.)
Pheidole sp. 11
Plagiolepis sp. 02
Plagiolepis sp. 03
Platythyrea lamellose Roger
Platythyrea shultzei Forel
Plectroctena sp. 01
Plectroctena sp. 02
Polyrhchis schistacea
Ponera sp. 01
Pseudoponera sp. 01
Rhoptomyrmex sp. 02
Rhotomyrmex transversinodis
Solenopsis sp. 01
Solenopsis sp. 02
Strumigensy pretoriae
Tapinolepis sp. 01
Tapino sp. 01? Lutem Emery
Technomyrmex pallipes Smith
Tetramorium sp. 17 (simillimun gp.)

Tetramorium baufra
Tetramorium cf setigerum mayr
Tetramorium notiale
Tetramorium sepositum Santschi
Tetramorium setuliferum
Tetramorium sp. 01 (squaminode Emery gp.)
Tetramorium sp. 04 (gabonensa gp.)
Tetramorium sp.05 (sereiceventre gp.)
Tetramorium sp. 07 (weitzeckeri gp.)
Tetramorium sp. 08 (simillimun gp.)
Tetramorium sp. 10 (squaminode Emery gp.)
Tetramorium sp. 11 (squaminode Emery gp.)
Tetramorium sp. 12 (squaminodis gp.)
Tetramorium sp. 13
Tetramorium sp. 14 (sereiceventre gp.)
Tetramorium sp. 16 (sereiceventre gp.)
Tetramorium sp. 18 (simillimun gp.)
Tetramorium sp. 19 (simillimun gp.)
Tetramorium sp. 21 (squaminode Emery gp.)
Trachymesopus sharpi forel

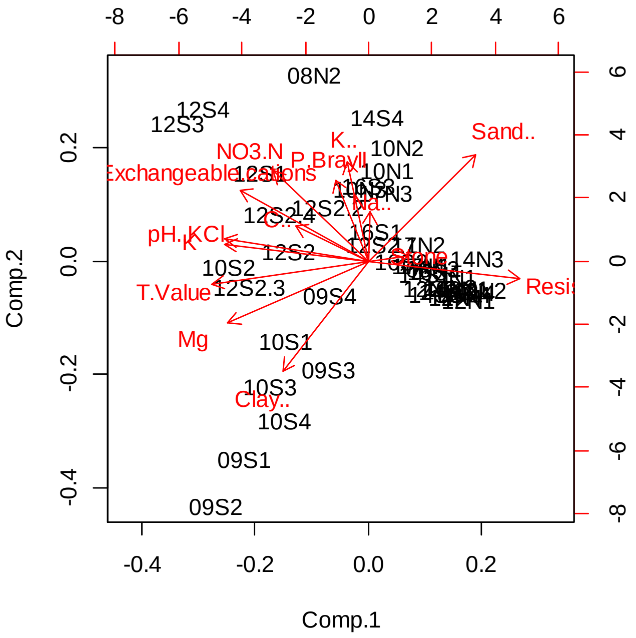
Appendix 2.C The PCA biplot of the centroids for the 40 hits measured at each plot for vertical habitat structure for 15 surveys.



