Insect macroecological patterns along an altitudinal gradient: the Greater Cederberg Biodiversity Corridor

by

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DECLARATION

I, the undersigned, hereby declare that the work contained in this dissertation is my own, original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

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ABSTRACT

The central goal in macroecology is to determine species diversity patterns across ecological gradients. Altitudinal and latitudinal patterns in species richness are often assumed to be analogous. Furthermore, the primary mechanisms underlying richness patterns along these two gradients might be similar. To date, few studies have tested whether the hypotheses proposed to explain latitudinal richness variation apply to patterns across altitude. This study therefore tests several hypotheses proposed to explain patterns in species diversity (i.e. ambient energy, productivity, area and geometric constraints) and their underlying mechanisms using altitudinal gradients in epigaeic ant and beetle species richness in the Greater Cederberg Biodiversity Corridor (GCBC) (Western Cape, South Africa). The study was conducted across an altitudinal gradient that was laid out from sea level to the top of a mountain (approximately 2000 m above sea level) and down the other side thereof. First, it was determined how the ant and beetle assemblages differ between the main vegetation types included in the transect and which environmental variables might underlie these differences. Thereafter, the variation in species richness and range size patterns of the two groups was investigated across the full altitudinal gradient. This is the first study that tests the applicability of two mid-domain models across such an altitudinal gradient using both complete and partial assessments. The models explained large proportions of the variance in range sizes across three domains but the ranges could have been constrained to show peaks in the middle of the domains due to the way in which the boundaries of the domains were selected. By contrast, the mid-domain models were not important in explaining species richness patterns, which suggests that they cannot explain diversity across the gradient. The species richness patterns of the two groups did not show the predicted mid-altitudinal peak. Moreover, it was demonstrated that different processes structure ant and tenebrionid assemblages across the same altitudinal transect. Ant species diversity was highly correlated to contemporary climatic variables, while historical factors appear to play a more important role in structuring tenebrionid beetle assemblages. Furthermore, support was found for the species energy theory in the ant assemblages, as well as for two of its underlying mechanisms, namely the more individuals hypothesis and the niche position mechanism. These results suggest that there are likely to be substantial and complex changes to ant assemblages under the predicted climate change scenarios for the region. Given the crucial role played by this group in ecosystem functioning (e.g. myrmecochory) it is suggested that these responses are

not likely to be a response solely to vegetation changes, but might also precipitate vegetation changes. This study also forms the basis of a long-term monitoring programme to establish baseline data for the epigaeic ants and tenebrionids and to monitor changes in these communities due to climate change.

OPSOMMING

Een van die sentrale idees in makro-ekologie is om die patrone in spesies diversiteit oor ekologiese gradiënte te ondersoek. Verder word daar aangeneem dat spesie rykheidspatrone oor hoogte- en breedtegradiënte analoog is aan mekaar en dat die primêre onderliggende meganismes van die patrone dieselfde kan wees oor hierdie twee gradiënte. Tot dusver het min studies getoets of die voorgestelde hipoteses wat breedtegradiënte in spesie rykheid verduidelik van toepassing is op hoogtegradiënte. Hierdie studie toets dus verskeie van hierdie hipoteses (aanvoelbare temperatuur, produktiwiteit, area en geometriese beperkinge) en hulle onderliggende meganismes in mier en kewer spesie rykheid in die Groter Cederberg Biodiversiteits Korridor (GCBK) (Wes Kaap, Suid Afrika). Die studie is uitgevoer oor 'n hoogtegradiënt wat vanaf see vlak tot ongeveer 2000 meter bo seevlak en weer aan die ander kant van die berg af uitgelê is. Eerstens is daar bepaal hoe die mier en kewer diversiteit verskil tussen die hoof planttipes wat oor die hoogtegradiënt voorgekom het en watter omgewingsveranderlikes daarvoor verantwoordelik is. Daarna is die variasie in spesie rykheid en area van verspreiding van die twee groepe ondersoek oor die hele hoogtegradiënt. Hierdie is die eerste studie wat die toepaslikheid van twee mid-domein modelle oor so 'n hoogtegradiënt toets met behulp van volledige en gedeeltelike ondersoeke. Die modelle het baie van die variasie in area van verspreiding verduidelik oor drie domeine maar die areas van verspreiding kon beperk gewees het om pieke in die middel van die domeine te vorm as gevolg van die manier waarop die grense van die domeine gekies is. In teenstelling, het die modelle nie spesie rykheid verduidelik nie en dus kan hulle nie spesie diversiteit oor hierdie gradiënt verduidelik nie. Die spesie rykheidspatrone van die twee groepe het nie die verwagte piek by midhoogte gewys nie. Verder het verskillende prosesse mier en kewer groeperings oor die hoogtegradiënt gestruktureer. Mier diversiteit was hoogs gekorroleer met kontemporêre klimaatsveranderlikes, terwyl historiese faktore belangriker was vir die kewers. Die spesie-energie teorie was ondersteun deur die data, asook die meer individue hipotese en die nis posisie meganisme. Hierdie resultaat dui daarop dat daar moontlik komplekse veranderinge in mier groeperings gaan plaasvind soos die klimaat verander. Miere vervul belangrike ekologiese prosesse in ekosisteme, wat beteken dat die laasgenoemde verandering nie bloot net gaan plaasvind as gevolg van veranderinge in die plantegroei nie, maar dat hulle self ook veranderinge kan veroorsaak. Hierdie studie vorm ook die basis van 'n langtermyn moniteringsprogram om basislyn data vir hierdie twee ekologies belangrike groepe vas te stel

en om veranderinge wat in hierdie gemeenskappe plaasvind, as gevolg van klimaatsverandering, te monitor.

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"DON'T PANIC!"

From *The Hitchhiker's Guide to the Galaxy* – Douglas Adams

TABLE OF CONTENTS

GENERAL INTRODUCTION

Variation in species richness across latitude is one of the oldest and most significant patterns in macroecology. Typically, the relationship between species richness and latitude is negative (Rosenzweig, 1995; Brown & Lomolino, 1998). Evidence for this negative association has been found in several major taxa such as molluscs (Rex *et al.*, 1993; Roy *et al.*, 1994, 1998, 2000), marine invertebrates (Rex *et al.*, 2000), marine and freshwater arthropods (France, 1992; Astorga *et al.*, 2003), marine and freshwater fish (Macpherson & Duarte, 1994; Oberdorff *et al.*, 1995; Stevens, 1996), terrestrial arthropods (Cushman *et al.*, 1993; Davidowitz & Rosenzweig, 1998; Lobo, 2000; Rodriguero & Gorla, 2004), terrestrial plants (Gentry, 1988; Ellison, 2002; Hunter, 2005), amphibians and reptiles (Kiester, 1971; Schall & Pianka, 1978; Currie, 1991), birds (Schall & Pianka, 1978; Currie, 1991; Blackburn & Gaston, 1996; Rahbek & Graves, 2001; Cardillo, 2002) and mammals (McCoy & Connor, 1980; Currie, 1991; Pagel *et al.*, 1991; Ruggiero, 1994; Kaufman, 1995, 1998; Cowlishaw & Hacker, 1997; Davidowitz & Rosenzweig, 1998; Andrews & O'Brien, 2000; Lyons & Willig, 2002). Strong latitudinal gradients have also been found at higher taxonomic levels such as genus, family and superfamily levels (e.g. Fischer, 1960; Stehli & Wells, 1971; Qian, 1998). However, several exceptions exist to the general pattern where the relationship between species richness and latitude is positive, modal (i.e. richness peaks outside of the tropics) or nonsignificant (e.g. Rabenold, 1979; Janzen, 1981; Hawkins & Compton, 1992; Poulsen & Krabbe, 1997; Price *et al.*, 1998; Pyšek, 1998; Lambshead *et al.*, 2003; Kryštufek & Griffiths, 2002; Andrew & Hughes, 2005). These exceptions are often the result of studies being conducted over narrow latitudinal extents, low species numbers, localized occurrences, or unique habitat requirements (e.g. parasitic species, aquatic plants) (Gaston, 1996; Willig *et al.*, 2003).

A large number of hypotheses have been proposed to explain the relationship between species richness and latitude (Pianka, 1966; Brown, 1988; Rohde, 1992, 1999; Gaston, 1996; Gaston & Blackburn, 2000; Whittaker *et al.*, 2001). However, the primary mechanisms underlying this well-documented pattern remain contentious. These can be separated into three main categories, namely null models, historical hypotheses and ecological hypotheses (Pimm & Brown, 2004).

NULL MODELS

Geometric constraint models have been advocated as appropriate null models to test species richness patterns across environmental gradients (Colwell & Lees, 2000; Jetz & Rahbek, 2001). These models predict that when different sized ranges are randomly placed within a bounded domain, free of environmental or historical gradients, the result would be a mid-domain peak in richness (Colwell *et al.*, 2004). Such models have been generated by placing species' ranges within one-dimensional (Colwell & Hurtt, 1994; Pineda & Caswell, 1998; Willig & Lyons, 1998; Lees *et al.*, 1999; Colwell & Lees, 2000) and more recently within two-dimensional (Bokma *et al.*, 2001; Jetz & Rahbek, 2001) bounded areas or domains. These studies have shown that a species richness peak in the middle of the bounded region is inevitable, whether empirical (Willig & Lyons, 1998; Lees *et al.*, 1999; Jetz & Rahbek, 2001) or theoretical (Colwell & Hurtt, 1994; Lyons & Willig, 1997; Pineda & Caswell, 1998; Bokma *et al.*, 2001) data are used. Colwell and Lees (2000) called the species richness patterns generated by these geometric constraint models the mid-domain effect and the geometric constraint models are collectively called mid-domain models. Moreover, geometric constraint models (or mid-domain models) also predict a unimodal, mid-elevational or bathymetrical species richness peak (Colwell & Hurtt, 1994; Pineda & Caswell, 1998; Lees *et al.*, 1999).

Some of the assumptions underlying mid-domain models have recently been severely criticized (Brown, 2001; Koleff & Gaston, 2001, Whittaker *et al.*, 2001; Hawkins & Diniz-Filho, 2002; Laurie & Silander, 2002; Zapata *et al.*, 2003, 2005; but see Colwell *et al.*, 2004, 2005). Moreover, Zapata *et al.* (2003) qualitatively assessed the empirical evidence for the mid-domain effect and found that in most cases the match between observed and predicted species richness was weak. For example, Koleff and Gaston (2001) have shown that, although mid-domain models acceptably predicted latitudinal species richness patterns of New World parrots and woodpeckers, the fit between observed and predicted patterns in species turnover and latitudinal range extent is particularly poor. They found that mid-domain models provide better predictions of observed diversity patterns the more rigorously the observed data is specified in constructing the models (e.g. using actual latitudinal midpoints). Moreover, Hawkins *et al.* (2005) recently criticized mid-domain models because the range size frequency distribution that generates the mid-domain peak in species richness within a bounded domain using mid-domain models cannot exist without environmental and historical influences (see also Zapata *et al.*, 2003, 2005). However, these models claim to generate a null expectation in the absence of any such factors (Colwell *et al.*, 2004).

HISTORICAL FACTORS

Historical factors such as vicariance events and climate change have also been suggested to shape species richness gradients (Ridley, 1996; Brown & Lomolino, 1998; Qian & Ricklefs, 2004; Ricklefs, 2004). According to this hypothesis areas that have experienced historical changes are not saturated because species have not had enough time to colonize (ecological time hypothesis) or adapt through speciation (evolutionary time hypothesis) to these areas (Pianka, 1966). In other words, older areas are more diverse (Pianka, 1966). Pleistocene glaciations and climatic change at polar and temperate latitudes have been invoked to explain lower species richness at these latitudes while the high species richness of the tropics is explained by more stable environments and hence the survival of many taxa (Fischer, 1960). However, Rohde (1992) argued that evolutionary time cannot be a general explanation of latitudinal gradients in species richness, but that it can explain differences in species richness between ecosystems at the same latitudes. Nonetheless, several recent studies have provided evidence that historical factors do play significant roles in current species distribution patterns (Fraser & Currie, 1996; Qian & Ricklefs, 2004; Ricklefs, 2004; Svenning & Skov, 2005).

ECOLOGICAL HYPOTHESES

Several ecological mechanisms have been proposed to explain latitudinal gradients in species richness (for review see Rohde, 1992; Willig *et al.*, 2003). However, Rohde (1992) refuted most of the mechanisms because they are either circular or insufficiently supported. He classified explanations for species richness gradients based on competition, mutualism, predation, epidemics, biotic spatial heterogeneity, population size, niche width, population growth rate, patchiness, epiphyte load, host diversity and harshness as circular because these mechanisms are usually the result of increased species diversity and not the cause (Rohde, 1992). Mechanisms for species richness gradients that were classified as insufficiently supported by the literature include environmental stability and predictability, productivity, abiotic rarefaction, physical heterogeneity, solar angle, area, aridity, seasonality, number of habitats and latitudinal ranges (i.e. Rapoport's rule) (Rohde, 1992). The studies that tested these mechanisms gave conflicting and inconsistent results, or the mechanisms were not applicable to all habitat types (Rohde, 1992). He therefore argued that none of these mechanisms could be regarded as general explanations for the latitudinal gradient in species richness (Rohde, 1992).

Willig *et al.* (2003) thoroughly reviewed those mechanisms which, to date, have received the most support (or are difficult to refute based on current information) and are the

3

most general. These are geographic area, the Rapoport-rescue hypotheses, evolutionary speed, productivity and ambient energy hypothesis. The geographic area hypothesis states that the tropics can support more species than low latitudes because of its larger geographic area (Rosenzweig, 1995). The latter consequently results in an increase in speciation and a decline in extinction rates (Chown & Gaston, 2000). Even though evidence for this mechanism has been provided (see Rosenzweig, 1995; Rosenzweig & Sandlin, 1997) the effect of area on species richness is difficult to test (Chown & Gaston, 2000) and there is little concrete support for this mechanism.

According to Stevens (1989) the Rapoport effect (the range size of species increase with an increase in latitude) may be the mechanism underlying latitudinal species richness gradients. It is thought that the wide range sizes of species at higher latitudes are the result of wider climatic tolerances relative to those of low-latitude species (Stevens, 1989). Stevens (1989) further argued that equal dispersal abilities of high and low-latitude species would result in tropical species spilling over into climatically unsuitable areas (higher latitudes), therefore inflating the species richness in these areas. This pattern was termed the Rapoport-rescue hypothesis and is a combination of the "rescue effect" described by Brown and Kodric-Brown (1977) and the range size gradient (Stevens, 1989). However, it seems increasingly unlikely that the Rapoport-rescue hypothesis explains the latitudinal gradient in species richness (Rohde *et al.*, 1993; Roy *et al.*, 1994; Rohde & Heap, 1996; Gaston *et al.*, 1998; Gaston & Chown, 1999; Kerr, 1999; Taylor & Gaines, 1999).

The evolutionary speed hypothesis posits that species richness is higher at low latitudes as a result of greater evolutionary rates (Rohde, 1992). The evolutionary rate of species is elevated as a consequence of increased mutation rates, shorter generation times and increased selection pressures, which in turn are a result of higher temperatures (energy levels) at these latitudes (Rohde, 1992). Few studies have tested this mechanism but the ones that did found no support for negative associations between latitude and evolutionary rate (Cardillo, 1999; Bromham & Cardillo, 2003).

It has been suggested that an increase in energy availability will result in an increase in species richness (Hutchinson, 1959; Turner *et al.*, 1988; Currie, 1991; Wright *et al.*, 1993; Gaston, 2000; Willig *et al.*, 2003). To date the species-energy relationship has gained wide support (Fraser & Currie, 1996; Kerr & Packer, 1997; Hawkins *et al.*, 2003; Evans *et al*., 2005a). Two versions of this hypothesis exist, namely the productivity and the ambient energy hypothesis. The productivity hypothesis states that a positive relationship exists between productivity and species richness and an inverse relationship between latitude and

productivity (Pianka, 1966; Mittelbach *et al.*, 2001; Willig *et al.*, 2003). This hypothesis was originally developed by Hutchinson (1959), Connell and Orians (1964), Brown (1981) and Wright (1983) and proposes that species richness is limited by energy through trophic cascades (see Hawkins *et al.*, 2003 for discussion). The shape of the relationship between productivity and species richness, however, remains controversial (Waide *et al.*, 1999; Mittelbach *et al.*, 2001). It has been shown that, even though a modal relationship occurs most frequently, positive and negative linear relationships are also common (Waide *et al.*, 1999; Mittelbach *et al.*, 2001). Furthermore, it has been suggested that the species richness-productivity relationship is scale dependent (Waide *et al.*, 1999; Mittelbach *et al.*, 2001; Whittaker *et al.*, 2001; Chase & Leibold, 2002; van Rensburg *et al.*, 2002; Storch *et al.*, 2005). The relationship is often unimodal at small spatial scales (Abramsky & Rosenzweig, 1984; Rosenzweig, 1995; Ritchie & Olff, 1999; Waide *et al.*, 1999; Dodson *et al.*, 2000; Mittelbach *et al.*, 2001; Chase & Leibold, 2002) while richness typically increases monotonically with increasing productivity at larger (regional) scales (Currie & Paquin, 1987; Currie, 1991; Rosenzweig, 1995; Waide *et al.*, 1999; Mittelbach *et al.*, 2001; Chase & Leibold, 2002, but see Kerr & Packer, 1997; Chown & Gaston, 1999).

The ambient energy hypothesis states that at low latitude organisms are closer to their physiological optima than they are likely to be at higher latitudes (low energy) areas (Turner *et al.*, 1987; Currie, 1991; Hawkins *et al.*, 2003). This hypothesis serves as an umbrella hypothesis for other explanations such as environmental and climatic variability, seasonality and environmental predictability (Willig *et al.*, 2003) because these explanations can be linked to variations in ambient energy.

Mechanisms explaining the species-energy relationship

The species-energy relationship is regarded as one of few general ecological rules (Huston, 1994; Rosenzweig, 1995). Nevertheless, the actual mechanism responsible for the species energy relationship is contentious and tests of proposed mechanisms are scarce. In a comprehensive review Evans *et al.* (2005a) critically assessed nine mechanisms that may generate positive relationships between species richness and available energy at the macro-scale. These are sampling, increased population size, niche position and breadth, dynamic equilibrium, more trophic levels, consumer pressure, range limitation and diversification rate (Evans *et al.*, 2005a). Here I provide a summary of the predictions made by these mechanisms and tests thereof.

5

Sampling and increased population size mechanisms

The sampling mechanism predicts a positive, decelerating relationship between species richness and abundance in an assemblage. This mechanism assumes that available energy in an area, and the number of individuals that can be supported in that area, are positively correlated, and that individuals in an assemblage is selected at random from a regional species pool where some species are more common than others (Evans *et al.*, 2005a). Therefore, if higher energy availability translates into higher total abundance, species richness will also increase in a decelerating fashion because common species will be selected faster than rare species (Preston, 1962a, b; Rosenzweig, 1995). The diagnostic prediction is that the sampling mechanism produces an abundance-species richness relationship identical to that predicted by random sampling (Evans *et al.*, 2005a). Similarly, the increased population size mechanism (Wright, 1983) assumes that most species will increase their abundance with an increase in available energy, which in turn will reduce their extinction risk (Preston, 1962a, b; MacArthur & Wilson, 1963). The relationship between population size and the probability of extinction is positive and decelerating (Leigh, 1981; Pimm *et al.*, 1988), and thus the relationship between abundance and species richness will also be positive and decelerating. Both the sampling and the increased population size mechanisms predict a positive, decelerating relationship between species richness and abundance. However, after controlling for sampling effects this relationship disappears if the sampling mechanism holds, but persists under the increased population size mechanism (Kaspari *et al.*, 2003; Evans *et al.*, 2005a).

