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Ant diversity across an elevational gradient; functional versus taxonomic perspectives in the Soutpansberg Mountains, South Africa

A PhD thesis submitted to the Department of Ecology and Resource Management in the School of Environmental Sciences, University of Venda in fulfilment of the requirements for the degree

of

Doctor of Philosophy

in

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By

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"You have a choice: you can keep up with the literature or you can contribute to it"

Robert MacArthur

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Declaration

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

Signature……

Date……..

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Publication timeline and disclaimer

Please note that chapters' two to five of this thesis were written as stand-alone papers (see below), and therefore some repetition was unavoidable.

The following chapters have been accepted or are in preparation for submission for publication in journals:

Chapter 2: Munyai, T. C. & Foord, S. H. 2015. An inventory of epigeal ants of the western Soutpansberg Mountain Range, South Africa. Koedoe 57 (1), 1-12.

Chapter 3: Munyai, T. C. & Foord, S. H. 2015. Temporal patterns of ant diversity across a mountain with climatically contrasting aspects in the tropics of Africa. PloS ONE 10 (3), e0122035.

Chapter 4: Munyai, T.C. & Foord, S.H. Monitoring turnover of ants across an elevational transect: niche, space and time's relative importance (in preparation).

Chapter 5: Munyai, T.C., Foord S.H. & Parr, C.L. Dominance hierarchies of ant communities across an elevational transect, Soutpansberg Mountain (in preparation).

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Overall summary

Invertebrates constitute the bulk of ecosystem diversity. However, they are often ignored in conservation plans because of several shortfalls that include the lack of inventories and public awareness, a paucity of distribution and abundance data as well as their unknown way of life and sensitivity to habitat change. Environmental gradients are central in our attempt to address these shortfalls, gauging these organisms' responses to environmental change and ultimately in the search for general rules of community assembly.

In this study I focus on ants in a long-term monitoring study (5-year period) across an elevational gradient, that includes 11 sites on two climatically contrasting aspects of the Soutpansberg Mountain Range in Southern Africa. Ants were sampled using pitfall traps (September 2009 – January 2014) and baits (November 2011 and October 2012). Ants form a dominant component of terrestrial ecosystems, which both respond to and affects ecosystem processes, and this thesis aims to: 1) provide a check list and baseline data for ant species collected over a 5-year period across the study area, 2) report on the long-term biannual (wet and dry seasons) trends of species richness and test the relative contribution of geometric constraints, energy, available area, climate, local environmental variables, time, and space in explaining ant species richness patterns, 3) identify the relative role of spatial, environmental and spatially structured environmental variables in explaining variation in ant species turnover over the 5-year period of the study and 4) define a dominance hierarchy for ants species along the transect to describe variation of these dominance groups' abundance and distribution in space (elevation and habitat) and time (time of the day and season) and infer possible underlying processes structuring these assemblages.

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Chapter One introduce ant diversity along environmental gradients and how its relevant to long-term monitoring. Chapter Two provides data on standardised pitfall surveys over the study period and yielded a total of 133 species in 38 genera and 6 subfamilies, with 21% of these species restricted to the southern slope of the mountain and 14% to the northern slope. Forty two percent of the species had significant indicator values (IndVal) larger than 70 and several of these were restricted to elevational zones pointing to a narrow and restricted distribution of several ant species along this altitudinal gradient. Observed richness was the highest at a low-altitude mesic and lowest at the summit site (sedgeland). Richness estimation and extrapolation, however, suggests an increase in richness at a southern aspect site 1600 m a.s.l. with increasing sampling effort.

Chapter Three reports on the large seasonal variability in richness with evidence of decreasing seasonal variation in species richness with increasing elevation. Diversity patterns across the study were mainly determined by geometric constraints and temperature while soil characteristics (clay and carbon content) accounted for smaller but significant amounts of the variation.

Chapter Four suggests that ant species turnover was consistently explained by spatially structured environmental variables followed by pure spatial variables while pure environmental variables explained less than 2% of the variation, except for one survey that followed an extraordinarily wet period. The spatially structured component reflects the strong gradient along the transect. The importance of space points to the importance of mass effects or some environmental variables which were not measured, particularly factors that vary at finer scales such as competition. Energy proxy variables (NDVI, Mean Monthly Temperature, and Minimum Monthly Temperature) consistently explained most of the variation in ant species turnover.

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Available area, soil characteristics (percentage clay in the soil), also contributed to the explanatory power of the models.

Chapter Five reveal that dominant ant abundance increased with elevation, experienced seasonal decrease in winter and had a daily minimum during the warmest part of the day. The abundance of subdominant ants was highest at mid-elevational short forest site (1200 m a.s.l.) and was also highest during the warmest part of the day, while subordinate ants were present together with dominant ants throughout the day except in the morning. Subordinate ants had the highest abundance in woodland habitat.

Chapter Five also shows that various mechanisms might affect alpha diversity at a site across environmental gradients. On top of the mountain (sedgeland habitat), dominant ants control species richness at baits through competitive exclusion while habitat heterogeneity together with low abundance of dominant ants (open woodland habitat), environmental filtering (short forest habitat) and disturbance (shrubland habitat) might structure ant assemblages in the remaining habitats of the study area.

Across the study area, predicted increases in temperature should see an increase in species richness on the mountain but indicator taxa associated with high elevations are predicted to become locally extinct. Although ant assemblage responses were mainly driven by energy, structural changes will be confounded by the effects of bush encroachment on the southern aspect that will act as a filter while thermal tolerance limits will determine the response of species on the north. Developing a functional classification for the ants of the mountain might provide a more predictive framework for both assemblage and ecosystem functioning.

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Chapter 1: Ant diversity along gradients and its relevance to long term monitoring in a changing environment

Invertebrate inventories and long-term monitoring

Cardoso et al. (2011) list seven reasons why invertebrates are not included in conservation programmes. Three of these reasons (scientific shortfalls) are particularly relevant to how science is practiced: 1) unknown distribution of invertebrates species (Wallacean), 2) invertebrate abundance and their changes in space and time are unknown (Prestonian) and 3) their way of life and sensitivity to habitat types is largely unknown (Hutchinsonian) (Cardoso et al. 2011). Others include a lack of public awareness in recognizing their importance (Public dilemma) leading to a situation where policymakers and stakeholders are not aware of the invertebrate conservation problem (Political dilemma) and the lack of basic science and funding for invertebrate research (Scientific dilemma) (Cardoso et al. 2011). To overcome these shortfalls, inventories that follow standardized, comparable protocols and the identification of indicator taxa are essential (Cardoso et al. 2011).

Although they are sometimes consigned into the 'too hard basket' (Andersen and Majer 2004) invertebrates contribute the bulk of diversity in the ecosystems (Woinarski et al. 2002). They meet the criteria required for taxa to be included in biodiversity studies as they constitute the most diverse group and contribute to various important ecosystem services (Alonso and Agosti 2000, McGeoch et al. 2011). They are particularly well suited for monitoring programmes as they are easy to sample, could be processed efficiently and can be sampled over large scales (Oliver and Beattie 1996, Andersen and Majer 2004) and respond to the environment at small scales.

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The paucity in our understanding of invertebrates' distribution in space is eclipsed by the very limited consideration given to the role of temporal dynamics in species and assemblage properties (Juan and Hewit 2014). Standardized sampling protocols in long-term monitoring programmes are particularly timely if we are to understand ecosystem responses to global change drivers. In addition to requiring a considerable amount of time and investment, long-term monitoring studies are hampered by a lack of baseline information. The latter would provide a representation of the current status of the ecosystem and such information is vital in detecting changes, in particular, changes that are above the natural threshold for any particular ecosystem in question (Vaughan et al. 2001).

As much as baseline data are important for a monitoring programme, an effective target organism/taxon which is diverse, forms a large proportion of the biomass and performs diverse ecosystem services as compared to charismatic taxa e.g. most big mammals which are not abundant and not found in all ecosystem is crucial (Magurran and McGill 2011). Ants are an ideal candidate organism in this regard (Alonso and Agosti 2000). They thrive in almost every terrestrial ecosystem, except for a few inhospitable and remote islands (Hölldobler and Wilson 1990) and they are also easy to sample (Alonso and Agosti 2000). Ants are widespread and constitute an important part of terrestrial ecosystems. Their biomass is estimated to be one of the highest of any taxonomic group (Hölldobler and Wilson 1990) with more than 12,500 described species and an estimated 25,000 undescribed species (Ward 2010). Ants play vital roles in the functioning of terrestrial ecosystems (Del Toro et al. 2012) including pollination (Carvalheiro et al. 2010), myrmecochory (Fokuhla et al. 2012), nutrients recycling (Verchota et al. 2003), mutualistic relationships with other insects (Ness et al. 2010) as well as predation and scavenging (Philpott and Armbrecht 2006). As a result, they have been the recent focus of

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several monitoring programs e.g. the response of ants to long term fire regimes (Parr et al. 2004, Andersen et al. 2006, 2014), drivers of ants in the face of global change along elevational transects (Botes et al. 2006, Munyai and Foord 2012, Bishop et al. 2014), response to pastoral and military land use (Woinarski et al. 2002) and monitoring changes within and surrounding the endangered monsoon vine thickets (Fisher et al. 2014).

Despite their importance, ants, just like any other insect group are often not included in conservation plans and mostly ignored in conservations initiatives (Cardoso et al. 2011). Although studies have included ants as indicators in monitoring programmes e.g. studies on mining rehabilitation and land management (Andersen and Majer 2004), forest clearing (Majer et al. 2007) and soil quality (Lobry de Bruyn 1999, Frouz and Jilková 2008), there is a concern that invertebrates are almost completely absent from long term monitoring programmes (Magurran and McGill 2011).

Studies of diversity along gradients could provide the baseline data for biodiversity assessment and monitoring. The global significance of this is evident in the establishment of various long-term monitoring programs in different parts of the world such as the Long Term Ecological Research Program (LTER) started in 1980 in the United States of America (Hobbie et al. 2003) and in Australia, Terrestrial Ecosystem Research Network (TERN). Also the recent development of the Environmental Long-Term Observatories Network of Southern Africa (ELTOSA) (see Henschela et al. 2003) and the International Long Term Ecological Research Network (ILTER) (Gosz 1996). All these programs emphasise the need for long-term studies as they investigate the temporal dynamics of diversity across various envioronmental gradients. These programs are therefore very important in identifying space-time interation (Laliberte´ et al. 2009) and this is of particular interest in the changing environment.

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Importance of gradients in a changing environment

Environmental gradient refers to a gradual change in abiotic factors (for example humidity, temperature, soil fertility, precipitation and others) through space and time. The variation in environmental factors such as resources or conditions such as stress (temperature) and disturbance affects the variation in the number of individuals creating a gradient. Two commonly explored gradients are latitudinal (Willig et al. 2003) and elevational (Werenkraut et al. 2015) gradients. Although studies across these gradeints are increasingly being documented, their causes remain a challenge to biologist (Rosenzweig 1995, Sanders and Rahbek 2012).

Across gradients, biologists measures the abiotic factors that explain the distribution of organisms and ecosystems in terms of environmental tolerances. Therefore studying these gradients provide crucial information which aid in understanding the geographic distribution of species and ecosystems. Understanding the geographic distribution of organism is critically important in achieving the goal of maintaining biodiversity in the face of global climate change (Gaston 2000). Along gradients, three measures of biodiversity are commonly studied, i.e. alpha, beta and regional/gamma diversity. Two of these, apha and beta diversity, will be discussed here.

Gradients and alpha diversity

Alpha diversity is the total number of species in a single site or sampling unit (Anderson et al. 2006) and its pattern across environmental gradients (elevational, latitudinal, ecotones and bathymetric) have gained much interest amongst biologists (Sanders and Rahbek 2012). The most documented pattern is the decrease in species richness with an increase in elevation or latitude (Rosenzweig 1995, McCain 2007, Dunn et al. 2009). There has been, however, growing support for richness peaking at mid-elevation (Rosenzweig 1995, Gaston 2000). Interestingly, a

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few studies have even observed an increase of richness with elevation e.g. for ants (Sanders et al. 2003).

The drivers and correlates of these patterns have also received attention in the past few decades (Pimm and Brown 2004, Gavin and Stepp 2014) with more than 30 hypotheses proposed (Rhode 1992, Hawkins et al. 2003), although recent studies have focused on a smaller number (Willig et al. 2003, Dunn et al. 2010) that can be grouped into four main groups. The first group is hypotheses related to area/spatial constraints, viz. the mid-domain effect (Colwell et al. 2004), available area (Rahbek 1995, Rosenzweig 1995) and Rapoport's Rule (Stevens 1992, Gaston et al. 1998).

The second group of hypotheses is climate related and includes environmental factors such as humidity and temperature (Hawkins et al. 2003, Sanders et al. 2007, McCain 2007), precipitation (Hawkins et al. 2003, Delsinne et al. 2010) and energy (Kaspari et al. 2000, Kaspari et al. 2004, Braschler et al. 2012). Climatic variables directly and indirectly explain patterns in species richness as they mediate the biotic interactions and influence the distribution of survival resources along gradients (Hawkins et al. 2003). The third group is historical hypotheses and they argue that time is a limiting factor of species diversity along gradients where certain areas have not had sufficient time for species to either colonise or evolve and increase their diversity (Rhode 1992, Pimm and Brown 2004, Gillman et al. 2009).

The last group is related to local ecological interactions, habitat structure and edaphic factors (Currie 1991, Willig et al. 2003). The local interaction of biotic factors such as competition (Parr et al. 2005, Cerda et al. 2013), predation (Hobaek et al. 2002, Barros 2005), parasitism (Roche et al. 2010, dos Santos et al. 2013) and mutualism (Rudgers and Clay 2008) have been documented to affect alpha diversity for various taxa.

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Soil properties have been identified as one of the major influences of species richness, e.g. Medinski et al. (2010) and references therein. Soil can have an indirect effect on ants e.g. through its effects on plant distribution which also affect ant richness (Jacquemin et al. 2012), and can also have direct effects on species richness e.g. increased ant richness in Ecuadorian Andean forests resulting from clay availability (Ramon et al. 2013).

Habitat complexity has been widely documented in various studies as a major influence of species diversity in taxa such as small mammals (Lam and Maguire 2013), fish (Wilson et al. 2014) and invertebrates (Parr et al. 2010, Galle et al. 2014). There is a growing body of evidence emphasizing the negative effects of habitat complexity on species richness of ants in particular (Brühl et al. 1999, Araújo and Fernandes 2003, Lassau and Hochuli 2004).

Across gradients (elevational and latitudinal) on this regard, one of the first study to attempt to quantify latitudinal gradients in ant diversity was by Kusnezov (1957) at a regional scale incorporating Utah, Cuba, Trinidad, Alaska, Iowa, parts of Argentina, and Brazil. Since then, this subject has exprienced a growing number of studies *inter alia* Cushman et al. (1993) and Kaspari et al. (2003). To date, much focus has been on biodiversity patterns along elevational gradients. Sanders and Rahbek (2012) showed that > 300 studies by the year 2011 have investigated elevational variation in biodiversity while Gaston (2000) also reviewed the patterns along latitudinal gradients, also see Rosenzweig (1995) and Gaston and Blackburn (2000) for critical reviews. The majority of these studies along elevational gradients have not investigated the temporal dynamics of species richness patterns and their drivers and correlates, but see Bishop et al. (2014) in the Maloti Drakensberg Mountain of South Africa for a notable exception.

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Gradients and beta diversity

Whittaker (1960, 1972) defined beta diversity as a measure for the variation in the identities of species among habitats/sites between ecosystems/geographical areas or along environmental gradients (Legendre et al. 2005, Terlizzi et al. 2008). It compares habitat diversity of different study systems and indicates the degree to which habitats have been partitioned by species (Wilson and Shmida 1984).

Although there is increasing awareness that beta diversity measures a fundamental aspect of spatial biodiversity patterns, it has received less attention than studies dealing with local or alpha diversity (Terlizzi et al. 2008, Paknia and Pfeiffer 2014). The same applies when beta diversity is contrasted to regional or gamma diversity (see Koleff et al. 2003, Harborne et al. 2006). Legendre et al. (2005) and Legendre (2006) argue that beta diversity is a key concept for understanding conservation of biodiversity and ecosystem management as it provides key information to identify areas of conservation importance, understanding the effects of fragmentation and estimation of global diversity (Harrison et al. 1992). Harborne et al. (2006) pointed out that it can be used to establish appropriate scales for management and that it is a potential substitute for a range of ecosystem functions and processes.

A combination of environmental (niche based) and space (dispersal) processes drives beta diversity but the relative importance of these factors is dependent on the scale of measurement and taxonomic group (Bestelmeyer et al. 2003, Qian and Ricklefs 2007). Quantifying the role of pure environmental, pure spatial positioning and the shared effects of the spatially structured environmental factors can aid in improving the understanding of how each of these factors affect beta diversity (Baselga 2008, Legendre et al. 2009, Paknia and Pfeiffer 2014). Very few studies have considered the impact of spatial structure on ant beta diversity, but see Del Toro (2013) in

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eastern North America. While some studies (Vasconcelos et al. 2010, Mezger and Pfeiffer 2011) have also examined the combined effects of environment and spatial factors, where they had weak effects on ant species turnover.

Myrmecologists have historically focused much of their attentions on factors and mechanisms related to variation in alpha diversity (Botes et al. 2006, Munyai and Foord 2012, Bishop et al. 2014) and there have been few studies dealing with mechanisms determining ant beta diversity along gradients (but see Bishop et al. 2015). Recent advancements in analyzing beta diversity have allowed for improved understanding of variation in beta diversity across gradients (Laliberte´ et al. 2009).

Competition and ants

The negative interaction of individuals sharing limited resources is defined as competition. Interspecific competition is one of the fundamental processes in ecology and it results in increased fitness of one species compared with another, owing to a superior ability to access the limited resource (Parr and Gibb 2010, Blight et al. 2014). As a mechanism shaping community structure, competition has had the oldest history in ecology and it is also seen as the central pillar upon which evolutionary and ecological theory rests (Koeppel and Wu 2014). A synthesises of studies on interspecific competition have reported on its effect on both plants and animals (Begon et al. 2006). It causes poor competitors to have smaller population sizes in the semi-arid grassland plant communities (Martorell and Freckleton 2014) and tree species assemblages in the tropical cloud forests (Long et al. 2013) while it determines community structure in a group of neotropical catfishes (Alexandrou et al. 2011).

Two earlier studies, Schoener (1983), examined a total of 164 studies in terrestrial plants and animals, and marine organisms, found that 90% of these studies report the existence of

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interspecific competition. Connell (1983) reviewed a total of 72 studies and found support in 40% of these studies. However in contrast, a review by Strong et al. (1984) suggest a relatively rare detection of interspecific competition in phytophagous insects. Similarly, a Hairston et al. (1960) review suggests a relatively rare influence of interspecific competition among herbivores in general and more particularly plant eating insects.

Competition has had a long history in ant ecology and much of the debate around it have been its role in structuring assemblages (Parr and Gibb 2010, Gibb and Johansson 2011). Although competition, through competitive exclusion by dominant ants, controls assemblages at local scales (Parr 2008), other mechanism such as habitat heterogeneity (Pacheco and Vasconcelos 2012, Parui et al. 2015), disturbance (Gibb et al. 2015, Vonshak and Gordon 2015) and environmental filtering (Wiescher et al. 2012, Fowler et al. 2014) play a significant role in influencing ant species diversity.

Building on the importance of competition, as well as detectability studies have proposed that ant species in assemblages can be classified into dominance hierarchies (Savolainen and Vepsäläinen 1988). Within the hierarchy, the most competitive (behaviourally dominant) ants are at the top of the hierarchy while the least competitive are at the bottom. Although recent review by Parr & Gibb (2010) agree that competition is one of the most contentious issue and that there is a need to further discuss its dectatability and importance in structuring ant assembalges, evidence of competitive exclusion in previous ant studies exist (e.g. Andersen, 1992, Parr et al. 2005, Parr, 2008).

Three types of ant with distinct behaviour based on their competitive interaction and resource exploitation are recognized i.e. the extirpators, opportunist and insinuators (Hölldobler and Wilson 1990). Arnan et al. (2011) also recognises a three-tiered competition hierarchy based on a

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widely used ant functional group scheme (Andersen 1995) i.e. dominant, subdominant and subordinate. The dominant ant species correspond to "extirpators" described in Hölldobler and Wilson (1990) and territorials as in Savolainen and Vepsäläinen (1988). These are highly competitive ants with large territories, numerically abundant and aggressively defending all different types of resources. The subdominant ants are almost equivalent to the "encounters" species group in Savolainen and Vepsäläinen (1988) and "opportunists" in Hölldobler and Wilson (1990). Species in this group recruit individuals to food resources quickly because they are mostly the first to arrive at baits (Parr and Gibb 2010).

The subordinate group consists of poorly competitive ants that correspond to the "insinuators" reported in Hölldobler and Wilson (1990) and "submissive" as observed in Savolainen and Vepsäläinen (1988). They mostly recruit less individuals to food resources and are able to gain access to resources unnoticed by dominant species because some of them are adapted to forage at night to avoid interaction with superior competitors (Bestelmeyer 2000, Parr and Gibb 2010, Aranda-Rickert and Fracchia 2012). However, Parr and Gibb (2010) argue that not all ants fit neatly into these hierarchies because most species defend territories, but only against conspecifics or closely related species.

Mountains as natural laboratories

Transects across mountains can act as surrogates of medium to large-scale spatial and temporal diversity patterns and dynamics (Longino and Colwell 2011). Although area and isolation could have a more significant impact on diversity in mountains than in other ecosystems, the shorter distances between different habitats largely negates the impact of dispersal limitation and assemblages should therefore respond to environmental gradients and change. These ecosystems could therefore be ideal indicators of the rate and impacts of global change. Sanders and Rahbek

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(2012) proposed that future studies across mountains should demonstrate the effects of climate change on current and future biodiversity patterns and they report on the growing number of studies on elevational diversity. Furthermore, Sanders and Rahbek (2012) provide four reasons why elevational gradients are of special importance in revealing the processes and mechanism leading to variation in diversity. These include that elevational gradients are easy to replicate given the number of available mountains, the possibility to carry out manipulative experiements and that field data can be readily collected along these gradients as compared to latitudinal gradients (Sanders and Rahbek 2012).

Long term monitoring of elevational transects provide an understanding of drivers of biodiversity in both space and time and is particularly relevant within the context of global change (Magurran and Dornelas 2010). Botes et al. (2006) established the first long-term invertebrate monitoring site along an elevational transect in South Africa towards the end of 2002. Their study area included both Fynbos and Succulent Karoo with 17 elevational sites and two aspects (west and east) in the Cederberg Mountains of the Western Cape Province. A second transect was established in the grasslands of the Drakensberg Mountains in 2006 with seven elevational sites all in one aspect (Bishop et al. 2014). Towards the end of 2008, a third site was initiated across the western parts of the Soutpansberg Mountain Range in the north-eastern corner of South Africa which consists of five habitat types (woodland, herbland/sedgeland, forest, thicket and shrubland) with eleven sites and two aspects (north and south) and it is the first long term monitoring project of invertebrates in the tropics of Africa (Munyai and Foord 2012). All three sites follow a similar sampling protocol i.e. sample invertebrates during the wet and dry season with pitfall traps. They aim to identify drivers and correlates of invertebrate diversity within the context of global change especially given the prediction for changes leading to an increase in

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temperature and rainfall in the north-eastern part of South Africa (Davis et al. 2010, van Wilgen et al. 2015).

Study site

The Soutpansberg Mountain Range is a centre of endemism and is the focal point for the newly proclaimed Vhembe Biosphere Reserve, which is one of the United Nations Educational, Scientific and Cultural Organisation (UNESCO) World Network of Biosphere Reserves (www.unesco.org). It has the highest plant generic and family level diversity among the 18 recognized Centres of Plant Endemism for southern Africa (van Wyk and Smith 2001). The region also contains 33% of South Africa's reptiles, 60% of mammal species and 75% of its avifauna (Berger et al. 2003).

Recent work on terrestrial invertebrates and small mammals of the region reported rich generic and higher taxonomic diversity for spiders (Foord 2008, Foord et al. 2013), ants (Munyai and Foord 2012), scorpions (Foord et al. 2015), bats (Taylor et al. 2013) and other small mammals e.g. rodents, sengis and shrews (Taylor et al. 2015). Chase Grey et al. (2013) also recorded the highest leopard density outside of protected areas in Sub-Saharan Africa. The high levels of biological diversity of the Soutpansberg gives it a high long-term priority for conservation (Van Wyk and Smith 2001).

Thesis objectives and outline

The objectives of the thesis are to 1) provide baseline results of a standardised inventory of epigeal ants collected over a five year period (2009 – 2014) along an elevational transect in the Western Soutpansberg mountain (Chapter Two), 2) detail seasonal, annual and long-term trends as well as testing the relative contribution of correlates of species richness in the study area (Chapter Three), 3) identify the relative role of spatial, environmental and spatially structured

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environmental variables in explaining variation in ant species turnover over the period of the study (Chapter four) and 4) define a dominance hierarchy for ant species and describe variation of these dominance groups across the study area (Chapter Five).

The following section briefly describe the objectives of each chapter within the context of the main themes of the thesis:

Chapter 2: An inventory of epigeal ants of the western Soutpansberg mountain range, South Africa

Invertebrates contribute the bulk of diversity but are often excluded in conservation planning. One way in which this paradox can be resolved is through inventories that follow standardized and comparable protocols. Chapter Two of this thesis summarizes the results of a standardized pitfall survey across the eleven elevational sites of the study area, provides baseline data of ant indicator taxa and their distribution and a *posteriori* define distinct ant assemblages across the transect and test for differences between these groups.

Chapter 3: Temporal patterns of ant diversity across a mountain with climatically contrasting aspects in the tropics of Africa

Factors that drive species richness over space and time are still poorly understood and are often context specific. To date, more than 30 hypotheses have been developed and tested to explain patterns of species richness along environmental and geographic gradients (Rohde 1992). Chapter Three tests some of these hypotheses across the study area as well as details the seasonal, annual and long-term trends of species richness over a five year period (2009 – 2014). I test the relative contribution of geometric constraints, energy, available area, climate, local

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environmental variables, time, and space in explaining ant species richness patterns across the study area.

Chapter 4: Monitoring turnover of ants across an elevational transect: niche, space and time's relative importance

Factors and mechanisms responsible for driving alpha diversity are better understood than those that drive beta diversity (Beck and Khen 2007, Paknia and Pfeiffer 2014). Recent studies argue that our ability to disentangle variation in diversity into the contributions of different processes affecting it and the scale of measurement at which these processes and correlates act will help us better understand the drivers of species beta diversity (Laliberte´ et al. 2009, Legendre et al. 2009). Chapter Four aims to test the effect of space-time interaction on ant species turnover, identify environmental and spatial variables that consistently explain significant amounts of this turnover and partition the relative roles of pure environmental, pure spatial and spatially structured environmental variables in determining this variation.

Chapter 5: Dominance hierarchies of ant communities across an elevation transect, Soutpansberg Mountain

Competition has been described as a "hallmark of ant ecology" (Hölldobler and Wilson 1990). However, its role in ant ecology is still a contentious issue despite its long history. Previous studies have used observation of interspecific competitive interactions to classify ants into dominance hierarchies (Savolainen and Vepsäläinen 1988, Arnan et al. 2011). Chapter Five of this study aims to define a dominance hierarchy for ants along the study area, describe variation of these categories in space (elevation and habitat) and time (time of the day and season), describe the variation in ant morphospace along the transect and determine the relative role of

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competition (resources), habitat heterogeneity/structure, disturbance and environmental filtering (stress) in the coexistence of ant species across the mountain.

The final chapter (Chapter Six) contextualizes results of this thesis within a regional and global context, discusses the implications of these results for future monitoring across the transect and predicts the impact of global change on ant assemblages of the Soutpansberg Mountain.

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Chapter 2: An inventory of epigeal ants of the western Soutpansberg Mountain Range, South Africa

Abstract

The distribution, abundance and sensitivity of invertebrates to habitat change are largely unknown. Long-term monitoring of ecological gradients with standardised and comparable protocols can form the basis of a better understanding. Altitudinal gradients are particularly relevant within this context. Here we provide baseline data of ant indicator taxa and their distribution that was collected over a five year period across the Soutpansberg mountain range, South Africa. Standardised pitfall surveys across 11 sites yielded a total of 133 species in 38 genera and 6 subfamilies. Of these species, 21% were restricted to the southern slope of the mountain and 14% to the northern slope. Forty two percent of the species had significant Indicator Value larger than 70 and several of these were restricted to elevational zones pointing to a narrow and restricted distribution of several ant species along this altitudinal gradient. Sample coverage of epigeal ants was 0.98 for the transect as a whole. Extrapolated richness estimates reached an asymptote for all, except three sites. These were the only sites impacted by bush encroachment. Observed richness was the highest at a low-altitude mesic site that is exposed to considerable disturbance by megaherbivores and mechanical clearing of woody vegetation. Structural classification of vegetation was predictive of a broad-scale ant assemblage structure. On a smaller scale, however, the assemblage structure was a function of elevation, space and temperature. Future monitoring should use identified indicator taxa to monitor expansion of bush encroachment, particularly with reference to its impact on grasslands. Bush encroachment could endanger several ant species associated with mesic grasslands and

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woodlands on the mountain, as well as ant diversity, as these were the habitats with the highest ant diversity.

Introduction

Although invertebrates comprise the bulk of diversity in an ecosystem, they are often excluded from conservation initiatives. Cardoso et al. (2011) identified seven reasons for this. Three of the shortfalls had to do with the unknown 1) distribution (Wallacean), 2) abundance, its dynamics in space and time (Prestonian) and 3) species' way of life and sensitivity to habitat types (Hutchinsonian). These three shortfalls are particularly relevant to how ecologists practise their science, as the distribution, abundance in time and space, and sensitivities to habitat change are largely unknown for most species. These constraints can be resolved through inventories that follow standardised and comparable protocols (Cardoso et al. 2011).

Ants respond to the environment at small scales and considerable support exists for their use as indicators of disturbance and habitat degradation (see Andersen and Majer [2004] for review). Ants are easily collected and species or morpho-species level determination are aided through readily available taxonomic expertise (Ward 2010). In addition to being diverse, abundant and a dominant component of animal biomass in terrestrial ecosystems (Hölldobler and Wilson 1990), they also perform important functions in ecosystems, including pollination, myrmecochory and nutrient cycling, among others (Wielgoss et al. 2014).

The Soutpansberg Mountain Range is a centre of endemism (Hahn 2002) and is the focal point for the newly proclaimed Vhembe Biosphere Reserve, one of the United Nations Educational, Scientific and Cultural Organisation (UNESCO) World Network of Biosphere Reserves (www.unesco.org). It has the highest plant generic and family level diversity among the 18 recognised

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Centres of Plant Endemism in southern Africa (van Wyk and Smith 2001). Recent results suggest that this diversity and endemism is mirrored by spiders (Foord 2008) and reptiles (Kirchhof et al. 2010). As an inselberg that rises 1000 m above the surrounding plains, the Soutpansberg Mountain Range has provided a refuge for several taxa during periods of climate change and will once more play a biogeographic role in the region as regional climate changes take effect in response to elevated global greenhouse gases (Tshiala et al. 2011).

Transects can provide valuable diversity, distribution and abundance information as well as population trends. Altitudinal transects are particularly relevant within the context of contemporary climate changes. Here we summarise the results of a standardised inventory of epigeal ants over a 5-year period (2009–2013), along a transect across the western Soutpansberg Mountain Range. We provide a checklist of epigeal ants with a sample coverage of 0.98 for the whole transect, a *posteriori* defined distinct ant assemblages across the transect and tests for differences between these groups. Lastly we identified indicator species associated with each of the groups that will act as baseline information for longer term studies along this transect.