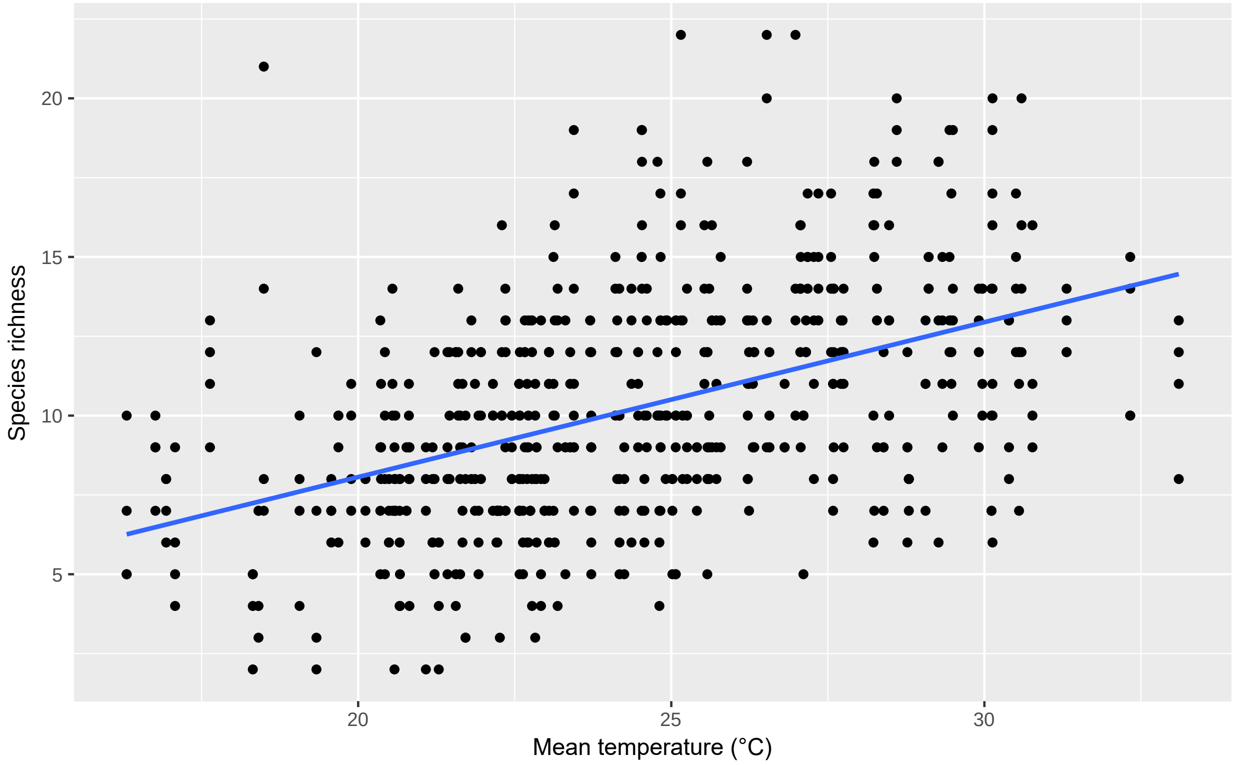
Appendix 2.D PCA biplot for the horizontal habitat structure quantified for all surveys.



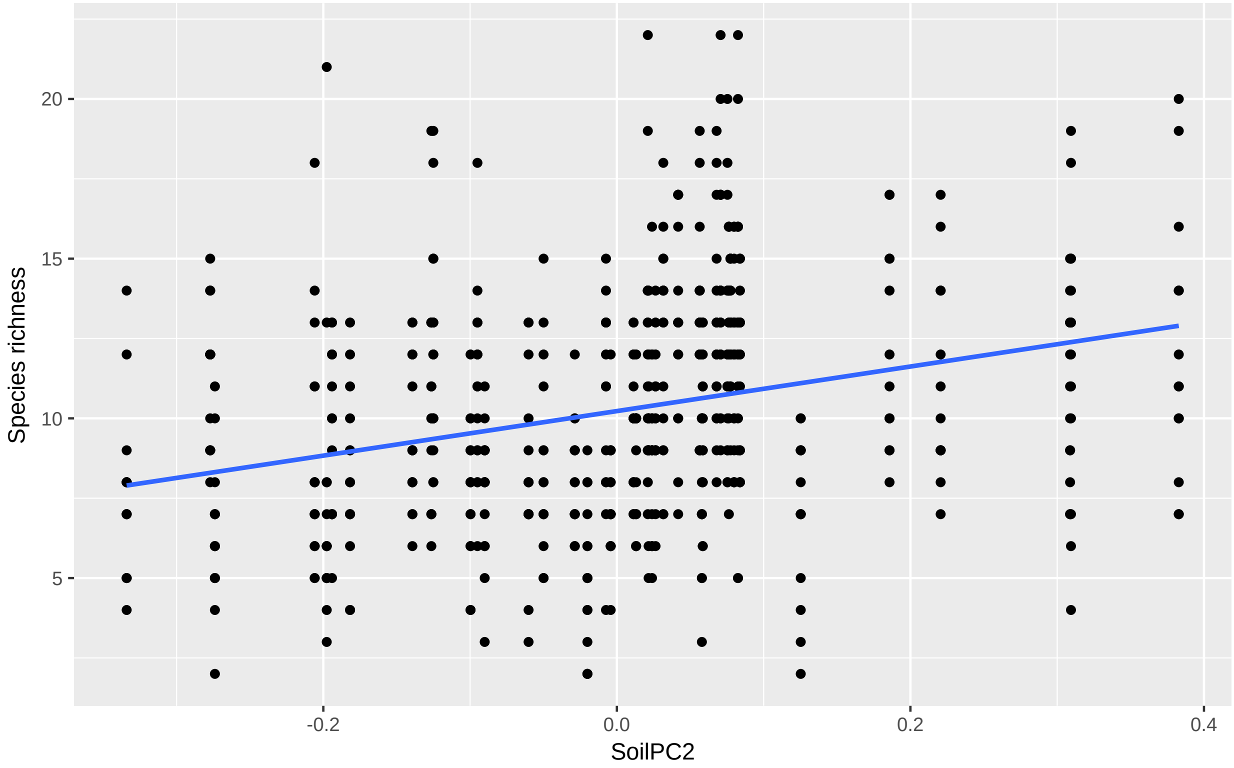
Appendix 2.E PCA biplot for soil properties sampled in January 2010.