Kaspari *et al.* (2003) tested the sampling and increased population size mechanisms using ant assemblages at 49 localities covering the net primary productivity gradient across North and South America. They determined the species diversity and number of ant colonies at each site from 1994 to 1997 and tested the mechanisms at three spatial grains ranging from a 1-m^2 plot, a transect of 30 1-m^2 plots to the local scale (all the plots combined) (Kaspari *et al.*, 2003). Fisher's α was used as a measure of species richness after the effects of sampling were removed (Kaspari *et al.*, 2003). Their results indicated that the sampling and increased population size mechanism explains the diversity gradient at the smallest scale (Kaspari *et al.*, 2003). The increased population size mechanism has also been tested using detritivorous aquatic insect communities in tree holes (Srivastava & Lawton, 1998) and bird communities (Hurlbert, 2004). Hurlbert (2004) found support for the increased population size mechanism in bird communities in North America across a productivity gradient ranging from desert and grassland to deciduous forest. He argued that this mechanism did not operate in isolation to determine the richness patterns, but that the relative abundance distributions of these bird

6

communities and habitat heterogeneity also played significant roles (Hurlbert, 2004). By contrast, Srivastava and Lawton (1998) tested this mechanism in aquatic tree hole communities by experimentally manipulating productivity. They found that the mechanism was not supported in these communities because more productive tree holes supported more species, but not more individuals (Srivastava & Lawton, 1998). Evans *et al.* (2005b) recently tested two of the key predictions of the increased population size mechanism, namely that extinction rates will be lower in energy rich areas and that these relationships are stronger in rare species (see niche position mechanism), in British breeding birds. They found support for the former prediction, but found the opposite pattern for the latter (Evans *et al*., 2005b).

Niche position

The niche position mechanism (Abrams, 1995) is similar to the increased population size mechanism in the sense that both mechanisms predict positive relationships between species richness, abundance and energy after the effects of sampling have been controlled for (Evans *et al.* 2005b). However, the niche position mechanism predicts that niche position specialists will show much stronger species-energy responses while the opposite trend is true for the increased population size mechanism (Evans *et al.*, 2005a). In addition, the niche position mechanism makes the assumption that the amount of rare resources will increase as available energy increases (Evans *et al.*, 2005a). Kaspari (2001) found limited support for this mechanism in ant assemblages in the Americas along a productivity gradient ranging from desert to rain forest: detritivore specialists only occurred in high energy areas. Evans *et al.* (2005b) found no evidence that the niche position mechanism structure British breeding bird communities because the relationship between extinction and energy availability was stronger in generalist and not in specialist species.

Niche breadth

The niche breadth mechanism makes the prediction that increased energy availability may increase the abundance of resources (Evans *et al.*, 2005a). If such a resource is favoured by a species that is utilizing less preferred resources, that species might reduce its consumption of the latter and increase its consumption of the preferred resource, which leads to smaller niche breadths in energy rich areas (Evans *et al.*, 2005a). This may lead to positive species-energy relationships when niche overlap and competitive exclusion is reduced (Evans *et al.*, 2005a). However, reductions in niche breadths because of an increase in certain resources' availability

7

are usually short-term (e.g. Feinsinger & Swarm, 1982; Evans & Jarman, 1999) and this mechanism may therefore result in non-permanent changes in communities.

More trophic levels

The more tropic levels mechanism predicts a positive relationship between the number of trophic levels and the available energy in an area (Evans *et al.*, 2005a). When more trophic levels are added more novel species can be supported and a positive relationship between available energy and species richness arises (e.g. Oksanen *et al.*, 1981; Kaunzinger & Morin, 1998). According to Evans *et al.* (2005a) the number of trophic levels is rarely limited by available energy and other factors such as history, disturbance and available area can also shorten food chains.

Consumer pressure

The consumer pressure mechanism (Paine, 1966; Janzen, 1970) posits that abundance and species richness of consumers will increase with increasing energy availability, which will increase consumer pressure on their prey. This will decrease competitive exclusion between prey species (Kullberg & Ekman, 2000; Shurin & Allen, 2001), which will in turn result in positive species-energy relationships (Evans *et al.* 2005a). However, the other mechanisms described by Evans *et al.* (2005a) predict that prey populations will also increase with increasing energy availability, resulting in a buffer effect (Evans *et al.*, 2005a). It is therefore unlikely that this mechanism will be a general one (Evans *et al.*, 2005a). Indeed, Evans *et al.* (2005b) did not find support for this mechanism in British breeding birds. They argued that rare species are most vulnerable to competitive exclusion and should therefore show the strongest species-energy responses. However, they found the opposite trend and thus no support for the mechanism (Evans *et al.*, 2005b)

Dynamic equilibrium

A seventh mechanism proposed to account for positive species-energy relationships is dynamic equilibrium (Huston, 1979). This mechanism suggests that extinction rates are lower in high-energy areas after disturbance, which will result in a positive species-energy relationship (Huston, 1979; deAngelis, 1995), and that populations in these areas recover faster following a disturbance event (Evans *et al.*, 2005a). To date no studies have tested how the available energy in an area influences the responses of populations to disturbance (Evans *et al.*, 2005a).

Range limitation

This mechanism predicts that species always occur in areas where their physiological needs can be met and the physiological requirements of more species can be met in energy rich than in energy poor areas (see Evans *et al.*, 2005a). However, the relationship between solar energy and species richness is unimodal because few species are adapted to withstand the conditions in extremely hot areas such as deserts (Evans *et al.*, 2005a). This can result in a nested species distribution with species occurring in energy rich areas having a narrower range of climatic tolerances than those in energy poor areas. However, the sampling, increased population density, niche position and breadth, more trophic levels, consumer pressure and dynamic equilibrium mechanisms also predict nested species distributions (Evans *et al.*, 2005a).

Diversification rate

The diversification rate mechanism is the only mechanism linking positive species-energy relationships with speciation rate. Rohde (1992) proposed that 'energy levels do not determine species numbers but evolutionary speed'. Increases in mutation rates are directly linked to increases in solar energy (Rohde, 1992) and there will thus be a positive relationship between diversification rate and energy. Cardillo (1999) tested this mechanism in passerine bird and swallowtail butterflies by comparing species richness in sister clades across latitude. He found that diversification rate is higher at lower than in higher latitudes (Cardillo, 1999), which provides some evidence for the diversification rate mechanism. Allen *et al.* (2002) found evidence that species diversity of terrestrial (trees, amphibians), freshwater (riverine fish) and marine taxa (gastropods, ectoparasites of fish) is related to ambient temperature along latitudinal and altitudinal gradients. They argued that their results provide evidence that the biochemical reactions that control speciation rates will accelerate with an increase in temperature (Allen *et al.*, 2002).

BATHYMETRIC AND ALTITUDINAL PATTERNS

The species-energy pattern is also complex in more than a single dimension. Not only does richness vary with latitude but also with altitude in terrestrial systems and depth in marine ones, as well as across longitude for both systems. Several studies on species distributions have taken this into account in terrestrial (e.g. Currie & Paquin, 1987; Currie, 1991; Jetz & Rahbek, 2001; Hawkins & Porter, 2003a, b) and marine (e.g. Macpherson & Duarte, 1994; Hughes *et al.*, 2002; Connolly *et al.*, 2003; Harley *et al.*, 2003; Brandt *et al.*, 2005) systems.

To date, studies have shown that species richness either declines with increasing depth (Stevens, 1992; Smith & Brown, 2002) or peak at mid-depths (Pineda 1993; Rosenzweig & Abramsky, 1993 and references therein; Macpherson & Duarte, 1994; Pineda & Caswell 1998; Brandt *et al.*, 2005).

Altitudinal variation in species richness has also long been of interest. At first, species richness was thought to be a linearly declining function of altitude. According to Rahbek (1995), this generalization is attributable to two frequently sited studies on birds. The first of these deals with land birds in New Guinea and shows that species richness declines steadily across an altitudinal gradient from sea level to 4000 m above sea level (Kikkawa & Williams, 1971). In the second study, Terborgh (1977) showed that Andean bird species richness also declines monotonically with increasing altitude across a gradient ranging from 400 – 3600 m above sea level. Several other studies have also shown that monotonically declining species richness patterns exist across altitude in birds and mammals (Graham, 1983, 1990; Patterson *et al.*, 1998), isopods (Sfenthourakis, 1992), land-snails (Tattersfield *et al.*, 2001), insects (Claridge & Sinhrao, 1978; Hebert, 1980; Ichijo *et al.*, 1982; Wolda, 1987) and plants (Hamilton, 1975; Hamilton & Perrott, 1981; Rawal & Pangtey, 1991; Mark *et al.*, 2001; Jones *et al.*, 2003; Pauchard & Alaback, 2004). However, Rahbek (1995, 2005) showed that, even though the general trend seems to be a linear decline in species richness with altitude, unimodal relationships are more typical. Early in his paper Rahbek (1995) argued that Terborgh's (1977) study is sited as a "textbook example" of a monotonically decreasing species richness trend across altitude, but a unimodal richness pattern emerged after sampling effect has been controlled for (see Rahbek, 1995). A more recent group of studies has shown that species richness peaks at mid-altitude. These mainly include studies on plants (Vetaas & Grytness, 2002; Grytness, 2003; Bachman *et al.*, 2004; Bhattarai *et al.*, 2004), birds (Rahbek, 1997), mammals (Brown, 2001; Heaney, 2001; Rickart, 2001; Sánchez-Cordero, 2001; McCain, 2005) and insects (Janzen, 1973; Janzen *et al.*, 1976; McCoy, 1990; Olson, 1994; Rahbek, 1995, 1997; Lees, 1996; Fisher, 1998, 1999; Lees *et al.*, 1999; Blanche & Ludwig, 2001; Sanders, 2002). However, this relationship is dependent on the study region, scale and taxon and few studies have standardized for sampling effort and area when investigating species richness patterns across elevational gradients (McCoy, 1990; Rahbek, 1995).

OBJECTIVES OF THIS STUDY

It is often assumed that altitudinal and latitudinal species richness patterns are analogous (MacArthur, 1972; Brown, 1988; Rohde, 1992; Stevens, 1992). However, Rahbek (2005)

recently argued that, this might not be the case (mainly due to differences in the extent of the two gradients), but the primary mechanisms underlying species richness patterns along these two gradients might still be the same. Nonetheless, few studies have tested whether the hypotheses proposed to explain latitudinal richness variation (available area, ambient-energy, productivity, null models and the Rapoport rescue effect) apply to altitudinal species richness gradients. For example, only six studies have explicitly tested for an altitudinal Rapoport effect to date (Stevens, 1992; Patterson *et al.*, 1996; Fleishman *et al.*, 1998; Ruggiero & Lawton, 1998; Sanders, 2002; Fu *et al.*, 2004) and researchers have only recently started investigating whether null models might explain species richness patterns along altitudinal gradients (Rahbek, 1997; Lees *et al.*, 1999; Jetz & Rahbek, 2001; Kessler, 2001; Sanders 2002; Grytnes, 2003; Bachman *et al.*, 2004; McCain, 2005). Furthermore, altitude has conventionally been regarded as a surrogate for productivity (Orians, 1969; MacArthur, 1972; Terborgh, 1977) and altitudinal species richness gradients have regularly been cited as support for hypotheses associated with ambient-energy and productivity (e.g. Stevens, 1989, 1992; Currie, 1991; Abrams, 1995; Whittaker *et al.*, 2001; see also Rahbek, 2005). Even though this relationship has been shown to exist across altitudinal gradients, no studies have investigated the mechanisms underlying the altitudinal species-energy relationship.

This study therefore tests these hypotheses (i.e. ambient energy, productivity, area and geometric constraints) and their underlying mechanisms using altitudinal gradients in epigaeic ant and beetle species richness in the Greater Cederberg Biodiversity Corridor (GCBC) (Western Cape, South Africa). First, I aimed to determine if and how epigaeic ant and beetle assemblage structure differs between the main vegetation types in the GCBC, and which environmental variables might underlie such differences. Second, I investigated variation in ant and beetle species richness and range sizes across a full altitudinal gradient in the GCBC.

A major departure from other studies is that this one extends over the top of the altitudinal gradient (the highest altitudinal band sampled was at approximately 2000 m above sea level in the Cederberg where no permanent snowline exists) and is thus not restricted to one aspect of the mountain range as most other studies have been (but see Mark *et al.*, 2001). To date, several investigations of species richness patterns across altitudinal gradients have been undertaken in areas where the highest altitudinal band sampled has formed a hard boundary for species distribution; the distribution of species is limited by a permanent snowline (e.g. Vetaas & Grytnes, 2002) or is limited by the distribution of their habitat (e.g. Lawton *et al.*, 1987, Lees *et al.*, 1999). For example, Lawton *et al.* (1987) investigated richness patterns on insect assemblages feeding on bracken and, although bracken is

widespread in Britain, it is restricted to elevations lower than 600 m above sea level (Page, 1976). Similarly, Lees *et al.* (1999) examined richness patterns of taxa occurring in the rainforest biome of Madagascar. This rainforest spans 13 degrees of latitude (12,25ºS – 25,25ºS) and 2100 m of elevation.

The difference between this study and others is important because no other studies have tested patterns in range size and species richness along an altitudinal gradient that was laid out from sea level to the top of a mountain and down the other side thereof. Moreover, the applicability of mid-domain models has not yet been tested across such an altitudinal gradient. Because the transect runs from Lamberts Bay (sea level on the western slope) to Wuppertal (approximately 500 m a.s.l. on the eastern slope), a peak in species richness and range size is predicted by mid-domain models approximately at the highest altitude sampled because this area lies in the middle of the bounded area (Colwell & Hurtt, 1994; Colwell & Lees, 2000) (i.e. the Mountain Fynbos is bounded by Strandveld and Succulent Karoo). This is in contrast to the predicted mid-altitudinal species richness and range size peak found in many other studies (Colwell & Hurtt, 1994; Pineda & Caswell, 1998; Lees *et al.*, 1999). Thus, investigating a full transect has the potential to clearly distinguish the predictions of geometric constraint models and other mechanisms. For example, the former would result in a richness peak at high altitude accompanied by the largest average range size (see Colwell & Lees, 2000; Colwell *et al*., 2004). By contrast, other mechanisms might result in a peak in range size at high altitude (a consequence of the climatic variability hypothesis – see Gaston & Chown 1999), but higher richness elsewhere, which would suggest that the geometric constraints model does not hold.

WHY EPIGAEIC ANTS AND BEETLES IN THE CEDERBERG?

The taxa

Epigaeic ants and beetles were chosen because they are extremely diverse and widespread throughout South Africa (Scholtz & Holm, 1985). Ants also occur at high abundances and both taxa can be collected efficiently using pitfall traps (Krasnov *et al.*, 1996; Majer, 1997; Bestelmeyer *et al.*, 2000). Ants are important ecosystem engineers because of their effects on soil structure (physical and chemical) and function, which in turn affects vegetation and microclimate profiles in ecosystems (Hölldobler & Wilson, 1990; Dean & Yeaton, 1993; Lobry de Bruyn, 1994; Folgariat, 1998). Ants also play a crucial role in seed dispersal in the Fynbos biome (Bond & Slingsby, 1983; Johnson, 1992; Le Maitre & Midgley, 1992) and, in

doing so, disperse seeds to nutrient-enriched sites and enable seeds to avoid competition, predation and fire damage (see Johnson (1992) and references therein). Tenebrionids are typically important processors of organic matter (Slobodchikoff, 1978; Allsopp, 1980; Thomas, 1983), and carabids constitute a significant assemblage of ground-dwelling predators (Thiele, 1977).

The study area

The Greater Cederberg Biodiversity Corridor (GCBC) is the first biodiversity corridor in South Africa and includes large areas of the Cape Floristic Region (CFR) and Succulent Karoo (Figs. 1 and 2). It forms part of both the Cape Action for People and the Environment (CAPE) and the Succulent Karoo Ecosystem Plan (SKEP). The main objective of these two conservation planning programmes is to secure the conservation of the exceptional biodiversity of the Cape Floral Kingdom and, through this, to deliver sustainable economic benefits to the people of the region (Younge & Fowkes, 2003, Cowling & Pressey, 2003 and Driver *et al*., 2003). The GCBC project further aims to extend biodiversity conservation outside protected area with a focus on private land (Anonymous, 2004).