Materials and methods

Study area

The 16.5 km altitudinal transect extends over the highest point of the Soutpansberg Mountain Range, Lajuma (1748 m), in the Luvhondo Nature Reserve. It includes the northern and southern slopes of the mountain and consists of 11 sites, spaced at 200 m altitudinal intervals. It starts at 800 m. a.s.l. in the Limpopo valley to the north of the mountain, ascends 900 m to Lajuma, and descends another 800 m to the plains south of the range (Figure 1).

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The study area stretches across five broad structural vegetation types, namely woodland, sedgeland-herbland, forest, thicket and shrubland. All the sites on the northern aspect (all arid sites) are woodland (total tree cover 0.1% – 75%; shrub cover < 10%; mean crown-gap ratio > 0.1). They can be characterised as low (1 m – 5 m-tall trees), open (crown-gap ratio of 2–8.5) woodland (Figures 2a–2d), mostly on shallow quartzitic soils (Figures 2b–2d). One site is characterised by deep sandy soils (Figure 2a). Dominant trees species include *Burkea africana*, *Ochna pulchra*, *Diospyros dichrophylla*, *Rhus magalismontanum*, *Boscia albitrunca*, *Adansonia digitata*, *Senegalia nigrescens* and *Terminalia sericea*. Vegetation types along the plains and lower southern foothills are largely thicket (Figure 3d, mesic site) and shrubland (Figure 3e), located on red loamy-clay soils dominated by woody species such as *Dichrostachys cinerea*, *Senegalia caffra* and *Olea europaea*.

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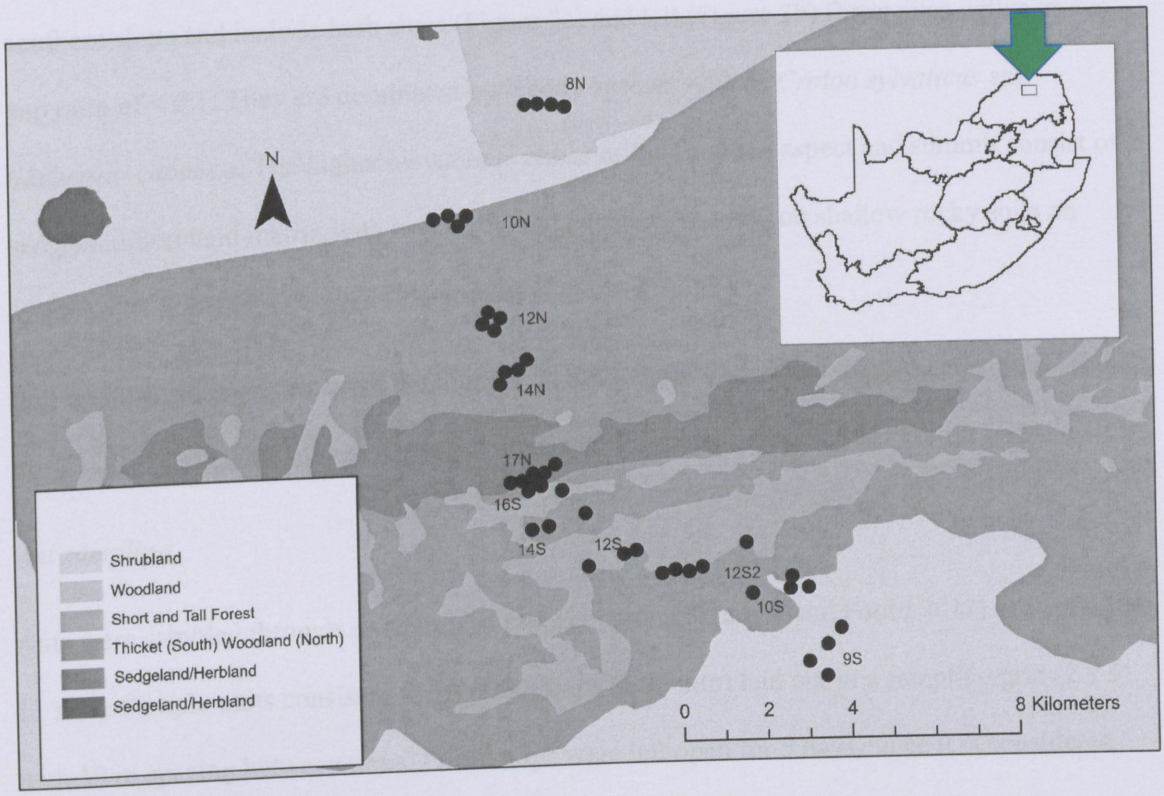

Figure 1: Location of the Soutpansberg transect in South Africa (inset) and the position of the 44 replicates with the 5 structural habitat types. Northern aspect: 800 m. a.s.l. (8N), 1000 m. a.s.l. (10N), 1200 m. a.s.l. (12N), 1400 m. a.s.l. (14N), 1700 m. a.s.l. (17N/summit); southern aspect: 1600 m. a.s.l. (16S), 1400 m. a.s.l. (14S), 1200 m. a.s.l. (12S), 1200 m. a.s.l. (12S2), 1000 m. a.s.l. (10S), 900 m. a.s.l. (9S).

Structurally, the lowest site on the southern aspect (Figure 3e) is tall, closed shrubland (< 0.1% tree cover). It is dominated by a *D. cinerea* matrix with patches that are mechanically cleared of all woody plants. Site 10S (Figure 3d) is low thicket (10% – 100% tree cover and > 10% shrub

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cover). The forests are found at mid-elevation, between 1200 m. a.s.l. and 1400 m. a.s.l. on the southern slope and include both short (Figure 3c) and tall (Figure 3b) forest sites with a crown-gap ratio of < 0.1. They are dominated by woody species such as *Croton sylvaticus* and *Ekebergia capensis*. The higher elevational zones of the southern aspect and summit consist of a sedgeland-herbland matrix with low shrubland patches that grow on shallow rocky soils on quartzite, dominated by *Coleochloa* species (Figures 2e–3a).

Soil temperature extremes were the highest on the summit of the mountain (mean annual range 10 °C – 55 °C) and the lowest in the tall forests of the southern aspect (14 °C – 32 °C).

Ant sampling

Ants were sampled through standardised pitfall trapping (Munyai and Foord 2012) at each of the 11 sites. Sample units consisted of 10 pitfall traps (ø 62 mm) laid out in a sampling grid (2 x 5) with 10 m spacing between traps. Pitfall traps were left open for 5 days, since it is considered representative and does not sample excessive ants (see Munyai and Foord [2012] and references therein). The first five surveys were not replicated, because during this period samples where collected biomonthly. However, from September 2009 onwards (Appendix 1), sampling units were spatially replicated four times at each site. Replicates were separated by at least 300 m to avoid pseudo-replication (Ness et al. 2004). The traps contained a 50% solution of propylene glycol as a preservative that neither attracts nor repels ants (Abensperg-Traun and Steven 1995).

The ant samples were washed in a laboratory and stored in 70% ethanol. They were sorted to morpho-species and, where possible, identified to species by comparison with reference collections housed in the Kruger National Park in South Africa and the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Tropical Ecosystems Research Centre

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in Darwin, Australia. Bolton (1994) was used to identify some specimens to genus level, while valid names were confirmed using AntCat (http:// www.antcat.org) and AntWeb (http://www.antweb.org). The unidentified (morpho) species were given the following number codes: University of Venda Collection_01, 02, etc. (i.e. UVOC_01, 02, etc.).

Bothroponera, *Mesoponera*, *Ophthalmopone* and *Pseudoponera* were considered valid genera rather than being subsumed under *Pachycondyla* (Schmidt & Shattuck 2014). Subfamilies Aenictinae and Cerapachyinae were both considered invalid and therefore subsumed under Dorylinae, as treated by Brady et al. (2014). Reference collections are housed at the University of Venda and CSIRO Tropical Ecosystems Research Centre (Darwin, Australia).

Data analysis

Chao 2 and ICE, in EstimateS version 9.1.0 (Colwell 2013), were used to estimate species richness. Sample coverage at each site and the transect as a whole was computed with sample-based rarefaction and extrapolation of the incidence matrix. Sample coverage represents the proportion of the total number of individuals in the ant assemblage along the transect that belong to the species represented in our sample (Chao and Jost 2012). This is an appropriate measure of coverage and has been used in previous studies of ant richness along environmental gradients, see Del Toro (2013).

Both interpolation and extrapolation of samples was based on the Bernoulli product model as well as unconditional variance estimates for the rarefaction (interpolation) (Chao and Jost 2012) and extrapolation curves. This sample-based estimation provides both unconditional variance abundance data of this study and species richness predicted by a 1000 pitfall samples and were considered to be a fair reflection of the richness at a site.

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For the multivariate analysis samples within each replicate were pooled over the period of the study. This resulted in a species abundance matrix consisting of 44 records, one for each replicate. Ant assemblage structure was mapped using non-metric multidimensional scaling (MDS) ordination of Bray-Curtis similarities (Clarke and Warwick 2001). A *posteriori* groups of ant assemblages were defined based on hierarchical clustering with group average linking. Support for these groups was tested with the permutational procedure SIMPROF in PRIMER v.6.1.6 (Clarke and Gorley 2006). The degree of specificity (uniqueness to a particular group) and fidelity (frequency of occurrence within the group) was assessed (van Rensburg et al. 1999) through the Indicator Value Method (IndVal) (Dufrene and Legendre 1997). This index is symmetric and reaches a maximum of 100 when all the individuals of a species are only found in one group and the species occurs in all the sites of that group. Species with significant IndVal's greater than 70 were selected (van Rensburg et al. 1999).

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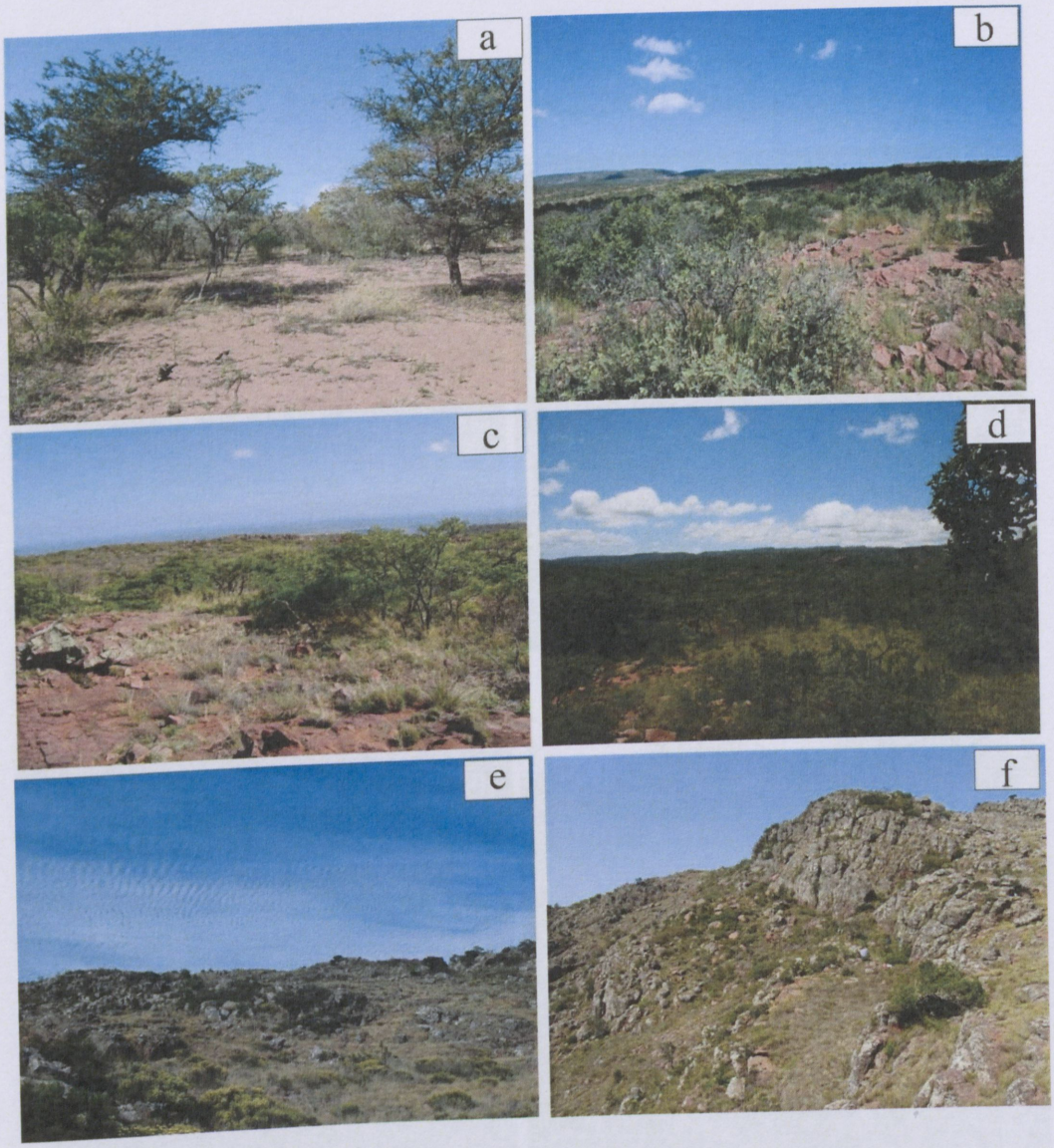

Figure 2: Sites with deep sandy soils, a) 08N characterised by trees such as *Adansonia digitata* and b) 12N *Senegalia nigrescens* and *Terminalia sericea* while (c) 10N and (d) 14N are on shallow quartzitic soils and include *Burkea africana*, *Ochna pulchra*, *Diospyros dichrophylla*, *Rhus magalismontanum*, *Boscia albitrunca* and *Terminalia sericea*. Higher elevation sites (e) 17N and (f) 16S are low shrubland patches with shallow rocky soils on quartzite, dominated by *Coleochloa* species.

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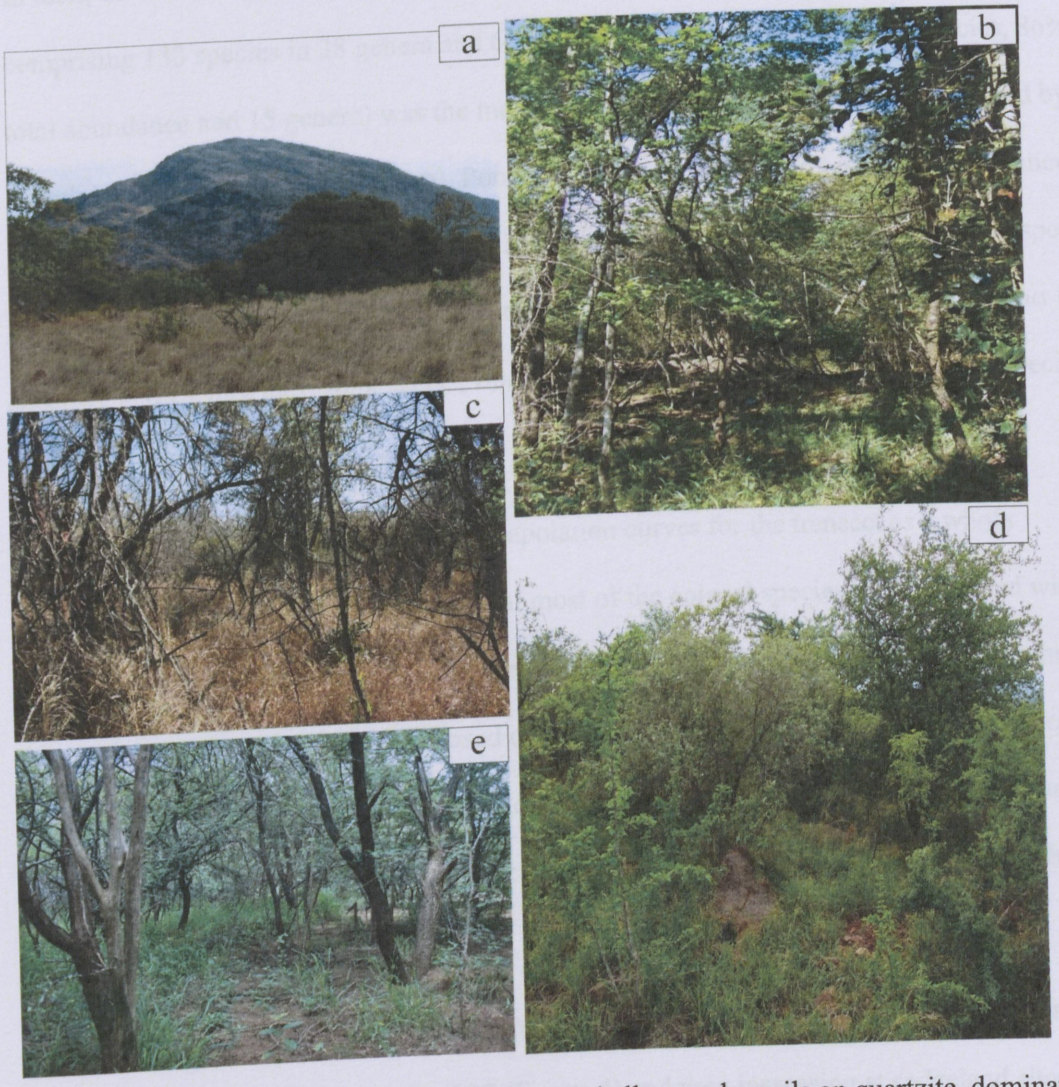

Figure 3: Low shrubland patches, a) 14S, with shallow rocky soils on quartzite, dominated by *Coleochloa* species, b) Tall forest (12S) dominated by woody species of *Croton sylvaticus* and *Ekebergia capensis* and c) Short forest (12S2). Low elevation sites of the southern aspect than include d) Thicket (10S) on clay soils dominated by woody species such as *Senegalia caffra* and *Olea europaea* and e) Shrubland (09S) on clay soils dominated by woody species such as *Dichrostachys cinerea*.

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Results

In total, 85 759 ant specimens were collected during the 13 sampling periods (Appendix 1), comprising 133 species in 38 genera and 6 subfamilies. Myrmicinae (with 72 species, 86% of the total abundance and 15 genera) was the most diverse and abundant subfamily, followed by Formicinae (27 species and 6 genera). Ponerinae (12 genera) had the second highest generic diversity. The most specious genera were *Tetramorium* (22 species), *Camponotus* (19 species), *Monomorium* (13 species), *Pheidole* (9 species), *Crematogaster* (6 species), *Meranoplus* (4 species), and *Ocymyrmex*, *Anochectus*, *Bothroponera* and *Plectroctena*, each with 3 species (Appendix 2).

Sample-based species rarefaction and extrapolation curves for the transect as a whole approximated an asymptote, indicating that most of the epigeal species were collected with a sample coverage of 0.98. Sample coverage for all sites was > 0.95, while coverage for the forest site, 12S, was the lowest, at 0.955. Based on richness estimations (Table 1) and species richness extrapolations (Figures 4 and 5), ant richness peaked at mid-elevations on the northern aspect. Only at woodland site 14N was species richness significantly greater than that of 17N, the summit (Figure 4).

The pattern on the southern aspect was more complex, with richness decreasing significantly from shrubland site 9S to forest site 12S (Figure 4) and then increasing at sedgeland sites 14S and 16S before decreasing again towards the summit (Figure 4). Based on predicted richness of sites (Figure 5), the ranking of sites changes only for 14N. Notably, the predicted curve for 16S also suggests a considerable increase in richness with increased sampling. The sites with the highest and lowest variation in mean annual temperature variation (17N and 12S) also had the lowest species richness.

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Table1: Observed number of species (obs), abundance, richness estimates (Chao 2, ICE in EstimateS 9.1.0 package) and sample coverage for broad structural vegetation types and 11 sites with their geographical coordinates along the Soutpansberg transect.

Vegetation types	Obs	Abundance	Site	Geographical Coordinates	Obs	Chao2	ICE	Sample Coverage
Shrubland	77	4966	9S	23 03.846 °S, 29 29.400 °E	76	87.9	85.5	0.974
Thicket	60	16192	10S	23 02.961°S, 29 28.680 °E	60	79.3	75.1	0.968
Forest	68	8578	12S2	23 02.661 °S, 29 27.869 °E	56	74.9	72.9	0.958
			12S	23 02.417 °S, 29 27.033 °E	52	58.1	57	0.955
Sedgeland/herbland	85	15948	14S	23 02.071 °S, 29 25.863 °E	63	79.1	80	0.968
			16S	23 01.355 °S, 29 26.033 °E	55	75.9	85.5	0.959
			17N	23 01.445 °S, 29 25.745 °E	41	49.8	48.5	0.963
Woodland	92	40023	14N	23 00.018 °S, 29 25.545 °E	63	84.4	84	0.969
			12N	22 59.504 °S, 29 25.421°E	64	71	67.7	0.98
			10N	22 58.157 °S, 29 24.979 °E	57	70	68.1	0.972
			8N	22 56.683 °S, 29 26.359 °E	57	68	64.3	0.982

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In total, 104 species were collected along the northern slope and 117 species on the southern slope. Twenty-eight species were restricted to the southern slope and nineteen species to the northern slope. Ten species, *Camponotus* UOVC_18 (*maculatus* gp.), *Lepisiota* UOVC_01 (*capensis* gp.), *Monomorium albopilosum* Emery, *Monomorium* UOVC_07, *Monomorium*_08 (*monomorium* gp.), *Pheidole* UOVC_01 (*megacephala* gp.), *Tetramorium cf. setigerum* Mayr, *Tetramorium* UOVC_01 (*squaminode* gp.), *Tetramorium* UOVC_08 (*simillimum* gp.) and *Technomyrmex pallipes* Smith, occurred at all the sites (Appendix 2).

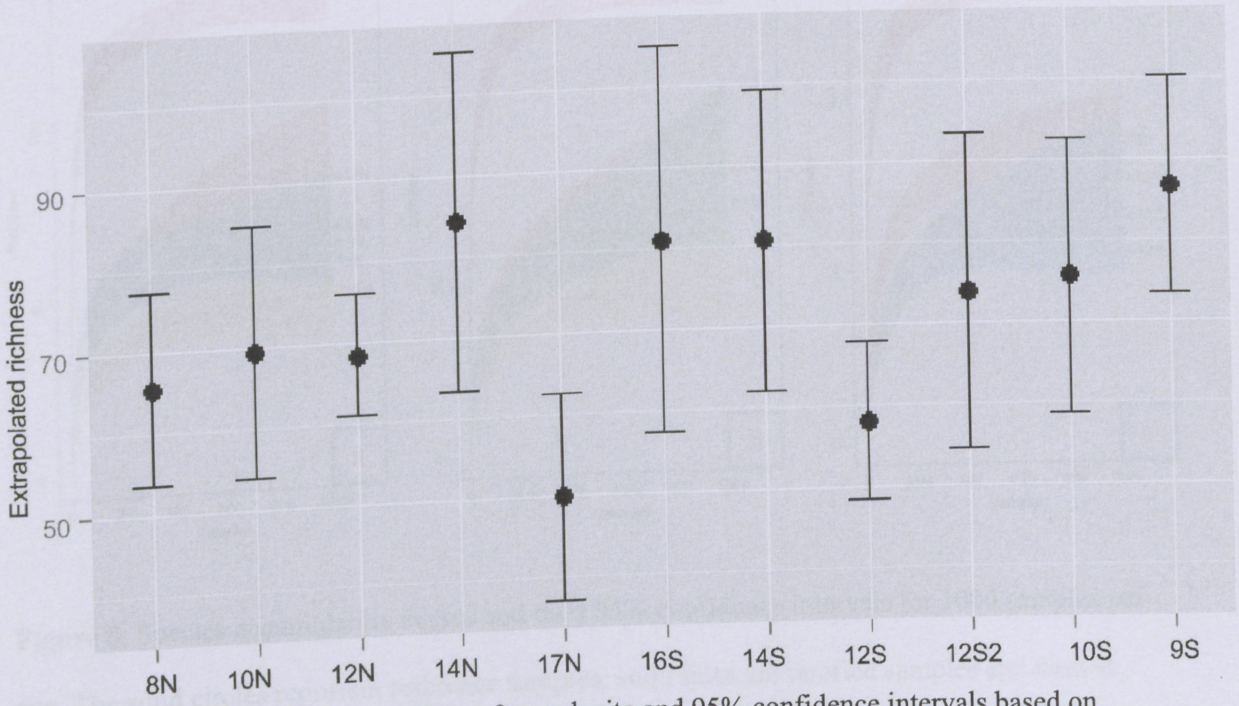

Figure 4: Extrapolated species richness for each site and 95% confidence intervals based on unconditional variance, from 1000 pitfall samples for each of the 11 sites across the Soutpansberg Mountain Range.

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A total of 20 Ponerine species were sampled from both the southern and the northern aspects. Fifty per cent of all Ponerine species, namely *Anochectus* UOVC_01, *Bothroponera ?strigulosa* Emery, *Bothroponera* UOVC_02, *Bothroponera* UOVC_03, *Hypoponera* UOVC_01, *Leptogenys intermedia* Emery, *Leptogenys schwabi* Forel, *Ophthalmopone* UOVC_01, *Plectroctena* UOVC_02 and *Pseudoponera* UOVC_01, were restricted to the southern slope of the mountain. The other 10 species occurred on both slopes of the mountain.

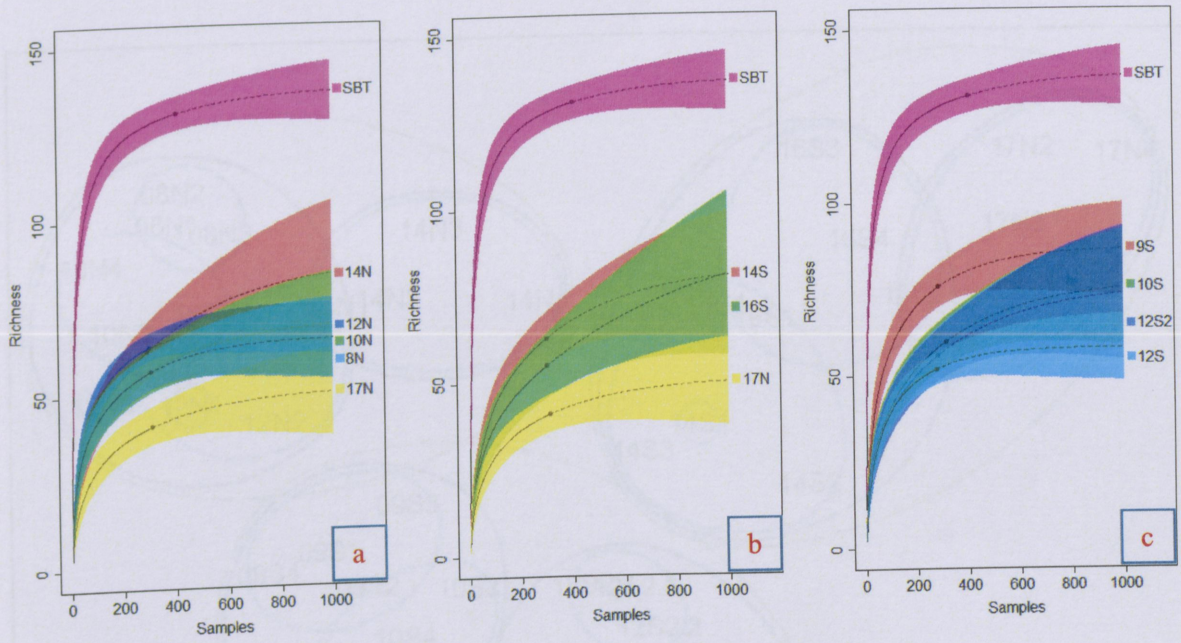

Figure 5: Species accumulation curves and their 95% confidence intervals for 1000 samples per site. The solid circles represent reference samples; solid lines are rarefied samples and dashed lines are extrapolations based on Mau Tau estimation. (a) Northern aspect, (b) higher elevational sites and (c) low to mid-elevation southern aspect. SBT, accumulation curve for the whole transect.

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The non-metric multidimensional scaling plot identified three major groupings: the high elevation sedgeland-herbland sites (14S – summit); woodlands (08N – 14N); and shrubland, thicket and forest sites (09S – 12S) (Figure 6). At Bray–Curtis similarity measures of 50, each of the 3 groups divides into 2 (Figure 6). The groupings reveal distinct assemblages associated with the summit (17N) at higher elevations, while 14N was distinct from all the lower elevation sites on the northern aspect. Low elevation (shrubland and thicket sites 09S – 10S) and mid-elevation (forest sites 12S2 – 12S) of the southern aspect formed a distinct grouping.

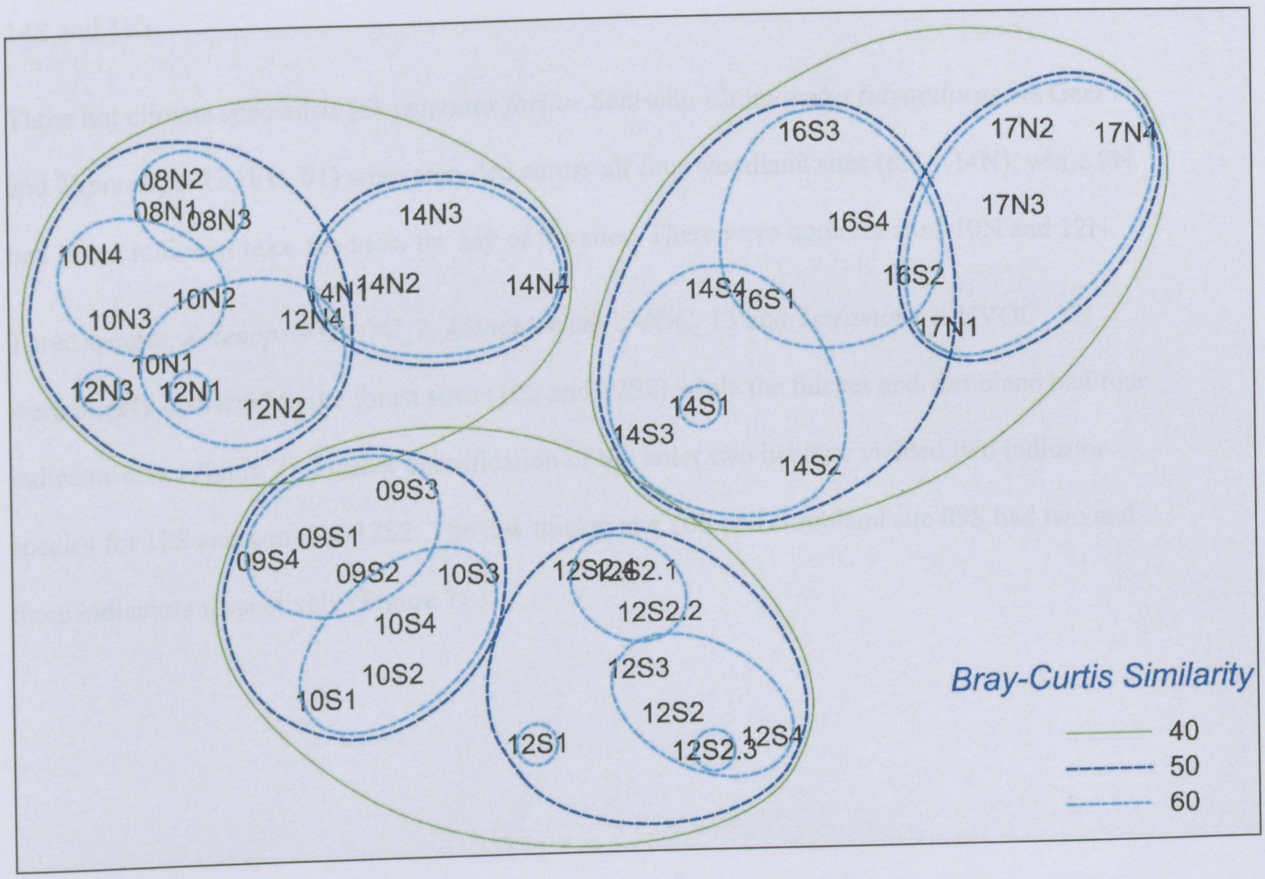

Figure 6: Non-metric multidimensional scaling of ant assemblages for samples pooled within each of the 44 replicates across 11 sampling sites in the Soutpansberg Mountain Range.