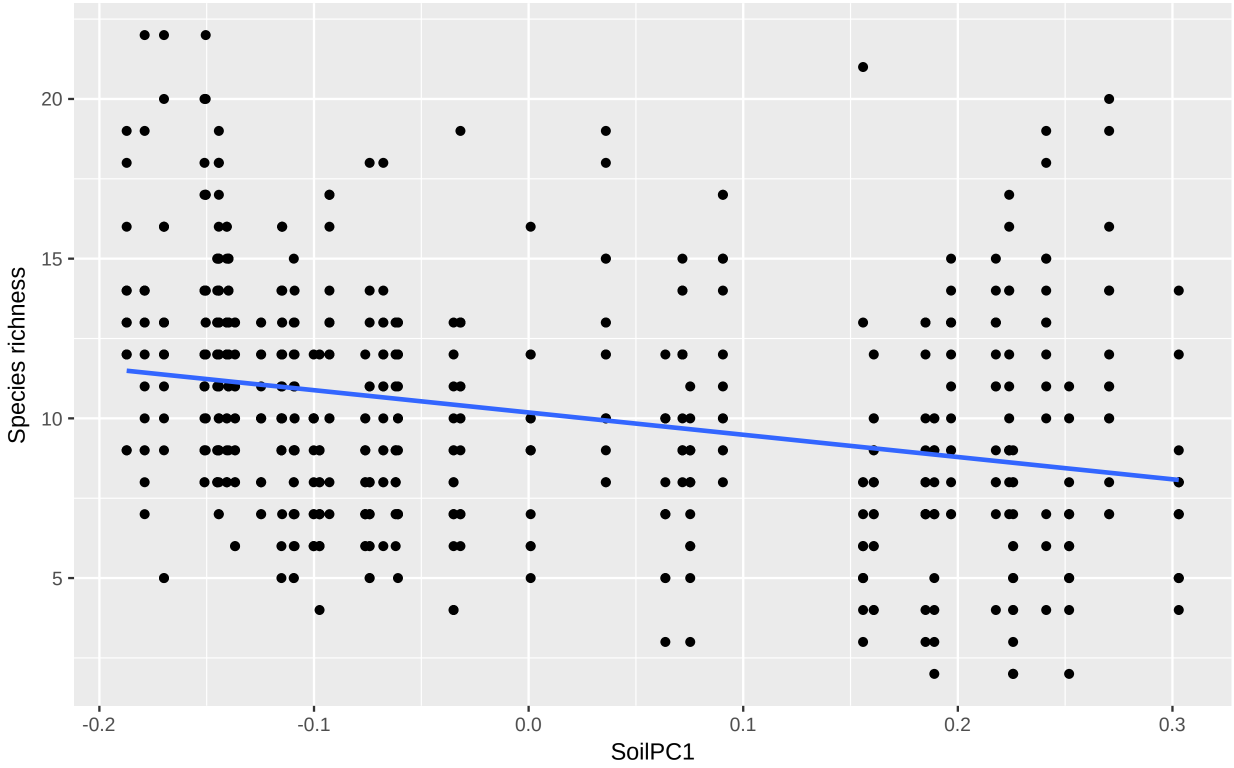
Appendix 2.F Scatterplot of the response of the taxonomic diversity to mean soil monthly temperature (^{o} C).