Such conservation strategies are imperative in light of the predicted changes due to land use (Todd & Hoffman, 1999; Rouget *et al*., 2003a, b) and especially climate change (Midgley *et al*., 2002, 2003; Hannah *et al*., 2005) in this region within the next few decades. Climate-modelling exercises have demonstrated that the CFR is likely to be highly sensitive to climate change (Rutherford *et al.*, 1999; Midgley *et al*., 2002, 2003; Thomas *et al.*, 2004; Hannah *et al*., 2005). Rutherford *et al.* (1999) provided the first assessment of the possible effects that climate change might have on protected areas in the arid regions of South Africa. They demonstrated that, due to local extinctions of plant species and projected migrations as a result of changes in the climate, it would not be possible to sustain species in fixed protected areas and up to 42.4% of the plant species were predicted to go extinct within these areas (Rutherford *et al*., 1999). Several studies have used various climate change scenarios to model the future distributions of Proteaceae species (Midgley *et al*., 2002, 2003; Thomas *et al.*, 2004; Hannah *et al*., 2005). Using three different bioclimatic models, Midgley *et al.* (2002) investigated possible changes in distributions and extinctions for 330 Proteaceae species and for the Fynbos biome as a whole. They showed that the Fynbos biome will suffer between 51% and 65% loss by the year 2050 and these losses will mainly be concentrated in the northern latitudes (Midgley *et al*., 2002). A major concern is that 29 of the 330 endemic
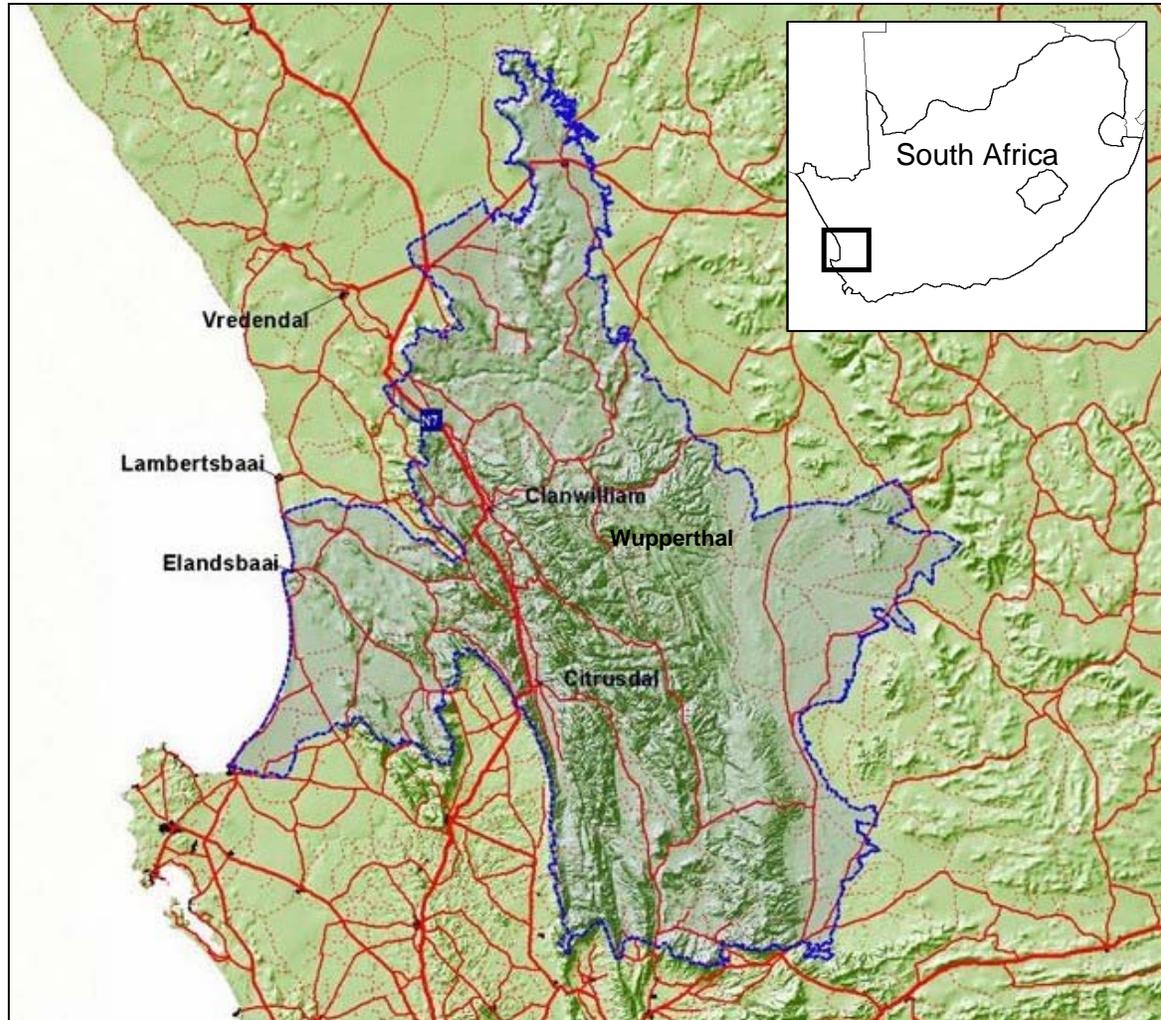
Figure 1 Map of the Greater Cederberg Biodiversity Corridor (GCBC) (Western Cape, South Africa).

a) Strandveld
Succulent Karoo

c) Mountain Fynbos

d) Succulent karoo

Figure 2 Images of the main vegetation types within the Greater Cederberg Biodiversity Corridor.

15

Proteaceae species have ranges that are situated entirely within these areas (Midgley *et al*., 2002). Midgley *et al*. (2002) showed that one third of endemic Proteaceae species will go extinct and that only 5% will retain more than two thirds of their current range under the most extreme scenarios. In a second study, Midgley *et al*. (2003) modelled responses of 28 Proteacea species. They found that the species may display a diverse array of responses: five species were predicted to suffer range elimination, 12 species showed range reductions with a mean range loss of 84% of their range size, and 23 species displayed south-eastward range shifts. Thirteen of the latter species showed no geographic overlap with current ranges. In the last study, Thomas *et al.* (2004) incorporated land use estimates in their models and predicted that 27% of the 243 Proteaceae species investigated would become extinct by 2050.

The GCBC was therefore selected as a study area because of the prediction that Fynbos will disappear from the region due to climatic changes. It is thus crucial to collect baseline data on taxa that are critical for ecosystem functioning in this area. Baseline data on insect diversity in conservation areas are often not available (McGeoch, 2002) and this impedes our understanding of the structure and functioning of insect communities in different ecosystems. This is especially true for the CFR where there is little monitoring of diversity (particularly for insects) at present. Although many predictions have been made of how the CFR is going to change under future climatic conditions, few attempts have been made to monitor what is actually happening. This work forms the basis of such a monitoring programme by establishing the baseline data for two ecologically important taxa in the early 2000s, and by examining altitudinal variation in the assemblages of these taxa in the northern CFR.

STRUCTURE OF THE THESIS

Chapter 2 serves as a detailed description of the study area and sites. In addition, this chapter deals with epigaeic ant assemblage structure (i.e. variation in species richness and abundance), and the environmental correlates thereof, within the main vegetation types across the altitudinal gradient. Chapter 3 is an investigation of the same issues in the epigaeic beetle fauna (darkling beetles and ground beetles) across the altitudinal gradient. In Chapter 4, I determine whether an altitudinal Rapoport effect exist in the epigaeic ant and beetle fauna and test the principal mechanism proposed by Stevens (1989, 1992, 1996) to explain the Rapoport effect across environmental gradients. In Chapter 5, I conduct a full investigation of the variation in the ant and beetle species richness across the full altitudinal gradient and test the main hypotheses proposed to explain species richness gradients across altitude (ambient

energy, productivity, area, the vertical complexity of vegetation or geometric constraints). Furthermore, I explicitly test the predictions underlying the hypotheses that explain the obtained patterns in the taxa. In Chapters 4 and 5 I mainly concentrate on the tenebrionid beetles because the carabid fauna was depauperate across the transect. Finally, Chapter 6 revisits the main aims and findings of the thesis and proposes further topics for research in this area.

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CHAPTER 2

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ANTS, ALTITUDE AND CHANGE IN
THE NORTHERN CAPE FLORISTIC REGION

INTRODUCTION

The Cape Floristic Region (CFR) is a major biodiversity hotspot of global significance (Myers, 1990; Cowling & Richardson, 1995; Mittermeier *et al.,* 1998). It is both the smallest and richest floral kingdom with approximately 8700 plant species (Low & Rebelo, 1996), of which 68 % are endemic (Bond & Goldblatt, 1984). The region has a high concentration of Red Data Book plant species (i.e. 1406 species) (Cowling & Hilton-Taylor, 1994), and is listed as a Centre of Plant Diversity (WWF and IUCN 1994) and a Global 200 Ecoregion (Olson & Dinerstein, 1998). It is also home to several endemic vertebrate species and is an Endemic Bird Area (Stattersfield *et al.*, 1998). The CFR includes five biomes (Nama- and Succulent Karoo, Thicket, Forest and Fynbos) of which the dominant and most characteristic biome is the Fynbos (Low & Rebelo, 1996). However, the Succulent Karoo is also a biome of considerable significance. It has the richest succulent flora (*c*. 1000 sp.) globally, like Fynbos is extremely species rich at both regional and local scales, and is the only semi-arid region that qualifies as a biodiversity hotspot of global significance (Cowling & Hilton-Taylor, 1994; Cowling *et al.*, 1999).

The considerable biodiversity of the CFR is threatened by land transformation for agriculture and urban development, and by alien plant invasions (Todd & Hoffman, 1999; Rouget *et al*., 2003a). At present, approximately 30 % of the area is transformed by agriculture (25.9 %), urbanization (1.6 %) and alien vegetation (1.6 %) (Rouget *et al*., 2003a). Some of the lowland habitats have been reduced by as much as 90 % (Rouget *et al*., 2003b), and it is predicted that at least 30 % of the remaining natural vegetation will be transformed within the next 20 years (Rouget *et al*., 2003a). Moreover, climate-modelling exercises have demonstrated that the Fynbos in the Cape Floristic Region (CFR) is likely to be highly sensitive to climate change (Midgley *et al*., 2003; Hannah *et al*., 2005). It is thought that within 50 years Fynbos will be largely replaced with a different, unknown vegetation type. Climate change models predict that, over this period, the CFR will experience a 1.8ºC

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increase in mean annual regional temperature and that this area will be faced with significantly more arid conditions (Midgley *et al.*, 2003). The Fynbos biome will apparently lose large areas near its northern limits (retaining less than 10 %, Midgley *et al.*, 2002), especially those along the west coast and in the Cederberg mountains (Midgley *et al.*, 2002, 2003). Biome loss will occur at all altitudes, and will only be less than 50 % at altitudes between 1800 m and 2100 m. Slopes at lower altitudes along the northern borders of the Cape Fold Belt will also become unsuitable for this biome and it is predicted that the range of Fynbos will contract southwards into this mountain range (see Midgley *et al.*, 2003). In addition, the Nama- and Succulent Karoo are also under threat and it is predicted that between 0.3% and 42.4% of species will go extinct within protected areas in these biomes (Rutherford *et al.*, 1999).

Given the predictions of significant loss of biodiversity in the CFR, conservation planning strategies for a future of change in the area are in place (including Cape Action for People and the Environment (CAPE) and the Succulent Karoo Ecosystem Plan (SKEP) (see Younge & Fowkes, 2003, Cowling & Pressey, 2003 and Driver *et al.*, 2003 for extensive overviews of aims and progress)). These ecoregional conservation planning strategies not only incorporate current richness assessments, but also processes such as migration, major areas of evolution such as ecotones, and expected local-scale range shifts in response to climate change (Pressey *et al.*, 2003). Furthermore, the plans include consideration of ecosystem functioning aspects such as specialist pollination relationships, plant-herbivore interactions, and fire regimes (Pressey *et al.*, 2003). The strategic plans have largely been based on information on plants (especially the Proteaceae), as well as expert knowledge regarding medium- and large-sized mammal, freshwater fish, amphibian and reptile distributions (Cowling *et al.*, 2003, Cowling & Pressey, 2003; Kerley *et al.*, 2003). However, other groups will also be affected by landscape transformations and climate change (e.g. Erasmus *et al.*, 2000), and the processes included in the strategies are a subset of those that need to be taken into consideration if conservation is to be successful over the longer term (see e.g. Rodrigues *et al.*, 2000). Nevertheless, their absence in these plans and the planning processes that gave rise to them is not a consequence of lack of concern, but rather the absence of adequate information (Cowling *et al.*, 2003). A prime example is ant diversity, and one of the most significant processes in which ants are involved, myrmecochory.

Myrmecochory (seed dispersal by ants) is an important ecological process in the Fynbos biome (Le Maitre & Midgley, 1992). Indeed, approximately 20 % of the 6500 strictly Fynbos plant species (i.e. 1300 species) are dependent on myrmecochory for their survival

(Johnson, 1992). The only other comparable area is Australia with 1500 ant-dispersed plants, with the rest of the world containing a mere 300 species (Berg, 1975). In South Africa, myrmecochorous plants are mainly restricted to the Fynbos biome. A total of 29 families and 78 genera of Fynbos plants has been identified as containing species that are ant-dispersed (see Table 1 in Bond & Slingsby, 1983). Myrmecochory occurs only in two plant families outside Fynbos, the Euphorbiaceae and Zygophyllaceae (Bond & Slingsby, 1983).

Myrmecochorous ants belong to four subfamilies: Dolichoderinae, Formicinae, Myrmicinae and Ponerinae (Gómez & Espadaler, 1998). In the CFR the dominant myrmecochorous ants are *Pheidole capensis*, *Anoplolepis* sp. (c.f. *custodiens*), *Anoplolepis* sp. (c.f. *steinergroeveri*), *Tetramorium quadrispinosum*, and *Camponotus niveosetosus* (Bond & Slingsby, 1983, 1984). However, information on the extent of the habitat specificity of myrmecochorous ants is not widely available, especially for the areas in the CFR predicted to change rapidly in the next few years. Slingsby and Bond (1985) concluded that *Anoplolepis* sp. (c.f. *custodiens*), *Anoplolepis* sp. (c.f. *steinergroeveri*) *and P. capensis* are ubiquitous in both mesic and arid areas of Fynbos, and the presence of *Anoplolepis* sp. (c.f. *custodiens*) has been reported throughout Africa (Prins, 1963; Breytenbach, 1988). Moreover, no myrmecochorous ant species have been studied in terms of their likely direct and indirect (via vegetation change) responses to climate change. If they were to be substantially influenced by such change, thus also affecting the plant species with which they interact, then conservation plans that are based partially on plant data might prove to be inadequate for capturing likely change. To date only the influences of invasive ant species such as the Argentine ant, *Linepithema humile* (e.g. Bond & Slingsby, 1984; Midgley & Bond, 1995; Gómez & Oliveras, 2003), and exotic plant species, such as Australian *Acacia* (French & Major, 2001), on seed dispersal by ants have been investigated. Indeed, no monitoring systems exist for insect assemblages in the CFR.

Here we address these issues by investigating ant assemblage structure within the main vegetation types in a northern CFR area, the Cederberg. In particular, we determine if and how ant assemblage structure differs between the main vegetation types in the Greater Cederberg Biodiversity Corridor (GCBC), how restricted ants, and in particular the major myrmecochores, are to specific vegetation types, and which environmental variables might underlie differences in the ant assemblages and in the specificity of species to particular areas.

MATERIAL AND METHODS

Study site

This study took place in the Greater Cederberg Biodiversity Corridor. This mega-reserve spans a west-east gradient from coastal lowlands, Mountain Fynbos to Succulent Karoo and includes the northern most extremity of the CFR with the Cederberg Wilderness Area forming the core (Anonymous, 2004). Specifically, this study was conducted across an altitudinal transect covering the major vegetation types on both aspects of the Cederberg, encompassing the full range of vegetation. The transect ranged from sea level at Lambert's Bay, to Sneeukop (1926 m a.s.l.), and down the eastern slopes to Wupperthal (approximately 500 m a.s.l.). A total of seventeen altitudinal bands was sampled at 200 m altitudinal intervals across the transect (Table 1) representing Strandveld Succulent Karoo (one site), Mountain Fynbos (15 sites) and Lowland Succulent Karoo (one site).

Strandveld Succulent Karoo is characterized by low, scattered succulent shrubs such as *Zygophyllum morgsana* (Tortoisebush), *Euphorbia mauritanica* (Fragmenting Milkbush) and *E. burmannii* (Poison Milkbush) and stretches from the Berg River Mouth in the south to Alexander Bay in the north (Hoffman, 1996). Rainfall is generally low (50 - 300 mm) (Hoffman, 1996), and the geology of this biome is characterized by dune sand with highly calcareous areas.

Three main plant families characterize Mountain Fynbos: Restionaceae (restios), Ericaceae (heaths) and Proteaceae (proteas) (Rebelo, 1996). In the Cederberg district the Proteaceae constitutes the dominant overstorey in Fynbos (63 species of which seven are endemic to the area) and the majority of species are confined to the Fynbos biome (Rebelo, 1996). The geology of these areas is mostly quartzitic sandstone with shale and conglomerate lenses. Rainfall varies from 200 to over 2000 mm per year (Low & Rebelo, 1996).

The Mountain Fynbos can be further classified into structural units (or types) based on the dominant plant families at each of the sites (following Campbell, 1985, see also Cowling & Holmes, 1992). These structural units are Restioid Fynbos, Proteoid Fynbos, and Ericaceous Fynbos. Three sampling sites were located in Restioid Fynbos along the transect, at 200 m and 900 m a.s.l. on the western slope and at 900 m on the eastern slope (see Table 1). At these sites the vegetation is dominated by a high cover (> 60%) of Restionaceae, or restios and sedges (900 m site on the western slope). *Protea nitida* and *Leucadendron salignum* occur at the 200 m site but constitute less than 10% of the cover. This site could

37

thus still be classified as Restioid Fynbos (see Campbell, 1985). All three sites have gentle slopes (see Table 1).

Proteoid Fynbos only occurs on the western slope of the transect at the 300, 500 and 700 m sites (see Table 1). At the 300 m site (Sawadee), the vegetation type is ecotonal, with both Fynbos and Succulent Shrubland elements, such as non-ericaceous, ericoid-leaved shrubs (e.g. *Passerina* and *Phylica*) (L. Agenbag, personal communication). However, the dominant vegetation is proteoid and this site was thus included in the Proteoid Fynbos structural unit (Campbell, 1985). The 500 and 700 m sites are dominated by dense protea-dominated vegetation with restioids in the mid- to under storey. The sites in this vegetation type have steeper slopes than those sites in Restioid Fynbos (Table 1).

The vegetation turns to Ericaceous Mountain Fynbos above 900 m along the transect on both western and eastern slopes (see Table 1) (Campbell, 1985). Eight sites were located in this structural unit, four on the western slope and four on the eastern slope (Table 2). The western and eastern slope Ericaceous Fynbos are very similar, both with a high restioid component. The two sites at 1700 m just below Sneeukop were placed on very steep slopes compared with the other sampling sites (see Table 1).

In drier areas (e.g. between the Cederberg mountain range and Wupperthal) Mountain Fynbos is replaced by Lowland Succulent Karoo (Low & Rebelo, 1996), which is dominated by small, scattered shrubs such as Mesembryanthemaceae (vygies), Crassulaceae (stonecrops) and Asteraceae (daisies). This biome is extremely arid and one sampling area was located in this habitat type on top of Singkop in Wupperthal (see Table 1). The geology of this area is dominated by siltstone and shale. Rainfall ranges between 50 and 200 mm per year (Low & Rebelo, 1996).

Vegetation sampling

Vegetation structure was recorded at each sampling grid in October 2002 and March 2003 to determine the horizontal and vertical distribution of the vegetation. The horizontal distribution of vegetation was determined by estimating the coverage of the soil surface by vegetation, leaf litter, exposed rock and bare ground following the methods outlined by Rotenberry and Wiens (1980), Bestelmeyer and Wiens (1996) and Parr *et al*., (2004). A 1 m^2 grid was placed over each pitfall trap (see Ant sampling below) and the percentage of ground covered by the four categories within the grid was estimated. Mean ground cover was calculated for each sampling grid (i.e. each group of 10 pitfall traps).

Table 1 Sampling areas and vegetation types along the altitudinal gradient stretching from Lamberts Bay over the Cederberg down to Wuppertal. CWA = Cederberg Wilderness Area. "Last fire" refers to the date of the last recorded fire at each site. Where two dates are given the sampling grids at a particular site burnt in different years.