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Figure 7 summarizes the indicator species associated with each of the a *posteriori* defined groups for which there was significant support in SIMPROF. Among the 133 species analysed, 56 species had significant IndVal's above 70 (Figure 7). Nine species were indicators of the transect as a whole, i.e. they were consistently found in all the sites. Four species were consistently associated with the sedgeland at higher elevations whereas three were restricted to the lower elevations on both sides of the mountain (Figure 7). The summit (17N) and 16S had a distinct array of indicator taxa, whereas one species (*Pheidole* UOVC_05) was an indicator species at 14S and 16S.

Three hot climate specialists (*Ocymyrmex fortior* Santschi, *Camponotus fulvopilosus* De Geer and *Tapinolepis* UOVC_01) were recorded across all four woodland sites (8N – 14N), while 8N had seven indicator taxa, the most for any of the sites. There were none for sites 10N and 12N.

Three species, *Solenopsis* UVOC_2, *Monomorium* UVOC_13 and *Tetramorium* UVOC_12) were largely restricted to the forest sites (12S and 12S2) while the thicket and shrubland had four indicator taxa (Figure 7). Further classification of the latter two habitats yielded two indicator species for 12S and none for 12S2. The low thicket site 10S and shrubland site 09S had two and three indicators respectively (Figure 7).

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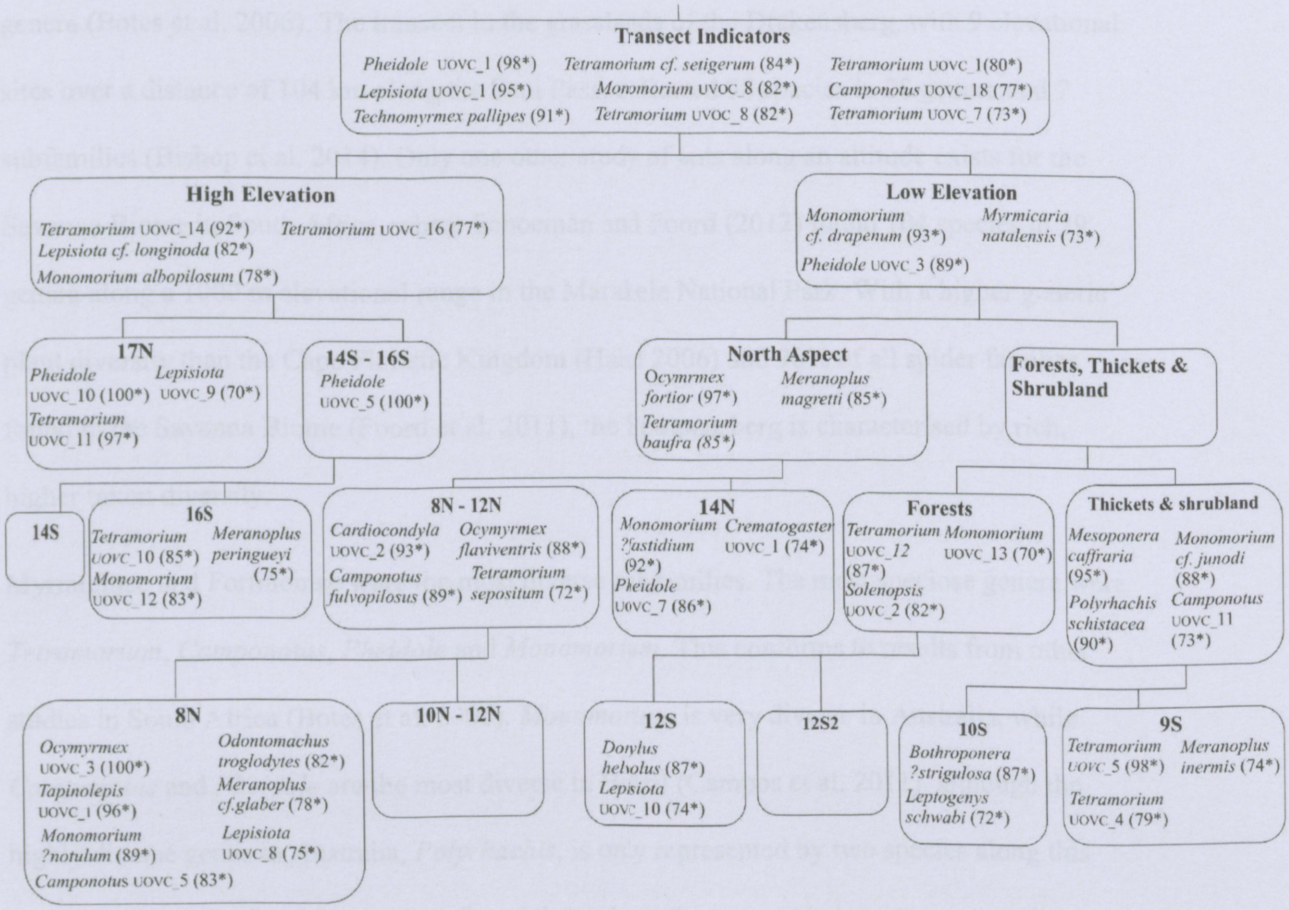

Figure 7: Indicator species identified for the different levels of the hierarchical typology across the Soutpansberg mountain range with their significant indicator values in brackets (*).

Discussion

The species level and higher taxon diversity of this study compares favourably with that of similar studies in the Cederberg and Drakensberg mountains, both of which employ a protocol similar to the one used in this study. The Cederberg transect located in the Cape Floristic Kingdom includes 17 sites over a distance of 160 km. That study recorded 86 species in 24

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genera (Botes et al. 2006). The transect in the grasslands of the Drakensberg, with 9 elevational sites over a distance of 104 km along the Sani Pass, collected 98 species in 28 genera and 7 subfamilies (Bishop et al. 2014). Only one other study of ants along an altitude exists for the Savanna Biome in South Africa, where Schoeman and Foord (2012) found 104 species in 29 genera along a 1000 m elevational range in the Marakele National Park. With a higher generic plant diversity than the Cape Floristic Kingdom (Hahn 2006) and 90% of all spider families found in the Savanna Biome (Foord et al. 2011), the Soutpansberg is characterised by rich, higher taxon diversity.

Myrmicinae and Formicinae were the most diverse subfamilies. The most speciose genera were *Tetramorium*, *Camponotus*, *Pheidole* and *Monomorium*. This conforms to results from other studies in South Africa (Botes et al. 2006). *Monomorium* is very diverse in Australia, while *Camponotus* and *Pheidole* are the most diverse in Brazil (Campos et al. 2011), although the highly diverse genus in Australia, *Polyrhachis*, is only represented by two species along this transect. Except for *Lepisiota*, genera found throughout the transect belong to cosmopolitan genera (*Camponotus*, *Monomorium*, *Pheidole* and *Tetramorium*). This includes a tramp species in the subfamily Dolichoderinae, *Technomyrmex pallipes* Smith, which is widely distributed throughout Afrotropical and Malagasy region (Antweb 2014a).

All indicator species associated with the northern aspect were hot climate specialists, e.g. three *Ocymyrmex* taxa and *Camponotus fulvopilosus* De Geer, known to be thermophilic and characteristic of arid or well drained soils of the Afrotropical Region (Bolton & Marsh 1989; Robertson & Zachariades 1997). *Camponotus fulvopilosus* De Geer nesting habit of constructing nests in the soil under large rocks and fallen logs have been reported in Robertson and Zachariades (1997). *Dorylus helvolus* Linnaeus, preferred the forests. This species is also known

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from forest and grassland habitats of Western Cape and Kwazulu Natal in South Africa (Antweb 2014b).

This study provides a thorough inventory of ground-dwelling ants, with a sample coverage of 0.98. The sample coverage represents the proportion of the total number of individuals in the ant assemblage along the transect that belongs to the species represented in our sample (Chao and Jost 2012).

Most of the species accumulation curves of predicted richness based on 1000 pitfall samples reached an asymptote. There were two exceptions: a woodland site 14N and sedgeland site 16S, both of which also had the lowest coverage. Although 14N is in the woodland vegetation type, it is near the ecotone between sedgeland and woodland. The large turnover of taxa at this site could be the result of mass effects from taxa found in sedgeland. The steep slope of the 16S accumulation curve might suggest a temporal change in the ant assemblages of this site.

Based on photographic records at each of the pitfalls, the *Coleochloa* species that dominate 16S site are being invaded by short woody shrubs. Turnover at this site might be linked to this encroachment and could probably lead to increased abundance of taxa associated with sites that are structurally more complex, such as forest sites 12S and 12S2 and shrubland site 9S. This has particularly important implications for the management of the few remaining grassland habitats in the Soutpansberg.

The high diversity of Ponerinae species at the base of southern aspect might be due to more productive ecosystems associated with the basalt intrusions, and higher rainfall. Disturbance also seems to positively impact Ponerine richness, which peaks in shrubland site 9S. This site is inside a wildlife sanctuary that is stocked with buffalo where the bush is mechanically cleared.

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The three major groupings of ant assemblages across the study area conform to the broad structural classification of the vegetation used in this study (Edwards 1983).

Ant taxa identified as indicators of different habitat types could be used in monitoring of the rate of bush encroachment and the associated impacts. A single site on the lowest elevation of the southern aspect (09S) yielded 57% of the total ant species. This site experiences higher levels of disturbance through herbivory and bush clearing and this could provides support for the important role of disturbance as a driver of ant diversity and its effect in the savanna biome.

The structural classification of vegetation in this study is a good predictor of broad-scale ant assemblage structure. Finer scale distinctions were linked to elevation, structural elements and temperature.

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Chapter 3: Temporal patterns of ant diversity across a mountain with climatically contrasting aspects in the tropics of Africa

Abstract

Factors that drive species richness over space and time are still poorly understood and are often context specific. Identifying these drivers for ant diversity has become particularly relevant within the context of contemporary global change events. We report on a long-term biannual (wet and dry seasons), standardized sampling of epigeal ants over a five year period on the mesic and arid aspects of an inselberg (Soutpansberg Mountain Range) in the tropics of Africa. We detail seasonal, annual and long-term trends of species richness, test the relative contribution of geometric constraints, energy, available area, climate, local environmental variables, time, and space in explaining ant species richness patterns through Generalized Linear Mixed Models (GLMM) where replicates were included as random factors to account for temporal pseudo-replication. Seasonal patterns were very variable and we found evidence of decreased seasonal variation in species richness with increased elevation. The extent and significance of a decrease in species richness with increased elevation varied with season. Annual patterns point to an increase in ant diversity over time. Ant density patterns were positively correlated with mean monthly temperature but geometric constraints dominated model performance while soil characteristics were minor correlates. These correlates accounted for all the spatio-temporal variability in the database. Ant diversity was therefore mainly determined by geometric constraints and temperature while soil characteristics (clay and carbon content) accounted for smaller but significant amounts of variation. This study documents the role of season, elevation and their interaction in affecting ant species richness while highlighting the importance of neutral processes and temperature in driving these patterns.

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Introduction

Understanding the overall importance of processes and correlates that determine diversity patterns has been an on-going challenge to biologists (Laliberte´ et al. 2009) as they act at different scales and require consideration of the taxa involved (Bestelmeyer et al. 2003). More than 30 hypotheses have been developed and tested that explain patterns of species richness along environmental and geographic gradients (Rohde 1992). As a first approximation these hypotheses have been grouped into three categories, viz. null models, historical and ecological hypotheses (Pimm and Brown 2004, McCain 2007a). Recent studies have focused on a smaller number of these hypotheses (Willig et al. 2003). Among these, the mid-domain effect (Colwell and Lees 2000), available area (Rosenzweig 1995, Kattan and Franco 2004), species-energy theory (Strivastava and Lawton 1998), soil properties (Botes et al. 2006) and habitat structure have been tested for many taxa (mammals (Lyons and Willig 2002, McCain 2007b), birds (Rahbek 1997), plants (Cowling and Samways 1995, Ellison 2002), and insects (Lobo 2000, Botes et al. 2006).

The importance of understanding the impact of global change on biodiversity has brought renewed focus on mountains as living laboratories (Cerda et al. 1997). Their role in the study of richness patterns is, *inter alia*, to provide a predictive framework for the response of diversity to climate change (Colwell and Rangel 2010). An understanding of drivers of diversity along these gradients also identifies useful environmental filters for conservation initiatives (Crous et al. 2014). Macro-ecological studies of species richness in mountains have documented the role of the mid-domain effect (Sanders 2002), temperature (Sanders et al. 2007, Bishop et al. 2014), energy, and available area (Sanders et al. 2003). However, only a handful of studies have

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investigated temporal dynamics of diversity and very few have done so for more than a year (but see Bishop et al. 2014).

The potential of mountains as replicated tests of the generality of these drivers (Cerdar et al. 1997) prompted the initiation of standardized long-term monitoring sites across three mountains in the major biomes of South Africa. These are the Cederberg Mountains in the Cape Floristic Kindom (Botes et al. 2006), the Drakensberg Mountains in the grassland biome (Bishop et al. 2014) and the Soutpansberg Mountain Range in the savannah biome (Munyai and Foord 2012). The Soutpansberg mountain is an inselberg in the north-eastern corner of South Africa. It lies north of the tropic of Capricorn and its eroded surface, varied topography, climate and erosion resistant quarzitic rock on diabase intrusions, dated at two billion years, have acted as a refuge and evolutionary hub for several endemic species (Hahn 2002, Berger et al. 2003, Hahn 2006, Jocqué 2008, Kirchhof et al. 2010). The climate of the mountain is strongly influenced by its East North East to West South West orientation (Hahn 2006) resulting in an arid northern aspect characterized by open dry savannah and a mesic southern aspect with thicket, sedgeland/herbland, forest, and thicket/bushland habitats.

The role of ants in ecosystem dynamics has become increasingly important as the Anthropocene progresses (Leal et al. 2014) and developing an understanding of the factors that affect their diversity are both timely and relevant. Ant richness studies on mountains have reported a mid-elevation peak (Samson et al. 1997, Sanders 2002, Sanders et al. 2003, Sabu et al. 2008, Chaladze 2012, Bishop et al. 2014), monotonic decrease with increased elevations (Olson 1994, Robertson 2002, Sanders et al. 2003) or no clear pattern at all (Botes et al. 2006). Most of the studies that measured and identified drivers and correlates of these patterns found temperature to be a significant factor while precipitation had a limited effect. Drivers such as available area

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played a minor role in two of the studies (Sanders et al. 2007) whereas geometric constraints (mid-domain effect) was only relevant in one study (Sanders 2002). These studies were done over short (< 1 year) temporal scales and assume that spatial patterns are constant in time (de Juan and Hewitt 2014). Recent work has however focused on temporal variability over seasons (Beck et al. 2010) and among years (Bishop et al. 2014). Long-term sampling designs have observed new phenomena along elevations and allows for the investigation of hypotheses that cannot be tested with spatial designs only (Bishop et al. 2014).

In a study of ants across the Soutpansberg, Munyai and Foord (2012) identified a peak at mid-elevation on the arid northern aspect and a more complex pattern on the southern mesic aspect but did not consider temporal dynamics of diversity. This study aims to test whether there is any seasonal, annual and long-term trends of richness over a five year period (2009-2014) along this transect representing one of the longest time series of standardized sampling available for ants in the world and certainly the only one that falls within tropical regions of Africa. We test for a decrease in the seasonal variation in species richness with increased altitude, as documented in a sister project (Bishop et al. 2014) and we contrast the importance of correlates (soil, energy, habitat structure, temperature, area, and mid-domain effect) in explaining variation in ant richness with that explained by spatial and temporal predictors.

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Materials and methods

Study area

This study was carried out along a transect that extends over the highest point of the Soutpansberg Mountain Range (1748 m. a.s.l.). The significance of this region has recently been affirmed by its inclusion into the UNESCO Man and Biosphere Program (MaB). The Soutpansberg is the main geographic feature within the Vhembe Biosphere Reserve (VBR), and includes several core conservation areas critical to biodiversity conservation. The transect was set out at 200 m elevation intervals on both sides (arid north and mesic south) of the mountain, with an altitudinal range of 900 m in the north (800–1700 m. a.s.l.), and 800 m (900–1700 m) in the south. The gradient includes 11 elevational zones and is *ca.* 16 km in length. It stretches over a variety of habitats, viz. thicket/shrubland (900 m. a.s.l. (9S); 1000 m. a.s.l. (10S)), forests 1200 m. a.s.l. (12S, tall forest); 1200 m. a.s.l. (12S2, short forest)), sedgeland/herbland (1700 m. a.s.l. (17N/summit); 1600 m. a.s.l. (16S); 1400 m. a.s.l. (14S)) in the south, open woodland (800 m. a.s.l. (08N); 1000 m. a.s.l. (10N); 1200 m. a.s.l. (12N); 1400 m. a.s.l. (14N)) in the north see (Munyai and Foord 2012) and (Foord et al. 2015) for further details.

Ant sampling

Sampling units consisted of 10 pitfall traps, each 62 mm in diameter, laid out in a grid (2 x 5) with 10 m spacing between traps. Sampling units within sites were replicated four times for each of the 11 elevational sites (44 sampling units in total). Replicates (sampling units) within an elevational zone were > 300 m apart to avoid pseudo-replication (Munyai and Foord 2012). Pitfall traps were left open for five days each during September 2009, 2010, 2011, 2012 and 2013 (dry season), and January 2010, 2011, 2012, 2013 and 2014 (wet season) and contained

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50% solution of propylene glycol that neither attracts nor repels ants (Abensperg-Traun and Steven 1995; Adis 1979). The ant samples were washed in the laboratory and stored in 70% ethanol. They were sorted to morpho-species and where possible identified to species level.

Correlates

Soil. Soil samples were collected in January 2010 using a soil auger. A total of ten soil subsamples in each of the 4 replicates of a site were pooled. Soils were dried and then analysed for composition: pH, conductivity, stone volume, K, Na, Ca, and Mg, C, NO3-N, H+, C, T-value, pBrayll, and the percentage clay, silt and sand by BemLab (Pty) Ltd laboratories, Somerset West, South Africa (Appendix 4). All 16 variables were standardized and principle component analysis performed to deal with co-linearity. The first four components explained 83% of the variation. Principal component axes one (Soil-PC1) and two (Soil-PC2) both represents a gradient from sandy to clayish soil, Soil-PC3 is associated with increased carbon content of the soil, and Soil-PC4 is linked to increased phosphate and sodium (Appendix 5). Soil characteristics were sampled during only one sampling period and were therefore assumed to remain stable over the period of the study. Although this might not be true for many of the variables, the relative percentage of sand and clay that represents most of the variation between sites (Soil-PC1 and Soil-PC2) can be expected to remain relatively stable over a five year period.

Energy. Energy which is retained in the biomass produced by plants is available to consumers in the form of chemical energy (Clarke and Gaston 2006). Plant productivity is considered an appropriate measure of available energy (Braschler et al. 2012). Normalised difference vegetation index (NDVI) was derived for all sites during the sampling month i.e. from September 2009 to January 2014 (Appendix 6). NDVI values were derived from MODIS (Moderate Resolution Imaging Spectroradiometer)

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/TerraVegetationIndicesMonthlyL3Global0.05DegCMGV005https://lpdaac.usgs.gov/lpdaac/products/modis_product_table/vegetation_indices/monthly_l3_global_0_05deg_cmg/v5/terra (Braschler et al. 2012).

Habitat structure. Fine scale vertical and horizontal habitat structure were quantified during each of the 10 surveys (Munyai and Foord 2012). The horizontal distribution of vegetation was determined by visually estimating percentage area covered by vegetation, leaf litter, exposed rock and bare ground on a 1 m^2 grid which was placed over each pitfall trap. For the vertical distribution of vegetation, the number of hits on a 1.5 m rod (i.e. the number of contacts with vegetation) was recorded at 25 cm intervals at four points located at 90° angles from a 1.5-m radius centred on each pitfall trap. An assessment of whether the rod would touch any vegetation anywhere above the rod (1.5 m) was also made. This provides a measure of canopy cover. Principle component analysis was performed on the horizontal and vertical measures respectively to account for co-linearity. For vertical habitat structure, each of the seven intervals along the rod was used as input variables. The PCA therefore not only accounts for the number of hits but also represents the location of the hits. The first two principal components accounted for 78% of the variation. Principal component axis one (Vert-PC1) represents a gradient from sites with dense canopy cover and very little ground cover to sites with low ground cover and the absence of canopy cover while Vert-PC2 is negatively related to increased complexity in vegetation structure (Appendix 7).

The first two principle components of horizontal habitat structure explained 81% of the total variation. Axis one (Hor-PC1) summarizes a gradient from sites dominated by bare ground and leaf litter to sites covered with vegetation, whereas axis two (Hor-PC2) contrast sites with rock cover with those dominated by leaf litter (Appendix 8).

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Temperature. Two Thermocron iButtons (Semiconductor Corporation, Dallas /Maxin, TX and USA) record soil temperature at 1 hour intervals at each site over the period of the study. The iButtons were buried 1 cm below the soil surface at locations that had direct exposure to sunlight except where canopy cover was > 70%. Temperature sequences from January 2009 to January 2014 were plotted and inspected for iButtons that malfunctioned or became exposed (Appendix 9). The monthly mean, minimum, maximum temperature and variation in temperature (SD) at each site during the month of sampling were calculated (Appendix 10 and Appendix 11). Temperature data for the two iButtons were averaged for each elevational site.

Area. The area covered by each elevation zone (200 m contour sampling zone) was calculated by creating a Minimum Convex Polygon of all replicate points with a 40 km buffer which encompasses the area under study, see Munyai and Foord (2012) for further details.

Mid-domain effect. The eroded peneplain surrounding the Soutpansberg inselberg represents a hard boundary at lower elevations and the predictions of a null model was generated in RangeModel 5 (Colwell 2006) with similar protocols employed by Dunn et al. (2006). The boundaries were defined by the base of the mountain and the summit, i.e. model predictions included both the southern and northern aspects respectively. A species' range was measured as the number of bins (bin = 200 m elevation intervals) between the highest and the lowest elevation site at which a species occurs. Occupancy was measured as the total number of bins at which a species occurs (Dunn et al. 2006). This was done for each of the aspects respectively.

Spatio-temporal variables

Season (dry and wet) were included as categorical variables, year as numerical, aspect as a categorical variable, while spatial structures in the data were identified and modelled using

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principal coordinates of neighbor matrices (PCNM) by computing principle coordinates analysis (PCoA) of a truncated euclidean distance matrix that only have the distances between replicates that are close neighbours (Borcard and Legendre 2002) (Appendix 12) with the 'stats' package in R (R Development Core Team 2013). This is an eigenvector-based approach that allows for the modelling of spatial structures as predictor variables of variation in species richness from broad to fine scales (Paknia and Pfeiffer 2014). This is done by constructing spatial variables of all structures at relevant scales. The largest truncation distance determines the smallest scale perceived and large distances means the loss of smaller spatial scales. Four additional points (Appendix 13) were therefore added to this design to reduce the threshold value, the PCNM values were calculated and the additional points removed from the PCNM matrix (Borcard and Legendre 2002). Thirty one eigenvectors (spatial variables) with significant positive spatial correlations were extracted and included as spatial variables for further analysis in the final model. This approach has several benefits as the size of eigenvalues is related to the scale it represents, spatial variables are orthogonal, represents a wide range of spatial scales and can model any type of spatial structure (Borcard and Legendre 2002).

Statistical analysis

Sample coverage works on the principle that samples of equal completeness and not equal size should be compared between communities. Here, sample completeness, was estimated with coverage-based rarefaction and prediction (Chao and Jost 2012).

Variation in species richness was analysed at three levels. We first modelled species richness in response to correlates (soil, habitat structure, temperature, energy and mid-domain). The second analysis modelled the ability of spatial (elevation and the eigenvectors of the principal components of neighbour matrices (PCNM's) and temporal (season and year) to explain patterns

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in species richness. This analysis also allowed us to determine if there are any intra-annual (season) and inter-annual (longer-term) trends in ant species richness. These spatio-temporal predictors were then used to analyse the residuals of the first (environmental) model. This provides a measure of the variation in species richness that is explained by pure spatial and temporal predictors (Bishop et al. 2014).

Analysis was done with Generalized Linear Mixed Models (GLMM) using a loglink function and poisson error distribution. Replicates were included as random factors in the model to account for temporal pseudoreplication while all predictor variables were included as fixed variables. Observed species richness were weighted using sample coverage (Del Toro 2013). An information theoretic approach was used to assess models with different combinations of the explanatory variables. Bias corrected Akaike's information criterion (AICc) values were used to compare models. Marginal R^2 (R^2m, due to fixed effects only) and conditional R^2 (R^2c, due to fixed and random effects) were calculated for the best model to determine how much of the variation is explained by fixed and random effects respectively (Nakagawa and Schielzeth 2013).

The effect of elevation on seasonal variation was quantified by treating each replicate as a time series with ten data points from which the seasonal variation in species richness was extracted with classical decomposition of moving averages (Fleishman et al. 1998) Values were then regressed against elevation where a negative relationship indicates a decreased seasonal variation in species richness at higher elevations. Species pool effects were corrected for by expressing species richness as a proportion of the total number of species observed at the replicate over the period of the study and also as a proportion of the total number of species observed at a site over the period of the study (see Bishop et al. 2014).

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Results

A total of 86502 ants comprised of 130 species in 38 genera and six subfamilies were collected. Sample coverage for the whole survey varied from 0.98–0.99 for a site while the mean coverage was 0.82 ± 0.005 (SE) for replicates during a sampling occasion. Species richness observed in a replicate averaged at 15 species with the highest richness observed in the open woodlands followed by the thicket/bushland of the lower southern elevations and sedgeland/herblands of the higher elevations, while forest sites had the lowest observed species richness (Figure 8a). Scatterplots suggest that there is positive relationship between the average temperature during the month of the survey and the number of species observed (Figure 9A—D). This pattern is the most evident for the thicket/shrubland and sedgeland/herbland habitats (Figure 9c and d).

Correlates

The best model of species richness retained average monthly temperature during the month of the survey, mid-domain effect, Soil-PC2, Soil-PC 3 and Soil-PC 4 as correlates (Table 3). The mid-domain effect's estimate was highly significant ($p < 0.001$) and positive (Table 3). Average monthly temperature stood central to model performance and also performed the best when included as the only predictor in the model (Table 2). Average monthly temperature during the month of the survey also resembled the general form of ant richness patterns across the mountain (Appendix 9). The best model had a marginal R^2 of 0.33 while temperature alone explained 22% of the variation. Temperature's estimate was positive (0.1 ± 0.02) suggesting that species richness increases with increasing temperature. The model describes a pattern that is consistently higher along the lower elevations of the southern aspect, lower in the forests and summit and hump-shaped or unchanged on the northern aspect (Figure 10). Sites of the open woodlands on the northern aspect generally had the highest observed and predicted species richness.

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Table 2: Model AIC values, marginal and conditional R^2 for generalized linear mixed models of all correlates, spatio-temporal and the residuals of the best driver model.

Correlates					
		ΔAIC (next best)	Worst model	R^2_m	R^2_c
Best Model	1450 (Average Temperature + Mid-domain + Soil-PC2 + Soil-PC3 + Soil-PC4)	1452	1463.7	0.33	0.38
Average Temperature	1497.073			0.22	0.32
Mid-domain	1484.767			0.16	0.37
Soil-PC2	1540.136			0.06	0.27
Soil-PC3	1544.527			0.03	0.27
Soil-PC4	1547.546			0.005	0.27
Spatio-temporal					
		ΔAIC (next best)	Worst model	R^2_m	R^2_c
Best model	1489.437 (Elevation:Season+Year + Season + PCNM2 + PCNM3 + PCNM11 + PCNM13 + PCNM14 + PCNM17 + PCNM25)	1490		0.32	0.32
Year	1532.8			0.06	0.3
Season	1529.6			0.05	0.3
PCNM2	1537			0.08	0.26
Residuals of correlates model				0.04	0.52

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Spatio-temporal covariates

Species richness was higher during the wet seasons (Table 3) but there was an exception to this rule in the 2013/2014 sampling season when some sites on the southern aspect recorded higher species richness during the dry season than during the wet season (Figure 10).The interaction of elevation with season was negative and significant. This points to a more pronounced decrease in species richness with elevation. There has also been a significant annual increase in species richness over the period of the study (Table 3). Seven of the 31 spatial eigenvectors (PCNM's) were retained in the best model and their spatial structure is shown in Appendix 14. These seven variables represent spatial structuring of ant species richness patterns from the largest to the smallest spatial scale.

Analysis of model residuals

Spatio-temporal variables explained a small amount of variation in the residuals of the best driver model, $R^2m = 0.04$, which suggests that there was no spatio-temporal pattern in the residuals of the best driver model and that all the variation is explained by temperature and middomain effect.

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Table 3: Estimates of significant terms in spatio-temporal and driver-correlate models of species richness observed over the period of the study. ., < 0.01; *, < 0.05, **, < 0.01, ***, < 0.001

Spatio-temporal	
Term	**Estimates**
Year	0.04 ± 0.015*
Dry Season ↔ Wet Season	0.4 ± 0.04 *
Elevation : Wet Season	$-0.0004 \pm 0.9 \times 10^{-4}$ *
Elevation : Dry Season	$-0.0001 \pm 0.9 \times 10^{-4}$
PCNM2	$0.0001 \pm 0.1 \times 10^{-4}$ ***
PCNM3	$-0.00004 \pm 0.1 \times 10^{-4}$ *
PCNM11	$-0.00007 \pm 0.3 \times 10^{-4}$ *
PCNM13	$0.0001 \pm 0.4 \times 10^{-4}$ **
PCNM14	$-0.00007 \pm 0.3 \times 10^{-4}$ **
PCNM17	$0.00009 \pm 0.4 \times 10^{-4}$ *
PCNM25	$0.0006 \pm 0.3 \times 10^{-4}$.
Correlates	
Mid-domain	0.12 ± 0.02 ***
Monthly Average Temperature	0.1 ± 0.02 ***
Soil-PC2	0.48 ± 0.14 ***
Soil-PC3	-0.26 ± 0.15 .
Soil-PC4	0.26 ± 0.14 .