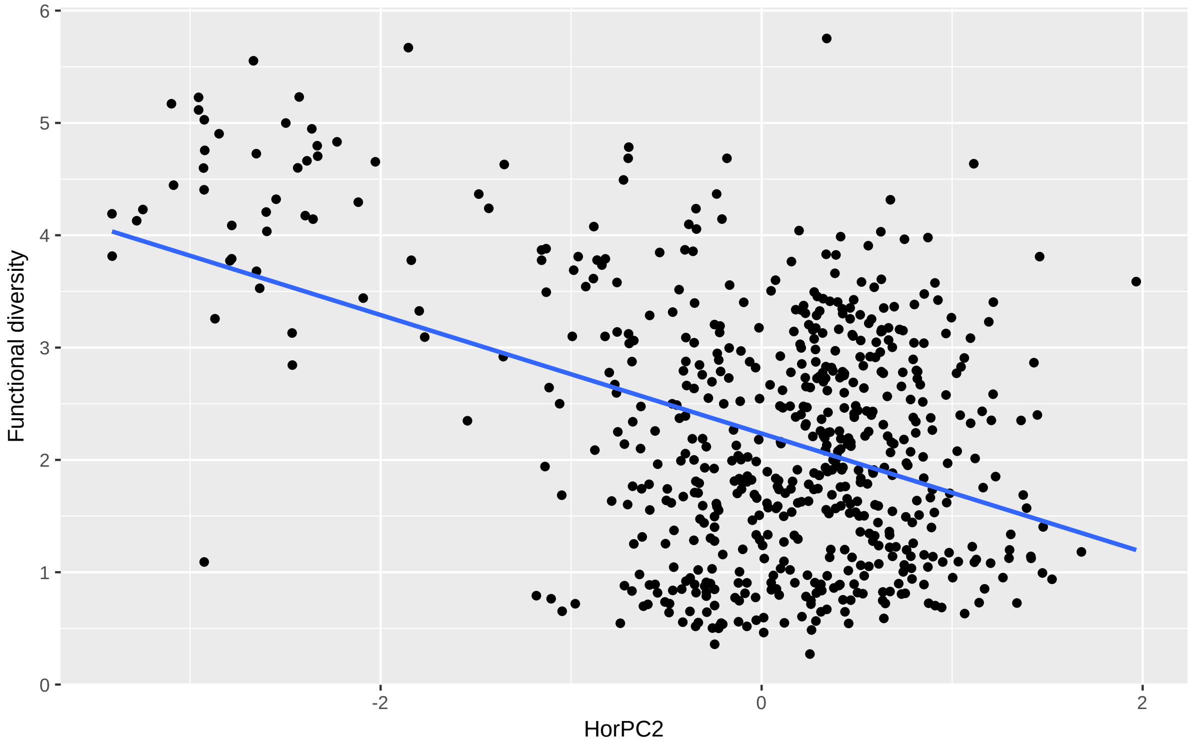
Appendix 2.G Scatterplot of the response of taxonomic diversity to soilPC2 (sandy soil+, clay soil-).



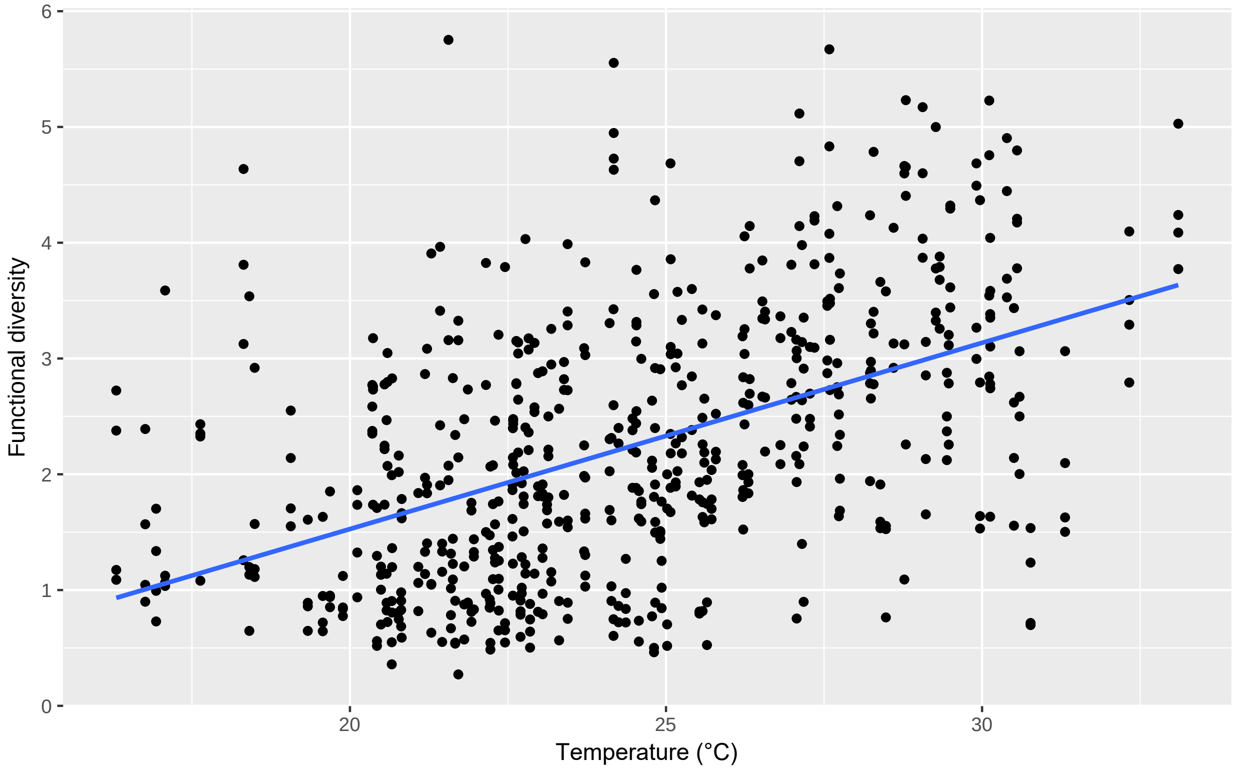
Appendix 2.H Scatterplot of the response of taxonomic diversity to soilPC1 (acidic soils+, basic soils-).