Area	GPS	Altitude	Slope (º)	Last fire	Area (km^2)	Vegetation type	Geology
Western slope:							
Lamberts Bay (Fig. 1a)	32º 10,682'S 18º 18,858'E	5 m	0.820	-	3082.58	Strandveld Succulent Karroo	Dunesand, in areas highly calcareous
Farm "Aan het Berg" (Fig. 1b)	32º 16,598'S 18º 31,799'E	256 m	3.867	-	1531.61	Restioid Mountain Fynbos	Quartzitic sandstone with minor shale and
Sawadee (Cederberg) (Fig. 1c)	32º 20,518'S 18º 59,491'E	370 m	7.873	1988	1531.61	Ecotonal, Succulent Karoo and Proteoid Mountain Fynbos	conglomerate lenses
Niewoudt's Pass CWA) (Fig. 1d)	32º 21,067'S 19º 00,417'E	537 m	13.516	1988	765.43	Proteoid Mountain Fynbos	
Uitkyk Pass (CWA) (Fig. 1e)	32º 24,471'S 19º 05,079'E	766 m	17.674	1959; 1988	447.53	Proteoid Mountain Fynbos	
Driehoek (CWA) (Fig. 1f)	32º 25,445'S 19º 09,970'E	922 m	6.981	1999	370.14	Restioid Mountain Fynbos	
Jeep track between Welbedacht and	32º 27,581'S 19º 14,459'E	1133 m	7.003	1979	282.66	Ericaceous Mountain Fynbos	
Sneeukop (CWA) (Fig. 1g, h)	32º 26,100'S 19º 13,969'E	1337 m	7.870	1979; 1984	206.59	Ericaceous Mountain Fynbos	

Table 1 (continued)

Area	GPS	Altitude	Slope (º)	Last fire	Area (km^2)	Vegetation type	Geology
Jeep track between Welbedacht and Sneeukop (CWA) (Fig. 1i)	32º 21,435'S 19º 08,753'E	1543 m	9.792	1999	106.73	Ericaceous Mountain Fynbos	Quartzitic sandstone with minor shale and conglomerate lenses
(Fig. 1j)	32º 21,310'S 19º 08,938'E	1687 m	27.387	1985	21.47	Ericaceous Mountain Fynbos	
Sneeukop (CWA) (Fig. 1k)	32º 21,305'S 19º 09,695'E	1926 m	8.670	1985; 2001	3.40	Alpine Mountain Fynbos	Quartzitic sandstone with thin shale and conglomerate lenses
Eastern slope:							
Between Sneeukop hut and Sneeukop (CWA) (Fig. 1l)	32º 21,241'S 19º 10,018'E	1740 m	36.979	1959; 1985	6.76	Ericaceous Mountain Fynbos	
Sneeukop hut (CWA) (Fig. 1m)	32º 20,888'S 19º 10,213'E	1543 m	15.230	1985; 2000	39.32	Ericaceous Mountain Fynbos	Quartzitic sandstone with minor shale and conglomerate lenses
Sneeukop to Wuppertal (CWA) (Fig. 1n)	32º 20,340'S 19º 10,899'E	1365 m	8.448	2000	76.94	Ericaceous Mountain Fynbos	
(Fig. 1o)	32º 20,140'S 19º 11,623'E	1158 m	2.471	2000	232.54	Ericaceous Mountain Fynbos	
(Fig. 1p)	32º 19,637'S 19º 12,086'E	965 m	10.397	2000	607.88	Restioid Mountain Fynbos	
Wupperthal (Fig. 1q)	32º 16,674'S 19º 13,161'E	520 m	9.207	-	1353.37	Lowland Succulent Karoo	Siltstone, shale

a) Lambert's Bay (W)

b) 200 m a.s.l. (W)

c) 300 m a.s.l. (W)

Figure 1 (a-c)

d) 500 m a.s.l. (W)

e) 700 m a.s.l. (W)

f) 900 m a.s.l. (W)

Figure 1 (d-f)

g) 1100 m a.s.l. (W)

h) 1300 m a.s.l. (W)

i) 1500 m a.s.l. (W)

Figure 1 (g-i)

j) 1700 m a.s.l. (W)

k) 1900 m a.s.l.
(Summit)

l) 1700 m a.s.l. (E)

Figure 1 (j-l)

44

m) 1500 m a.s.l. (E)

n) 1300 m a.s.l. (E)

o) 1100 m a.s.l. (E)

Figure 1 (m-o)

p) 900 m a.s.l. (E)

q) 500 m a.s.l. (E)

Figure 1 Images of representative sampling grids at each of the 17 sites. The sites are described in Table 1 and altitudes of the sites are given at each image. W = western slope, E = eastern slope.

The vertical distribution (relative vertical complexity) of the vegetation was measured by determining foliage height profiles using techniques similar to those of Rotenberry and Wiens (1980) and Bestelmeyer and Wiens (1996). Vegetation height was measured at four points located at 90º angles on a 1.5 m radius centred on each pitfall trap. At each of these sampling points a 1.5 m rod was placed vertically through the vegetation and the number of contacts with vegetation (hits) was recorded at 25 cm height increments (0-25 cm, 26-50 cm, 51-75 cm, 76-100 cm, 101-125 cm, 125-150 cm, 150 cm +). The average total number of hits per sample point was calculated as a measure of the changing vertical distribution of vegetation (Rotenberry & Wiens, 1980). The maximum height at each sampling point was taken as the highest 25 cm height interval where vegetation contacts were recorded (Rotenberry & Wiens, 1980).

One soil sample of 20 cm^3 (see Tan 1996) was taken during October 2002 at each sampling grid to ascertain soil characteristics. At each sampling grid twenty sub-samples were taken randomly and then mixed to make up one sample from which the 20 cm^3 was taken. The soil samples were air-dried in the laboratory for at least 10 days. The soil samples were analysed for composition (sand, silt, clay and rock), pH (McLean 1982), K, Na, Ca, Mg (Chapman, 1965), P (Bray & Kurtz, 1945), C (Nelson & Sommers, 1982), NO_3, H and conductivity (United States Salinity Laboratory Staff, 1954) by BemLab (Pty Ltd.), Somerset West, South Africa.

Two Thermocron iButtons (Semiconductor Corporation, Dallas/Maxim, Model DS 1920) were buried 10 mm beneath the soil surface at each sampling site (in an area where vegetation cover was low to ensure minimum shade cover) to measure soil temperature. This was done in June 2002 and data recordings are currently ongoing. The iButtons were set to record temperature at one-hour intervals. The data collected from June 2002 to October 2003 were used to calculate the following temperature parameters for each altitudinal band across the 16 month period: mean monthly temperature; mean monthly maximum and minimum; mean monthly temperature range, and absolute maximum and minimum temperature.

Ant sampling

Epigaeic ants were sampled along the altitudinal gradient during October 2002 and March 2003 by pitfall trapping. A total of forty pitfall traps, divided into four groups of ten pitfalls each, was placed at each site during each sampling event (Fig. 2). The four groups of pitfall traps were placed in such a way that they were at least 300 m apart. GPS readings were taken of the location of each group of ten pitfalls for spatial analyses. The ten traps were laid out in

a grid (2 x 5) with traps spaced at 10 m intervals (Fig. 2). The disturbance caused by placing the pitfall traps was minimized and the vegetation around the traps was not cleared. The "digging-in" effect (Greenslade, 1973) was thus considered negligible and the traps were set immediately. The traps contained 50 ml of a 50 % propylene glycol solution as preservative, which does not significantly attract or repel ants (Adis, 1979). All pitfall traps were left open for a period of five days per sampling event. The samples were washed and placed in 70 % ethanol in the laboratory and then sorted for ants. Ants were identified to species where possible or assigned to morphospecies. Voucher specimens of each species collected are held at the University of Stellenbosch and will be placed in the Iziko Museums of Cape Town.

Data analysis

Sample-based rarefaction curves for the ants were compiled separately for the sites to determine the degree of sampling representivity (EstimateS V5, R.K. Colwell, 1997, http://viceroy.eeb.uconn.edu/estimates, see also Gotelli & Colwell, 2001). The non-parametric Incidence Coverage Estimator (ICE) and Michaelis-Menten richness estimate provided by EstimateS were used to evaluate sample size adequacy (Colwell & Coddington, 1994). Sampling may be considered adequate when the sample-based rarefaction curves and the two estimators converge closely at the highest observed values (Longino *et al*., 2002). The ICE is a robust measure indicating sampling completeness because it stabilises well and is independent of sample size (Longino *et al*., 2002).

When sample-based rarefaction curves are used to compare different data sets, the comparison made is one of species density (the number of species per unit area) and not species richness (Gotelli & Colwell, 2001). To compare the species richness values of sites, individual-based rarefaction must be used (Gotelli & Colwell, 2001). These curves standardise different datasets on the basis of number of individuals and not on number of samples. Individual-based rarefaction curves were computed in EstimateS using the Coleman method (Coleman, 1981). Thereafter, the curves were rarefied to the lowest number of individuals recorded at a site to ensure valid comparisons of species richness between different sites (Gotelli & Colwell, 2001).

Because of the influence that available area has on species richness patterns (Rosenzweig, 1995), the species-area relationship was determined for both species richness and density across the altitudinal gradient using Generalized Linear Models assuming a Poisson error distribution (log link function, Type III model) (Dobson, 2002). The available
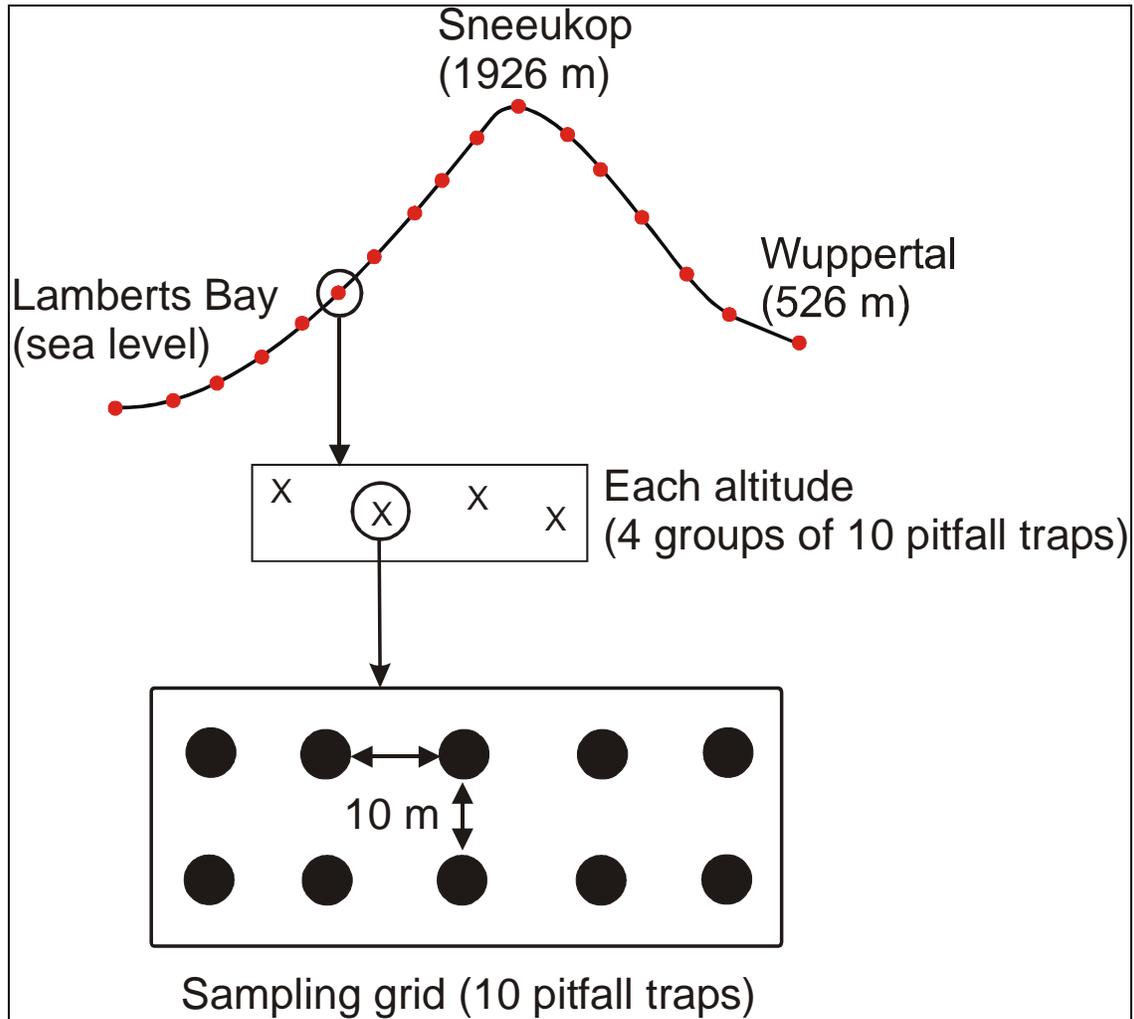
Figure 2 Sampling layout of the transect ranging from Lambert's Bay, over the Cederberg, and down to Wupperthal. Sampling was conducted in October 2002 and again during March 2003 in the same areas.

area was calculated across the Cederberg region (18°15' - 19°45'E; 32°00' - 32°45'S). The range of altitudes was divided into 200 m bands (each site was situated in an altitudinal band) and the total area in each altitudinal band within the Cederberg region was calculated using ArcView GIS 3.3 (see Table 1). This was done separately for the eastern and western slopes.

Collinearity in the abiotic variables (six temperature and 15 soil parameters, available area, altitude) and biotic variables (six vegetation parameters and post-fire vegetation age in Mountain Fynbos) was determined using Pearson's product-moment correlations. This was done separately for the abiotic and biotic variables. When variables were significantly correlated (and with $r > 0.50$) one of them was excluded from further analyses, based on a consideration of its likely biological relevance. The structure of the correlograms (see below) of the independent variables was also compared to assist in decisions about which variables to exclude. This approach did not alter the final choice of variables and therefore the full set of correlograms is not shown. The relationships between the abiotic and biotic variables chosen for analyses were then determined, again using Pearson's product-moment correlations, to refine the selection of variables by excluding collinear variables. When abiotic and biotic variables were significantly correlated (and with $r > 0.50$), one of the variables was excluded using the above protocol. These and the following analyses were performed for both the full transect and for a subset thereof in Mountain Fynbos. Mountain Fynbos constituted over 85% of the transect, and the climate change predictions for the region are for this biome (Midgley *et al*., 2002; 2003). Differences in ant assemblage structure between the within (the dominant biome only) and across biome predictors were also examined.

The proportion of the variation explained in ant species density and abundance by spatial position and the environmental variables (abiotic and biotic) was determined using trend surface analysis and partial regression approaches (Legendre & Legendre, 1998). This was done for total species density and total abundance per site across the whole transect, then for total species density and total abundance in each site in Mountain Fynbos, and finally for the total abundance of the dominant myrmecochorous species separately collected at each site across the whole transect. Generalized Linear Models assuming a Poisson error distribution with a log link function (Type III model corrected for over-dispersion) were used.

Following Legendre & Legendre (1998), trend surface analysis was first applied to determine the best-fit combination of spatial variables that contributed significantly to explaining the variation in the dependent variables. The spatial component of the variation in species density and abundance was modelled using a third-order polynomial that extracts linear and more complex spatial features (e.g. patches and gaps) from the data: $f(x, y) = b_0 +$

$b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$, where x and y are longitude and latitude respectively (Borcard *et al.*, 1992; Legendre, 1993). Generalized linear models were then performed for the environmental variables on species density and abundance, and the best fit model including only significant terms obtained (Legendre & Legendre, 1998; the only difference to the method was that we used generalized, rather than general, linear regression to accommodate the distribution of the dependent variables (see also McGeoch & Price 2004)).

Thereafter, partial linear regression analyses were conducted in which the terms from the best fit trend surface (spatial component) and environmental models were combined. Thus, the final model included both spatial and environmental terms, and was used to partition the explained variance (deviance) in species density and abundance into four components: (a) non-environmental spatial (the proportion of the variance explained by purely spatial components); (b) spatially structured environmental (the proportion of the variance explained by both spatial and environmental components); (c) non-spatial environmental (the proportion of the variance explained by environmental variables independent of any spatial structure); and (d) unexplained or residual variation (Legendre & Legendre, 1998). This procedure identifies the relative contribution of the environmental variables and spatial components to the explained variation in ant density and abundance, but it does not quantify the importance of individual variables (Legendre & Legendre, 1998, see also Lobo *et al.*, 2002, van Rensburg *et al.*, 2002).

To further understand the spatial structure in the selected environmental variables, spatial autocorrelation analysis (Moran's *I*, see Legendre & Fortin, 1989; Legendre & Legendre, 1998) and specifically SAAP V4.3 (Wartenberg, 1989) was used. Spatial correlograms based on 12 equal-frequency classes (i.e. same number of point pairs = 764) were used to graphically present the changes in the Moran's *I* coefficients (Legendre & Legendre, 1998). Overall significance of each correlogram was assessed with progressive Bonferroni correction and used to correct individual distance class *I* values for multiple comparisons (Wartenberg, 1989).

Canonical Community Ordination was used to relate the species composition of the assemblages to the environmental variables (Canoco V4.5, ter Braak & Šmilauer, 2002). The relationship between ant assemblage structure within the different vegetation types and environmental variables was examined using redundancy analysis (RDA) (ter Braak, 1994). The analysis was first conducted for assemblages in all six vegetation types together and then separately for those occurring in Mountain Fynbos. The species data were log_{10}-transformed

51

prior to analysis (Lepš & Šmilauer, 2003). A forward selection procedure of environmental variables was used to initially determine which of the variables significantly explained ant assemblage structure. The significance of each variable was judged using a Monte-Carlo permutation test (ter Braak, 1994). The model was then rerun with only significant explanatory variables to determine the percentage of assemblage variation accounted for by these variables. The results were displayed as biplots in which environmental variables are depicted as arrows and samples as symbols (Lepš & Šmilauer, 2003). Based on sample scaling, the length of the arrows indicates the relative importance of the environmental variables in explaining species composition of the samples and the arrows point in the expected direction of the steepest increase thereof (Lepš & Šmilauer, 2003). Species-sample relationships were also displayed as biplots to determine which species contribute to differences between assemblages. Only those species with more than 30% of their variability explained by the ordination subspace were included in the biplots (Lepš & Šmilauer, 2003). Species are depicted as arrows with arrows pointing in the direction of steepest increase in abundance (Lepš & Šmilauer, 2003).

Dufrêne and Legendre's (1997) Indicator Value Method was used to identify characteristic ant species for each vegetation type (based on hierarchical clustering) and altitudinal site (non-hierarchical clustering) (see McGeoch & Chown, 1998 for discussion). Using this method, measures of specificity (uniqueness to a site) and fidelity (frequency within that site) are combined for each ant species independently. An Indicator Value (IndVal) is then provided, as a percentage, for each species. A high indicator value indicates that a species has high fidelity and specificity to the site(s) within which it occurs and that it can be regarded as characteristic of that particular area. The significance of the IndVal measures for each species was tested using a random reallocation procedure of sites among site groups (Dufrêne & Legendre, 1997). Species with significant IndVals greater than 70 % (subjective benchmark, see van Rensburg *et al*., 1999; McGeoch *et al*., 2002) were then regarded as indicators of a particular site.

RESULTS

Species density, richness and abundance

A total of 81 ant species representing 24 genera (72 379 individuals) was collected during the two sampling periods (see Appendix A). Thirteen ant species were collected only in October 2002 while seven species were collected only during March 2003. Most species and genera

belonged to the subfamily Myrmicinae (48 and 12 respectively), followed by the Formicinae (28 and 4 respectively) (see Appendix A). The most speciose genera were *Camponotus* (20 species), *Tetramorium* (13 species) and *Monomorium* (12 species). Four myrmecochore species were sampled (see Appendix A), although the ecological roles of species that could not be identified to the species level are not known.

Ericaceous Fynbos had the highest total species density, while the highest total abundance was found in Proteoid Fynbos (Table 2). Proteoid Fynbos also had the highest mean species density and abundance (Table 2). Strandveld and Alpine Fynbos had the lowest mean species density, and Alpine Fynbos had the lowest mean abundance (Table 2).