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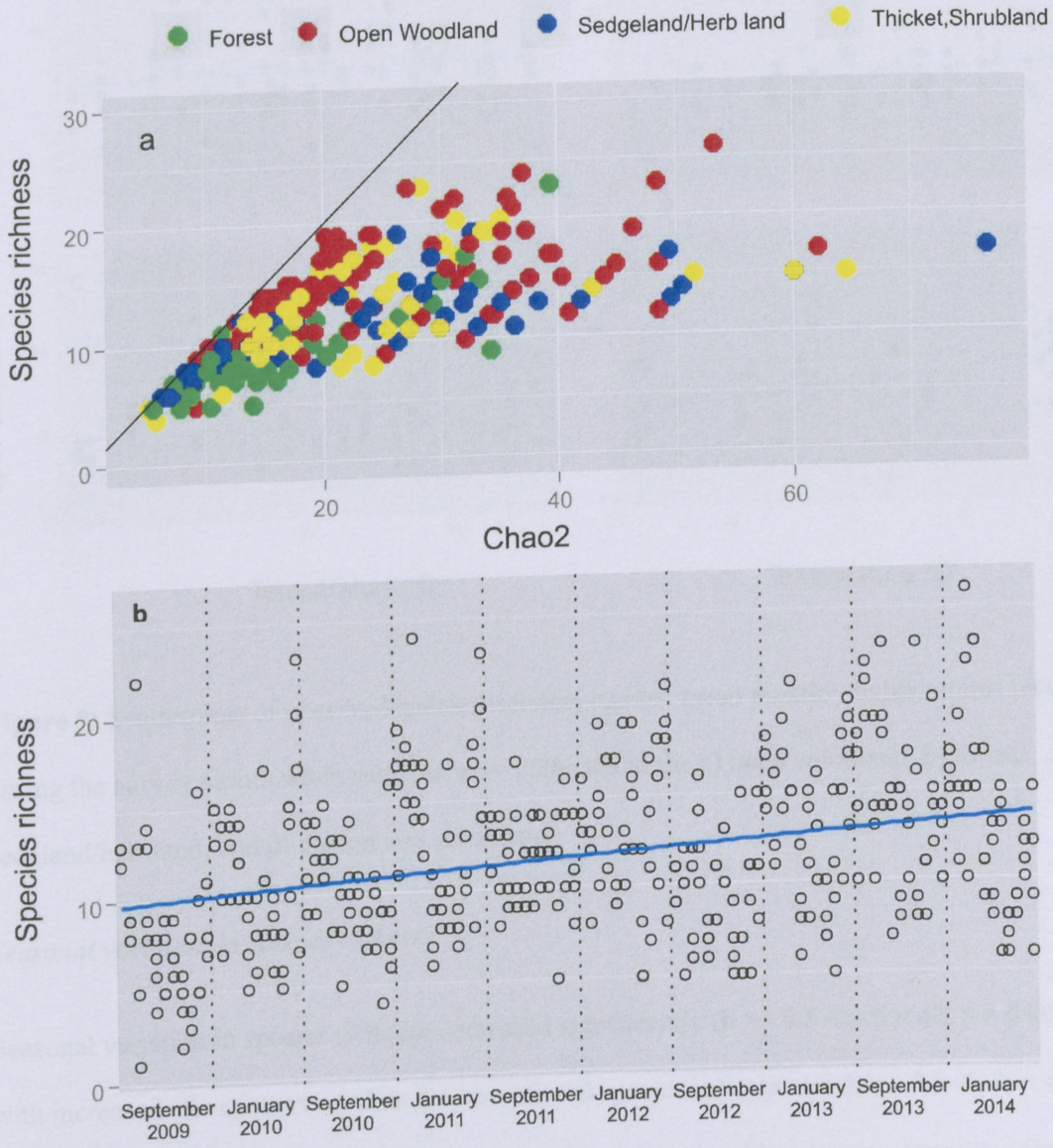

Figure 8: a) Scatterplots of observed species richness and Chao 2 estimates of species richness at replicates in the four habitat types along the transect and b) a scatterplots of species richness collected at the 11 sites as a function of the chronological order of surveys.

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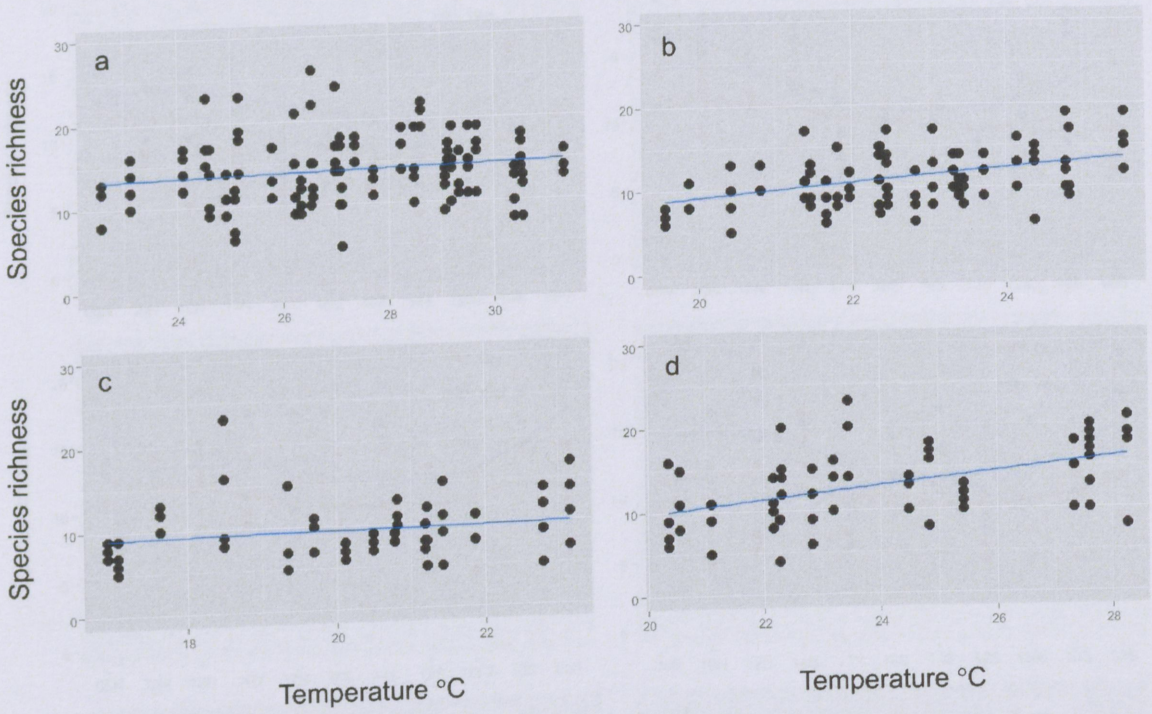

Figure 9: Scatterplots of observed species richness against mean monthly temperatures recorded during the survey month when samples were collected in the a) open woodland, b) forests, c) sedgland/herbland, and d) thicket and shrubland.

Seasonal variation in species richness

Seasonal variation in species richness decreased significantly (b = −0.5–2, df = 42, p = 0.002) with increased elevation even when the size of total species in replicates (b = −0.9–4, df = 42, p = 0.001) and sites (b = −0. 9–4, df = 42, p = 0.003) or elevational bands were accounted for (Figure 11).

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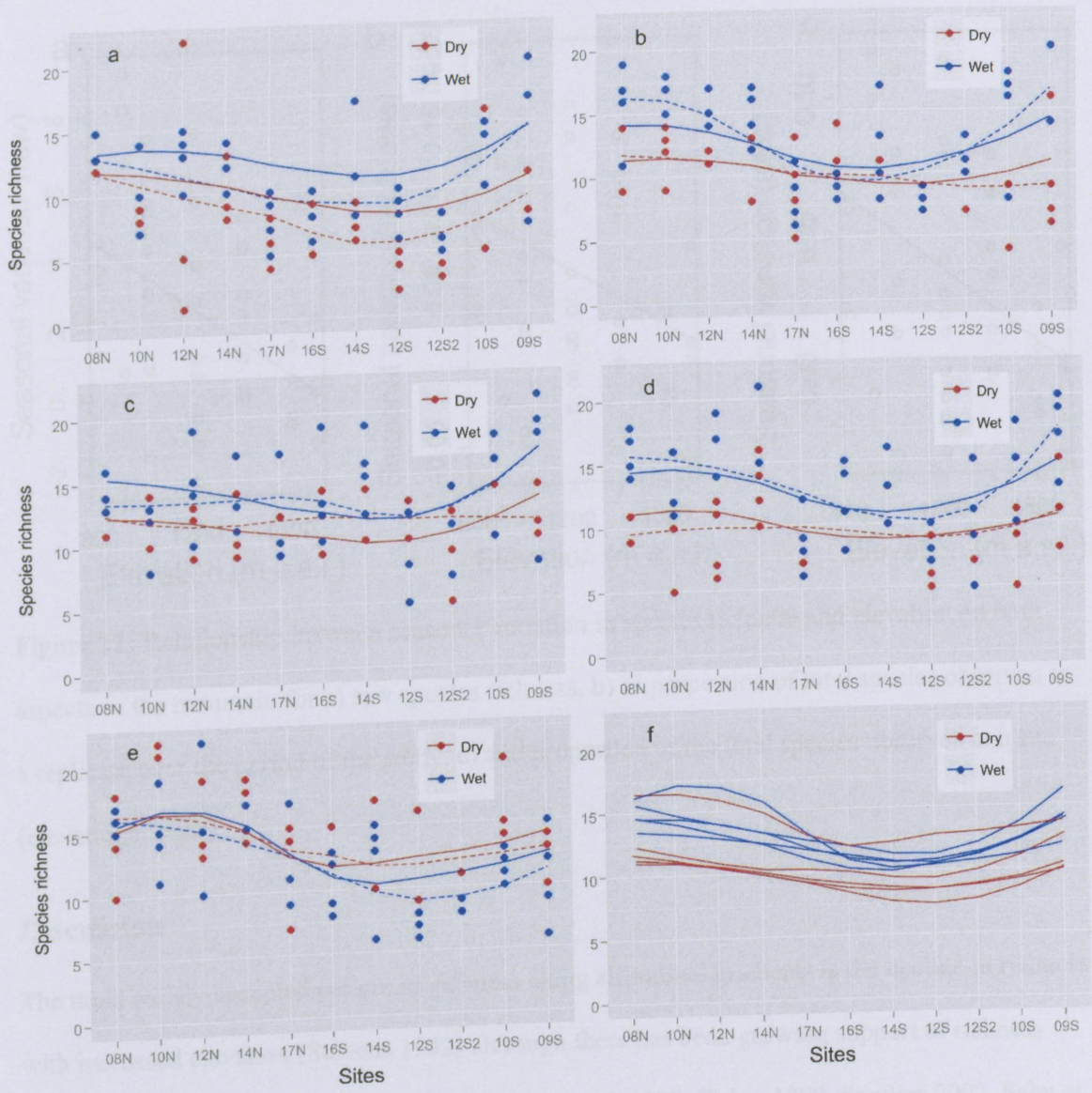

Figure 10: Species richness for different sampling events (10 surveys) across the elevational sites in the Soutpansberg mountain range (2009–2014) predicted from the model, red lines (dry season) September survey and black lines (wet season) January surveys and also for all years (ten in total) combined (f). Also a plot for species richness against all 10 surveys (a – e) for all elevational sites from northern aspect to southern slope overtime (September 2009—January 2014), similarly top lines, red line = dry season and black lines = wet season.

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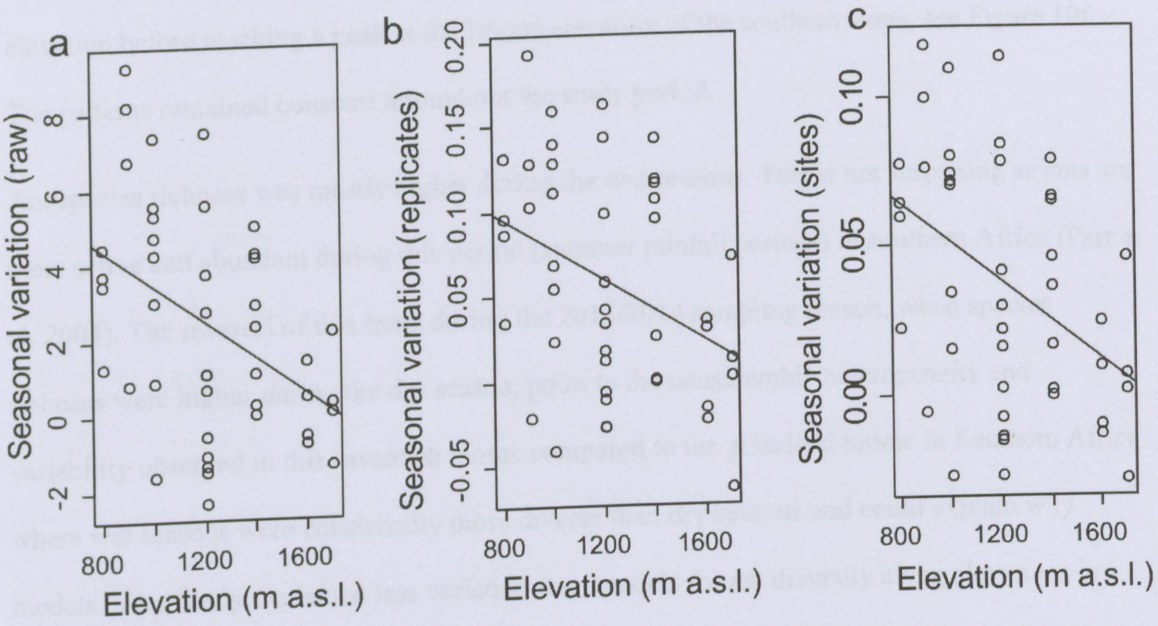

Figure 11: Relationship between seasonal variation in species richness and elevation on both aspects of the mountain for a) raw species richness, b) as proportion of total species observed in a replicate over the period of the study, c) and proportion of the total species observed at a site (elevational band).

Discussion

The most widely accepted pattern of richness along altitudinal gradients is the decline in richness with increased elevation (Stevens 1992) although there has been growing support of richness peaking at mid-elevation (Rahbek 1995, Samson et al. 1997, Fisher 1998, Sanders 2002, Sabu et al. 2008, Chaladze 2012, Bishop et al. 2014). Richness patterns along the soutpansberg transect are more complex however not suprising as McCain and Grytnes (2010) mainted that across various elevation four main patterns are usually reported. Diversity on the northern slope peak at mid-elevation of the mountain and decreasing at higher elevations (Collins 1980, Atkin and Proctor 1988, Olson 1994, Robertson 2002) followed by a small intermediate peak towards mid-

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elevation before reaching a peak at the lowest elevation of the southern slope, see Figure 10f. The patterns remained constant throughout the study period.

Ant species richness was mostly higher during the wet seasons. This is not surprising as ants are most active and abundant during this period (summer rainfall periods) in southern Africa (Parr et al. 2004). The reversal of this trend during the 2013/2014 sampling season, when species richness were higher during the dry season, point to the considerable heterogeneity and variability observed in this savannah biome compared to the grassland biome in Southern Africa where wet seasons were consistently more diverse than dry seasons and could explain why models in our study explained less variation than models for ant diversity along elevations in grassland (Bishop et al. 2014). After controlling for the size of species pools (Figure 10), the seasonal variation in species richness still decreased with elevation, strengthening support for the impact of elevation on seasonal effects (Bishop et al. 2014). Thus an increased richness was not the result of dispersal from the regional species pool but caused by decreased activity levels of ant colonies during cold and resource poor periods (dry season). These conditions have a disproportionately higher impact on lower elevation species. These taxa are often less tolerant of colder temperatures experienced during the dryer seasons. Many of the specialist predator, several of which were restricted to lower elevations e.g. ponerinae ants (Munyai and Foord 2015) were also only active during the wet season when prey availability peaked. Ant species richness showed a significant increase over the period of the study (Figure 8b).

The mid-domain effect played a prominent role in explaining variation in species richness. Evidence for the importance of mid-domain effect has been found in other studies (Dunn et al. 2006) but support also exists for the contrary (Kerr et al. 2006, Sanders et al. 2007). Sanders (2002) in a regional elevational gradient study, reported on the importance of geometric

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constraints in explaining ant richness variation where the mid-domain effect together with available area explained 90%, 99% and 57% in Colorado, Nevada and Utah respectively. In contrast, a study in southern Appalanchians of leaf-litter ants along an altitudinal gradient found no support for geometric constraints models (Sanders et al. 2007). Kaspari et al. (2004) also found no support for these models at a continental scale in North America. While Bishop et al. (2014), although not directly testing for these models, argued that it is unlikely that neutral models are responsible for driving patterns across their study area and pointed to the importance of temperature and area in explaining diversity patterns observed. Our results highlight the importance of geometric constraints and not area in explaining variation in richness.

There was a significant positive association between species richness and percentage clay in the soil (Soil-PC2). Percentage clay negatively affected the dominance levels of dominant ants in the Kruger National Park (Parr 2008) and distribution of *Anoplolepis cf. custodiens* in the Cederberg (Botes et al. 2006). In North Californian grasslands the abundance of the dominant ant *Messor andrei*, was negatively associated with percentage clay levels (Boulton et al. 2005), while there was a positive relationship with the occurrence of more common ant species, *Acropyga fuhrmanni* in Ecuador (Jacquemin et al. 2012). In our study high percentage clay of the soil was associated with high species richness which corresponds with Ramon et al. (2013) observation that clay contributes to high species richness in the Ecuadorian Andean forests. Although Delsinne et al. (2010) found no relationship between soil texture and alpha diversity, their study suggests the indirect effect of soil (Jacquemin et al. 2012) on ant diversity through its impacts on plants e.g. excess salt in the soil negatively affect ant diversity through its effect on plant diversity.

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At a larger and regional scale, Braschler et al. (2012) observed a unimodal relationship between ant richness and NDVI with a peak at average productivity in sites of the Fynbos biome. The smaller scale of this study might explain why energy failed to have an effect (Kaspari et al. 2000). NDVI might also be a poor proxy of available energy in this study. Particularly for the forests and habitats with considerable canopy cover where very little of this biomass will be available for epigeal ants.

Studies along an arid elevational transect stressed the importance of temperature which, in combination with precipitation, explained 80% of ant species variation (Sanders et al. 2003). Temperature constrains ant foraging activities as it restricts their foraging times of the day (Jayatilaka et al. 2011). It is also widely accepted as a principal factor that determines distribution and activities (Hölldobler and Wilson 1990, McCain and Grytnes 2010) and there is a growing evidence that low temperature is a primary stress that controls patterns in ants as well as community structure (Andersen 2000, Araújo and Fernandes 2003). In contrast a study in Indonesian cacao plantations by Wielgoss et al. (2010) observed a negative correlation between temperature and ant species richness due to the presence of aggressive dominant Dolichoderinae ant species in the study area. Complex environments also have an influence on temperature indirectly, where open habitats tend to have high temperatures compared to closed/complex environment (Andersen 2000).

Similar to our study, complex habitats and low temperatures at higher elevations of Serra do Cipó (Araújo and Fernandes 2003) sampled less ant species. Soil temperatures in the thickets/shrubland and sedgeland/ herbland habitats were a better predictor of species richness than in the open woodlands and forest. Thermal ranges in the forests are small (Appendix 10 (12S and 12S2)) and might act as a filter for a small subset of cold tolerant species. In contrast,

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open woodlands are characterised by considerable variation in micro-climates over very small scales. The two iButtons per site might therefore not capture the varied thermal regimes of this habitat and fail to capture some of the variation in observed species richness.

In conclusion, we found that geometric constraints were the most important driver of species richness patterns followed by temperature while soil characteristics played a minor role. Energy, habitat structure and area failed to explain significant amounts of variation while spatiotemporal predictors were accounted for by the best model of correlates. In contrast to our sister transect in the Drakensberg mountains (Bishop et al. 2014), we have observed an increase in species richness over time. Similar to their study, we found that seasonal variation in species richness decreased with elevation. There was a significant decrease in richness with elevation during the wet season while this decrease was not significant during the dry season. The strength of patterns therefore varied with season and elevation.

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Chapter 4: Monitoring turnover of ants across an elevational transect: niche, space and time's relative importance

Abstract

Factors and mechanisms responsible for driving alpha diversity are better understood than those that drive beta diversity. Recent methodological advances allow for the disentanglement of variation in beta diversity into the contributions of different processes affecting it and identification of the scale at which these processes and correlates act. Here we focus on ant turnover across a mountain in the savanna biome of South Africa. Ants were sampled over a five year period (2009 – 2014), twice each year, at 11 sites at regular ranges of elevation. We test for the effect of space-time interaction on ant turnover, identify environmental and spatial variables that consistently explain significant amounts of turnover and partition the relative role of pure environmental, pure spatial, and spatially structured environmental variables in determining this variation. We furthermore assess the contribution of space and environment at various scales. Average and minimum temperature, NDVI and percentage sand in the soil consistently explained significant amounts of species turnover. Spatially structured environmental variables consistently explained the largest amount of variation in ant species turnover, followed by pure spatial while the contribution of pure environmental variables were negligible. The spatially structured component reflects the strong gradient associated with the transect while the dominant role of space points to the importance of mass effects or some environmental variable that we did not measure, particularly one that varies at fine scales. We predict that the relative role of pure space will decrease and that of niche processes (environment and spatially structured environmental variables) will increase in response to global change drivers because of the increased importance

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of environmental filtering associated with predicted elevated temperatures of the arid northern aspect and CO_2 induced bush encroachment of the southern aspect.

Introduction

Historically most community ecology studies have focused on factors and mechanisms that determines variation in local/alpha diversity (Sanders et al. 2003, Parr 2008, Dunn et al. 2009, Carvalho et al. 2012). Due to this, we now better understand what determines alpha diversity than what determines beta diversity (Beck and Khen 2007, Vasconcelos et al. 2010, Paknia and Pfeiffer 2014). However, beta diversity is at the heart of community ecology, as it deals with that which makes assemblages of species more or less similar to one another at different places and times (Vellend 2010). Beta diversity also measures the rate of variation in species composition across habitats/sites between ecosystems/geographical areas or along environmental gradients (Legendre et al. 2005, Terlizzi et al. 2008) and can reveal the mechanisms responsible for driving this variation (Bishop et al. 2015).

Understanding mechanisms which are responsible for maintaining biodiversity depends more on our ability to disentangle variation in diversity into the contributions of different processes affecting it and the scale of measurement at which these processes and correlates act (Laliberte´ et al. 2009, Legendre et al. 2009). A combination of both environmental (niche based) and space (dispersal) factors drive beta diversity (Baselga 2008) but the importance of these factors are dependent on the scale of measurement, taxonomic group and taxonomic level (Qian and Ricklefs 2007, Qian et al. 2009). In order to understand what shapes metacommunity structure or biogeographical patterns of species turnover, it is crucial to determine the relative weighting of each of these drivers i.e. niche based and dispersal (Duivenvoorden et al. 2002, Genner et al. 2004).

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Earlier studies (Whittaker 1960) suggested that beta diversity is mainly determined by variation in environmental differences, i.e. where environment is similar the flora and fauna is more similar. Thi is particularly relevant to small organisms with large population sizes and high dispersal abilities, e.g. periphyton and phytoplankton (Padial et al. 2014). Contrastingly, pure spatial variables (dispersal) explain a substantial amount of variation in beta diversity of endemic beetles on an island (Boieiro et al. 2013).

Environmental factors are also spatially structured and determine beta diversity for various taxa including European longhorn beetles (Baselga 2008), tenebrionid beetles (Fattorini and Baselga 2012) and spiders (Carvalho et al. 2011), and are particularly important in natural systems (Sattler et al. 2010). For ants in particular, existing evidence points to the importance of pure environmental and spatially dependent environmental variables in explaining beta diversity variation (Paknia and Pfeiffer 2014) and most studies report a weak effect of spatial variables on their own (Vasconcelos et al. 2010, Mezger and Pfeiffer 2011).

All these ant studies were performed over short (< 1 year) periods of time and did not consider seasonal and inter-annual changes. There is a real possibility that space and time can interact which could point to temporal changes in the relative importance of processes (dispersal vs. niche-based processes) that drive ant beta diversity (Laliberte´ et al. 2009). Here, we focus on ants (Hymenoptera: Formicidae), a taxon that could provide crucial data for conservation planning and management. Ants are abundant (Hölldobler and Wilson 1990), their taxonomy is increasingly well understood (Ward 2010) and they play vital ecological functions in the ecosystem (Del Toro et al. 2012). They can act as indicators for long-term monitoring studies (Alonso and Agosti 2000, Majer et al. 2007). Monitoring across elevational gradients has received increased attention, because mountains are biodiversity hotspots and taxa associated

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with the higher altitudes of mountains are particularly sensitive to change as the result of global warming (Gaston and Chown 1999, Munyai and Foord 2012, Werenkraut et al. 2015).

We sampled ants over a five year period (2009 – 2014), twice each year, across 11 sites, along an elevational gradient in the Soutpansberg Mountain Range. Firstly, we asked whether patterns in turnover are explained by space-time interactions. No space-time interactions in patterns of turnover would imply the relative role of space and environment remain constant over time. Secondly we identified environmental and spatial variables that explained significant amounts of turnover in ant diversity for each of the 10 surveys. Finally we partition the relative role of pure environmental, pure spatial, and spatially structured environmental variables in determining variation in beta diversity.

Materials and methods

Study area

Ants were sampled following a standardised and comparable protocol in the Soutpansberg Mountain Range (Munyai and Foord 2015a, 2015b). The transect was set out at 200 m elevation intervals on both sides (arid north and mesic south) of the mountain (*ca.* 16 km long), with an altitudinal range of 900 m. a.s.l. on the northern aspect (800–1700 m. a.s.l.), 800 m. a.s.l. (900–1700 m. a.s.l.) on the southern aspect. Habitat types across the transect include woodland on the northern aspect, sedgeland/herbland on the highest elevations, forests at mid-elevations, thicket and shrubland on the lowest elevation of the southern aspect, See Munyai and Foord (2015b) for details.

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Ant sampling

Ground dwelling ants were sampled using pitfall traps during dry (September) and wet (January) seasons between 2009 and 2014 in all 11 elevational sites. Each elevational site had four replicated grids. Grids consisted of pitfall traps laid out in a 2 × 5 array with 10 m between traps. Replicates were spaced at least 300 m from each other. Pitfall traps contained a 50% solution of propylene glycol and they were left open for five days. Ant samples were washed in the laboratory, preserved in 70% ethanol and sorted to species where possible otherwise they were identified to morpho-species level, See Munyai and Foord (2015b) for details.

Correlates

Soil. A total of 16 soil variables (pH, conductivity, stone volume, K, Na, Ca, and Mg, C, NO3-N, H+, C, T-value, pBrayll, and the percentage clay, silt and sand) were analysed by BemLab (Pty) Ltd laboratories, Somerset West, South Africa). A total of ten soil subsamples in each of the 4 replicates of a site were pooled. Principal component axes one (Soil-PC1) and two (Soil-PC2) both represent a gradient from sandy to clayish soil, Soil-PC3 is associated with increased carbon content of the soil, and Soil-PC4 is linked to increased phosphate and sodium (Appendix 5). Soil characteristics were only sampled once and were therefore assumed to remain stable over the period of the study. Although this might not be true for some of the variables, the relative percentage of sand and clay that represents most of the variation between sites (Soil-PC1 and Soil-PC2) can be expected to remain relatively stable over a five year period (Munyai and Foord 2015a).

Energy. Normalised difference vegetation index (NDVI) was derived for all sites during the sampling month (Appendix 6). NDVI values were derived from MODIS (Moderate Resolution

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Imaging Spectroradiometer)/TerraVegetationIndicesMonthlyL3Global0.05DegCMGV005https://lpdaac.usgs.gov/lpdaac/products/modis_product_table/vegetation_indices/monthly_l3_global_0_05deg_cmg/v5/terra (see Munyai and Foord 2015a). At each site, two Thermocron iButtons (Semiconductor Corporation, Dallas /Maxin,TX and USA) record soil temperature (buried 1 cm below the soil surface) at 1 hour intervals over the period of study and temperature sequences from January 2009 to January 2014 were plotted and inspected for iButtons that malfunctioned or became exposed (Appendix 9). Data for the two iButtons were averaged for each elevational site and monthly mean, minimumand maximum temperature and variation in temperature (SD) at each site during the month of sampling were calculated (see Appendix 10; 11 and Munyai and Foord 2015a).

Habitat structure. We quantified fine scale vertical (the number of hits on a 1.5 m rod) and horizontal (estimating percentage area covered by vegetation, leaf litter, exposed rock and bare ground) habitat structure for each of the 10 surveys. Details are provided in Munyai and Foord (2015a). To account for co-linearity, principle component analysis was performed on the horizontal and vertical measures. The first two principal components accounted for 78% of the variation. Principal component axis one (Vert-PC1) represents a gradient from sites with dense canopy cover and very little ground cover to sites with low ground cover and the absence of canopy cover while Vert-PC2 is negatively related to increased complexity in vegetation structure (Appendix 7). The first two principle components of horizontal habitat structure explained 81% of the total variation. Axis one (Hor-PC1) summarizes a gradient from sites dominated by bare ground and leaf litter to sites covered with vegetation, whereas axis two (Hor-

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PC2) contrast sites with rock cover with those dominated by leaf litter, see Appendix 8, (Munyai and Foord 2015a).

Area. The area covered by each elevation zone (200 m contour sampling zone) was calculated by creating a Minimum Convex Polygon of all replicate points with a 40 km buffer which encompasses the area under study. Further details provided in Munyai and Foord (2012).

Spatial variables

Spatial structures in the data were identified and modelled using principal coordinates of neighbor matrices (PCNM) by computing principle coordinates analysis (PCoA) of a truncated euclidean distance matrix that only has the distances between close neighbours (Borcard et al. 2004) with the 'stats'package in R (R Development Core Team 2013). This provides a spectral decomposition of the spatial relationships between all replicates along the transect and generates variables that correspond to all spatial scales that can be perceived for the study design. However, the largest truncation distance determines the smallest scale perceived and large distances means the loss of smaller spatial scales. Four additional points were therefore added to this design to reduce the threshold value, the PCNM values were calculated and the additional points removed from the PCNM matrix (Borcard and Legendre 2002). Fifteen eigenvectors with significant positive spatial correlations were extracted and included as spatial variables in the multiple regression analysis. This approach has several benefits as the sizes of eigenvalues are related to the scales they represent, spatial variables are orthogonal, represents a wide range of spatial scales and can model any type of spatial structure (Borcard and Legendre 2002).

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Statistical Analysis

A major objective of sampling at larger temporal scales is to identify the processes that drive patterns in diversity. In contrast to snapshot studies, identifying space-time interactions is particularly important, e.g. the discovery of interactions in ant assemblage patterns of this study would point to temporal changes in the relative importance of processes (stochastic vs. deterministic) that drive ant turnover (Laliberte´ et al. 2009). The absence of such interactions would warrant analysing data from one sampling event as results for other periods would be qualitatively similar (Laliberte´ et al. 2009). To test for space-time interactions we used a two-way crossed factor design with time and space as factors, in an RDA using orthogonal dummy variables or Helmert contrasts (Venables and Ripley 2002). As our sampling design was balanced and replicated, a two-way ANOVA approach can be used. Helmert contrasts were derived for each time period (ten in total), space (11 elevational sites with four replicates each) and their interactions using the 'stats' package in R (R Development Core Team 2013). This resulted in a total of 9 temporal, 10 spatial and 90 interaction contrasts (Borcard et al. 2011). The ability of environmental and spatial variables to explain ant beta diversity was assessed by redundancy analysis. A forward selection procedure on the environmental dataset was performed to identify spatial and environmental variables that made significant ($p < 0.05$ after 999 random permutations) contributions in explaining variation of ant beta diversity (See Blanchet et al. 2008). By performing this procedure, inflated Type I error and the over estimation of the amount of explained variance is avoided. The variation explained by the two selected sets of variables (space and environment respectively) was partitioned into the relative role of space, environment and spatially structured environmental variation in explaining ant beta diversity. Partitioning was done through a series of partial regressions using the 'varpart' command in vegan (Oksanen),

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(see Carvalho et al. 2012). Scale-specific importance of environmental variables (soil, energy, habitat structure and area) were assessed by describing two spatial models based on the PCNM vectors selected, broad-scale and fine scale, and fitting species turnover against each forward selected variable through redundancy analysis. Fitted values were then used in variation partitioning using the forward selected environmental variables to estimate their relative importance at each scale. Detailed descriptions can be found in Carvalho et al. (2012) and Laliberte´ et al. (2009).