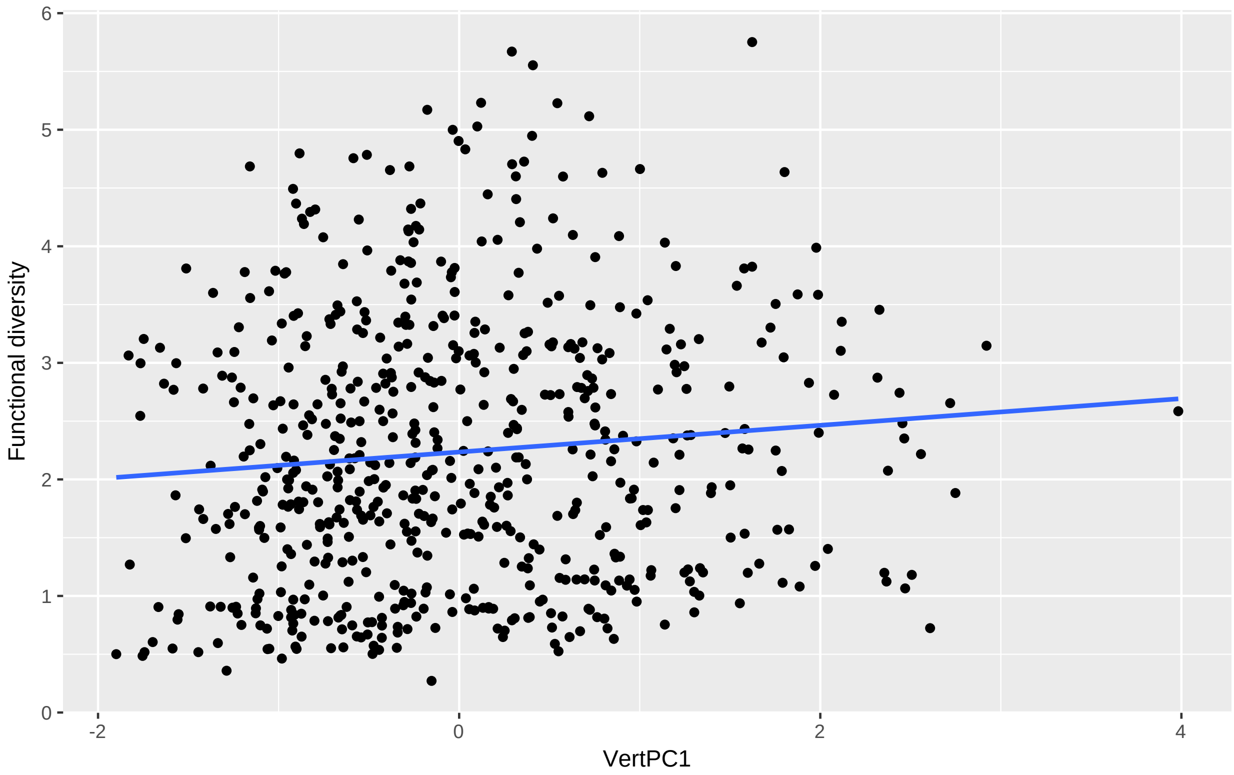
Appendix 2.I Scatterplot of the response of functional diversity to horPC2 (leaf litter cover+, rock cover-).