Table 2 Species density and abundance of ants collected in the different vegetation types. *n* = number of sampling grids, *S* = total species density, *N* = total abundance.

Vegetation	*n*	*S*	*N*	Species density Mean ± S.E.	Abundance Mean ± S.E.
Strandveld	8	14	6490	6.63 ± 0.26	811.25 ± 199.93
Restioid Fynbos	24	47	13155	12.08 ± 0.38	548.13 ± 106.12
Proteoid Fynbos	24	48	32203	14.38 ± 0.47	1341.80 ± 137.45
Ericaceous Fynbos	64	58	16824	10.13 ± 0.32	262.88 ± 57.32
Alpine Fynbos	8	23	707	5.88 ± 1.22	88.38 ± 39.84
Succulent Karoo	8	14	3000	7.50 ± 0.33	375.00 ± 55.940

Sample-based species rarefaction curves approximated asymptotes for the two sampling periods indicating that most of the species at the different sites were collected (see Fig. 3). In most cases the rarefaction curves and estimators converged closely at the highest observed species density for each site. Species density estimates for each of the sites are thus considered representative (Table 3). However, this was not the case for the 300 m site on the western slope and the 1500 m site on the eastern slope. The reason for the substantial difference between the observed and ICE values was the relatively high number of singletons and doubletons. Although we have no explanation for these exceptions, they should be kept in mind throughout.
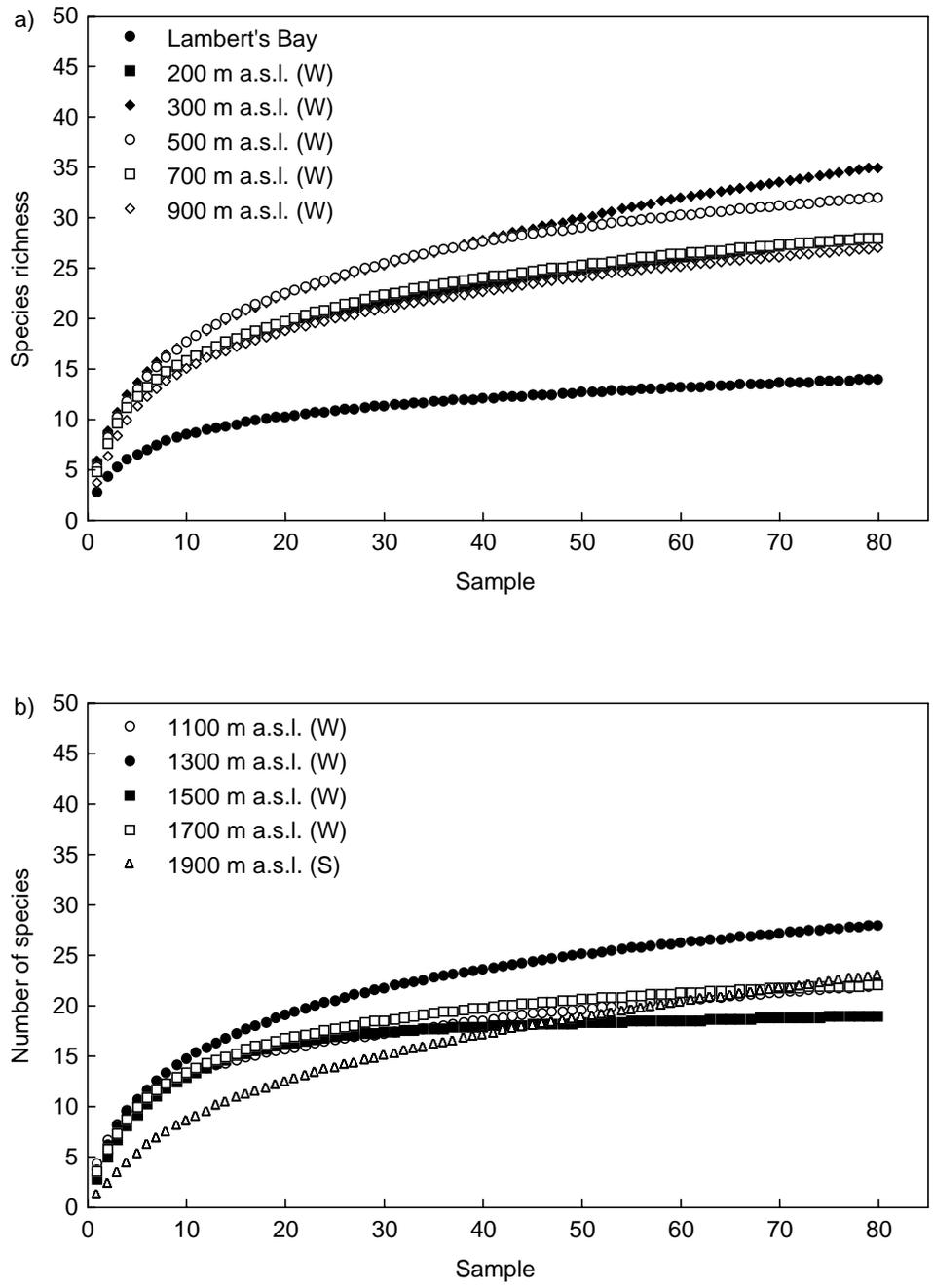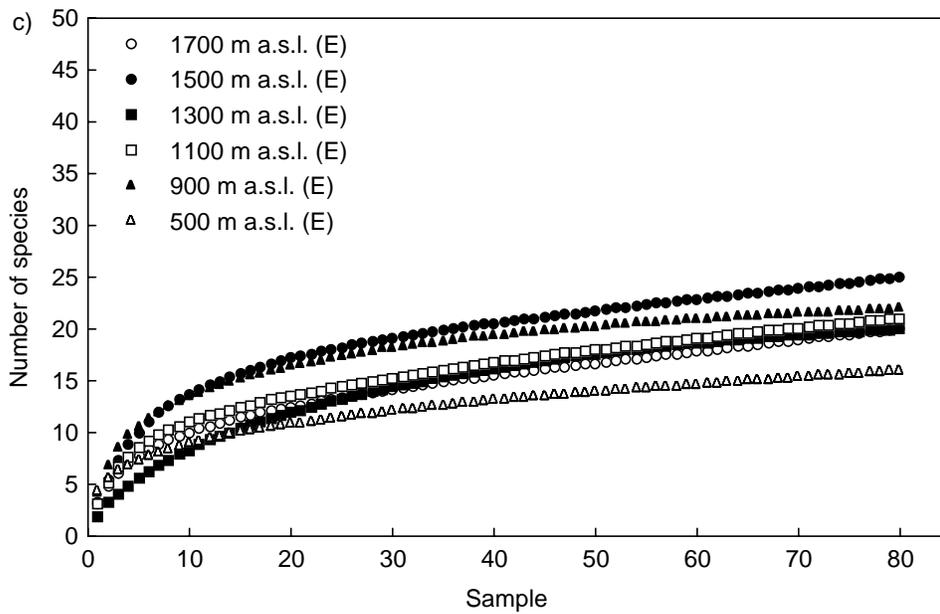
Figure 3 (a, b)

c)

Figure 3 Sample-based species rarefaction curves of ant assemblages of a) sea level to 900 m above sea level on the western slope (W), b) 1100 – 1900 m above sea level on the western slope and c) 1700 – 500 m above sea level on the eastern slope (E).

Individual-based rarefaction curves showed that, when the curves of the different altitudinal bands are rarefied to the lowest number of individuals collected at a site (1900 m, 670 individuals), the highest species richness (23 species) was recorded at 900 m on the western slope and at the summit (Fig. 4). The lowest number of species was recorded at sea level (10 species), followed by the 500 m and 1100 m altitudinal bands on the eastern slope (11 species) (Fig. 4).

Species richness across the entire transect was significantly related to available area (χ^2 = 9.86, P = 0.001, R^2 = 38.72, scaled deviance = 15.53, df = 16, estimate = +0.0002 ± 6.5 x 10^{-5}). There was no relationship between species density across the whole transect and available area (χ^2 = 0.28, P = 0.60, R^2 = 1.38; scaled deviance = 20.45, df = 16). Within Mountain Fynbos, species density was significantly related to area (χ^2 = 14.03, P < 0.001, R^2 = 51.99; scaled deviance = 12.21, df = 14), but with a negligible slope. There was no relationship between species richness and available area (χ^2 = 0.67, P = 0.41, R^2 = 4.70, scaled deviance = 7.47, df = 14).

The set of abiotic variables (six temperature and 15 soil parameters, altitude and available area) was reduced to 12 that were used in all subsequent analyses (see Appendix B). Four of the six temperature variables were selected: mean monthly temperature, mean monthly temperature range, absolute monthly maximum and absolute monthly minimum temperature. The highest mean temperature was found at Wupperthal (500 m on the Eastern slope) and the lowest on the summit (Fig. 5a). The highest absolute maximum temperature was 68.5 ºC (1500 m on the eastern slope) and the absolute minimum was –5.5 ºC (1700 m on the eastern slope) (Fig. 5a). The mean monthly temperature range was lowest between 1100 and 1500 m on the western slope (Fig. 5b). Seven soil parameters were selected for analyses of which five were chemical (pH, conductivity, P, C, NO_3; Appendix C) and two structural (proportion of clay and silt; see Appendix C) components. Available area was included in the set of abiotic variables, but the abiotic variables were highly correlated with altitude and this variable was thus not used in further analyses (see Appendix B).

Collinearity in the biotic variables was removed by excluding two variables (proportion of exposed rock and maximum vegetation height) (see Appendix B). The vegetation variables that were used in all subsequent analyses were therefore: proportion of ground covered by litter and vegetation, proportion of bare ground, and the average total number of hits per sample point (TOTHITS) (see Appendix C). Post-fire vegetation age in Mountain Fynbos was added as a biotic variable to the analyses of the species density and abundance of ants within Mountain Fynbos.

56

Table 3 The number of species observed in the pooled samples (Sobs), Incidence-based Coverage Estimator of species density (ICE) and the Michaelis-Menten richness estimator (MMMean) of the sample-based rarefaction curves.

| Sites (m a.s.l.)	Sobs	ICE (± S.D.)	MMMean
Western slope			
0 m	14	15.56 ± 0.00	14.04
200 m	23	24.94 ± 0.01	23.17
300 m	35	41.74 ± 0.02	35.07
500 m	14	15.75 ± 0.02	13.23
700 m	28	29.29 ± 0.01	28.88
900 m	24	25.55 ± 0.01	24.84
1100 m	22	26.26 ± 0.01	21.62
1300 m	27	29.64 ± 0.01	28.46
1500 m	19	19.57 ± 0.00	20.44
1700 m	21	21.35 ± 0.00	22.48
1900 m	23	26.79 ± 0.01	27.94
Eastern slope			
1700 m	19	29.96 ± 0.02	18.23
1500 m	25	36.21 ± 0.01	25.47
1300 m	21	22.24 ± 0.00	23.87
1100 m	21	25.40 ± 0.02	21.15
900 m	24	25.55 ± 0.00	24.84
500 m	14	15.75 ± 0.02	13.23
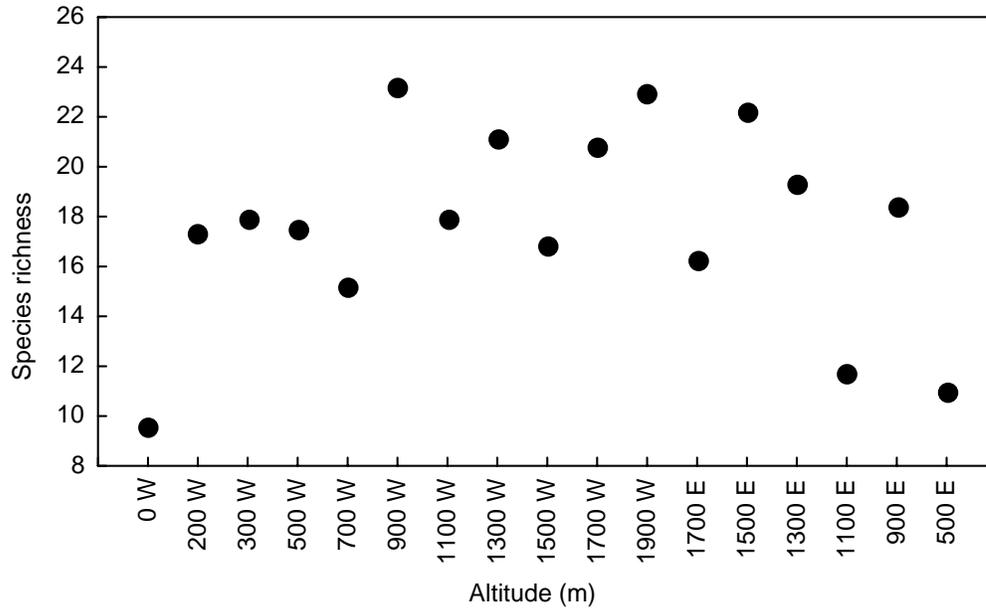
Figure 4 Species richness values derived from individual-based species accumulation curves of ant assemblages across the different altitudinal bands.
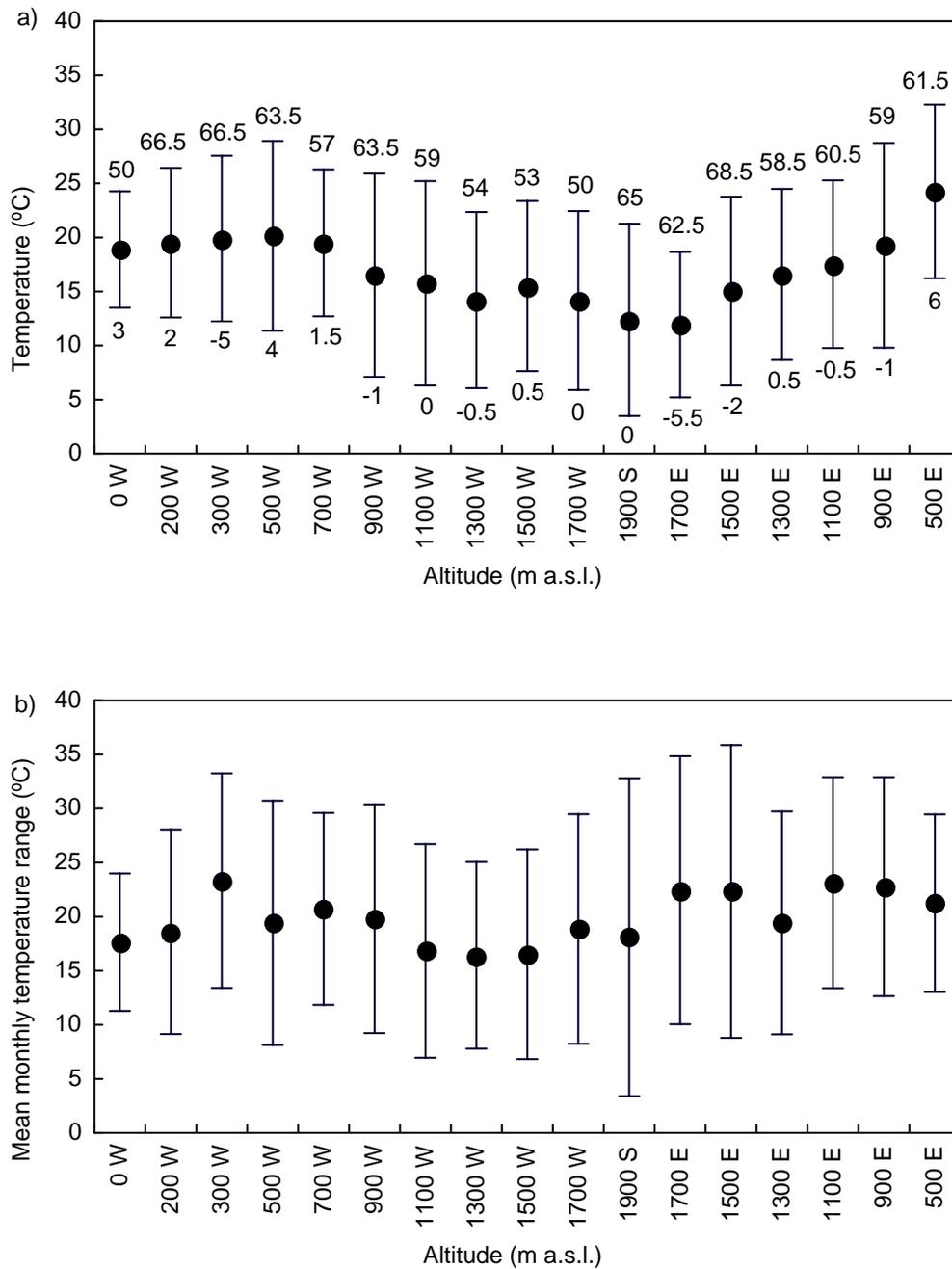
Figure 5 a) Mean monthly temperature, absolute maximum and absolute minimum temperatures and b) mean temperature range for the different sites.

Total species density of ants per site across the whole transect was significantly related to six environmental variables (Table 4). However, after controlling for spatial position, no environmental variables remained significant in the model. A similar result was found for species density of ants in Mountain Fynbos (Table 4). This outcome is a consequence of considerable spatial structure in the environmental variables, as is indicated by the relatively high proportion of variance explained by the spatially structured environmental component (Table 4), and the autocorrelation structure of the environmental variables (Fig. 6). In other words, the high degree of spatial structure shared by species density and the environmental component suggests in this case that the environmental variables might be responsible for variation in species density. By contrast, several of the environmental variables remained significant in the models for variation in total abundance per site, across the whole transect and for Mountain Fynbos (Table 4). Thus, the proportion of variance explained by the pure environmental components was higher than the variance explained by pure spatial components in the case of the abundance of ant occurring in Mountain Fynbos (Table 4). Nonetheless, a large proportion of the explained variance in abundance was again due to the spatially structured environmental component (Table 4). The abundance of ants across the whole transect was positively related to mean monthly temperature range and negatively to absolute maximum monthly temperature (Table 4). The abundance of Mountain Fynbos ants was negatively related to absolute maximum monthly temperature and vertical complexity of the vegetation, and positively related to the proportion of litter (Table 4). Neither the density nor the abundance of ants in Mountain Fynbos was significantly related to post-fire vegetation age.

Myrmecochores

The abundances of the four myrmecochorous ant species were related to different spatial and environmental variables in each case, and the overall variance explained varied considerably between the species. Generally, the spatially structured environmental component did not explain the largest proportion of the variance in the abundance of these species, and large proportions of the variance in abundance were explained by pure environmental components (Table 4). The abundance of *Anoplolepis* sp. (c.f. *custodiens*) was negatively related to the proportion of bare ground, while the abundance of *Anoplolepis* sp. (c.f. *steinergroeveri*) was negatively related to clay and positively to litter (Table 4). The

60

Table 4 Generalized linear model (Poisson error distribution, log link function, Type III model corrected for overdispersion) outcomes for the relationships between spatial terms plus environmental variables on species density and abundance of ant assemblages across the transect and within Mountain Fynbos, and on the abundance of myrmecochorous ants. Estimates are given in brackets. Dev = Deviance. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.01$. (a) Nonenvironmental spatial component, (b) spatially structured environmental component, (c) nonspatial environmental component. MMtemp = mean monthly temperature, Amin/Amax = absolute minimum/maximum monthly temperature, MMrange = mean monthly temperature range, Cond = conductivity, BG = bare ground, vegcover = percentage vegetation cover, TOTHITS = vertical complexity of vegetation.