Results

Space-time interaction

The main factors, space and time, showed that ant assemblages had a very strong spatial structure (R^2 adjusted = 0.57, $p < 0.001$) and significantly varied in time (R^2 adjusted = 0.04, $p < 0.001$), but their interaction on ant assemblage structure was not significant (Table 4). This suggests that there was no change over time in the processes that explain ant turnover in the study area. All ten surveys were analysed to determine the relative role of space and environment but we used one survey, September 2010 where the largest amount of variation was explained, to analyse the role of these factors at different scales.

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Table 4: RDA, testing the role of time and space and their interaction in explaining variation in ant assemblage patterns for the ten sampling periods between September 2009 and January 2014. Level of significance: * P <0.05, ** P <0.01, *** P <0.001.

	Species richness		
	R^2 adj (%)	**df**	**F**
Source			
Space × Time	0.1	90,348	0.45
Interaction excluded from the model			
Time	0.04	9,340	1.8**
Space	0.56	10,339	58.4***
Interaction included in the model			
Time	0.02	9,430	2***
Space	0.57	10,429	55.8***

Environment

Available area, percentage clay in the soil (SPC2), NDVI and minimum monthly temperature explained significant amounts of variation in 90% of the surveys. Two other environmental variables, percentage sand in the soil (eight times) and then average monthly temperature (seven times) were also consistently included in the forward selection procedure, Table 5. Structural

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components of the habitat, leaf litter (Hor2) and habitat complexity (Vert1) were only included twice in the most parsimonious models (Table 5 and Figure 12). Although not consistently included in the best model, average monthly temperature on average explained the largest amount of variation followed by minimum monthly temperature, energy and percentage sand in the soil (SPC1) respectively (Table 5).

Space

Large scale spatial structures (PCNM1 – 5) and one intermediate spatial structure (PCNM7) consistently explained significant amounts of variation in species turnover for all ten surveys while small scale spatial structures explained the least amount of variation and often only for one survey (Table 6). The largest variation in species turnover was explained by the largest spatial scale structure (PCNM1) while the other large scale spatial structures (PCNM2 – 5), including the intermediate spatial structure (PCNM7), follows successively in the exact order of their spatial resolution (Table 6).

PCNM1 reflects a broad scale spatial structure that distinguishes between the summit and lower elevation assemblages (Figure 13a), while PCNM2 describes a cluster of sites in the upper northern elevations (mainly *Burkea africana* dominated vegetation) as distinct from all other sites (Figure 13b). The remaining variables identify mid-elevations as distinct from lower elevations (PCNM3, Figure 13c), the spatial structuring of lower elevation sites of the two aspects, particularly the southern aspect (PCNM4, Figure 13d), the spatially distinct northern most site of 08N (PCNM5, Figure 13e) and lastly a finer scale structuring of sites (PCNM7, Figure 13f).

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Table 5: Environmental variables explaining significant variation of ant beta diversity for each of the ten survey's variables explaining variation of ant beta diversity between surveys (September 2009 – January 2014). Variables were selected through forward selection.*, < 0.05, **, < 0.01, ***, < 0.001.

Survey	Area	SPC2	NDVI	Temp (min)	SPC1	Temp (ave)	Vert2	SPC4	Hor1	SPC3	Vert1	Hor2	Total R^2 Adjusted
Sept 2009			0.06***		0.01*				0.06***	0.02*			0.16
Jan 2010	0.02*	0.03***	0.1***	0.10***		0.03**	0.02**		0.03**				0.32
Sept 2010	0.06***	0.02***	0.08***	0.02**	0.04**	0.03**		0.02*	0.09***		0.03**		0.39
Jan 2011	0.04***	0.02**		0.02**		0.1***	0.1***				0.03***	0.02**	0.33
Sept 2011	0.02*	0.02*	0.06***	0.04**	0.04**		0.02*						0.20
Jan 2012	0.02**	0.01*	0.08***	0.01*	0.03***	0.1***		0.03**					0.28
Sept 2012	0.03**	0.02**	0.07***	0.10***	0.04***			0.02*		0.01*			0.29
Jan 2013	0.03***	0.02**	0.02*	0.12***	0.04***	0.03**	0.06***		0.01*			0.05***	0.38
Sept 2013	0.03**	0.02*	0.01*	0.05***	0.12***	0.1***	0.02**	0.01*	0.03***	0.01*			0.55
Jan 2014	0.05***	0.03***	0.02**	0.11***	0.02*	0.08***		0.03**					0.44
Average	0.03	0.02	0.06	0.06	0.05	0.07	0.04	0.02	0.04	0.01	0.03	0.04	0.33
Count	9	9	9	9	8	7	5	5	5	3	2	2	

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Table 6: Spatial variables explaining significant variation of ant beta diversity for each of the ten surveys (September 2009 – January 2014). Variables were selected through forward selection. V1 – V24 = PCNM1 - PCNM24. *, < 0.05, **, < 0.01, ***, < 0.001

Survey	V1	V2	V3	V4	V5	V6	V7	V8	V9	V11	V13	V14	V16	V19	V20	V24	Total R^2 Adjusted
Sept 2009	0.09***	0.05***	0.03**	0.02**	0.02**		0.02**	0.02*							0.02*		0.26
Jan 2010	0.13***	0.08***	0.04***	0.07***	0.04***		0.02**	0.02**									0.39
Sept 2010	0.13***	0.05***	0.07***	0.05***	0.04***	0.03***	0.01*	0.05***	0.02*	0.01*		0.02*		0.01*	0.01*		0.50
Jan 2011	0.15***	0.08***	0.03***	0.08***	0.03***		0.02**	0.02**		0.02*							0.44
Sept 2011	0.08***	0.05***	0.03***	0.02*		0.03*	0.03**										0.27
Jan 2012	0.06***	0.05***	0.03***	0.03**		0.02**	0.02*	0.02**					0.02*				0.25
Sept 2012	0.12***	0.06***	0.07***	0.02**	0.07***		0.02*							0.02*			0.38
Jan 2013	0.13***	0.04***	0.06***	0.05***	0.06***		0.02*	0.01*	0.01*	0.02*	0.03*	0.02*					0.45
Sept 2013	0.04**	0.07***	0.06***	0.04***	0.06***		0.03**									0.02*	0.26
Jan 2014	0.11***	0.02***	0.08***	0.06***	0.05***					0.01*	0.02*						0.40
Average	0.10	0.06	0.05	0.04	0.04	0.03	0.02	0.02	0.02	0.02	0.03	0.02	0.02	0.02	0.02	0.02	0.36
Count	10	10	10	10	7	3	9	6	2	4	2	2	1	2	2	1	

PCNM 1 – 5 = Large scale, PCNM 6 – 9 = Intermediate scale and PCNM 11 – 24 = Fine scale

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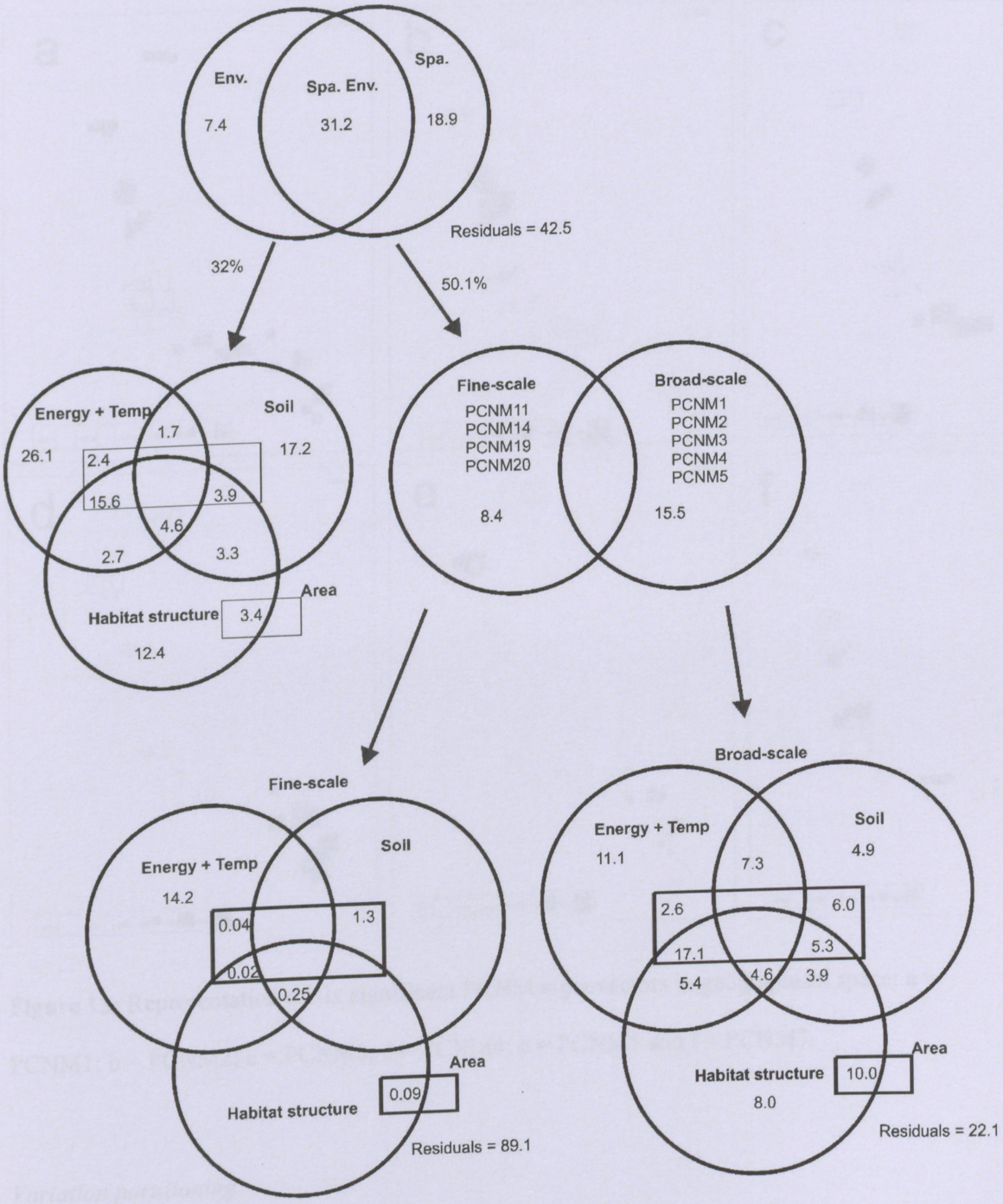

Figure 12: Venn diagram showing the results of the variation in partition procedure carried out on the forward selected environmental and spatial eigenvector variables for September 2010 ant species turnover across the transect.

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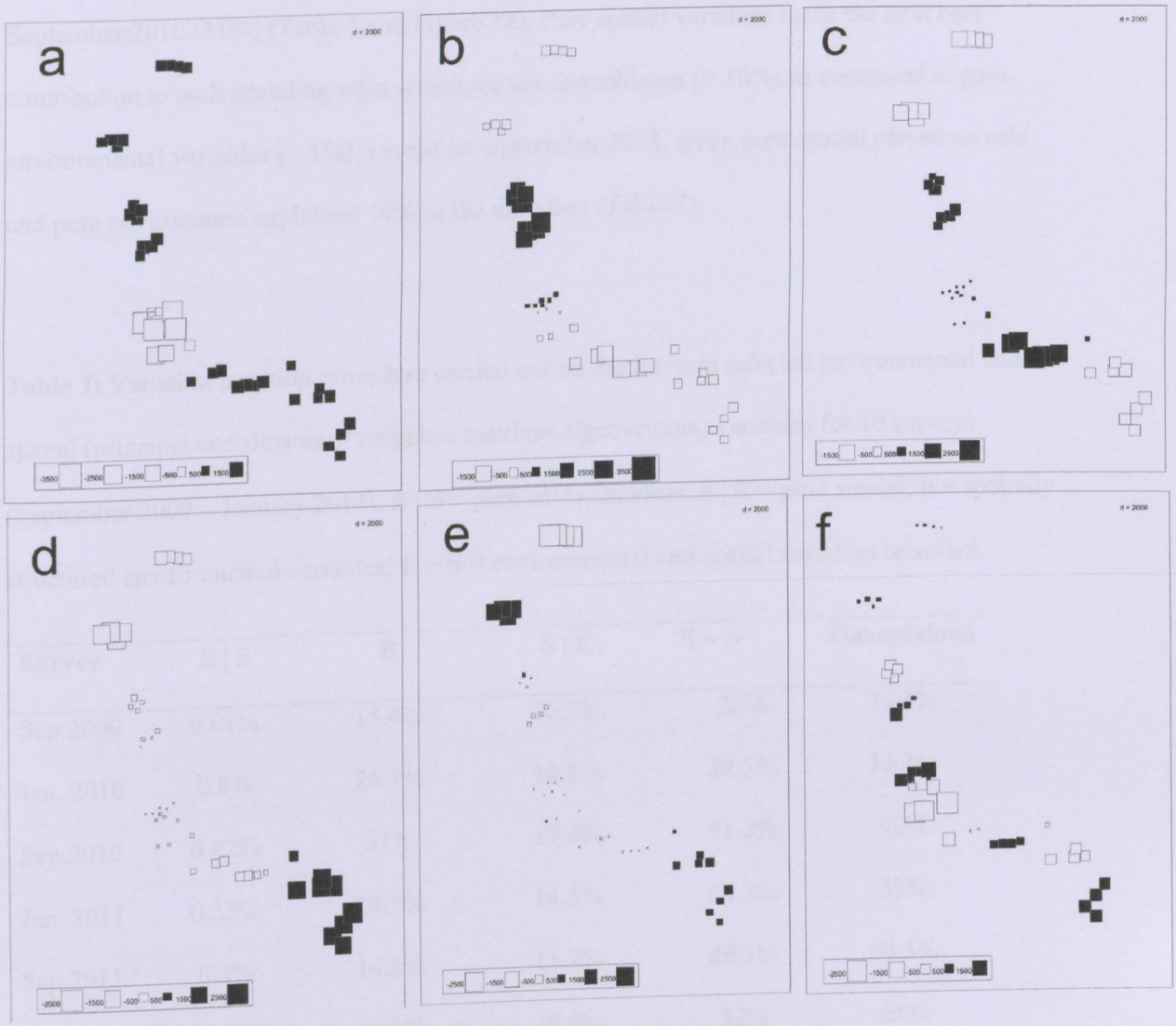

Figure 13: Representation of six significant PCNM eigenvectors in geographical space: a = PCNM1; b = PCNM2; c = PCNM3; d = PCNM4; e = PCNM5 and f = PCNM7.

Variation partitioning

Spatially structured environmental variables explained the largest amount of variation, on average (24.4%), the lowest was recorded for September 2011 (14.5%) and highest for

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September 2010 (31%) (Table 7 and Figure 12). Pure spatial variables made the next best contribution to understanding what structures ant assemblages (> 10%) as compared to pure environmental variables (< 1%), except for September 2013, when pure spatial played no role and pure environment explained 14% of the variation (Table 7).

Table 7: Variation partition procedure carried out on the forward selected environmental and spatial (principal coordinates of neighbor matrices eigenvectors) variables for 10 surveys (September 2009 – January 2014). **E | S** = pure environmental; **S | E** = pure spatial; **b** = spatially structured environmental variables; **E + S** = environmental and spatial variables recorded.

Survey	E | S	B	S | E	E + S	Unexplained
Sep.2009	0.01%	15.4%	10.2%	26%	74.3%
Jan. 2010	0.8%	24.1%	14.6%	39.5%	53.2%
Sep.2010	0.82%	31%	19.4%	51.2%	42%
Jan. 2011	0.33%	29.5%	14.5%	44.3%	53%
Sep.2011	0.6%	14.5%	11.2%	26.3%	68.3%
Jan. 2012	0.82 %	20.3%	10.9%	32%	61%
Sep.2012	0.33%	26%	12.1%	38.4%	59%
Jan. 2013	0.88%	29.3%	16%	46.1%	46%
Sep.2013	14%	27%	0.0%	41%	60%
Jan. 2014	0.73%	27%	14.5%	42.2%	51.5%
Average	2%	24.4%	12.3%	39%	57%

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Discussion

The lack of a space-time interaction on ant species composition suggests spatial patterns did not vary over the period of the study and that changes in time were common to all the sites. Furthermore, the relatively limited role of time in explaining changes in ant turnover suggests that there was little change in the ant assemblages over the five years of this study. Space, on the other hand, played a major role and although we still analysed all the surveys, much of the results of variation partitioning into niche and spatial processes were very similar over time.

The whole model, environmental and space (E + S), explained on average 39% and as much as 51% of assemblage turnover which contrasts with weaker model performance observed in other ant studies, e.g. 31.2% in Amazonian forests (Vasconcelos et al. 2010) and 16.2% in the Bornean rainforest (Mezger and Pfeiffer 2011). Notably, our model performance corresponds with another ant study in an arid region, e.g. the 62% explained in a study by Paknia and Pfeiffer (2014), 46.1% for spiders (Carvalho et al. 2011), and 31.9% for ground beetles of the Madeira Island Laurisilva (Boieiro et al. 2013).

Niche processes

The small amount (< 1%) of variation explained by pure environmental variables in this study contrasts with work done by Paknia and Pfeiffer (2014) in Iran where it explained the largest, 45%. However, the Paknia and Pfeiffer (2014) study was undertaken at a much larger spatial extent (1600 km) compared to the 16 km in this study. The overriding role of extreme environmental conditions (high temperatures and lack of rainfall) in the Iranian study points to the importance of environmental filtering of ants in deserts. The more mesic conditions along the

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Soutpansberg transect in association with the much shorter distances between sites limits the effects of niche-based processes except within the context of the strong environmental gradient.

The dominant role of spatially structured environmental variables (Table 6 and Figure 11) is in contrast with Paknia and Pfeiffer (2014) results where this joint effect explained a negligible amount of -0.06 of ant beta diversity. It does, however, correspond to the 46.1% of spider beta diversity on the coastal dunes along the Portuguese Atlantic coast (Carvalho et al. 2011), European longhorn (Baselga 2008) and tenebrionid (Fattorini and Baselga 2012) beetles where it explained up to 28.3% as well as 35% of turnover respectively.

The current study reported minimum (consistently) and average (significant amount) temperatures explaining ant turnover between surveys. Temperatures (mean annual and mean diurnal temperature) in Iran explained up to 39% of ant turnover (Paknia and Pfeiffer 2011) as well as in the dryland of central Asia (Pfeiffer et al. 2003). Wide fluctuations in temperature might prevent colonization in arid regions such as Iran as many ant species lack physiological or behavioural adaptations to them. Turnover between open and forested habitats also decreased with increased temperature (Del Toro 2013) while annual temperature was one of the variables retained in the best model explaining taxonomic and functional turnover of leaf-litter ants in the Atlantic rainforest of the eastern Brazil coastline (Silva and Brandao 2014).

Another important environmental variable, percentage clay in the soil, was also consistently included in the models. In the Black Belt Prairie Flatwoods regions of Mississippi, soil type combined with moisture availability had a considerable impact on ant colonization, preventing some species and supporting others (Hill et al. 2008). Paknia and Pfeiffer (2014) predicted that both soil texture and chemistry would be important in explaining ant beta diversity. The current study had a limited role as evidenced by the number of times and the average amount of

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significance with which they (SPC3 and SPC4) explained ant turnover. In Madeira Laurisilva, Boieiro et al. (2013) also reported on the influence of organic matter on ground beetles turnover.

Although energy was not important in explaining species richness across the same study area (Munyai and Foord 2015a), it played a significant and consistent role in all of the models of this study (Appendix 6). This is not surprising, as primary productivity (for which NDVI is used as a surrogate) is known to affect species extinction and abundance (Evans et al. 2005).

Habitat structure accounted for the smallest amount of variation in ant metacommunities (Table 4 and Figure 11) although there is a growing body of literature reporting the effects of habitat structure on ant assemblages (Ribas et al. 2003, Lassau and Hochuli 2004, Botes et al. 2006) and spiders turnover across various spatial scales (Carvalho et al. 2011). However, it might be that habitat structure mediates temperature and the energy input along the transect and therefore indirectly affects turnover in ants (Andersen 2000).

The consistent contribution of available area, i.e. 90% of all surveys, in explaining ant turnover in this study corresponds to the significant amount of variation in spider beta diversity (33.6%) at intermediate spatial scale and the unique contribution of area (6.4%) reported in Carvalho et al. (2011) while in contrast, Baselga (2008) found that area only explained 1% of the variation in European longhorn beetles.

Dispersal

In contrast to Paknia and Pfeiffer (2014) and Mezger and Pfeiffer (2011), pure spatial variables played a relatively larger role (14%) in explaining turnover in ants. This corresponds with studies in Madeira Natural Park (Island of Laurisilva) where pure spatial variables explained almost twice (16.4%) the amount of variation explained by pure environmental variables (9.8%) of

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endemic ground beetles (Boieiro et al. 2013), up to 16.8% of the turnover in European longhorn beetles (Baselga 2008) and 30.4% of tenebrionids turnover (Fattorini and Baselga 2012). Carvalho et al. (2011) also report the highest role of pure spatial variables compared to the role of pure environmental factors in explaining turnover of spiders along the Portuguese Atlantic coast.

The importance of broad scale spatial structures in the current study is similar to Goncalves-Souza et al. (2014) where it mainly explained beta diversity of spiders along the biogeographical scale of neotropical restinga vegetation in the Brazilian coast and along a gradient of mediterraneity in coastal dunes of Portugal (Carvalho et al. 2011). The dominant role of energy and temperature at the finer scale of this study indicates the need to consider both these variables as important correlates of ant diversity patterns across gradients. Carvalho et al. (2011) also found a dominant role of climate separately (37.2%) and a combined dominant role of temperature and vegetation (NDVI, which is used as a proxy for productive energy) explained up to 58.9 % of variation at the fine scale of their study.

In conclusion, we found no effects of space-time interaction on ant assemblages, strong spatial structuring and limited temporal structure. The importance of pure environmental variables was negligible relative to the role of pure spatial structures and spatially structured environmental variables. The predicted increase in temperature in the region coupled with CO_2 induced bush encroachment on the southern aspect should result in the increased importance of environmental filtering in the form of selecting for ant species with higher thermal tolerance on the northern aspect and species filtered by thickets on the southern aspect. It is therefore expected that the influence of pure spatial variables will decrease and that the role of spatially structured

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environmental variables and pure environmental (temperature and energy) variables would increase in response to an increased role of niche processes and environmental filtering.

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Chapter 5: Dominance hierarchies of ant communities across an elevational transect, Soutpansberg Mountain

Abstract

Competition has been described as the 'hallmark' of ant ecology. However, the outcome of competition is strongly context-depended and therefore its role should vary along environmental gradients. Here we focus on ants across an elevational transect in the Soutpansberg Mountain Range. We aim to define a dominance hierarchy for ants along the transect, describe variation in the abundance and distribution of these groups in space (elevation and habitat) and time (time of the day and season), describe the variation in ant morphospace along the transect and infer possible underlying processes structuring these assemblages. Ant activity patterns were observed at cat food, oats and sugar baits in each of the four seasons, three times during the day and once at night between November 2011 and October 2012. A combination of numerical and behavioural dominance metrics was used to rank ant species. The abundance of dominant ants increased with elevation, winter was the season of lowest abundance and least abundant during midday. Subdominant ants were most abundant during midday while subordinate ants were present together with dominant ants throughout the day except in the morning. Subdominant ants were most abundant in the short forest while the dominant ants were most abundant in the high elevation sedgeland. Ant morphospace was smallest at highest elevation and short forest while it was largest in the woodland sites. Our findings reveal that dominant ants control species richness at baits on top of the mountain (sedgeland) while habitat heterogeneity together with low abundance of dominant ants (open woodland), environmental filtering (short forest) and disturbance (shrubland) might structure ant assemblages in the remaining habitats of the study area.

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Introduction

Competition has had one of the oldest histories in ecology (Savolainen and Vepsäläinen. 1988; Parr and Gibb 2010; Stuble et al. 2013) and its role in structuring assemblages remains contentious. Overlapping niches could potentially result in competitive exclusion, leading to lower local species richness. Evidence for this exists for several taxa, e.g. butterflies (Kunte 2008), plants (Jakobsson and Eriksson 2003), mouse lemurs (Dammhahn and Kappeler 2008) and ants (Andersen 1992; Andersen and Patel 1994; Parr et al. 2005; Parr 2008). In contrast, multiple ant species with apparently similar niche requirements have been observed co-occurring in the same habitat or at a local level (Andersen 1991; Andersen 1992).

Interspecific competition is acknowledged as the key mechanism in ant ecology (Cerdá et al. 1998; Parr 2008; Parr & Gibb 2010; Vepsäläinen & Czechowski 2014).This also include studies on ant territoriality (Andersen and Patel 1994), dominance/competitive hierarchy (Savolainen and Vepsäläinen 1988; Lebrun 2005) and species co-occurrence (Arnan et al. 2011).

Studies have used the results of competitive interactions to classify ant assemblages into dominance hierarchies (Savolainen and Vepsäläinen 1988; Hölldobler and Wilson 1990) based on their ability to defend territories, resources and nests as well as differences in community organisation and behavioral ranks (Wilson 1971; Andersen 2000). Dominant ants tend to govern the utilization of resources in a community and exclude other species through competitive exclusion (Andersen 1992; Parr et al. 2005) resulting in lower species richness where dominant species are abundant at both local (baits) and assemblage level (Parr 2008; Campbell et al. 2015).

Although competition is one of the major influences of species diversity at local scale (Bengtsson et al. 1994), other mechanisms such as habitat heterogeneity (Hill et al. 2008,

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Pacheco and Vasconcelos 2012, Parui et al. 2015), disturbance (Kwon et al. 2014, Rivas-Arancibia et al. 2014, Chen et al. 2015, Gibb et al. 2015, Vonshak and Gordon 2015) and environmental filtering (Machac et al. 2011, Wiescher et al. 2012, Axen et al. 2014, Fowler et al. 2014) play a significant role in influencing ant species richness/diversity.

The habitat heterogeneity hypothesis assumes that species diversity will increase along structurally complex habitats due to increased niche diversity and diverse ways of environmental resources utilization (Tews et al. 2004; Pacheco and Vasconcelos 2012). Similar to dominance (competitive exclusion), disturbance also influence species diversity through what is known as the Intermediate Disturbance Hypothesis (IDH) (Connell 1978; Shea, Roxburgh & Rauschert 2004), although Fox (2012) suggests that there is little support for this hypothesis and argues that it has a disturbing history (Wilkinson 1999).

The Intermediate Disturbance Hypothesis postulates that at low levels of disturbance only dominant species persist and thereby reduce species diversity for an area while at intermediate levels, disturbance balances the loss of competitive exclusion and loss of competitive dominance and favour the co-existence of competitive species and disturbance-tolerant-species (Mackey and Currie 2001; Farji-Brener et al. 2002).

Environmental filtering hypothesizes that the environmental conditions should filter species into a new habitat thereby only allowing species with functional traits (life-history, physiological and morphological) compatible to specific environmental conditions should persist in such environments (Wiescher et al. 2012; Barnagaud et al. 2014). Because traits are measured at an individual level they therefore represent the effect of the environment on organisms and thereby reflect how organisms interact with their environment (Kaspari 1999, Violle et al. 2007; Diaz et al. 2013).

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Morphological characteristics of an organism reveal how an organism moves, its diet including where, how and on what it feeds (Weiser and Kaspari 2006). This is of critical importance as it represent the possible form, shape or structure of an organism, i.e. morphospace. Weiser and Kaspari (2006), however, argued that the most important morphological variable is body size as it affects an organisms' physiology, trophic biology and consequently the habitat where it occurs.

Environmental filtering together with a range of other processes, including competition, habitat heterogeneity and disturbance may determine species co-existence across environmental gradients. This study aims to define a dominance hierarchy for ants, describe variation of these categories in space (elevation and habitat) and time (time of the day and season), describe the variation in ant morphospace along the transect and determine the relative role of competition, habitat heterogeneity, disturbance and environmental filtering in ant species co-existence across the mountain.

Materials and methods

Study area

The Soutpansberg transect extends over the highest point of the mountain, Lajuma at 1748 m. a.s.l. (23.02408° S, 29.42908° E); descending to 800 m. a.s.l. in the north (22 56.683° S, 29 26.359° E) and 900 m. a.s.l. in the south (23 03.846° S, 29 29.400° E). The study area is characterised by five broad structural vegetation types, the northern aspect has four woodland sites (800 – 1400 m. a.s.l.), three sedgeland/herbland sites (1400, 1600 and 1700 m. a.s.l) on the highest elevation, two forest sites (1200 m. a.s.l. – both tall and short forest), one thicket site (1000 m. a.s.l.) and a shrubland site (900 m. a.s.l.) on the lowest elevation of the southern aspect as described in Munyai and Foord (2015a).

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Ant baiting

Ants were observed at three stations baited with cat food, sugar and oats respectively. Observations were conducted once in each of the four seasons of the year (November 2011 – October 2012) and at all 11 sites. At each site, three transects 10 m apart, each with 15 bait stations 5 m apart, were laid out. At each baiting station, a platform (60 mm x 50 mm) containing bait was placed to aid observation (Parr 2008). Each platform either had a teaspoon of fish-based cat food, oats, or a piece of cotton soaked in sugar solution placed on it depending on the transect. Ant activities were recorded after 15, 30 and 60 minutes at each baiting station. Baiting was repeated four times per day (i.e. three times during the day and once at night), per site, starting from 07h00, 12h00, 16h00 and 20h00 in summer and spring and 07h30, 12h30, 15h30 and 19h30 in winter and autumn.

Ants observed feeding at the bait, over a period of 10 seconds were counted and recorded. Species that could not be identified in the field were collected and stored in 96% ethanol for verification in the laboratory. Ants were identified to species level where possible otherwise they were assigned to morphospecies (See Munyai and Foord 2015b) for details.

Dominance analysis

A six-point scale was used to score abundances of all ants as follows: 1 = 1 ant, 2 = 2-5 ants, 3 = 6-10 ants, 4 = 11-20 ants, 5 = 21-50 ants and 6 ≥ 50 ants (Parr 2008) and references therein. Similar to Parr (2008), we defined a species' abundance per baiting session as the total of its abundance scores summed across 15 baits. The total abundance of each dominance category during a baiting session was the sum of each species in the category's total abundance for each

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baiting station (Parr 2008). The maximum abundance of each ant species per baiting session was 90 (abundance score 6 x 15 baits) similar to Parr (2008).