Appendix 2.J Scatterplot of the response of functional diversity to mean monthly soil temperature (**⁰ C)**



Appendix 2.K Response of functional diversity to vertPC1 (very little vertical structure-, more complex structure linked to increased vegetation+).



Appendix 3.A A list of species tested for $\mathrm{CT_{max}}$, N = 43 and $\mathrm{CT_{min}}$, N = 45.

$\mathrm{CT_{min}}$	$\mathrm{CT_{max}}$
Aenictus rotundatus	*Aenictus rotundatus*
Anochectus sp.02	*Anochectus sp.02*
Anoplolepis cf. custodiens	*Anoplolepis cf. custodiens*
Bothroponera? strigulosa	*Bothroponera? strigulosa*
Camponotus cubangensis dofleini	*Camponotus cubangensis dofleini*
Camponotus fulvopilosus	*Camponotus fulvopilosus*
Camponotus sp.02 (rufoglaucus gp.)	*Camponotus sp.02 (rufoglaucus gp.)*
Camponotus sp.03 niveosetosus group	*Camponotus sp.04 (etiolipes gp.)*
Camponotus sp.04 (etiolipes gp.)	*Camponotus sp.07 (empedocles gp.)*
Camponotus sp.07 (empedocles gp.)	*Camponotus sp.18 (maculatus gp.)*
Camponotus sp.18 (maculatus gp.)	*Cataulacus wissmannii*
Cataulacus wissmannii	*Cerapachys sp.01*
Cerapachys sp.01	*Crematogaster sp.01 subgenus sphaerocrema*
Crematogaster sp.02 (rufigena gp.)	*Crematogaster sp.06 (custanea complex)*
Crematogaster sp.01 subgenus Sphaerocrema	*Dorylus helvolus*
Crematogaster sp.06 (custanea complex)	*Meranoplus? perinqueyi*
Dorylus helvolus	*Monomorium albopilosum*
Meranoplus? perinqueyi	*Monomorium cf.junodi*
Monomorium albopilosum	*Monomorium damarense*
Monomorium cf. junodi	*Monomorium sp.01*
Monomorium damarense	*Myrmicaria natalensis*
Monomorium sp.01	*Ocymyrmex fortior*
Myrmicaria natalensis	*Ocymyrmex sp.03*
Ocymrymex fortior	*Pheidole sp.01 (megacephala gp.)*
Ocymyrmex sp.03	*Pheidole sp.02 (liengmei gp.)*
Pheidole sp.01 (megacephala gp.)	*Pheidole sp.05 (megacephala gp.)*
Pheidole sp.02 (liengmei gp.)	*Pheidole sp.07*
Pheidole sp.05 (megacephala gp.)	*Pheidole sp.10 (megacephala gp.)*
Pheidole sp.07	*Plectroctena sp.01*
Pheidole sp.10 (megacaphala gp.)	*Polyrhachis schistacea*
Plectroctena sp.01	*Rhoptomyrmex sp.02*
Polyrhachis schistacea	*Solenopsis sp.01*
Rhoptomyrmex sp.02	*Solenopsis sp.02*
Solenopsis sp.01	*Tapinolepis sp.01*
Solenopsis sp.02	*Technomyrmex pallipes*
Tapinolepis sp.01	*Tetramorium baufra*
Technomyrmex pallipes	*Tetramorium cf. setigerum*
Tetramorium baufra	*Tetramorium sepositum*
Tetramorium cf. setigerum	*Tetramorium setuliferum*
Tetramorium sepositum	*Tetramorium sp. 05 (sereiceventre gp.)*

Tetramorium setuliferum	*Tetramorium sp.07 (weitzeckeri gp.)*
Tetramorium sp.05 (sereiceventre gp.)	*Tetramorium sp.14 (sereiceventre gp.)*
Tetramorium sp.07 (weitzeckeri gp.)	
Tetramorium sp.14 (sereiceventre gp.)	
Tetramorium sp.16 (sereiceventre gp.)	

Appendix 3.B Correlation matrix between measured species traits (HW - Head width, HL - Head length, ML - Mandible length, SL - Scape length, CL - Clypeus length, EL - Eye length, EW - Eye width, WL - Weber’s length, HTL - Hind Tibia length, HFL- Hind Femur length. The strength of the correlation between traits is represented by the tone of the color.