Model	df	Dev	Selected environmental terms	Spatial terms	Percentage deviance explained			
					(a)	(b)	(c)	Total
Species density:								
Whole transect	123	136.57	area (+0.0002), MMtemp (+0.038), Amin (-0.0002), MMrange (-0.007), P (-0.004), TOTHITS (+0.006)	x (-0.654), x^2 (+25.359**), y^2 (+183.589*), xy (-44.283), x^2y (+591.665**), xy^2 (-1897.87**)	8.26	27.31	2.50	38.07
Mountain Fynbos	111	103.16	MMtemp (+0.011), pH (+0.219), P (-0.004), BG (-0.284)	x (-1.414), x^3 (+12.494), y^2 (+128.909*), y^3 (-1383.730**)	6.37	24.66	5.18	36.21
Total abundance:								
Whole transect	115	97.23	MMtemp (-0.174), MMrange (+0.338*), Amin (+0.140), Amax (-0.104*), pH (+0.156), Cond (+0.005), P (+0.003), C (-6.341), clay (+7.467), silt (+6.061), litter (+1.170), vegcover (+0.266), TOTHITS (-0.021)	y (-6.223), x (-15.932**), x^2 (-52.818), x^3 (-111.928), y^2 (-493.514), y^3 (-2969.520), x^2y (+632.357)	13.46	42.61	7.68	63.75

Table 4 (continued)

Model	df	Dev	Selected environmental terms	Spatial terms	Percentage deviance explained			
					(a)	(b)	(c)	Total
Mountain Fynbos	97	84.00	Area (+0.001), MMtemp (-0.168), MMrange (+0.342), Amin (+0.229), Amax (-0.146*), pH (-0.091), P (+0.002), C (-14.557), NO_3 (-0.016), clay (+8.430), silt (+7.970), litter (+3.295**), vegcover (+1.324), TOTHITS (-0.054*), age (-0.006)	x (-16.335), x^2 (+140.292), y^2 (+891.478), y^3 (+3404.883), xy (-319.695), x^2y (+3278.270), xy^2 (-10421.800)	6.86	49.86	12.97	69.69
Myrmecochores								
Anoplolepis sp. (c.f. *custodiens*)	78	66.79	BG (-3.454**)	y (-2043.890*), x (-4503.426*), x^2 (-48464.000*), x^3 (-170927.500*), y^2 (-7554.100), xy (+42677.060), x^2y (-216134.000*), xy^2 (+65857.380)	22.79	6.48	10.94	40.21
Anoplolepis sp. (c.f. *steinergroeveri*)	39	15.13	Amax (-0.682), pH (-3.587), C (-210.753), clay (-205.990**), litter (+6.642*)	y^3 (-29548.100), xy (+547.597), xy^2 (+11568.820)	2.93	31.57	41.70	76.20

Table 4 (continued)

Model	df	Dev	Selected environmental terms	Spatial terms	Percentage deviance explained			
					(a)	(b)	(c)	Total
Camponotus niveosetosus	65	92.69	area (+0.006***), MMtemp (-1.221***), Amax (-0.115*), pH (-3.004***), TOTHITS (-0.228**)	y (+7.726)	2.20	3.58	24.82	30.60
Tetramorium quadrispinosum	91	87.94	area (+0.003**), MMtemp (+0.849**), Amax (+0.124*), Amin (-0.349***), Cond (-0.001***), P (+0.011), C (-56.324**)	y (-15.687), x^2 (-53.962), xy (+177.411), x^2y (-513.919), xy^2 (+1258.633)	3.53	32.34	20.97	56.84
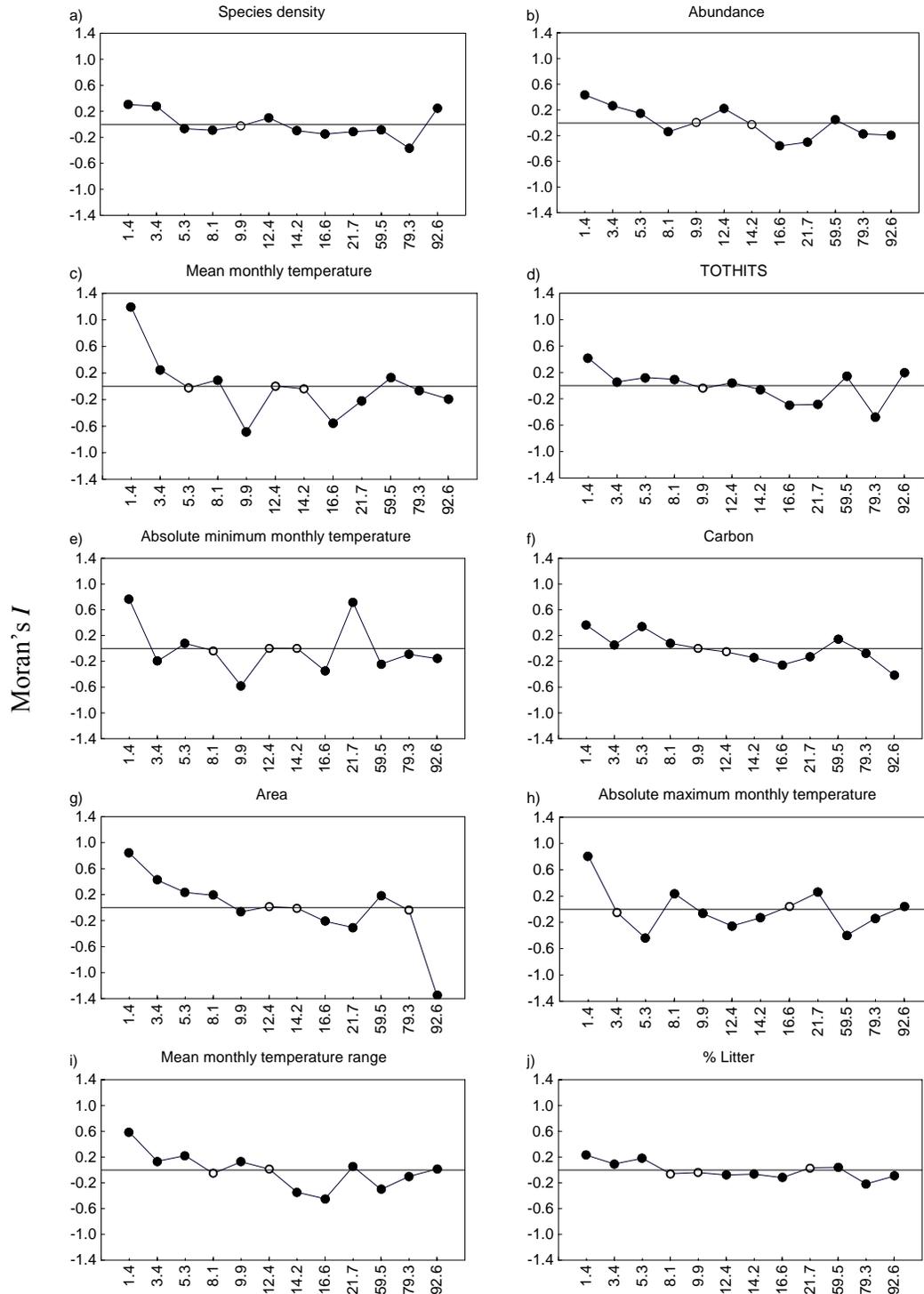
Figure 6 (a-j)
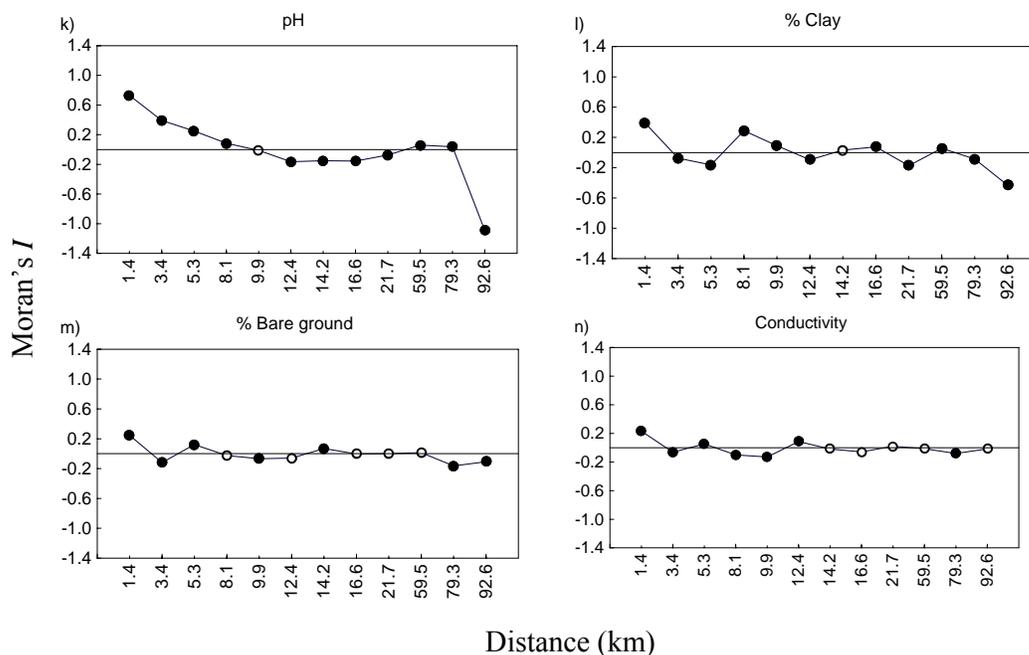
Figure 6 Spatial structure in species density and abundance, and the environmental variables that significantly explain the variance in species density and abundance. The correlograms were based on 12 equal-frequency classes (i.e. same number of point pairs = 764). Overall significance of each correlogram was assessed with progressive Bonferroni correction and used to correct individual distance class I values for multiple comparisons (Wartenberg, 1989). Significant Moran's I values (coefficient of autocorrelation) are indicated by closed circles.

abundance of *C. niveosetosus* was positively related to area, but declined with increasingmean monthly temperature range and absolute maximum temperature, as well as with increasing pH and vegetation complexity. By contrast, the abundance of *T. quadrispinosum* increased with area, mean monthly temperature range, and maximum temperature, but declined with increasing absolute minimum temperature (Table 4).

Assemblages

The first canonical axis in the RDA biplot (Fig. 7a) explained 29.7% of the sample-environment relation across the whole transect (F = 9.585, P = 0.002) and the first and second axes together explained 41.8%. Twelve of the environmental variables contributed significantly to the variance explained in the ant assemblages (Table 5).

The first axis represents an environmental gradient of increasing mean monthly temperature, absolute maximum monthly temperature, mean monthly temperature range, percentage bare ground and vertical complexity of the vegetation, and decreasing carbon content, nitrogen content and vegetation cover (Table 5, Fig. 7a). The second axis represents increasing absolute minimum monthly temperature and area (Table 5, Fig. 7a). Mean monthly temperature was the most important environmental variable explaining variance in assemblage structures (Table 5, Fig. 7a). Eight species had more than 30% of their variability explained by the ordination subspace across the whole transect (Fig. 7b). Five of these species were identified as species that are characteristic of particular vegetation types (see Table 5). One of these (*Myrmicaria* sp. 1) explained the difference between assemblages in Strandveld and the other vegetation types, even though this species was not identified as characteristic of this biome (see discussion below). Two species that were characteristic of Restioid and Proteoid Fynbos (*Camponotus mystaceous* and *Pheidole* sp. 2), contributed substantially to the differences between these two vegetation types and the other vegetation types.

Within Mountain Fynbos, the first canonical axis in the RDA biplot (Fig. 8a) explained 36.5% of the relationship between assemblages and the environmental variables (F = 10.002, P = 0.002) and the first and second axes together explained 51.6%. Ten environmental variables significantly explained the variation in assemblage structure of ants occurring in Mountain Fynbos (Table 5). Available area was the environmental variable that explained most of the variance in assemblage structure (Table 5). The first axis of the RDA biplot of samples vs. environmental variables represents an environmental gradient of increasing pH, mean monthly temperature, mean monthly temperature range, area and post-fire vegetation age. It further represented decreasing carbon content and percentage silt in the soil (Table 5, Fig. 8a). The second axis represents increasing absolute minimum monthly temperature and percentage clay in the soil (Table 5, Fig. 8a). Ten species had more than 30% of their variability explained by the ordination subspace within Mountain Fynbos (Fig. 8b). Three of these species were identified as characteristic of Fynbos vegetation types (*Monomorium fridae*, *Pheidole* sp. 2 and *Camponotus mystaceus* – Restioid and Proteoid Fynbos), and three were characteristic of Succulent Karoo (*Tetramorium quadrispinosum*, *Ocymyrmex* sp. 1 and *Monomorium* sp. 2) (see Table 6).

a)
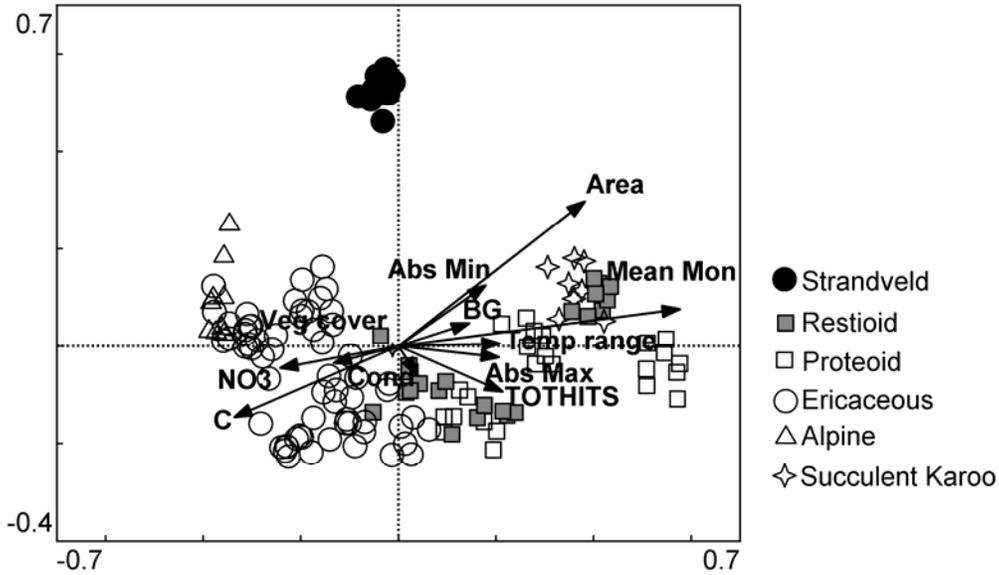
b)
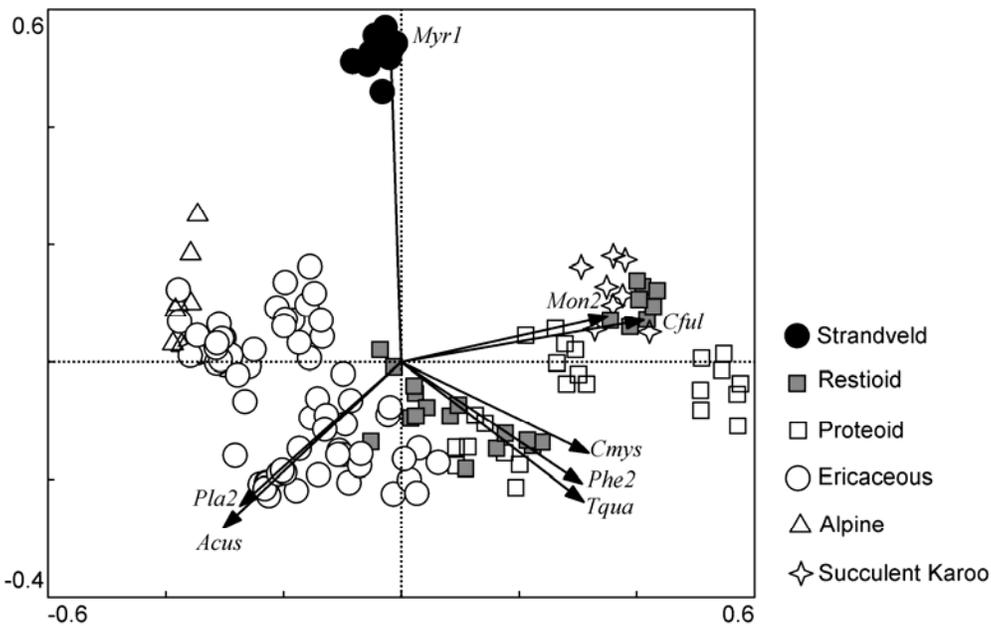
Figure 7 RDA ordination (biplot, sample scaling) of a) the ant assemblages occurring in the different vegetation types across the whole transect in relation to the environmental variables, and b) the ant assemblages, and species with more than 30% of their variability explained by the ordination subspace. *Acus = Anoplolepis* sp. (c.f. *custodiens*), *Phe2 = Pheidole* sp. 2, *Plagiolepis* sp. 1 *Tqua = Tetramorium quadrispinosum, Mon2 = Monomorium* sp. 2, *Myr1 = Myrmicaria* sp. 1, *Cful = Camponotus fulvopilosus, Cmys = C. mystaceus.*

67

Table 5 Significant species-environment correlation coefficients (R-values, ter Braak & Šmilauer, 2002) from redundancy analysis (RDA). The significance of the R-values was determined using Monte-Carlo permutation tests (P = significance and F = test statistic). Eigenvalues indicate the additional variance explained by each variable. Axis 1 and 2 are the first two ordination axes of the biplots of samples and environmental variables. A negative R-value reflects gradient direction in the RDA ordination. * indicates R-values that are significant at the table-wide level of α = 0.05.