Dominance hierarchies were based on numerical and behavioral dominance. Numerical dominant species occurred and occupied large proportions of the baits and monopolised (only ones present at a bait (Parr 2008; Gibb and Parr 2013)) most of the baits where they occurred. Behaviorally, dominant species won most of their encounters and this was assessed based on individual interaction with other taxa at baits, (Bestelmeyer 2000; Parr 2008). This involved counting the number of times individuals in a species behaviorally dominated or was subordinate in the interaction with other species (Parr 2008). During the three baiting periods (15, 30 and 60 minutes), any agonistic (biting, charging stigning or spraying of chemicals) interaction was recorded (see Parr and Gibb 2010). A dominance score was calculated as the percentage of encounters in which a species had won its interspecific encounters (Bestelmeyer 2000; Parr 2008; Parr and Gibb 2010).

Species were categorized into three dominance hierarchies based on all three bait types across four seasons and across all 11 elevational sites. Dominant ants were species with a dominance score > 50% and monopolised > 25% of the baits. Subdominant ants had a dominance index > 50% but monopolised < 25% (but > 10%) of the baits while subordinates ants were species with a dominance index < 40% and monopolised < 15% of the baits where they occurred.

Morphometric measurements

For each of the collected ant species in this study, we selected three specimens. For dimorphic species only minor ant specimens were selected as they are easily found for measurements. Standardized linear measurements for each ant were taken using an ocular micrometer mounted

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on a stereo microscope (Leica M205 C) which is accurate to 0.01 mm. Eleven morphometric measurements were taken: head length from the posterior edge of the clypeus to the posterior cephalic margin, head width across the top of the eyes and between the eyes, eye length and eye width, mandible length insertion to the tip, clypeus length, scape length, weber's length, pronotum width, hind tibia length and hind femur length.

Statistical analysis

The response of the three dominance groups to habitat, elevation, bait type, season and time of day was modelled with Generalized Linear Mixed Effects Models (GLMM) using a loglink function and poisson error distribution. The role of spatial and temporal variables was evaluated by alternating time (seasonal and time of the day), space (habitat and elevation) and bait type as fixed and random factors, accounting for either temporal or spatial pseudoreplication. Marginal R^2 (R^2m, due to fixed effects only) and conditional R^2 (R^2c, due to fixed and random effects) were calculated to determine how much of the variation is explained by fixed and random effects respectively (Nakagawa and Schielzeth 2013).

The ant morphospace at each site was quantified and visualized with linear discriminant analysis in PAST (Hammer et al. 2001) based on the average of the 11 morphometric measurements made for all of the species found at each site. Species that were included were those caught by pitfall trapping at the baiting sites in the 2012 survey. Therefore we included even taxa that did not come to the baits. Details of pitfall trapping methodology can be found in Munyai and Foord (2015b).

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Results

Ant species composition at baits

A total of 88 species and 127051 individuals from 23 genera and five subfamilies were observed during baiting. The three richest genera at the baits were *Camponotus* (16 species), *Tetramorium* (15 species) and *Monomorium* (9 species). Three species *Camponotus* UOVC_18 (maculatus gp.), *Technomyrmex pallipes* Smith and *Pheidole* UOVC_01 (*megacephala* gp.) occurred at all sites across the transect.

The most abundant genera were *Pheidole* (59%), *Monomorium* (14%), *Myrmicaria* (7%), *Crematogaster* and *Tetramorium* (5%). The most diverse sites were 10N (35 species), 09S and 12N (34 species) (Table 8). The sites where ants were the most abundant, 17N and 16S, had the least number of species at baits (Table 8).

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Table 8: Taxon richness at bait stations and pitfall traps (Pitfall trap data from trapping during 2012 surveys at baiting sites, data from Munyai and Foord (2015b)) with ratio of species richness at bait station and pitfall trap (species richness at bait/species richness at pitfall trap), proportional abundance at baits at eleven elevational sites across the transect sampled over all four seasons in 2012 and varying morphospace and dominance categories with their varying ranked abundance (Abundance ranked from 1 = lowest dominance value and 6 = highest dominance value) across the study area.

Sites	Subfamilies	Genera	Species	Species	Species	Morpho-space	Habitat	Ranked abundance			% total abundance (baiting)
	Baiting	baiting	baiting	pitfalls (2012) site	Ratio bait/ pitfall	pitfalls (2012)		Dominant	Subdominant	Subordinate	
08N	4	13	31	27	1.1	22.33	Woodland	3	5	6	7
10N	4	14	35	31	1.1	34.41	Woodland	3	5	6	8
12N	4	15	34	34	1	33.96	Woodland	3	5	6	7
14N	3	13	27	32	0.8	23.68	Woodland	3	5	6	10
17N	3	7	13	19	0.7	10.1	Sedgeland	4	2	4	15
16S	3	7	15	30	0.5	11.8	Sedgeland	4	2	4	12

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14S	3	9	21	34	0.6	14.29	Sedgeland	4	2	4	7
12S	2	9	17	26	0.7	18.65	Tall Forest	1	1	2	1
12S2	4	14	32	29	1.1	9.916	Short Forest	2	6	1	12
10S	3	8	18	29	0.7	17.44	Thicket	5	3	3	9
09S	4	15	34	35	1	27.21	Shrubland	6	4	5	11

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Dominance hierarchies on the Soutpansberg transect

Eight species (5 *Pheidole* species, 2 *Crematogaster* species and *Myrmicaria natalensis*) were identified as dominant (Table 9). A total of six species (3 *Monomorium* species, 1 *Pheidole* species; a *Tetramorium* species and *Meranoplus magretti*) were subdominant. Although four of these, *Meranoplus magretti* André, *Monomorium cf. drapenum*, *Pheidole* UOVC_07 and *Monomorium damarense* Forel, had dominance scores > 50%, they monopolized < 25% of the baits. *Monomorium albopilosum* Emery monopolized 35% of the 284 baits (highest number of bait occupied and percentage monopolised for all ants in this category) but had a dominance score of < 50% (Table 9). All other ants (74 species) were considered subordinate because they all had dominance scores < 40% and monopolized < 15% of the baits where they occurred (Table 9).

Dominant ants monopolised the highest number of baits ($F_{2,6} = 5.25$, $P < 0.05$) when compared with other groups at higher elevational sites (14S – 17N), see Figure 15 and 16. Similarly, they also occupied the highest number baits ($F_{2,6} = 15.88$, $P < 0.01$) at these higher elevation (Figure 15 and 16). Interestingly, at both aspects dominant ants monopolised and occupied the least amount of baits at mid-elevational sites (12N and 12S) while subordinate and subdominant ants were mostly monopolising and occupying baits at these sites, see Figure 15 and 16.

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Table 9: Dominance hierarchies of ant species across the Soutpansberg transect based on behavioural and numerical dominance at bait stations (*n* = total number of competitive interactions observed. Subordinate selected species = only species with enough data (i.e. where *n* is > 10)).

Dominance Category & Species/Morph species	*n*	Dominance scores	Sum of baits occupied	% monopolized
Dominant				
Pheidole UOVC_05 (*megacephala* gp.)	26	96	399	40
Pheidole UOVC_10 (*megacephala* gp.)	24	96	370	35
Crematogaster UOVC_01 subgenus *Sphaerocrema*	15	93	97	24
Crematogaster UOVC_03 (*rufigena* gp.)	8	88	15	47
Pheidole UOVC_01 (*megacephala* gp.)	30	84	403	26
Pheidole UOVC_02 (*liengmei gp.*)	6	83	115	25
Pheidole UOVC_03 (*megacephala* gp.)	21	77	278	40
Myrmicaria natalensis	11	64	185	34
Subdominant				
Meranoplus magretti	5	80	26	12
Monomorium cf. drapenum	17	71	204	13
Pheidole UOVC_07	13	69	119	14
Monomorium damarense	6	67	129	9
Monomorium albopilosum	49	31	284	35
Tetramorium UOVC_07 *(weitzeckeri* gp.)	17	29	174	11
Subordinate (selected species)				
Polyrhachis schistacea	23	35	118	6
Ocymyrmex fortiori	19	33	63	2
Lepisiota UOVC_01 *(capensis* gp.)	20	25	149	4
Camponotus cf. niveosetosus	18	22	36	8
Lepisiota crinite	10	20	14	7
Technomyrmex pallipes	14	14	163	13
Camponotus UOVC_18 *(maculatus* gp.)	21	10	40	0

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Effects of space (elevation and habitat), bait type (cat food, sugar and oats) and time (time of the day and season) on the abundance and distribution of dominance categories across the Soutpansberg transect

Dominant ants were abundant in the shrubland, thicket and sedgeland. They decreased in the woodland, short forest and had the lowest numbers in the tall forest (Table 10). Dominant ants also occupied lowest percentage baits at the tall forest (Figure 17). Subdominant ants were very abundant in the short forest followed by woodland as well as shrubland. Although not significant, subdominant ants were also the least abundant in the tall forest (Table 10). Subordinate ants were very abundant in woodland and thicket while they were significantly less abundant in the short forest. Our model suggests that abundance of dominant and subdominant ants increases with elevation, while subordinate ants decrease with elevation (Table 10).

Sugar was preferred by the subordinate ants whereas both dominant and subdominant ants preferred cat food. The abundance of dominant and subdominant ants decrease over the two other baits type (oats and sugar) and the decrease is more pronounced for dominant ants (Table 10). Oats was the least preferred bait type.

Dominant ant abundance peaked in summer and was the lowest in winter. The abundance of this group also varied the most between seasons (Table 10). Although less variable, subdominant and subordinate ant abundance peaked in autumn. Subdominant ants preferred to forage during midday, dominant and subordinate ants during the late afternoon and evenings (Table 10). Dominant ant abundance was the lowest at midday while subordinate ants reached their lowest abundance in the morning and subdominant ants in the evening (Table 10).

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Table 10: Abundance of the three dominance groups using GLMM. Habitat, elevation, bait types, season and time of the day; level of significance = * P <0.05, ** P <0.01, *** P <0.001. The contributions of fixed and random effects in explaining the abundance of dominance classes.

	Dominant	**Sub-dominant**	**Subordinate**
Space	$R^2_m = 0.17$	$R^2_m = 0.31$	$R^2_m = 0.1$
	$R^2_c = 0.49$	$R^2_c = 0.47$	$R^2_c = 0.5$
Variables	Z-value	Z-value	Z-value
Sedgeland ↔ Short Forest	-19***	105.5***	-6.8***
Sedgeland ↔ Shrubland	39.7***	29.6***	-1.1
Sedgeland ↔ Tall forest	-56.1***	-14.4***	-1.4
Sedgeland ↔ Thicket	25.4***	1	9***
Sedgeland ↔ Woodland	-12***	67***	12.9***
Elevation	55.7***	49.8***	-18.5***
Bait	$R^2_m = 0.21$	$R^2_m = 0.03$	$R^2_m = 0.26$
	$R^2_c = 0.59$	$R^2_c = 0.68$	$R^2_c = 0.55$
Variables	Z-value	Z-value	Z-value
Cat food ↔ Oats	-150.9***	-73.4***	-59.4***
Cat food ↔ Sugar	-86***	-16.4***	11.7***
Time	$R^2_m = 0.05$	$R^2_m = 0.06$	$R^2_m = 0.07$
	$R^2_c = 0.6$	$R^2_c = 0.75$	$R^2_c = 0.57$
Variables	Z-value	Z-value	Z-value
Autumn ↔ Spring	-29.5***	-58.5***	-37.4***
Autumn ↔ Summer	51.2***	-47.4***	-23.7***
Autumn ↔ Winter	-57.6***	-44.5***	-37.6***
Midday ↔ Evening	45.4***	-68.8***	8.1***
Midday ↔ Late Afternoon	53***	-24***	10.6***
Midday ↔ Morning	14.3***	-50.8***	-16.7***

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Ant morphospace along the mountain

The woodland habitat (14N, 12N, 10N and 08N) had the largest morphospace along the mountain with subordinate ant abundance peaking in this habitat (Figure 14 and Table 8). Although dominant ants were abundant and monopolized the third highest number of baits at shrubland (09S), the ant morphospace of this site was large, third only to the two woodland sites, 10N and 12N (Table 8 and Figure 14). Species richness in the shrubland was the highest at the baits, while this also was the habitat with most species caught in pitfall traps (Table 8).

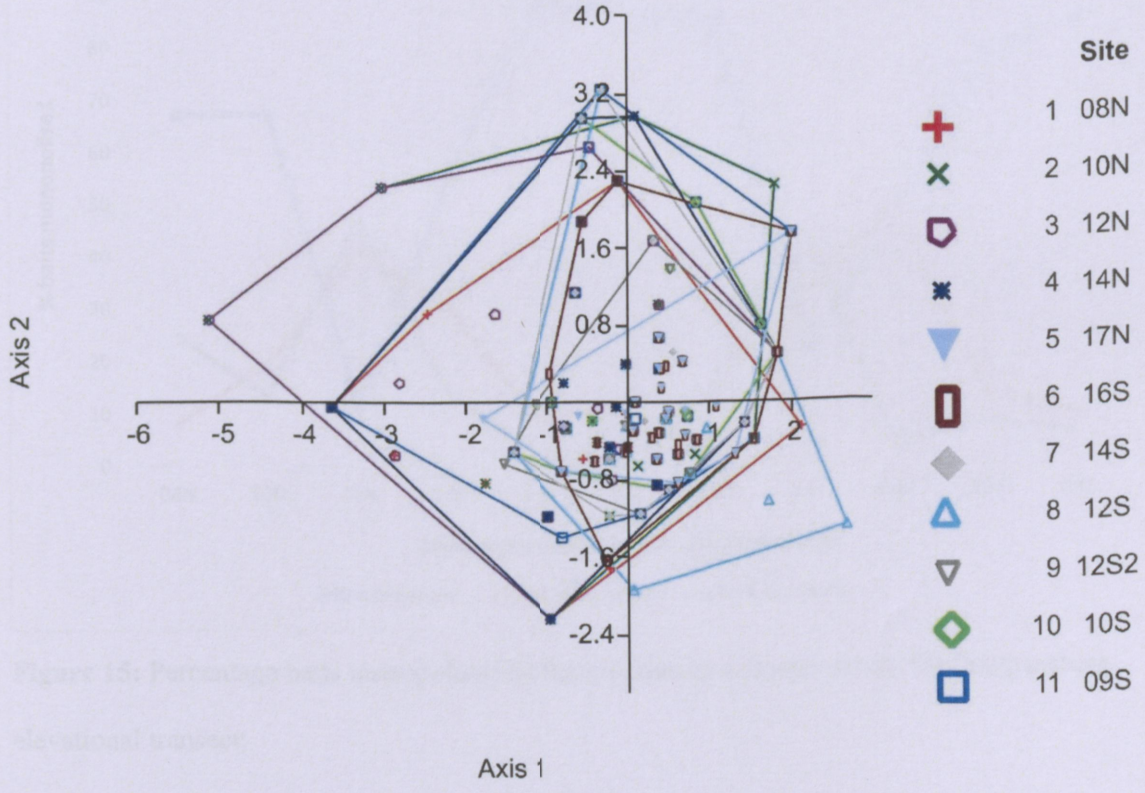

Figure 14: Graphic representation of variation of ant morphospace at 11 sites along the Soutpansberg elevational transect.

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The thicket (10S) and tall forest (12S) had the intermediate morphospace in this study with highest level of dominant ants in the thicket (Figure 14 and Table 8). Tall forest had the lowest abundance as well as species richness (Table 8). Sites in the sedgeland habitat (17N, 16S and 14S), had small morphospaces and the highest abundance of dominant ants. Although the short forest had a relatively large number of species, its morphospace was the smallest (Figure 14 and Table 8).



Figure 15: Percentage baits monopolised by three dominance classes across the Soutpansberg elevational transect.

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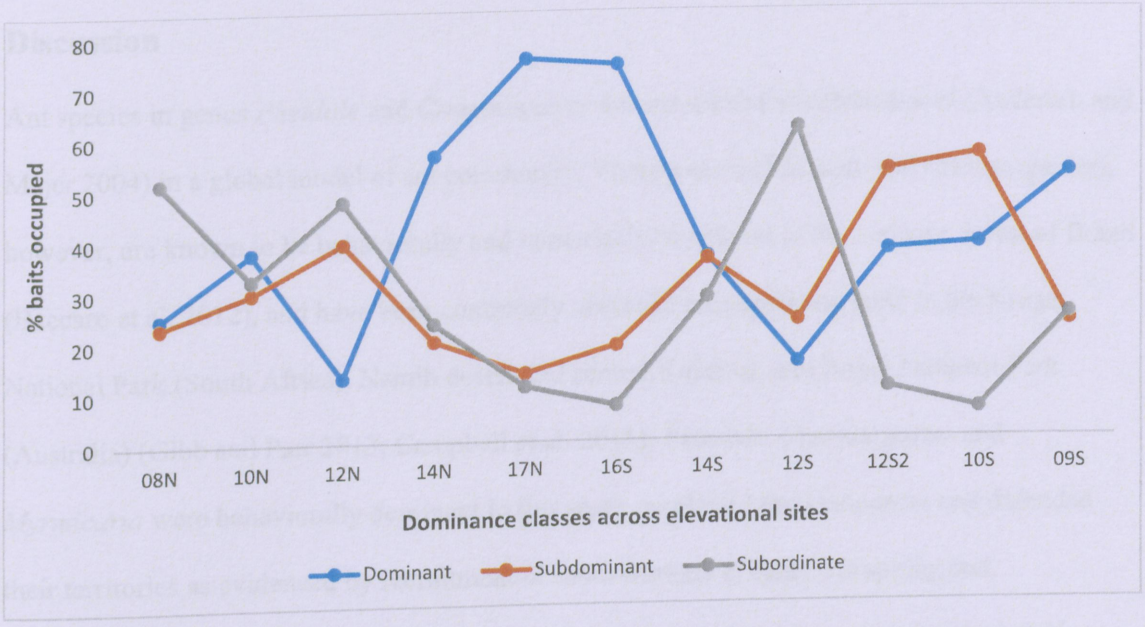

Figure 16: Percentage baits occupied by three dominance classes across the Soutpansberg elevational transect.



Figure 17: Percentage baits occupied by three dominance classes across five habitat types along the Soutpansberg transect.

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Discussion

Ant species in genus *Pheidole* and *Crematogaster* are considered as subdominant (Andersen and Majer 2004) in a global model of ant community. These genera (*Pheidole* and *Crematogaster*), however, are known to be behaviorally and numerically dominant in the Amazon forest of Brazil (Baccaro et al. 2012), and have been commonly observed monopolising baits in the Kruger National Park (South Africa), Namib desert and central Kalahari, and Royal National Park (Australia) (Gibb and Parr 2013; Campbell et al. 2015). *Pheidole*, *Crematogaster* and *Myrmicaria* were behaviorally dominant in this study, exploited food resources and defended their territories as evidenced by recruitment of more workers at baits, occupying and monopolizing more baits. Although these 'dominant' ants may not have such large territories as found in 'Dominant Dolichoderinae' (Arnan et al. 2011) they were territorial in sites where they occurred in the current study. The absence of 'Dominant Dolichoderinae' in southern African (Andersen 1997; Andersen and Majer 2004) has provided an opportunity for the subdominant species in this region to be dominant.

Dominant species in this study correspond to 'extirpators' and 'territorials' described in Hölldobler and Wilson (1990) and Savolainen and Vepsäläinen (1988) respectively. Across the mountain, abundances of dominant ants was positively associated with sedgeland, shrubland and thicket. Sedgeland had the lowest species richness while the same dominant groups were negatively associated with woodland and short forest habitat which were highly diverse (high species richness, baiting data Table 8). This suggests the negative effect that dominant ants (due to high percentage bait monopolisation and occupancy of baits), 'territorials', have on the species richness at a site where they are abundant (Morrison 1996).

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Previous studies propose that subdominant ants broadly defend food and nests only i.e. 'encounters' as described in Savolainen and Vepsäläinen (1988) and they are usually the first to arrive at baits and they are confident in the presence of more dominant species 'opportunists' as described in Hölldobler and Wilson (1990). Although subdominant ants in the current study were not the first to arrive at baits, in many cases they won encounters but failed to exclude other ant species at baits (low bait monopolisation) where they occurred (T. C. Munyai, personal observation).

The majority of species (74) categorized as subordinate species were generally submissive. Savolainen and Vepsäläinen (1988) reported that 'submissives' defend only their nests. Species in this group recruit few individuals at baits and they are also able to gain access to resource 'insinuators' by going unnoticed by dominant species (Hölldobler and Wilson 1990).

Dominant and subordinate species were at the same time at baits throughout the day except in the mornings was observed (Table 8). Subordinate ants were usually on top or the one side of the bait while the dominant species occupied the base of the bait or the other side, and the presence of subordinate ants went unnoticed.

Dominant ants were abundant at sedgeland habitat where morphospace was second smallest of the habitat types following short forest. The environmental conditions, e.g. climate, at highest elevation (sedgeland) favours dominant ant activities and there is probably very little filtering as evidenced by high competitive interactions at this habitat.

Factors other than competition that may influence local ant richness could include trade-off against thermal tolerance, parasitoids, predators and habitat complexity (Cerda et al. 2013). Arid environments of this study (across woodland habitat sites) had some of the lowest abundances of

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dominant ants. In the Namibian desert habitat, Campbell et al. (2015) reported a lack of aggressive interactions (interspecific competition) and suggested that it might be due to the absence of true dominant ants.

Shrubland had the highest abundance of dominant ants and third largest morphospace as well as the highest species richness (Table 8). The high abundance of dominant ants might be related to the considerable disturbances in this habitat as it is experiencing mechanical clearing of woody vegetation and grazing by native megaherbivores (Munyai and Foord 2015b).

Disturbance (Connell 1978) might therefore be the main reason for increase in ant species richness despite the presence of dominant species in the shrubland habitat. In the Madeira Natural Park (Island of Laurisilva) disturbance influenced second highest amount of pure environmental variables in species turnover and species richness differences of ground beetles (Boieiro et al. 2013). Also in the Drakensberg Mountains of South Africa, disturbance history (fire) was one of the important factors responsible for increasing species turnover for invertebrates (including ants) on burned compared to unburned valleys (Uys et al. 2009). Farji-Brener et al. (2002) suggest that after a disturbance, the increase or decrease in species diversity depends on the frequency, characteristics of the disturbance and the existence of competitive hierarchies as one example of many factors structuring communities.

The short forest (12S2) had the smallest morphospace and the most subdominant ants suggesting the effects of environmental filtering favouring this group (Figure 14 and Table 10). Despite the presence of dominant ants within the thicket habitat (10S), species richness (pitfall trap data, see Table 8) is the third highest on the southern aspect suggesting that it might be that habitat heterogeneity has increased species richness. The tall forest had the lowest abundance and

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species richness across the transect. The small morphospace (fifth smallest across the transect) suggests that environmental filtering is taking place and thereby reducing the number of species.

Dominant ants preferred to forage during the late afternoon and evening while subdominant ants were most active during the midday. In the Duke forest of USA, dominant ants were also most active during the evenings while subdominant were active during the day (Stuble et al. 2013). However these results contradict the findings of a study by Bestelmeyer (2000) in the semi-arid western Chaco region in the Salta Province of Argentina where behavioural dominants were active at moderately higher temperature (during the day) although subordinate ants were most common during the hottest part of the day.

Bestelmeyer (2000) also reported that the dominant ant group (*Solenopsis*) monopolized the most baits during summer. Temperature influences ants foraging behaviour (Cerdar et al. 1997) and high temperatures reduce the abundance of almost all ants at baits, including dominant species (Parr 2008; Arnan et al. 2012).

Dominant ants in the current study preferred cat food as compared to sugar and oats while the subordinate ants preferred sugar baits. Dominant ants exclusively occupied the most attractive high quality food while subdominant and subordinates occupy the less attractive food in the forest canopies of the Amazon (Bluethgen et al. 2000) while high protein value tuna baits always attracted the three most common species in the Teniente Enciso National Park in northeastern Paraguay (Delsinne et al. 2007).

Four possible processes may underly the distribution of ants across the mountain. At higher elevations (sedgeland), dominant ants are controlling ant species richness through competitive exclusion. The increased species richness at the low elevation shrubland habitat (09S) benefits

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from disturbance (Intermediate Disturbance Hypothesis) while filtering of species with small morphospace and resultant smaller specific traits may affect diversity at both forest habitat sites. On the northern aspect heterogeneous habitat types together with reduced abundance of dominant ants could have caused the increased species richness. A functional classification of taxa would provide an independent test of these predictions. With functional diversity predicted to be low in the forest (filtering) and sedgeland (competition), intermediate in the thicket and high in the shrubland (disturbance and patch dynamics) and high in open woodlands.

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Chapter 6: General discussion and conclusion

The need for ant inventories in long-term monitoring projects across elevational gradients

A key contribution of this study is the provision of an inventory and baseline data for ant species collected using standardised pitfall surveys over a 5-year period across the Soutpansberg Mountain Range, South Africa. There are several reasons for the omission of invertebrates from biodiversity conservation programmes the most critical of which is the lack of public awareness of their importance in ecosystems (Cardoso et al. 2011). Inventories that follow standardized and comparable protocols and the identification of indicator taxa are the first steps towards resolving these contraints (Cardoso et al. 2011). The long-term monitoring of impacts of global change would require time series baseline data, identification of taxa with credible indicator potential and a substantial improvement in the understanding of the casual links between global change and animal distributions (Erasmus et al. 2002). Chapter Two identified such a taxon, ants, and provided the time series data (standardized 5-year period data) and the taxon's abundance and distribution across the Soutpansberg Mountain Range transect. It also identified indicator species associated with each of the groups that will act as baseline information for longer term studies along this transect.

Chapter Two showed that most ant species were sampled, a sample coverage (0.98) for the whole transect and almost all elevational sites separately, indicating that sampling was representative of the ant assemblage of the study area. There was, however, an exception of site at 1600 m. a.s.l on the southern aspect for which extrapolation suggests a considerable increase in richness with increased sampling. This site might be expriencing temporal change in the ant assemblage resulting from the current short woody invasion replacing the sedgeland (*Coleochloa* species) which are in this site.

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Three major groupings (high elevation sedgeland, woodland and forests/thicket habitats) were identified by the non-multidimensional scaling indicating three important habitat types that need to be particularly monitored and conserved if ant diversity on this mountain is to be conserved. The importance of these habitat types is evidenced by the species restricted to each of these habitat types i.e. the twenty-eight species restricted to the southern (high elevation sedgeland, lower elevational shrubland and thicket to mid-elevation forests) and nineteen to the northern aspect (woodland) and the indicator species for each of these habitat types, aspect and some of the elevational sites. Species which were restricted to highest elevational sites (1400 – 1700 m. a.s.l) are probably in danger of extinction because of the predicted increase in temperature (van Wilgen et al. 2015), which will depend on how close the individual species are to the their thermal optimums and tolerances of their fundamental niches (Colwell et al. 2008), and increase in rainfall in this region (Davis et al. 2010) which will shift and change the habitat types as this will in turn have profound influence on the limiting resources that these species depend on.

Correlates ant alpha diversity across gradients

Another key findings of this study was the identification of correlates of ant species diversity (alpha and beta diversity) over spatio-temporal variability across the transect (Chapter Three and Chapter Four). Given that over space and time both correlates and drivers of species richness are still poorly understood and that they are often context specific in determining species richness patterns, this study provided the first of such results where the role of season, elevation and their interaction is affecting ant species richness and highlights the importance of neutral processes and temperature as correlates of variation in species richness patterns while soil characteristics (clay and carbon content) explained significant although small amounts of the observed variation (chapter three).

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Similarly, most studies along elevational gradients have documented the importance of temperature (Sanders et al. 2003, Sanders et al. 2007, Bishop et al. 2014, Werenkraut et al. 2015), geometric constraints (Sanders 2002) and soil characteristics (Botes et al. 2006, Munyai and Foord 2012) as the determinants of species diversity patterns. However, this study unlike many other studies provided temporal dynamics of diversity over a 5-year period while very few have done so for more than a year (but see Bishop et al. 2014).

The observed richness patterns consistently peaking at lowest elevation site of the southern aspect in this study is rarely observed. However, most ant studies report a decrease in richness at higher elevation which is similar as reported in this study, see Dunn et al. (2010) for a review. Other studies found no ants at the highest elevation (e.g. 3380 in Costa Rica (Janzen 1973) and 3200 m in Sudan (Weber 1943)) surveyed. The northern aspect had a mid-elevational peak of which there is a growing body of studies finding support for this pattern across elevational gradients, *inter alia* Chaladze (2012) and Bishop et al. (2014). This observed pattern did not change over time and also interestingly, elevation had an effect on seasonal variation where it decreased with elevation and this further supports that increased richness at lower to mid-elevation is not the result of dispersal from the regional species pool but caused by decreased activity levels of ant colonies during cold and resource poor periods (dry season) whereby taxa are often less tolerant of colder temperatures.

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Correlates of ant beta diversity across gradients

In chapter four, I identified both environmental and spatial variables that consistently explained the turnover for ant species across the study period. Available area, NDVI, percentage clay in the soil and minimum temperature explained a significant amount of species turnover. Other studies reported similar correlations e.g. available area in a spider study (Carvalho et al. 2011), and soil characteristics (Kaspari et al. 2000, Link et al. 2003) as well as temperature (Del Toro 2013, Paknia and Pfeiffer 2014, Silva and Brandao 2014) for ant studies.

This study also revealed that spatially structured environmental variables consistently and significantly explained the largest amount of variation in ant species turnover followed by pure spatial while the pure environmental variables explained the least amount (Chapter Four). The high explanatory power of spatially structured environmental variables have also been reported in spiders (Carvalho et al. 2011) and beetles (Baselga 2008). However, some ant studies have reported the weak effects of these variables in explaining turnover (Paknia and Pfeiffer 2014). The dominant role of pure spatial and spatially structured environmental variables emphasise the importance of spatially structured environmental variables (Sattler et al. 2010) in shaping communities in natural systems similar to the current study compared to urban habitat. The role of dispersal processes will, however, be less important as compared to pure environmental and spatially structured environmental variables resulting from predicted (Davis et al 2010, van Wilgen et al 2015) increase in temperature and rainfall in the region.

This study also revealed the dominant role of large spatial scale in explaining ant species turnover which proved to be similar to spider studies elsewhere, e.g. (Carvalho et al. 2011, Goncalves-Souza et al. 2014). Chapter Four also test the effect of space-time interaction and revealed that their interaction on ant assemblage structure was not significant. This result

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therefore suggested that the spatial patterns did not vary over the period of the study and that changes in time were common to all the sites and because space played a major role, much of the variation partitioned results into spatial and niche processes which were very similar over time.

The importance of competition in structuring ant species assemblages

In chapter five, I investigated some of the mechanisms that affect point diversity at a site across the study area and revealed that dominant ants only control species richness at baits on top of the mountain (sedgeland habitat) through competitive exclusion. This suggests that although competition is considered as the 'hallmark' of ant ecology (Hölldobler and Wilson 1990), its outcome is strongly context-depended and varies along environmental gradients. There is probably a combined role of dominance (competitive exclusion) with other mechanisms in structuring ant assemblages, but the latter were not investigated in the current study. The inferred alternative roles of habitat heterogeneity together with low abundance of dominant ants (open woodland), environmental filtering (short forest) and disturbance (shrubland) suggest that all these processes have to be considered if we are to understand ant assemblage structure and their response to change. For ants in particular, various studies at different scales have revealed the role of disturbance (Gibb et al. 2015), environmental filtering (Wiescher et al. 2012, Fowler et al. 2014) and habitat heterogeneity (Pacheco and Vasconcelos 2012, Parui et al. 2015).