| Variable	Eigenvalues	P	F	R (Axis 1)	R (Axis 2)
Whole transect:					
Mean monthly temp	0.06	0.002	8.32	0.852*	0.176*
Area	0.03	0.002	3.92	0.564*	0.678*
Absolute max temp	0.02	0.002	3.45	0.304*	-0.054
TOTHITS	0.02	0.002	3.40	0.315*	-0.218*
Absolute min temp	0.02	0.002	2.92	0.264*	0.289*
Temp range	0.03	0.002	3.85	0.306*	0.012
Bare ground	0.01	0.002	2.69	0.215*	0.109
Conductivity	0.02	0.002	2.09	0.057	-0.138
C	0.01	0.002	1.78	-0.497*	-0.338*
NO$_3$	0.01	0.014	1.56	-0.359*	-0.104
Vegetation cover	0.01	0.012	1.45	-0.197*	-0.081
Sum of all canonical eigenvalues: 0.24					
Mountain Fynbos					
Area	0.08	0.002	9.66	0.926*	-0.262*
Mean Monthly temp	0.02	0.002	3.75	0.884*	0.145
pH	0.03	0.002	3.39	0.648*	0.225*
Temp range	0.02	0.002	2.37	0.256*	-0.214*
Vegetation age	0.01	0.002	2.29	0.256*	0.061
Absolute min temp	0.02	0.002	1.91	0.159*	0.254*
C	0.01	0.002	2.13	-0.501*	-0.024
Vegetation cover	0.02	0.002	2.19	-0.115	-0.060
Clay	0.01	0.008	1.48	-0.178*	0.354*
Silt	0.01	0.016	1.51	-0.566*	0.478*
Sum of all canonical eigenvalues: 0.23					
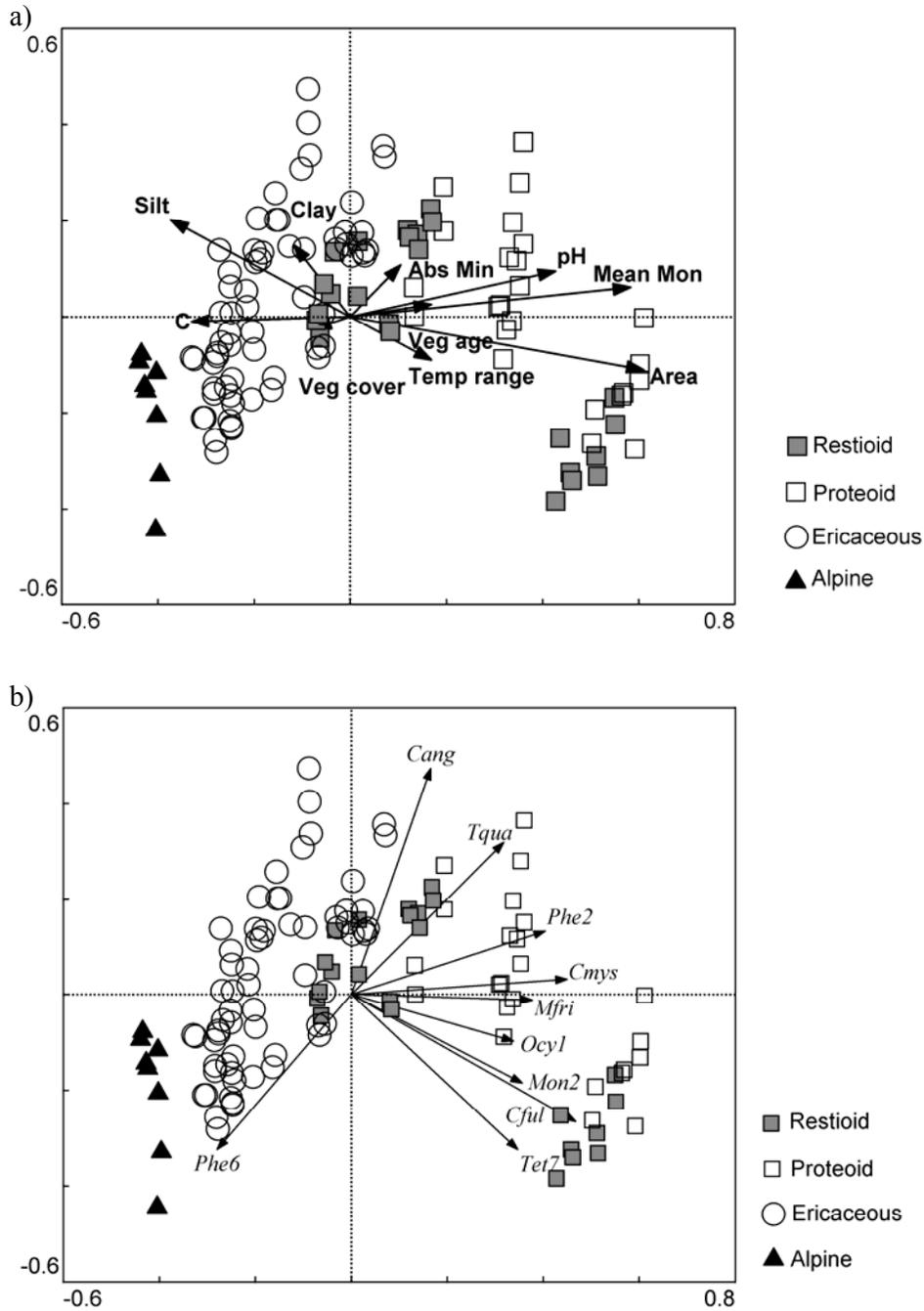
Figure 8 RDA ordination (biplot, sample scaling) of a) the ant assemblages occurring in the different vegetation types within Mountain Fynbos in relation to the environmental variables, and b) the ant assemblages, and species with more than 30% of their variability explained by the ordination subspace. *Cful = C. fulvopilosus, Cmys = C. mystaceus, Cang = C. angusticeps, Mon2 = Monomorium* sp. 2, *Mfri = M. fridae, Phe2 = Pheidole* sp. 2, *Phe6 = Pheidole* sp. 6, *Ocy1 = Ocymyrmex* sp. 1, *Tet7 = Tetramorium* sp. 7, *Tqua = T. quadrispinosum.*

69

Indicator species

The IndVal analyses revealed that nine species were characteristic of certain vegetation types, of which six were specific to Succulent Karoo and one to Strandveld (Table 6). There were no species that could be regarded as characteristic of any of the four Mountain Fynbos vegetation types (Table 6). However, two species were identified as characteristic of both Proteoid and Restioid Fynbos (Table 6). One species (*Myrmicaria* sp. 1) was restricted to Strandveld, but was not identified as specific to the biome. This species had a patchy distribution and was found in relatively low abundance, which translates into a low fidelity of the species to the biome (see Dufrêne & Legendre 1997). Therefore the species was not identified as specific to the biome using Dufrêne and Legendre's (1997) Indicator Value Method.

Furthermore, nine species were identified as characteristic of certain altitudes, and three of these were characteristic of a range of altitudes spanning more than one vegetation type (Table 6). Two species identified as characteristic of particular altitudes and vegetation types (*Anoplolepis* sp. (c.f. *custodiens*) and *T. quadrispinosum*) are myrmecochores.

DISCUSSION

The number of ant species collected in Proteoid Fynbos here (48 species) is comparable to that of other studies conducted in the same vegetation type (Donnelly & Giliomee, 1985; Schlettwein & Giliomee, 1987; Koen & Breytenbach, 1988). However, by comparison with ant assemblages in many other Southern African regions, with the exception of the arid Nama Karoo, total species (85) and generic (24) richness recorded in this study were low (Samways, 1983, 1990; Milton *et al*., 1992; Swart *et al*., 1999; Lindsey & Skinner, 2001; Parr *et al.,* 2002, 2004). These results suggest that ant species richness in the Cederberg (and in the Fynbos biome in particular) is intermediate between that of high-energy savanna environments and lower energy arid ecosystems in southern Africa. This would appear to be in keeping with large-scale patterns of variation in richness of other animals in southern Africa such as birds (van Rensburg *et al*., 2002) and frogs (Minter *et al*., 2004). It also suggests that ants are responding to energy availability in this region, as has been recorded elsewhere (Kaspari *et al*., 2004), though broader scale studies will be necessary to confirm this idea.

70

Table 6 Percentage indicator values (*IndVal* > 70 %) of ant species for each vegetation type (hierarchical clustering) and altitudinal band (non-hierarchical clustering). * = Maximum *IndVal* values. W = western slope, E = eastern slope.

Vegetation type/altitude	Species	*% IndVal*
Vegetation type		
Succulent Karoo	*Pheidole* sp. 1	98.66*
	Monomorium sp. 2	95.31*
	Tetramorium quadrispinosum	80.39*
	Tetramorium sp. 6	72.82*
	Messor sp. 1	72.29*
	Ocymyrmex sp. 1	71.73
Strandveld	*Technomyrmex* sp. 1	79.99*
Proteoid and Restioid Fynbos	*Camponotus mystaceus*	81.63*
	Pheidole sp. 2	80.33*
Altitude		
0 – 900 (W) m	*Monomorium fridae*	87.27*
	Lepisiota sp. 1	72.05
1100 (W) – 1700 (W) and	*Anoplolepis* sp. (c.f. *custodiens*)	73.75*
900 (E) – 1700 (E) m		
1900 m (Summit)	*Camponotus* sp. 1	96.37*
	Meranoplus sp. 1	90.00*
500 m (E)	*Pheidole* sp. 1	98.61*
	Monomorium sp. 2	95.17*
	Tetramorium quadrispinosum	79.89*
	Ocymyrmex sp. 1	71.08

71

In terms of local-scale variation in ant species density, and abundance, firmer conclusions can be reached. In the former case, much of the variation between sites was explained by spatially structured environmental variation, which was perhaps not surprising given the strong spatial gradient in the environmental variables (Fig. 6). In other words, strong spatial variation in a variable such as temperature is probably responsible for strong spatial variation in the dependent variable. Thus, variation in species density explained by the non-spatially structured environmental component only, tends to be low. Such an outcome is typical of studies undertaken over strong environmental gradients, although it is generally more characteristic of regional scale investigations (Borcard *et al*., 1992; Smith, 1994; Lobo *et al*., 2002; van Rensburg *et al*., 2002, McGeoch & Price, 2004). It has been suggested that if the residuals from a model including environmental variables only show no spatial structure, then the analysis can proceed without inclusion of the spatial variables (Diniz-Filho *et al*., 2003). However, this still leaves the problem of incorrect degrees of freedom in the model, which might lead to biased conclusions (see Lennon, 2000 for discussion). Therefore, we did not adopt the approach of residual inspection here. Rather we recognize that strong spatial variation in area, mean monthly temperature range, and mean monthly temperature are strong correlates with species density, with density tending to increase with area and with mean monthly temperature. These findings are in keeping with species energy theory (see Wylie & Currie, 1993; Rosenzweig 1995; Hawkins *et al*., 2003; Evans *et al*., 2004), and with results from investigations of ants, other insects, and ectotherms more generally (Turner *et al*., 1987; Kerr & Packer, 1999; Allen *et al*., 2002; Kaspari *et al*., 2004). However, variation in precipitation, which is apparently considerable across the transect (Cowling & Holmes, 1992 provide a qualitative estimate of rainfall variation for a nearby transect, but no quantitative data are available), may also have a substantial influence on variation in species density, thus accounting for the generally low total variance explained in our models. Indeed, Hawkins and Porter (2003) found that actual evapotranspiration was the primary explanatory variable for variation in butterfly species richness. Moreover, in water-limited systems such as those of the southwestern Cape (Deacon *et al*., 1992), water availability is much more likely to be a strong correlate of richness than is absolute energy availability (O'Brien *et al*., 2000; Hawkins *et al*., 2003). Linder (1991) found this to be the case for plant species richness in the southwestern Cape,

72

for which rainfall was the best predictor of species richness of several plant taxa typical of the Cape flora.

Variation in total abundance also had a pronounced spatially structured environmental component, for the same reasons as those discussed above. Increases in total abundance were strongly related to an increase in mean monthly temperature range and a decline in absolute maximum temperature, and in the Fynbos only were also positively related to increasing litter and declining vegetation complexity. Ant abundance and richness have been shown to vary considerably with temperature in several other studies (see Andersen, 1995; Parr *et al*., 2005). In general, abundance and richness increase with an improvement in habitat quality, which is often associated with increasing temperature (e.g. Bestelmeyer, 2000; Andersen, 1995; Cerdá *et al*., 1998) and then decline as habitats become more stressful (but see also Parr *et al.*, 2005). Several other studies have also found relationships between ant abundance and litter availability and vegetation complexity. For example, Bestelmeyer and Wiens (1996) found that species richness was dramatically greater in areas with higher litter load, but only in the dry season. They argued that the increased leaf litter development might buffer the ant assemblages against a decline in the habitat suitability (e.g. dryer conditions). Furthermore, Robertson (1999) found that reduced litter cover (as a result of fire) might result in a loss of cryptic species (but see also Lassau and Hochuli 2004).

An important difference between the models for species density and those for abundance was the considerably greater proportion of the variation in the latter explained by the full model (64-70%), by comparison with the former (36-38%). Why this should be the case is not entirely clear. However, the relationship between ant abundance (and especially the dominant ants) and species richness is typically unimodal (Anderson, 1992; Parr *et al*., 2005). Thus, species richness (or density) can be low at both low and high abundances. If the pattern is driven even partly by a combination of environmental stress and competition, which might well be the case (Parr *et al*., 2005), then the environment will appear to have a larger linear influence on abundance than on richness, so resulting in a greater proportion of the variance being explained in linear models of the former, than of the latter. This is precisely what we find.

Time since the most recent fire was never included as a significant variable in the models for variation in species density and abundance. It was likewise

unimportant in explaining differences between ant assemblages across the sites. Although these results are in keeping with a well-replicated experimental investigation of ant assemblage responses to fire in a southern African savanna system (Parr *et al.,* 2004), they contrast strongly with several other studies (Andersen & Yen, 1985; Andersen, 1991; Parr *et al*., 2002; Hoffman & Andersen, 2003), including one on Fynbos ant assemblages (Donnelly & Gilliomee, 1985). These differences may well be a consequence of the methods used, and certainly this study did not attempt to investigate post-fire age in a well-replicated explicit fashion (see Parr & Chown, 2003 for discussion). Rather, time since fire was included as a variable in the initial models and was never found to be significant. An explicit focus on time since fire, whilst holding other variables more constant in an appropriate experimental design, might well reveal affects of post-fire vegetation age on ant assemblages. Alternatively, it may turn out that like the ant assemblages in the fire prone system studied by Parr *et al*., (2004), those studied here may also be responsive only to whether the vegetation has burnt or not, rather than the subtleties of the burning regime, owing to considerable resilience and resistance born of a long-term exposure to a fire climax system (see Cowling, 1992 for a discussion of fire in Fynbos systems). Carefully replicated work will be required to distinguish these alternatives.

By contrast, temperature, area and several vegetation variables contributed significantly to the separation of the assemblages in the major vegetation types and biomes. These results are not surprising given that temperature and vegetation structure (including proportion of bare ground) have been found to be strong correlates of variation in ant assemblages in a variety of other studies. For example, Andersen (1986) found that ant assemblages were more diverse in Australian woodland, which represents greater structural complexity in terms of vegetation and litter (i.e. less bare ground), compared to the less structurally diverse heath. Furthermore, Perfecto and Vandermeer (1996) indicated that there is significant diversity loss in ground-foraging ant assemblages when the vegetation is altered in such a way to reduce shade and litter. However, they argued that this loss in diversity is rather a consequence of indirect (alterations in species interactions) than direct effects of habitat modifications (Perfecto & Vandermeer, 1996). Gotelli and Ellison (2002) showed that ant density in New England bogs and forests was related to vegetation complexity (and light availability), with higher density (and subsequently higher species richness) in the more complex forests, while Parr *et al*., (2004) showed

that bare ground and litter cover best explained overall patterns in ant diversity in an *Acacia* savanna in the Kruger National Park. In addition, Lassau and Hochuli (2004) found that ant assemblages in open habitats (which are generally hotter and drier) support a larger suite of opportunists, generalists and hot climate specialists than those in more complex habitats.

Perhaps of most significance is the fact that these strong relationships between temperature and vegetation variables, and ant assemblage structure suggest that climate change in this region will affect ant assemblages in two ways. First, alterations in climate such as the increase in temperature and increase in variability of temperature predicted for the region (Tyson, 1999; Giorgi *et al*., 2001; Midgley *et al*., 2002, 2003) will almost certainly push assemblages from left to right on Fig. 7 if these correlates have a causal basis. That is, higher altitude assemblages such as those typical of Alpine and Ericaceous Fynbos will slowly give way to those more characteristics of Proteoid and Restioid Fynbos, and ultimately Succulent Karoo. In other words, high altitude assemblages are likely to disappear, and along with them their characteristic species (*Camponotus* sp. 1, *Meranoplus* sp. 1, see Table 7). Second, changes in vegetation associated with alterations in temperature and water availability, an important driver of vegetation characteristics in the region (see Linder, 1991; Cowling & Holmes, 1992), are likely to exacerbate these changes owing to direct responses of ants to changes in vegetation cover and soil carbon. It has been shown that organic soil carbon and nitrogen decrease rapidly with an increase in temperature and decreasing precipitation in semiarid soils (see Smith *et al*., 2002; Link *et al.,* 2003). Such a reduction in organic matter can affect chemical, physical and biological properties of soil, which in turn contribute to ecosystem function and stability (Link *et al*., 2003). Moreover, such changes especially in organic carbon will ultimately affect plant distributions, which in turn will affect the ant assemblages.

The predicted changes are very much in keeping with those for other insect assemblages in montane regions, where the higher elevation assemblages are at most risk (Haslett, 1997; Fleishman *et al*., 1998, 2000; Hill *et al.*, 2002). They are also in keeping with predictions of vegetation change for the region, which suggest that only the higher elevations will support Fynbos, whilst the others will become more karroid, as was perhaps the case for other areas in the region that have altered from Fynbos to karroid vegetation as the region has dried out (Deacon *et al*., 1992). Of course, the changes are likely to be influenced by sharp discontinuities in geology and soil type,

as is clearly the case on the eastern edge of the study site where a sharp boundary exists between Fynbos and Succulent Karoo associated with a transition from Table Mountain Sandstone changing to shale (see Cowling & Holmes, 1992; Cowling *et al*., 1997; Milton *et al*., 1997; Lechmere-Oertel & Cowling, 2001) and on the western edge where dune sand and Table Mountain Sandstone abut, but the vegetation (Strandveld and Fynbos) and ant assemblages differ considerably.

Because of the functional importance of ants in Fynbos ecosystems as myrmecochores (Westoby *et al*., 1982; Bond & Slingsby, 1983; Slingsby & Bond, 1985; Breytenbach, 1988; Hanzawa *et al*., 1988; Handel & Beattie, 1990; Johnson, 1992; Le Maitre & Midgley, 1992; Midgley & Bond, 1995), there is unlikely to be a unidirectional influence of changing climate on vegetation and then on ants. Rather, the changing climate will directly affect ant assemblages, and will indirectly affect them via plant responses to climate. In turn, changes in the ant assemblages are also likely to affect the ways in which seeds are dispersed owing to differential responses of myrmechocorous species. For example, the abundance of *Camponotus niveosetosus* was negatively related to mean monthly temperature, absolute maximum temperature, and vegetation structural complexity, reflecting its numerical dominance at sites from 1300 to 1700 m. By contrast, the abundance of *Tetramorium quadrispinosum* covaried positively with mean monthly temperature and absolute maximum temperature reflecting is predominance at lower altitude (200 – 1300 m) sites. Increases in temperature in the region are thus likely to mean replacement of the former with the latter species.

Likewise, *Anoplolepis* sp. (c.f. *steinergroeveri*), which was collected only at low altitude sites (200 – 900 m), was positively related to litter and negatively to clay, reflected by its absence from Succulent Karoo. By contrast, *Anoplolepis* sp. (c.f. *custodiens*) was collected at higher altitudes (900 – 1700m) and had a negative relationship with bare ground. The altitudinal distribution of the two species only overlapped at 900 m on the western slopes. Both of these *Anoplolepis* species have previously been collected in the same areas, with *Anoplolepis* sp. (c.f. *steinergroeveri*) being numerically much less dominant (Lindsey & Skinner, 2001), as is the case here. However, *Anoplolepis* sp. (c.f. *custodiens*) is present throughout Africa (Prins, 1963) even though it has been hailed as one of the most dominant myrmecochores in the southwestern Cape (e.g. Midgley & Bond, 1995), and it is thus unlikely that this generalist species will be severely affected by climate change.