Dominant ants were abundant at sedgeland habitat (high elevations) which had the second smallest morphospace following short forest habitat indicating that environmental conditions e.g. climate at higher elevation (sedgeland habitat) favours dominant ants and there is little filtering as evident by highest competitive behaviour (highest number of baits occupied and monopolised by dominant ants) observed at this habitat. Further studies should develop a functional classification of taxa to provide an independent test of these predictions. I therefore predict that

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functional diversity will be lower in the forest (filtering) and sedgeland (competition), intermediate in the thicket and high in the shrubland (disturbance and patch dynamics) and woodlands (higher temperatures).

The role of dominant ants in structuring ant species assemblages have been reported in various studies (Bestelmeyer 2000, Parr 2008). Although this role is mediated by other factors e.g. habitat complexity in Gibb and Parr (2010) where foraging success of dominant ants were affected by it. Temperature has also been reported in many studies to affect dominant ant activities and thereby determining when they control resources (Cerdar et al. 1997, Bestelmeyer 2000, Arnan et al. 2012). Other biotic factors such as predation and parasitoids influence local ant richness (Cerda et al. 2013) because they promote species co-existence whereby they interrupt the process of competitive exclusion as well as influencing profoundly the outcome of competitive processes, and impose their own order on community organization (Begon et al. 2006). These processes, predation and parasitism, will need further investigation along this transect in order to uncover how they might be responsible for determining ant communities (if they do) across this study area.

Predicted future changes (Munyai and Foord 2012) should see the relative role of pure environmental and spatially structured environmental variables increase because of the filtering associated with bush encroachment (environmental filtering) on the southern aspect and increased importance of temperature on the northern aspect. It is therefore encouraged that further studies should investigate upper and lower critical thermal limits (CTLs) of ant species, because this will assist in monitoring the nature and pace of global change in the area as it unfolds. Future studies across the transect should also investigate ant functional diversity if ecosystem vulnerability and productivity across the mountain is to be predicted.

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Appendices

Appendix 1: Summary of number of replicates set out at each of the eleven sites during each of the 13 surveys along the Soutpansberg mountain range. A replicate within a site consisted of 10 pitfalls in a 2 × 5 grid. Pitfalls were separated by 10 m and replicates within a site were separated by at least 300 m to ensure independence.

	Survey												
Site	**Dec 2008**	**Feb 2009**	**April 2009**	**May 2009**	**July 2009**	**Sept 2009**	**Jan 2010**	**Sept 2010**	**Jan 2011**	**Sept 2011**	**Jan 2012**	**Sept 2012**	**Jan 2013**
08N	1	1	1	1	1	4	4	4	4	4	4	4	4
10N	1	1	1	1	1	4	4	4	4	4	4	4	4
12N	1	1	1	1	1	4	4	4	4	4	4	4	4
14N	1	1	1	1	1	4	4	4	4	4	4	4	4
17N	1	1	1	1	1	4	4	4	4	4	4	4	4
16S	1	1	1	1	1	4	4	4	4	4	4	4	4
14S	1	1	1	1	1	4	4	4	4	4	4	4	4
12S	1	1	1	1	1	4	4	4	4	4	4	4	4
12S2	1	1	1	1	1	4	4	4	4	4	4	4	4
10S	1	1	1	1	1	4	4	4	4	4	4	4	4
09S	1	1	1	1	1	4	4	4	4	4	4	4	4

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Appendix 2: Check list of subfamilies and ant species with their abundances collected during thirteen surveys in different broad structural vegetation types across an elevational transect across the western Soutpansberg mountain range in South Africa

Subfamilies and Species	**Five broad structural vegetation types**					
	Wood-land	Sedgeland /Herbland	Forest	Thickets	Shrub -land	Total
Dolichoderinae						
Tapinoma sp.01 *?luteum* Emery	121	15	5	0	1	142
Technomyrmex pallipes Smith	1143	748	27	44	40	2002
Dorylinae						
Aenictus rotundatus Mayr	787	0	0	0	7	794
Cerapachys UOVC_01	1	5	1	0	0	7
Cerapachys wroughtoni Forel	0	0	0	3	0	3
Dorylus helvolus Linnaeus	0	79	2104	2	193	2378
Dorylus UOVC_02	45	0	0	0	0	45
Formicinae						
Anoplolepis cf custodiens	92	1	0	0	3	96
Camponotus cf niveosetosus	2	9	1	24	6	42
Camponotus dofleini Forel	1	1	0	0	0	2
Camponotus fulvopilosus De Geer	463	0	0	0	0	463
Camponotus mayr Forel	35	1	0	2	2	40
Camponotus UOVC_02 (*rufoglaucus* gp.)	25	8	7	59	23	122
Camponotus UOVC_03 (*niveosetosus* gp.)	0	22	0	0	5	27
Camponotus UOVC_04 (*etiolipes* gp)	3	4	3	0	0	10
Camponotus UOVC_05	168	9	0	1	9	187
Camponotus UOVC_06 (*maculatus* gp.)	1	10	6	0	4	21
Camponotus UOVC_07 (*empedocles* gp.)	1	59	0	0	1	61
Camponotus UOVC_08 (*mystaceus* gp.)	0	1	0	0	0	1
Camponotus UOVC_11 (*cinctellus* gp.)	5	10	14	58	56	143

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Subfamilies and Species	Five broad structural vegetation types					
	Wood-land	Sedgeland /Herbland	Forest	Thickets	Shrub -land	Total
Camponotus UOVC_12 (*cinctelus* gp.)	1	16	0	2	20	39
Camponotus UOVC_17	0	0	1	0	0	1
Camponotus UOVC_18 (*maculatus* gp.)	54	14	16	18	32	134
Camponotus UOVC_20 (*niveosetosus* gp.)	11	0	0	0	0	11
Camponotus UOVC_21 (*cuneiscapus* gp.)	7	0	6	0	0	13
Camponotus UOVC_22	2	0	0	0	0	2
Lepisiota cf longinoda Arnold	1	35	0	0	0	36
Lepisiota crinita Mayr	0	1	42	5	1	49
Lepisiota UOVC_01 (*capensis* gp.)	476	303	79	232	110	1201
Lepisiota UOVC_02 (*spinosior* gp.)	57	2	2	0	3	64
Lepisiota UOCV_08 (*capensis* gp.)	72	0	0	0	0	78
Lepisiota UOVC_09 (*capensis* gp.)	0	15	0	0	1	16
Lepisiota UOVC_10 (*capensis* gp.)	6	1	440	0	0	441
Lepisiota UOVC_11	0	0	1	0	0	1
Plagiolepis UOVC_02	40	39	16	1	0	96
Plagiolepis UOVC_03	15	29	18	1	0	63
Polyrhachis schistacea Gerstäcker	18	0	0	61	20	99
Polyrhachis spinicola Forel	0	0	0	1	0	1
Tapinolepis UOVC_01	2325	0	0	0	25	2350
Myrmicinae						
Cardiocondyla UOVC_01	3	0	0	0	5	8
Cardiocondyla UOVC_02	4	0	0	0	0	4
Carebara UOVC_01	0	5	6	15	2	28
Cataulacus UOVC_01	4	0	1	0	0	5
Cataulacus wissmannii Forel	6	0	0	0	1	7
Crematogaster UOVC_01 subgenus *Sphaerocrema*	359	16	13	2	34	424
Crematogaster UOVC_02 (*rufigena* gp.)	37	13	7	3	1	61
Crematogaster UOVC_03 (*rufigena* gp.)	46	4	36	3	10	101
Crematogaster UOVC_04 subgenus *Sphaerocrema*	31	5	8	0	15	59
Crematogaster UOVC_05	8	0	0	0	0	8

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Subfamilies and Species	Five broad structural vegetation types					
	Wood-land	Sedgeland /Herbland	Forest	Thickets	Shrub -land	Total
Crematogaster UOVC_06 (*custanea* complex)	13	3	0	0	0	16
Meranoplus ?peringueyi	0	218	0	0	0	218
Meranoplus cf glaber Arnold	128	0	0	0	0	128
Meranoplus inermis Emery	0	0	1	4	13	18
Meranoplus magrettii André	214	0	0	0	7	221
Messor UOVC_01	0	0	0	42	0	42
Monomorium ?fastidium Bolton	163	23	0	0	0	186
Monomorium ?notulum Forel	1110	83	0	2	1	1535
Monomorium albopilosum Emery	1384	2627	254	118	192	4575
Monomorium cf. drapenum Bolton	4870	19	54	12	57	5328
Monomorium cf. junodi Forel	0	0	0	785	278	1063
Monomorium damarense Forel	1772	17	9	429	389	2666
Monomorium emeryi mayr	22	0	0	0	0	128
Monomorium UOVC_01	8	0	19	0	0	27
Monomorium UOVC_07	20	87	142	11	1	261
Monomorium UOVC_08 (*monomorium* gp.)	176	34	28	11	22	278
Monomorium UOVC_10 (*salomonis* gp.)	334	0	0	28	32	782
Monomorium UOVC_12 (*monomorium* gp.)	13	36	0	1	0	50
Monomorium UOVC_13	47	19	94	3	2	165
Myrmicaria natalensis Smith	1375	41	96	512	456	2480
Ocymyrmex flaviventris Santschi	153	0	0	0	0	153
Ocymyrmex fortior Santschi	2956	0	0	0	74	3030
Ocymyrmex UOVC_03	39	0	0	0	0	39
Pheidole UOVC_01 (*megacephala* gp.)	6097	940	1248	765	654	9704
Pheidole UOVC_02 (*liengmei* gp)	2788	20	11	17	42	2878
Pheidole UOVC_03 (*megacephala* gp.)	2857	92	1537	11738	962	17186

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Subfamilies and Species	Five broad structural vegetation types					
	Wood-land	Sedgeland /Herbland	Forest	Thickets	Shrub -land	Total
Pheidole UOVC_05 (*megacephala* gp.)	1	4807	0	0	0	4808
Pheidole UOVC_06 (*crassinoda* gp.)	305	21	1	331	107	765
Pheidole UOVC_07	1396	27	13	0	0	1436
Pheidole UOVC_09 (*crassinoda* gp.)	882	0	0	16	3	901
Pheidole UOVC_10 (*megacephala* gp.)	0	2835	0	0	0	2835
Pheidole UOVC_11	0	0	0	0	28	28
Pheidole UOVC_12	5	0	0	0	0	5
Rhoptromyrmex UOVC_02	0	14	0	0	0	14
Rhoptromyrmex transversinodis Arnold	0	2	11	32	1	46
Solenopsis UOVC_01	1	103	115	0	0	235
Solenopsis UOVC_02	6	9	80	8	0	149
Strumigenys ?arnodi Forel	0	1	0	0	0	1
Strumigenys pretoriae Arnold	0	2	0	0	0	2
Strumigenys UOVC_01	2	1	1	5	0	9
Strumigenys UOVC_02	0	0	1	0	0	1
Tetramorium baufra Bolton	1480	20	0	0	14	1514
Tetramorium cf. setigerum Mayr	64	197	67	49	28	405
Tetramorium notiale Bolton	0	4	18	27	16	65
Tetramorium sepositum Santschi	489	0	0	0	0	489
Tetramorium setuliferum Emery	315	38	0	0	2	355
Tetramorium UOVC_01 (*squaminode* gp.)	310	111	137	23	2	583
Tetramorium UOVC_04 (*gabonense* gp.)	14	0	2	15	87	118
Tetramorium UOVC_05 (*sericeiventre* gp.)	0	3	0	0	131	134
Tetramorium UOVC_07 (weitzeckeri gp.)	201	219	445	447	391	1703
Tetramorium UOVC_08 (*simillimum* gp.)	91	96	185	2	31	405
Tetramorium UOVC_10 (*squaminode* gp)	0	174	0	0	0	174

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Subfamilies and Species	Five broad structural vegetation types					
	Wood-land	Sedgeland /Herbland	Forest	Thickets	Shrub -land	Total
Tetramorium UOVC_11 (*squaminode* gp.)	6	229	0	10	0	245
Tetramorium UOVC_12 (squaminode gp.)	3	201	969	0	5	1178
Tetramorium UOVC_13	0	14	13	13	0	40
Tetramorium UOVC_14 (*sericeiventre* gp.)	0	527	1	0	0	528
Tetramorium UOVC_16 (*sericeiventre* gp.)	0	459	75	0	27	561
Tetramorium UOVC_17 (*simillimum* gp.)	0	0	3	0	0	3
Tetramorium UOVC_18 (*simillimum* gp.)	27	2	0	0	0	29
Tetramorium UOVC_19 (*simillimum* gp.)	32	8	22	2	10	74
Tetramorium UOVC_20	0	1	0	0	0	1
Tetramorium UOVC_21 (*squaminode* gp)	0	6	4	0	0	10
Tetramorium UOVC_22	0	0	0	0	3	3
Ponerinae						
Anochectus cf. traegaordhi Mayr	6	0	0	1	0	7
Anochectus UOVC_01	0	0	5	0	1	6
Anochectus UOVC_02	0	0	1	0	0	1
Bothroponera ?strigulosa Emery	1	2	15	116	8	142
Bothroponera UOVC_02	0	0	1	18	1	20
Bothroponera UOVC_03	0	0	0	0	9	9
Hypoponera UOVC_01	0	1	4	0	2	7
Leptogenys intermedia Emery	0	49	8	11	11	79
Leptogenys schwabi Forel	0	7	0	39	8	54
Mesoponera ?caffraria Santschi	2	6	6	39	159	212
Odontomachus troglodytes Santschi	35	0	0	0	12	47
Ophthalmopone UOVC_01	0	0	0	0	4	4
Platythyrea lamellosa Roger	93	1	1	1	2	98
Platythyrea shultzei Forel	27	0	0	2	0	29
Plectroctena ?mandibularis Smith	2	4	10	0	3	19

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Subfamilies and Species	Five broad structural vegetation types					
	Wood-land	Sedgeland /Herbland	Forest	Thickets	Shrub -land	Total
Plectroctena UOVC_02	0	0	2	1	0	3
Plectroctena ?subterranean Arnold	1	0	0	1	0	2
Ponera UOVC_01*	1	0	2	0	0	3
Pseudoponera UOVC_01	7	4	0	0	4	15
Pseudoponera UOVC_02	0	0	0	0	4	4
Pseudomyrmicinae						
Tetraponera UOVC_01	2	1	0	0	0	3

UOVC = University of Venda Collection

*, Introduced species.

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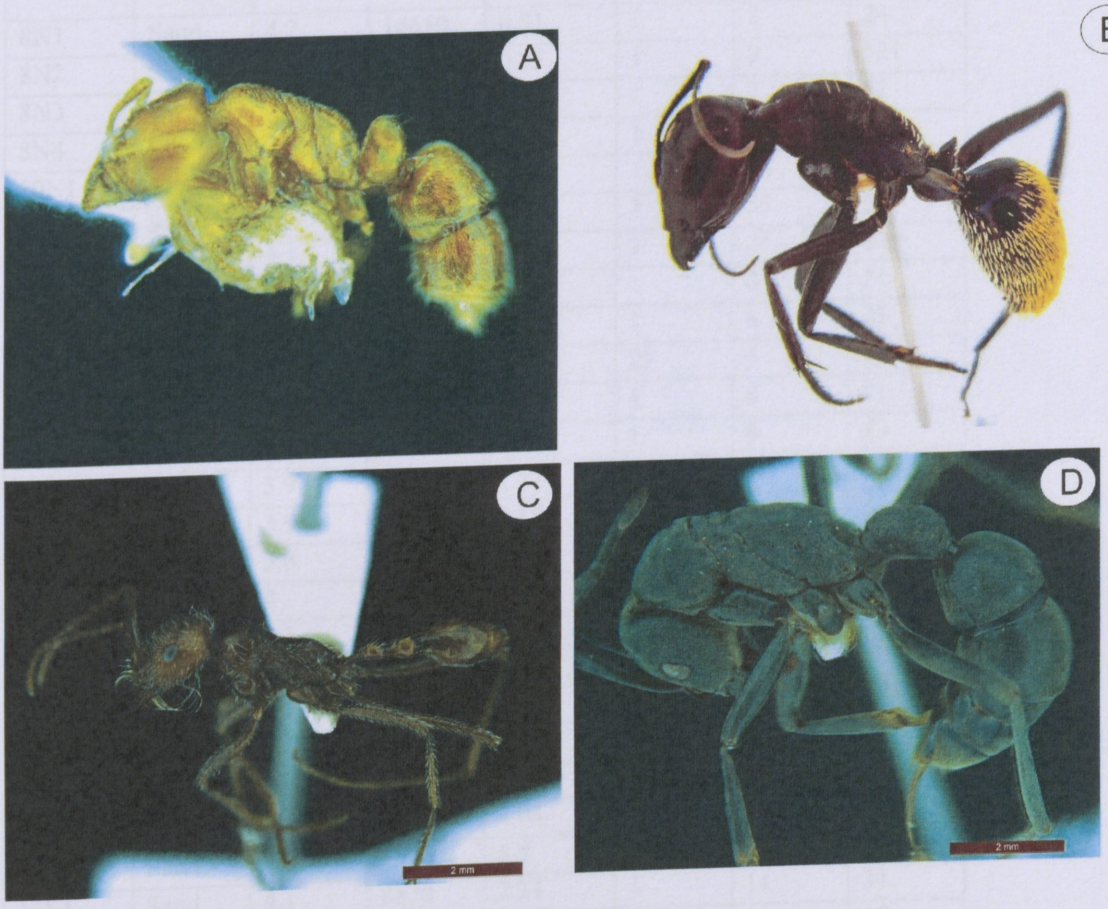
Appendix 3: Images of some notable and interesting species collected during 13 surveys: (a) introduced species *Ponera* UOVC_01, (b) *Camponotus fulvopilosus* De Geer, (c) *Ocymyrmex flaviventris* Santschi and (d) *Platythyrea lamellosa* Roger.



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Appendix 4: Soil properties of all 44 replicates along the Soutpansberg transect.

Replicate	Soil	pH	Resist.	H^+	Stone	P Bray II	K
Site	Soil	(KCl)	(Ohm)	(cmol/kg)	(Vol %)	mg/kg	
8N1	Sand	4.2	14650	0.51	1	2	24
8N2	Sand	5.6	770	0.35	1	9	521
8N3	Sand	4.4	8270	0.71	1	7	52
8N4	Sand	4	12900	0.71	1	7	21
10N1	Sand	4.4	1240	0.76	1	18	68
10N2	Sand	3.5	1760	2.93	1	55	50
10N3	Sand	5.3	3120	0.76	1	25	249
10N4	Sand	3.9	15600	0.96	1	8	21
12N1	Sand	3.7	12860	1.36	1	6	21
12N2	Sand	3.8	11000	1.41	27	4	24
12N3	Sand	3.1	6800	6.62	1	8	51
12N4	Sand	3.6	7370	1.77	1	6	23
14N1	Sand	3.9	7450	1.57	8	11	26
14N2	Sand	3.9	14240	1.57	1	9	36
14N3	Sand	3.8	18240	1.06	1	9	15
14N4	Sand	4	8000	1.26	1	6	23
17N1	Sand	4.2	9050	2.02	1	10	52
17N2	Sand	4	5130	3.03	19	13	67
17N3	Sand	3.7	5050	4.7	1	46	176
17N4	Sand	4	13190	3.33	1	21	60
16S1	Sand	3.9	2650	5.61	1	14	56
16S2	Sand	4	3590	4.04	4	12	46
16S3	Sand	3.9	1440	5.5	16	26	82
16S4	Sand	4.1	8870	2.37	1	11	34
14S1	Sand	4.1	5480	1.41	4	12	47
14S2	Sand	4.2	8420	1.26	1	8	21
14S3	Sand	3.9	5970	1.77	1	32	22
14S4	Sand	3.9	5300	1.77	1	53	227
12S1	Sand	6	1130	0.35	1	56	359
12S2	Sand	5.1	1400	1.31	1	16	262
12S3	Sand	6.4	690		1	42	382
12S4	Sand	6.2	650		1	4	725
12S2.1	Sand	4.5	3170	0.86	1	4	142
12S2.2	Sand	4.5	1580	1.67	1	7	291
12S2.3	Sand	5.4	1000	0.86	1	5	196
12S2.4	Loam	5	2680	1.26	1	6	404

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10S1	Sand	5.2	1260	0.86	1	4	119
Orchard	Soil	pH	Resist.	H^+	Stone	P Bray II	K
Site	Soil	(KCl)	(Ohm)	(cmol/kg)	(Vol %)	mg/kg	
10S2	Loam	5.8	1170	1.52	1	68	408
10S3	Sand	5.1	850	1.01	1	3	111
10S4	Loam	5.1	1400	0.86	1	3	117
9S1	Loam	4.8	970	1.36	1	4	186
9S2	Clay	5.1	820	0.86	1	3	183
9S3	Loam	4.5	2670	1.01	1	4	201
9S4	Sand	4.6	2940	0.96	1	3	269

Replicate	Exchangeable cations (cmol(+)/kg)				C	NO_3-N	Na	K
Site	Na	K	Ca	Mg	%	mg/kg	%	%
8N1	0	0.06	0.3	0.09	0.28	3.54	0	6.46
8N2	0.07	1.33	3.15	1.76	1.24	40.4	1.1	19.98
8N3	0	0.13	0.82	0.35	0.72	6.26	0	6.6
8N4	0	0.05	0.3	0.1	0.48	3.97	0	4.73
10N1	0.05	0.17	0.9	0.31	0.62	31.52	2.17	7.95
10N2	0.08	0.13	0.39	0.09	2.34	34.84	2.2	3.53
10N3	0.09	0.64	4.43	1.69	2.26	9.08	1.23	8.37
10N4	0.01	0.05	0.41	0.06	0.3	3.85	0.49	3.58
12N1	0	0.05	0.07	0.01	0.99	3.51	0	3.59
12N2	0	0.06	0.06	0.01	0.94	3.85	0	4
12N3	0.03	0.13	0.75	0.23	3.98	3.2	0.36	1.69
12N4	0	0.06	0.24	0.06	1.59	5.32	0	2.79
14N1	0.03	0.07	0.06	0.02	0.95	5.54	1.58	3.81
14N2	0.02	0.09	0	0.01	0.73	2.83	1.16	5.45
14N3	0.02	0.04	0	0	0.88	3.6	2.22	3.38
14N4	0	0.06	0.41	0.07	0.5	5.33	0	3.22
17N1	0.04	0.13	0.35	0.24	1.79	6.91	1.45	4.8
17N2	0.04	0.17	0.16	0.1	3.44	9.12	1.27	4.9
17N3	0.07	0.45	0.58	0.27	4.4	8.02	1.12	7.39
17N4	0.04	0.15	0.59	0.08	3.71	3.72	1.06	3.64
16S1	0.03	0.14	0.22	0.1	4.98	39.27	0.51	2.33
16S2	0.05	0.12	0.66	0.3	3.6	18.25	0.99	2.26
16S3	0.11	0.21	0.53	0.23	4.47	39.9	1.61	3.2
16S4	0.04	0.09	0.13	0.03	1.82	6.98	1.65	3.28
14S1	0.01	0.12	0.41	0.14	1.33	8.16	0.42	5.8

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14S2	0.02	0.05	0.15	0.06	0.71	6.93	1.06	3.53
Replicate	Exchangeable cations (cmol(+)/kg)				C	NO_3-N	Na	K
Site	Na	K	Ca	Mg	%	mg/kg	%	%
14S3	0	0.06	0.4	0.24	1.16	6.84	0	2.32
14S4	0.03	0.58	0.2	0.16	1.15	8.65	0.97	21.26
12S1	0.04	0.92	11.12	3.11	2.53	22.73	0.28	5.9
12S2	0.16	0.67	11.33	3.88	5.06	2.25	0.95	3.87
12S3	0.14	0.98	18.51	4.69	5.11	78.86	0.56	4.02
12S4	0.11	1.85	11.55	2.93	2.34	54.48	0.65	11.27
12S2.1	0.04	0.36	1.9	0.79	0.69	11.61	1.02	9.18
12S2.2	0.08	0.75	4.75	2.12	2.42	20.18	0.86	7.95
12S2.3	0.13	0.5	13.33	7.43	5.14	21.43	0.58	2.26
12S2.4	0.12	1.03	9.71	4.04	2.3	34.99	0.75	6.39
10S1	0.14	0.3	8.54	7.56	3.33	6.71	0.81	1.75
10S2	0.09	1.04	9.02	2.78	1.84	13.9	0.63	7.22
10S3	0.15	0.28	9.11	5.39	2.31	21.15	0.97	1.78
10S4	0.1	0.3	7.5	5.09	1.61	10.41	0.72	2.17
9S1	0.12	0.48	10.44	5.82	2.01	11.26	0.65	2.61
9S2	0.09	0.47	10.73	7.19	1.66	14.11	0.47	2.42
9S3	0.08	0.51	4.5	2.89	0.25	4.11	0.86	5.72
9S4	0.06	0.69	3.38	1.86	1.72	3.88	0.93	9.87

Orchard	Ca	Mg	T-Value	Clay	Silt	Sand	Classification
Site	%	%	cmol/kg	%	%	%	Classification
8N1	31.2	9.69	0.97	0.8	0.2	99	Sa
8N2	47.29	26.38	6.66	0.6	0.8	98.6	Sa
8N3	40.89	17.31	2.02	0.8	0.2	99	Sa
8N4	25.64	8.49	1.16	1	0.4	98.6	Sa
10N1	41.11	14.08	2.19	0.6	1.8	97.6	Sa
10N2	10.87	2.48	3.62	1	0.4	98.6	Sa
10N3	58.19	22.23	7.62	1	0.4	98.6	Sa
10N4	27.56	4.09	1.49	1	0.4	98.6	Sa
12N1	4.54	0.69	1.49	0.6	0.8	98.6	Sa
12N2	3.97	0.86	1.55	0.8	0.2	99	Sa
12N3	9.67	2.94	7.76	1	0.4	98.6	Sa
12N4	11.35	2.97	2.14	0.6	0.8	98.6	Sa
14N1	3.56	1.37	1.75	3.4	0.4	96.2	Sa
14N2	0.12	0.45	1.69	3	2	95	Sa

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14N3	0	0	1.12	0.6	0.8	98.6	Sa
Orchard	Ca	Mg	T-Value	Clay	Silt	Sand	Classification
Site	%	%	cmol/kg	%	%	%	Classification
14N4	22.88	4.08	1.8	0.4	1	98.6	Sa
17N1	12.47	8.55	2.78	3.4	0.4	96.2	Sa
17N2	4.44	2.74	3.5	3.4	0.2	96.4	Sa
17N3	9.57	4.53	6.07	3.6	0.2	96.2	Sa
17N4	14.03	2	4.2	3.4	1.4	95.2	Sa
16S1	3.57	1.59	6.1	3.4	0.2	96.4	Sa
16S2	12.75	5.83	5.17	3.4	0.2	96.4	Sa
16S3	8.13	3.45	6.58	3.4	0.2	96.4	Sa
16S4	4.75	1.17	2.66	3.4	0.2	96.4	Sa
14S1	19.73	6.54	2.09	3.2	0.2	96.6	Sa
14S2	9.86	3.62	1.54	3.2	0.2	96.6	Sa
14S3	16.19	9.61	2.46	3	2	95	Sa
14S4	7.24	5.7	2.73	3.2	2.2	94.6	Sa
12S1	71.57	19.99	15.54	3	1	96	Sa
12S2	65.3	22.34	17.35	3.2	0.2	96.6	Sa
12S3	76.11	19.31	24.31	3	3	94	Sa
12S4	70.24	17.84	16.45	1	6	93	Sa
12S2.1	48.04	20.01	3.95	2	5	93	Sa
12S2.2	50.75	22.61	9.37	1	3	96	Sa
12S2.3	59.9	33.39	22.25	2	4	94	Sa
12S2.4	60.05	25.02	16.16	0	9	91	Sa
10S1	49.07	43.43	17.4	3	6.4	90.6	Sa
10S2	62.43	19.2	14.45	13.2	8.2	78.6	SaLm
10S3	57.11	33.8	15.96	9.4	11.8	78.8	LmSa
10S4	54.14	36.77	13.85	11	13	76	SaLm
9S1	57.31	31.96	18.22	17.2	9.8	73	SaLm
9S2	55.46	37.2	19.34	21.4	9.8	68.8	SaKlLm
9S3	50.02	32.18	9	12	3.4	84.6	SaLm
9S4	48.61	26.78	6.96	9.6	1.8	88.6	LmSa

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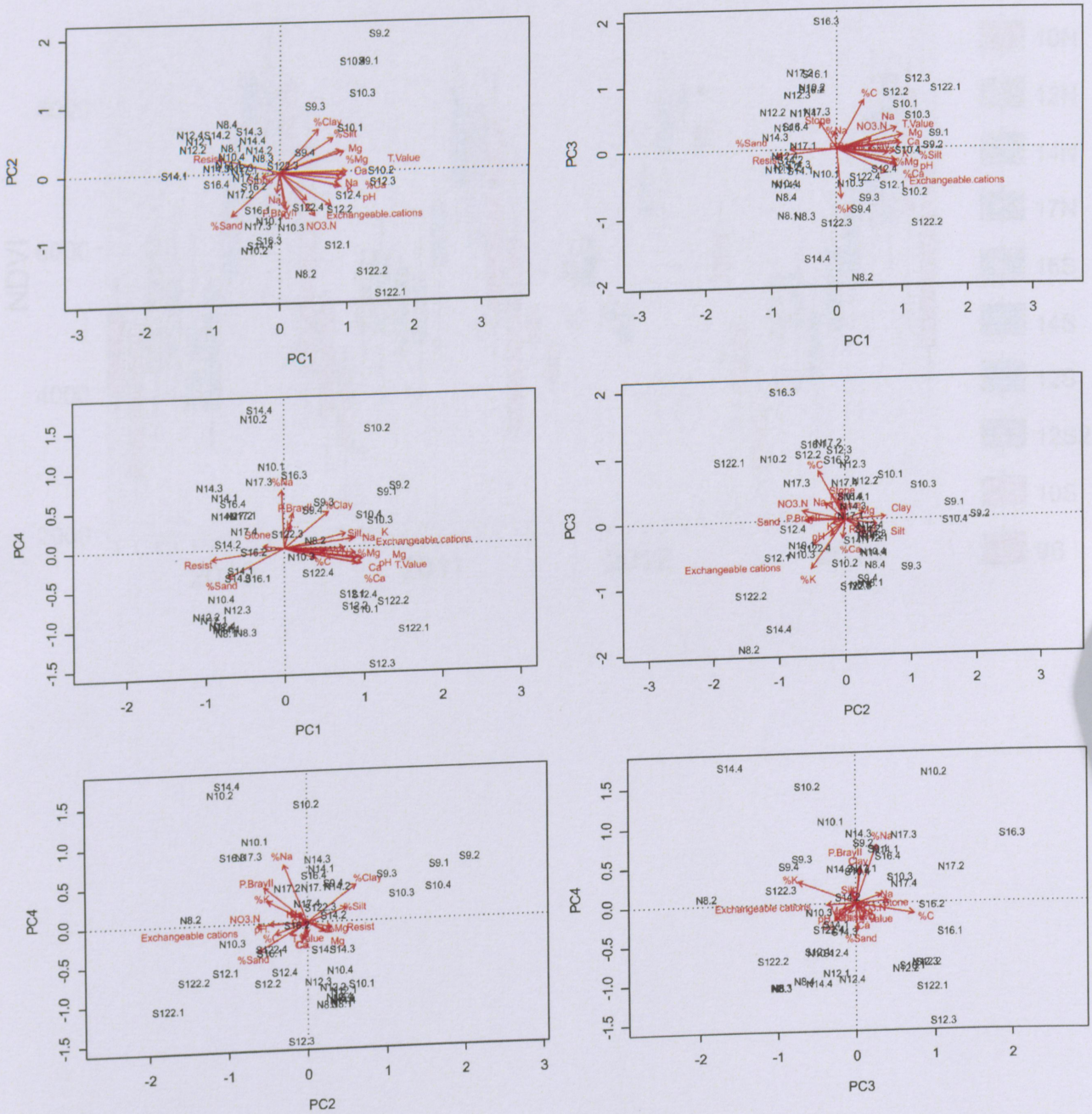
Appendix 5: Site and soil properties biplot of Principal Component Analysis. Red arrows indicate soil properties and black labels indicate replicates.



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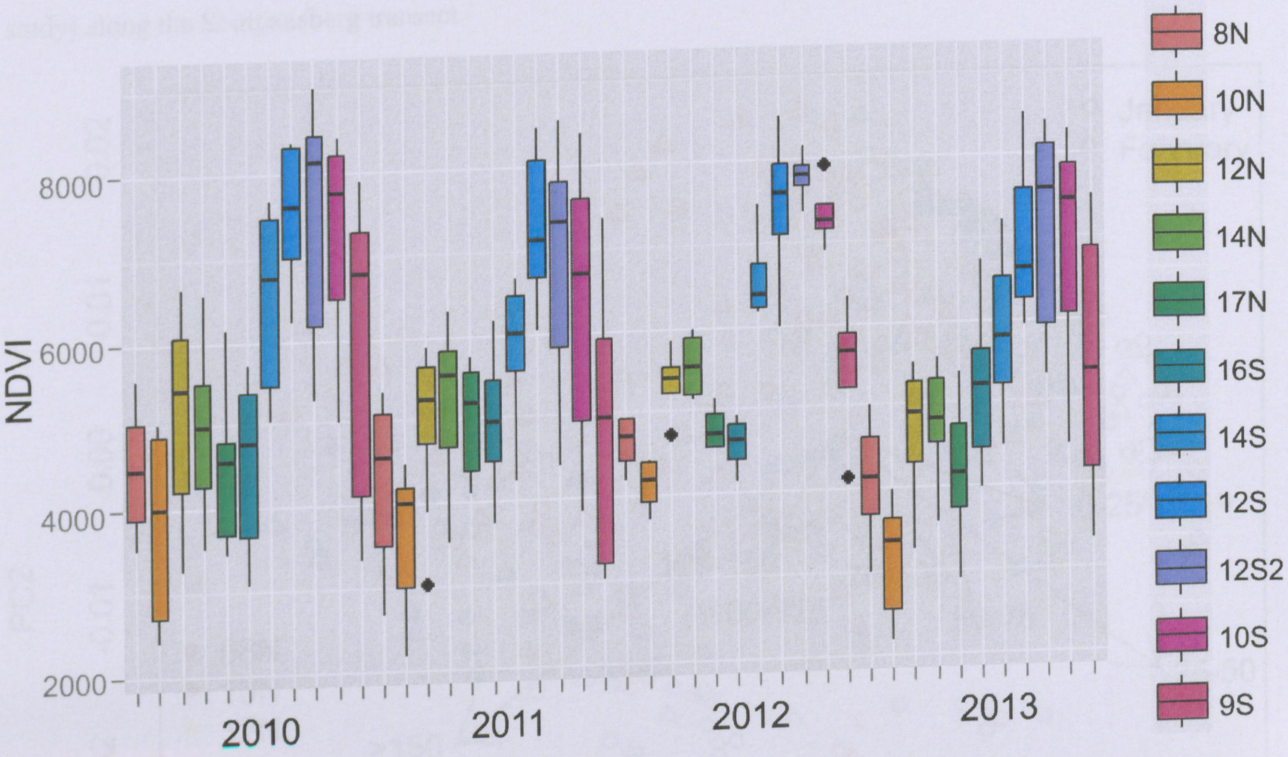
Appendix 6: Boxplot of NDVI at each site over the period of the study.



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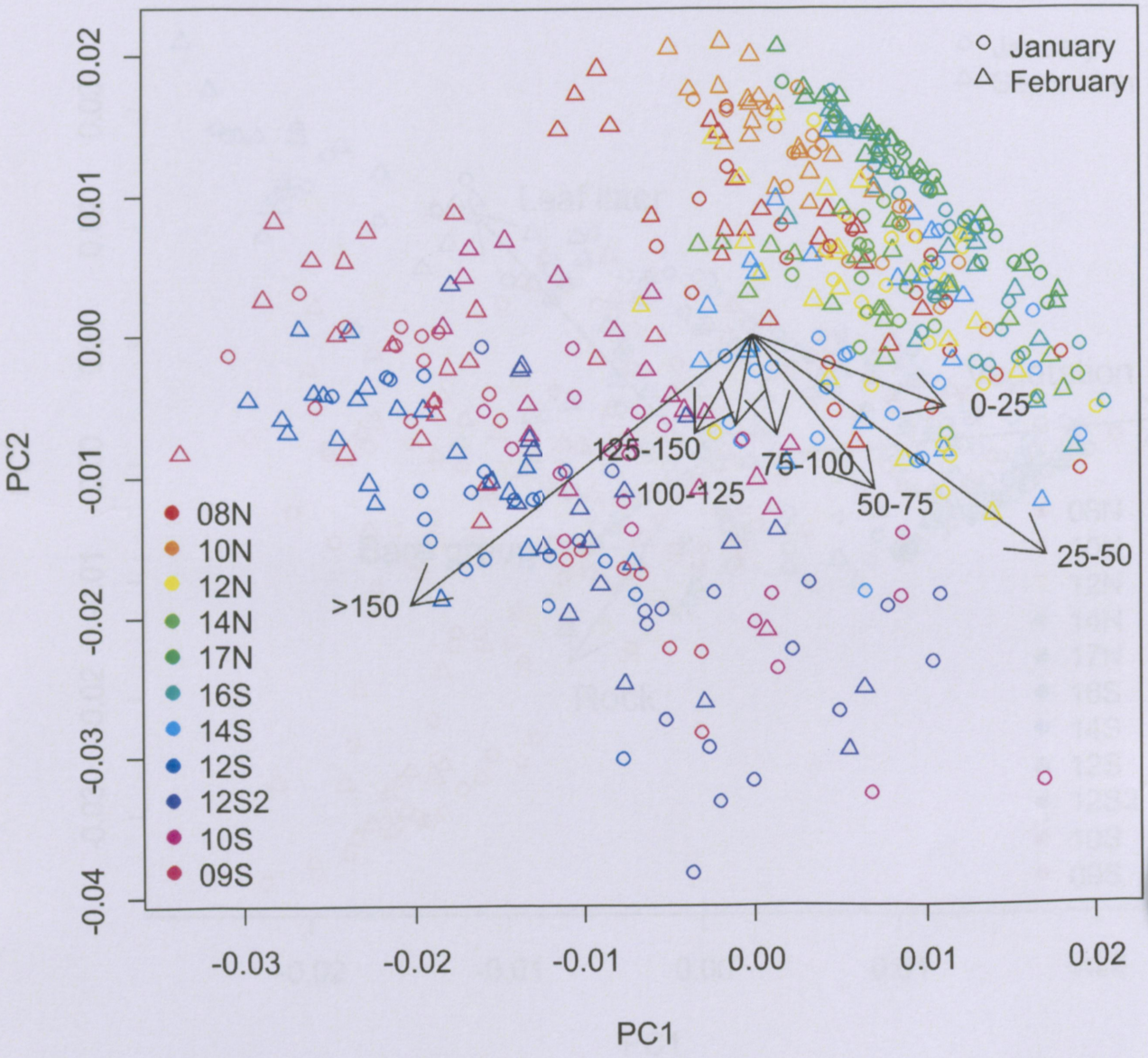
Appendix 7: Vertical vegetation structure of all 44 replicates (averaged over the period of the study) along the Soutpansberg transect.



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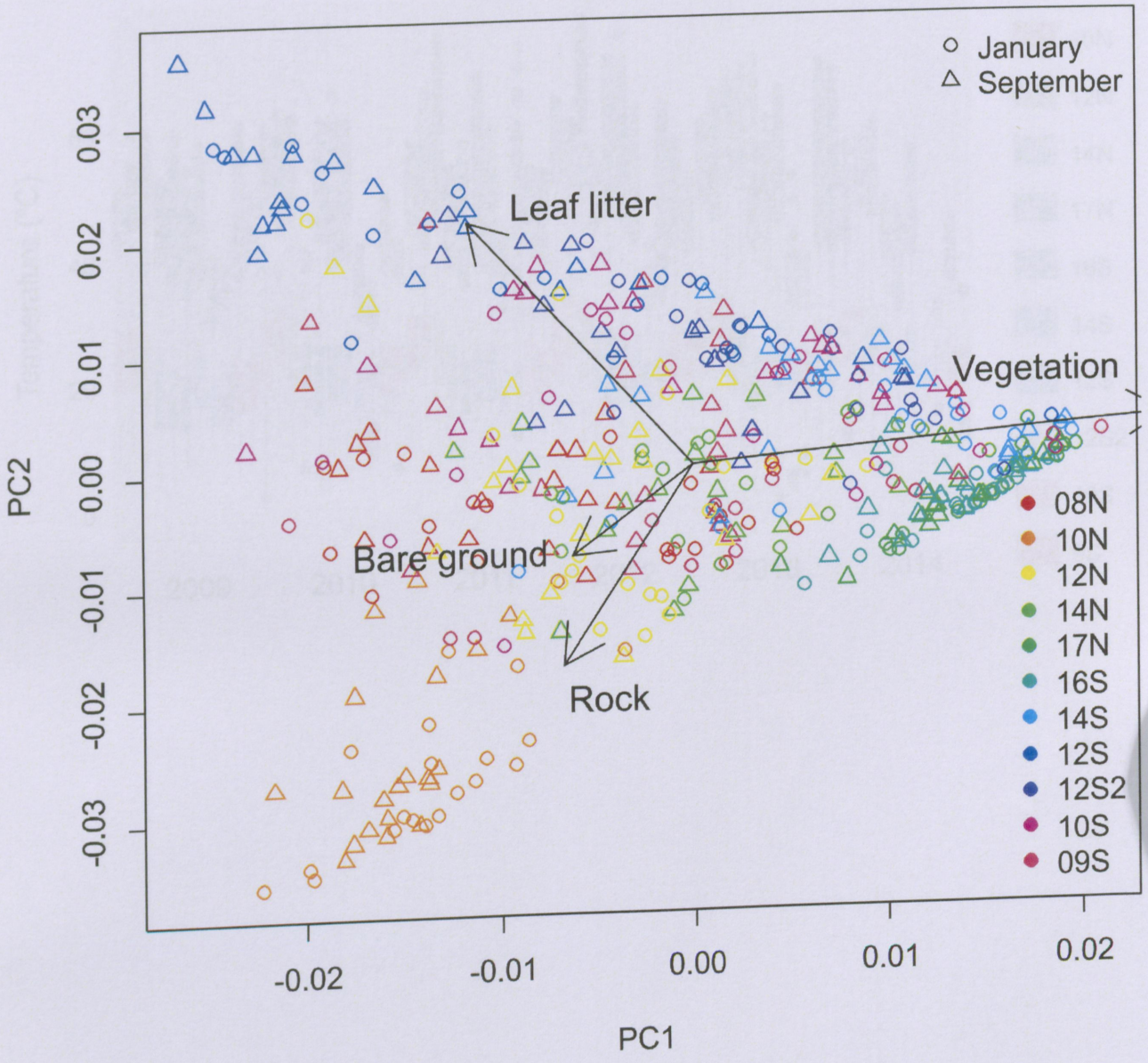
Appendix 8: Horizontal vegetation structure of all 44 replicates (averaged over the period of the study) along the Soutpansberg transect.



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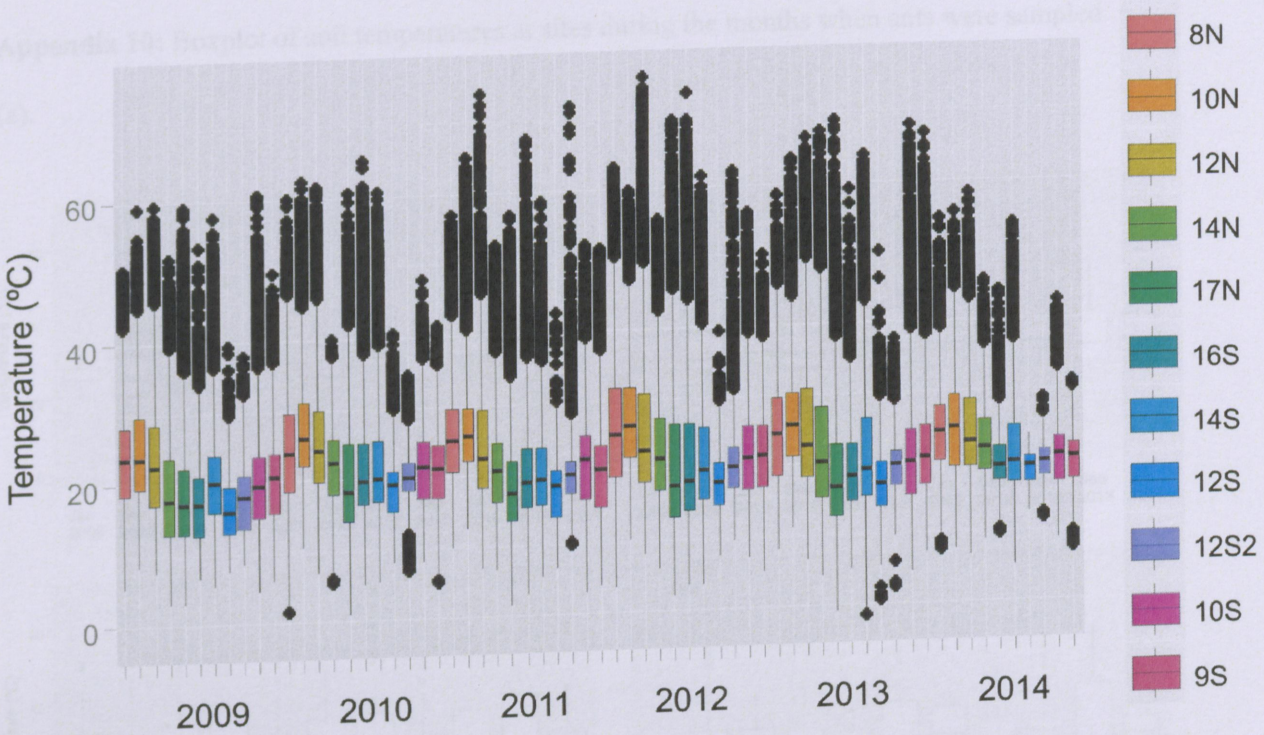
Appendix 9: Boxplot of soil temperature at each site over the period of the study.



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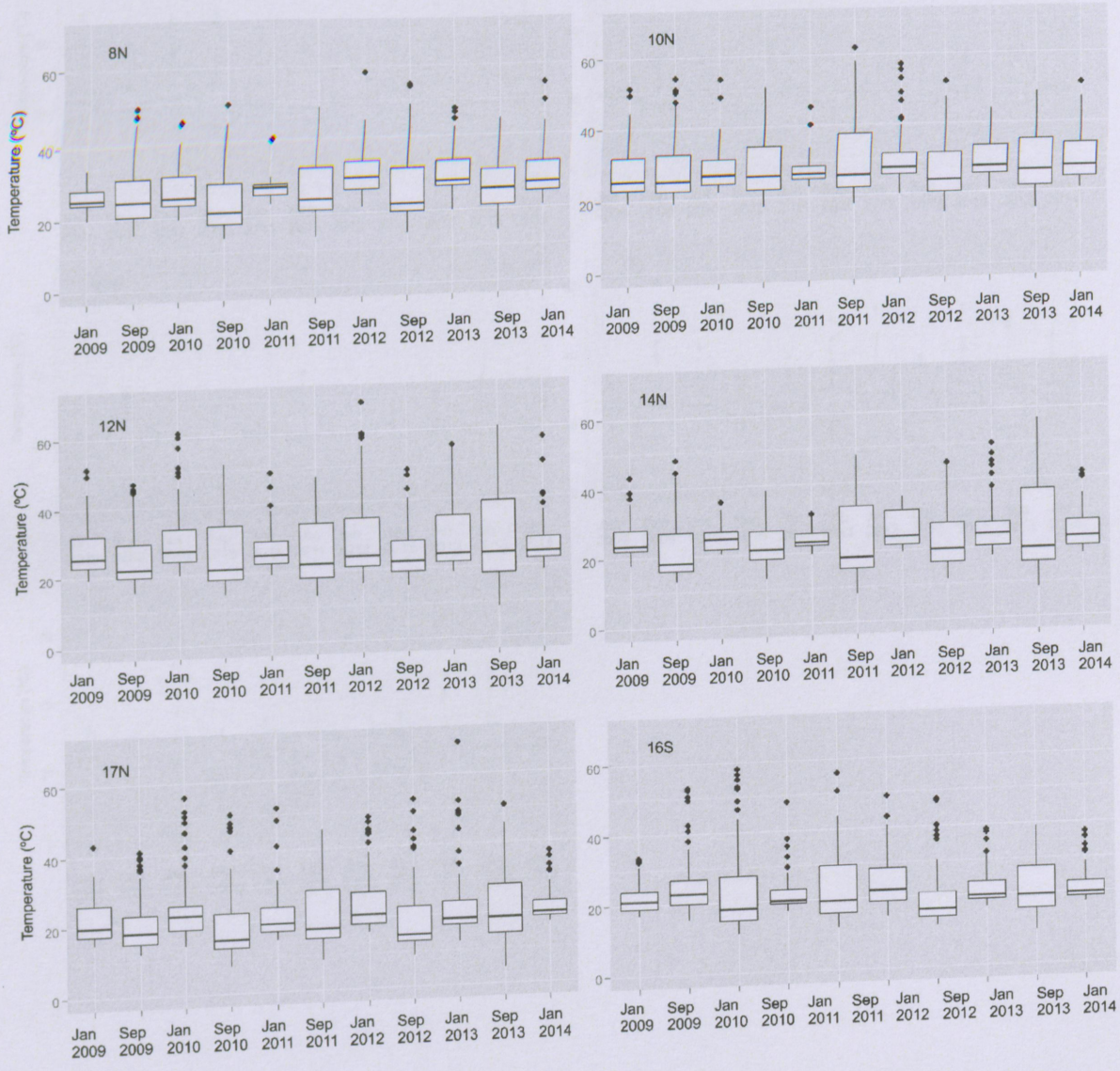
Appendix 10: Boxplot of soil temperatures at sites during the months when ants were sampled

(a).



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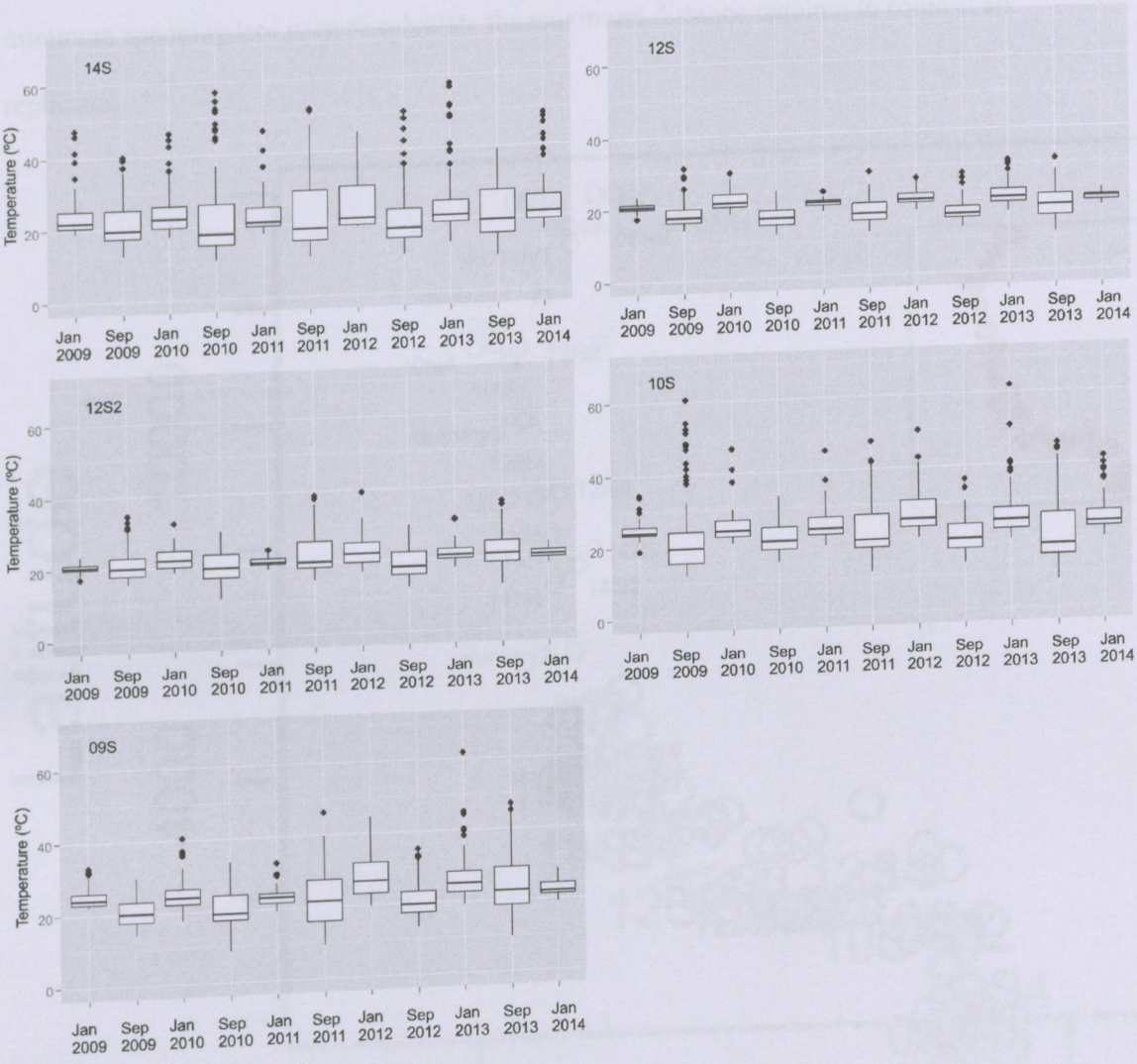
Appendix 11: Boxplot of soil temperatures at sites during the months when ants were sampled (b).



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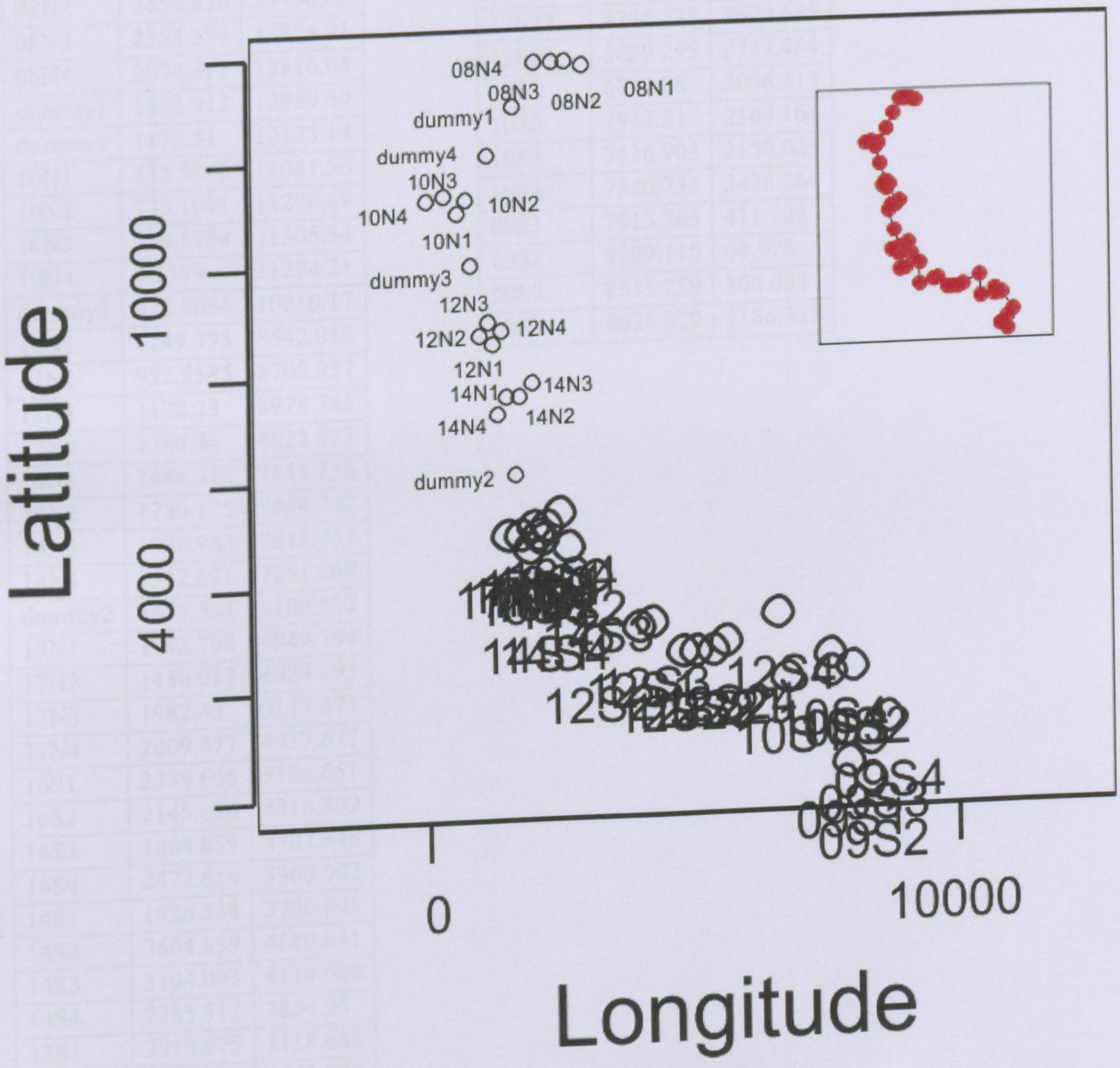
Appendix 12: UTM coordinates of 44 replicates along the transect as well as the four dummy variables included in the Principal Coordinate Analysis of Neighbourhood Matrices. Inset is the minimum spanning tree used to calculate the maximum distance required to connect all replicates.



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Appendix 13: UTM coordinates of replicates as well as dummy variables that were included to reduce the threshold value and reduce the smallest scale that can be perceived.

Site	x	y
08N1	2939.881	13723.02
08N2	2659.836	13790.83
08N3	2353.574	13824.71
08N4	2074.313	13816.04
dummy1	1623.912	12969.59
dummy4	1173.51	12123.14
10N1	535.5868	11041.56
10N2	723.1091	11276.69
10N3	328.5784	11305.34
10N4	7.1399	11224.21
dummy3	828.9084	10010.17
12N1	1249.393	8542.018
12N2	992.5585	8705.037
12N3	1122.23	8978.785
12N4	1389.44	8822.573
14N1	1444.212	7545.258
14N2	1736.175	7584.742
14N3	1938.953	7812.952
14N4	1332.671	7251.269
dummy2	1657.551	6100.532
17N1	1743.765	4949.794
17N2	1486.017	4929.693
17N3	1982.43	5117.573
17N4	2009.877	4917.677
16S1	2239.668	5106.651
16S2	2145.626	4816.809
16S3	1864.859	4707.348
16S4	2472.614	5300.002
14S1	1926.538	3790.005
14S2	2604.859	4680.641
14S3	3104.093	4114.989
14S4	2285.512	3854.95
12S1	3913.975	3118.638
12S2	3130.374	2863.603
12S3	4191.959	3184.893
12S4	6610.348	3264.923

Site	x	y
12S21	5335.447	2642.684
12S22	5030.98	2647.81
12S23	4736.225	2620.635
12S24	5629.295	2737.454
10S1	6712.08	2066.513
10S2	7943.21	2164.164
10S3	7536.903	2150.023
10S4	7580.735	2436.264
09S1	7913.365	411.728
09S2	8299.115	64.976
09S3	8311.759	806.053
09S4	8624.829	1186.315

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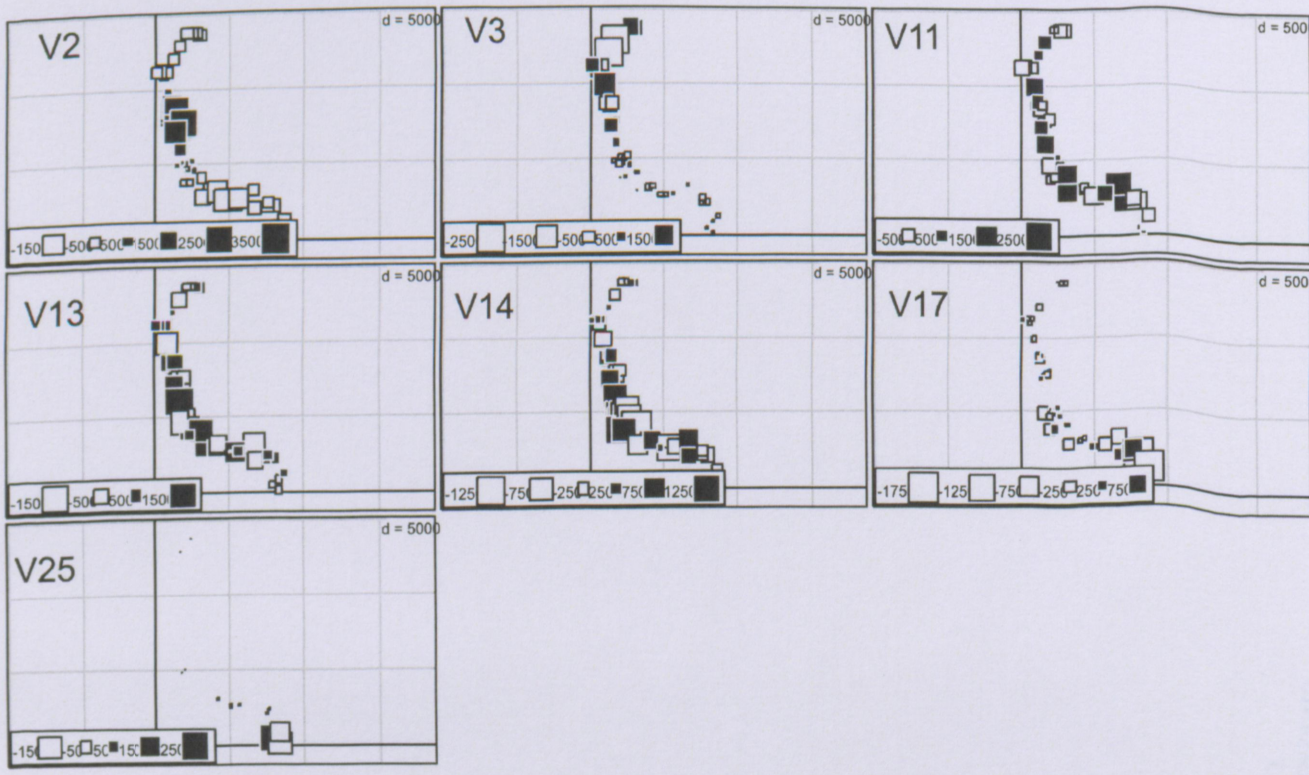
Appendix 14: Representation of significant eigenvectors in geographical space.



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