What these predicted changes are likely to mean for myremcochory is difficult to determine in the absence of more thorough experimental work. Several studies have indicated that even though myrmecochorous plants are clearly adapted to ant dispersal, ants have not evolved any particular trait (either morphological or behavioural) in response (Johnson, 1992; Midgley & Bond, 1995). Furthermore, seeds of myrmecochorous plants have very few physical structures that restrict their dispersal to specific ant species (Johnson, 1992; Midgley & Bond, 1995, see also Wheelright & Orians, 1982). Perhaps it is therefore unlikely that the displacement of one myrmecochorous species by another would affect seed dispersal. However, it has also been postulated that seed size plays a role in restricting the dispersal of large seeds by small ant species (Pudlo et al., 1980; Drake, 1981; Bond & Slingsby, 1983; Auld, 1986; Johnson, 1992; Witt & Giliomee, 2004). In addition, germination of seeds may be a function of burial depth (Brits, 1987; Bond et al., 1990). If different ant species have different seed gallery depths then the success of germination might be related to the ant species involved in dispersal of the seeds. Therefore, despite an apparent lack of specialization amongst myremcochores for some seed traits, their changing relative abundances and differences in behaviour and seed size preference could influence ecosystem functioning. Such a transformation in functioning would mean that conservation plans which seek to incorporate long-term change in the region (e.g. Younge & Fowkes, 2003, Cowling & Pressey, 2003 and Driver et al., 2003) might have underestimated the extent and nature of this change, and therefore may fail to capture the biodiversity they seek to maintain over the longer term.

In conclusion, this study has demonstrated that there are likely to be substantial and complex changes to ant assemblages as climates change in the northern Cape Floristic Region. The importance of ants for ecosystem functioning in both Fynbos and Succulent Karoo systems (e.g. Johnson, 1992; Le Maitre & Midgley, 1992; Milton et al., 1992) suggests that these responses are likely not to be a consequence solely of vegetation changes, but are likely also to precipitate such transformation. The dynamic aspects of the response of southern African ecosystems to climate change have enjoyed little attention (contrast the investigations of Rutherford et al., 1999, Erasmus et al., 2002, and Midgley et al., 2002, 2003, with those of the Aspen FACE project - Karnosky et al., 2003), although clearly such consideration is required. The changes that are predicted to take place in the next 50 years in Fynbos and Succulent Karoo ecosystems (Rutherford et al., 1999; Midgley,

2002, 2003) could be substantially exacerbated by synergistic effects of the kind outlined here, and only experimental work will determine whether this is likely to be the case. In the meantime, ongoing monitoring of this transect will reveal the nature and pace of the change as it unfolds.

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89

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GROUND-DWELLING BEETLE ASSEMBLAGES IN THE NORTHERN CAPE FLORISTIC REGION: PATTERNS, CORRELATES, AND IMPLICATIONS

INTRODUCTION

The Cape Floristic Region (CFR) is both the smallest and richest floral kingdom with approximately 8700 plant species (Low & Rebelo, 1996), of which 68 % are endemic (Bond & Goldblatt, 1984). In consequence, it has been identified as a major biodiversity hotspot of global significance (Myers, 1990; Cowling & Richardson, 1995; Mittermeier *et al.*, 1998). The region has a high concentration of Red Data Book plant species (i.e. 1406 species) (Cowling & Hilton-Taylor, 1994), and is listed as a Centre of Plant Diversity (WWF and IUCN, 1994) and a Global 200 Ecoregion (Olson & Dinerstein, 1998).

The patterns responsible for the exceptional diversity of the region's plants are reasonably well known (e.g. Cowling, 1992; Cowling & Lombard, 2002; Linder, 2003). For example, Linder (1991) found that rainfall was the best predictor of species richness of several plant taxa typical of the Cape flora. Cowling and Lombard (2002) hypothesised that regional diversity patterns are the product of different speciation and extinction histories. In a recent, comprehensive, review Linder (2003) argued that the considerable diversity of the CFR might be explained by diverse limitations to gene flow (such as dissected landscapes and pollinator speciation) and the complex environment that provides a diversity of selective regimes such as a geographically variable climate, altitudinal variation, regular fires, and different soil types and rocky terrain that provide many micro-niches.

By contrast, patterns of insect diversity in the CFR, and the processes underlying them, are poorly understood. The focus on the region's exceptionally high floristic diversity (e.g. Cowling *et al*., 1992; Cowling & Lombard, 2002) has somewhat overshadowed its faunal diversity and, in consequence, there is a dearth of information on insect species diversity within the CFR, although their functional significance is appreciated. The consensus view is that diversity is low (Johnson, 1992; Giliomee, 2003), although several local scale studies of specific host plants and their herbivores suggest that insect richness might be much

higher than is generally thought to be the case (e.g. Cicadellidae: Davies, 1988a, b; gall-forming insects: Wright & Samways, 1998). However, few groups have been subject to careful surveys, and most comparisons have been qualitative and based on examinations of studies that differ substantially in their methods (although the work by Wright and Samways (1998) on galling insect species richness is a notable exception).

Moreover, the determinants or correlates of insect diversity in this region are poorly explored. Only a few, recent studies have explored relationships between the diversity of certain groups and the environment. For example, Wright and Samways (1998) found that gall-insect species richness was positively correlated with Fynbos plant species richness and was not influenced by environmental variables such as elevation and aspect. In addition, it has been shown that Fynbos plant characteristics (e.g. infructescence openness and wall thickness) play a major role in determining the abundance, and frequency of occurrence of insect borers on *Protea* species (Wright & Samways, 2000). Botes *et al.* (in press, Chapter 2) showed that, across an elevational gradient in the Cederberg, temperature explained significant proportions of the variation in ant species density and abundance, and, together with area and several vegetation variables, contributed significantly to the separation of the ant assemblages in the major vegetation types and biomes in their study area.

The paucity of investigations of the determinants of insect diversity in the region is especially concerning because of the prediction that global climate change will have a substantial influence on the region (Midgley *et al.*, 2002, 2003, see also Hannah *et al.*, 2005). The Fynbos biome is predicted to lose large areas near its northern limits (retaining less than 10 %, Midgley *et al.*, 2002), especially those along the west coast and in the Cederberg mountains, and biome loss is expected to occur at all altitudes (Midgley *et al.*, 2002, 2003). These changes are expected to occur as a consequence of warming and drying in the region. What the direct and indirect effects of these changes in the environment are likely to mean for insects is not clear, largely because the insect fauna is poorly understood and the determinants, or even correlates, of variation in insect diversity in the region are so poorly understood.

In this paper, we therefore investigate patterns in, and correlates of, epigaeic beetle diversity in one of the most climate change sensitive areas in the CFR, the Cederberg (Midgley *et al.*, 2003). In particular, we determine whether ground-dwelling beetle assemblage structure differs between the main vegetation types in the Cederberg, how restricted these beetles are to specific vegetation types, and which environmental variables might be associated with site-related differences in beetle richness and abundance. The

92

epigaeic beetle fauna, which comprises mostly darkling and ground beetles, was selected for study because tenebrionids are typically important processors of organic matter (Slobodchikoff, 1978; Allsopp, 1980; Thomas, 1983), and carabids constitute a significant assemblage of ground-dwelling predators (Thiele, 1977).

MATERIAL AND METHODS

Study site

The study took place in the Greater Cederberg Biodiversity Corridor (GCBC), which is a large reserve spanning a west-east gradient from coastal lowlands to Mountain Fynbos and Succulent Karoo. It includes the northernmost extremity of the CFR, with the Cederberg Wilderness Area forming the core (Anonymous, 2004). Specifically, this study was conducted across an altitudinal transect covering the major vegetation types on both aspects of the Cederberg, encompassing the full range of vegetation. The transect stretched from sea level at Lambert's Bay, to Sneeukop (1926 m), and down the eastern slopes to Wupperthal (approximately 500 m) (see Chapter 2). A total of seventeen altitudinal bands was sampled at 200 m altitudinal intervals across the transect (see Table 1 in Chapter 2) representing Strandveld Succulent Karoo (one site), Mountain Fynbos (15 sites) and Lowland Succulent Karoo (one site). The Mountain Fynbos sites were further classified into four structural units (or types) based on the dominant plant families at each of the sites (following Campbell, 1985, see also Cowling & Holmes, 1992), namely Restioid (three sites), Proteoid (three sites), Ericaceous (eight sites) and Alpine Fynbos (one site).

Beetle sampling

Ground-dwelling beetles (Carabidae and Tenebrionidae) were sampled along the altitudinal gradient during October 2002 and October 2003 using the same sampling protocol outlined in Chapter 2. Several tiger beetle species (Cicindellidae) were also collected, and given their role as predators were included within the carabids. A total of forty pitfall traps, divided into four groups of ten pitfalls each, was placed at each site during each sampling event. The four groups of pitfall traps were placed in such a way that they were at least 300 m apart. GPS readings were taken of the location of each group of ten pitfalls for spatial analyses. The disturbance caused by placing the pitfall traps was minimized and the vegetation around the traps was not cleared. The "digging-in" effect (Greenslade, 1973) was thus considered negligible and the traps were set immediately. The traps contained 50 ml of a 50 % propylene

glycol solution as preservative. All pitfall traps were left open for a period of five days per sampling event. The samples were washed and placed in 70 % ethanol in the laboratory and all ground-dwelling beetles were pinned. The beetles were identified to species where possible or assigned to morphospecies. Voucher specimens of each ground-dwelling beetle species collected are held at Stellenbosch University and will be placed in the Iziko Museums of Cape Town.

Predictor variables

Twelve abiotic variables and five biotic variables were used to evaluate the effect of environmental conditions on species density and abundance. The abiotic variables comprised four temperature variables (mean temperature, mean monthly temperature range, absolute maximum and minimum temperature), seven soil parameters (chemical: pH, conductivity, P, C, NO_3; structural: proportion of clay and silt), and available area. The biotic variables included the proportion of ground covered by litter and vegetation, proportion of bare ground, the vertical complexity of the vegetation, and post-fire vegetation age in the case of Mountain Fynbos. Details on data collection for these the 17 variables are provided elsewhere (Chapter 2).

Data analysis

Sample-based rarefaction curves for all the beetles were compiled separately for the sites to determine the degree of sampling representivity (EstimateS V5, R.K. Colwell, 1997, http://viceroy.eeb.uconn.edu/estimates, see also Gotelli & Colwell, 2001). The non-parametric Incidence Coverage Estimator (ICE) and Michaelis-Menten richness estimate provided by EstimateS were used to evaluate sample size adequacy (Colwell & Coddington, 1994, see also Longino *et al*., 2002).

When sample-based rarefaction curves are used to compare different data sets, the comparison made is one of species density (the number of species per unit area) and not species richness (Gotelli & Colwell, 2001). To compare the species richness values of sites, individual-based rarefaction must be used (Gotelli & Colwell, 2001). These curves standardise different datasets on the basis of number of individuals and not on number of samples. Individual-based rarefaction curves were computed in EstimateS using the Coleman method (Coleman, 1981). Thereafter, the curves were rarefied to the lowest number of individuals recorded at a site to ensure valid comparisons of species richness between different sites (Gotelli & Colwell, 2001).

Because of the influence that available area has on species richness patterns (see Rosenzweig, 1995) the species-area relationship was determined for both beetle species richness and density across the altitudinal gradient using Generalized Linear Models assuming a Poisson error distribution (log link function, Type III model corrected for over dispersion) (Dobson, 2002).

The proportions of the variation in beetle species density and in beetle abundance explained by spatial position and the environmental variables (abiotic and biotic) were determined using trend surface analysis and partial regression approaches (Legendre & Legendre, 1998). This was done for total species density and total abundance per site across the whole transect, then for total species density and total abundance in each site in Mountain Fynbos, and finally for the total abundance and species richness of the tenebrionids and carabids separately collected at each site across the whole transect. Generalized Linear Models assuming a Poisson error distribution with a log link function (Type III model corrected for over-dispersion) were used.

Following Legendre and Legendre (1998), trend surface analysis was first applied to determine the best-fit combination of spatial variables that contributed significantly to explaining the variation in the dependent variables. The spatial component of the variation in species density and abundance was modelled using a third-order polynomial that extracts linear and more complex spatial features (e.g. patches and gaps) from the data: $f(x, y) = b_0 + b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$, where x and y are longitude and latitude respectively (Borcard et al., 1992; Legendre, 1993). Generalized linear models (assuming a Poisson error distribution with a log link function, Type III model corrected for over-dispersion) were then performed for the environmental variables on species density and abundance, and the best-fit model including only significant terms obtained (Legendre & Legendre, 1998; the only difference to the method was that we used generalized, rather than general, linear regression to accommodate the distribution of the dependent variables (see also McGeoch & Price, 2004)).

Thereafter, partial linear regression analyses were conducted in which the terms from the best-fit trend surface (spatial component) and environmental models were combined. Thus, the final model included both spatial and environmental terms, and was used to partition the explained variance (deviance) in species density and abundance into four components: (a) non-environmental spatial (the proportion of the variance explained by purely spatial components); (b) spatially structured environmental (the proportion of the variance explained by both spatial and environmental components); (c) non-spatial

95

environmental (the proportion of the variance explained by environmental variables independent of any spatial structure); and (d) unexplained or residual variation (Legendre & Legendre, 1998). This procedure identifies the relative contribution of the environmental variables and spatial components to the explained variation in beetle density and abundance, but it does not quantify the importance of individual variables (Legendre & Legendre, 1998, see also Lobo *et al*., 2002, van Rensburg *et al*., 2002).

Multivariate community analysis (PRIMER V5 1994) (Clarke & Warwick, 1994) was used to assess differences in beetle assemblages. Bray Curtis similarity measures (Bray & Curtis, 1957) were used to determine whether beetle assemblage structure differed between sampling periods and vegetation types. The data were fourth-root transformed before analysis to reduce the weight of common species (Clarke & Warwick, 1994). Analyses of Similarity (ANOSIM – Clarke, 1993) were used to determine whether there were significant differences between the beetle assemblages in the two sampling periods (October 2002 and 2003), the three main vegetation types (Strandveld, Mountain Fynbos and Succulent Karoo) and within the Mountain Fynbos between the four structural types (Restioid, Proteoid, Ericaceous and Alpine Fynbos). The ANOSIM procedure of PRIMER is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke, 1993). This method generates a global *R*-statistic, which is a measure of the distance between groups. An *R*-value that approaches one indicates strongly distinct assemblages, whereas an *R*-value close to zero indicates that the assemblages are barely separable (Clarke, 1993). These *R*-values were used to compare beetle assemblages between sampling periods and vegetation types. The false discovery rate criterion (see García, 2004) was used to correct for multiple comparisons.

The relationships between beetle assemblages in the three main vegetation types and the four structural types within Mountain Fynbos were displayed using non-metric multi-dimensional scaling (nMDS) ordinations (Clarke, 1993). These were iterated several times from 10 different starting values to ensure that a global optimum was reached, i.e. no decline in the stress value occurs (Clarke & Warwick, 2001).

Dufrêne and Legendre's (1997) Indicator Value Method was used to identify characteristic beetle species for each vegetation type (based on hierarchical clustering) and altitudinal site (non-hierarchical clustering) (see McGeoch & Chown (1998) for discussion). Using this method, measures of specificity (uniqueness to a site) and fidelity (frequency within that site) are combined independently for each beetle species. An Indicator Value (IndVal) is then provided, as a percentage, for each species. A high indicator value indicates

that a species has high fidelity and specificity to the site(s) within which it occurs and that it can be regarded as characteristic of that particular area. The significance of the IndVal measures for each species was tested using a random reallocation procedure of sites among site groups (Dufrêne & Legendre, 1997). Species with significant IndVals greater than 70 % (subjective benchmark, see van Rensburg *et al*., 1999; McGeoch *et al*., 2002) were then regarded as indicators of a particular site.

RESULTS

A total of 49 ground-dwelling beetle species (5 596 individuals) was collected during the two sampling periods (Appendix D). Thirty-three of these belonged to the family Tenebrionidae and 16 species to Carabidae (Appendix D). Eleven beetle species were collected only in October 2002 while no species were unique to the October 2003 period (Appendix D). Proteoid Fynbos had the highest total species density while the highest total abundance was found in Ericaceous Fynbos (Table 1). Ericaceous Fynbos also had the highest mean abundance (Table 1). The highest mean species density was found in Strandveld (Table 1). Alpine Fynbos had the lowest total abundance, mean abundance and mean species density (Table 1). Furthermore, Ericaceous Fynbos had the highest total carabid (including cicindellid) species density and abundance (Table 1). The total abundance of tenebrionids was also highest in Ericaceous Fynbos, but the total species density was highest in Proteoid Fynbos (Table 1).

Sample-based species rarefaction curves approximated asymptotes for the two sampling periods indicating that most of the species at the different sites were collected (Fig. 1). In most cases the rarefaction curves and estimators converged closely at the highest observed density for each site (Table 2). Species density estimates for each of the sites are thus considered representative. However, this was not the case for the 700 m site on the western slope. The reason for the substantial difference between the observed and ICE values was the relatively high number of singletons (five out of eight species). Although we have no explanation for this exception, it should be kept in mind throughout.

Few individuals were collected at three sites (1900 m, 25 individuals; 900 m on the eastern slope, 57 individuals; 700 m on the eastern slope; 113 individuals) compared to the rest of the sites. Therefore, the curves of the different altitudinal bands were rarefied to the fourth lowest number of individuals collected at a site (i.e. individual-based rarefaction curves; 200 m on the western slope, 149 individuals) and the species richness of three sites

Table 1 Species density and abundance of ground-dwelling beetles collected in the different vegetation types. n = number of sampling grids, S = total species density, N = total abundance.

Vegetation	n	S	N	Species density	Abundance	Carabidae, incl. Cicindellidae		Tenebrionidae	
				Mean ± S.E.	Mean ± S.E.	S	N	S	N
Strandveld	8	16	277	7.00 ± 0.57	34.63 ± 3.80	3	57	13	220
Restioid Fynbos	24	20	576	3.67 ± 0.49	24.00 ± 3.26	8	90	12	486
Proteoid Fynbos	24	23	627	4.83 ± 0.53	26.13 ± 3.58	6	32	17	595
Ericaceous Fynbos	64	19	3870	3.27 ± 1.19	60.47 ± 9.23	11	611	8	3259
Alpine Fynbos	8	6	25	1.13 ± 0.23	3.13 ± 0.97	5	24	1	1
Succulent Karoo	8	6	220	2.88 ± 0.23	27.50 ± 7.09	2	2	4	218

a)

Legend:
- Lambert's Bay
- 200 m a.s.l. (W)
- 300 m a.s.l. (W)
- 500 m a.s.l. (W)
- 700 m a.s.l. (W)
- 900 m a.s.l. (W)

b)

Legend:
- 1100 m a.s.l. (W)
- 1300 m a.s.l. (W)
- 1500 m a.s.l. (W)
- 1700 m a.s.l. (W)
- 1900 m a.s.l. (S)

Figure 1 (a, b)

c)
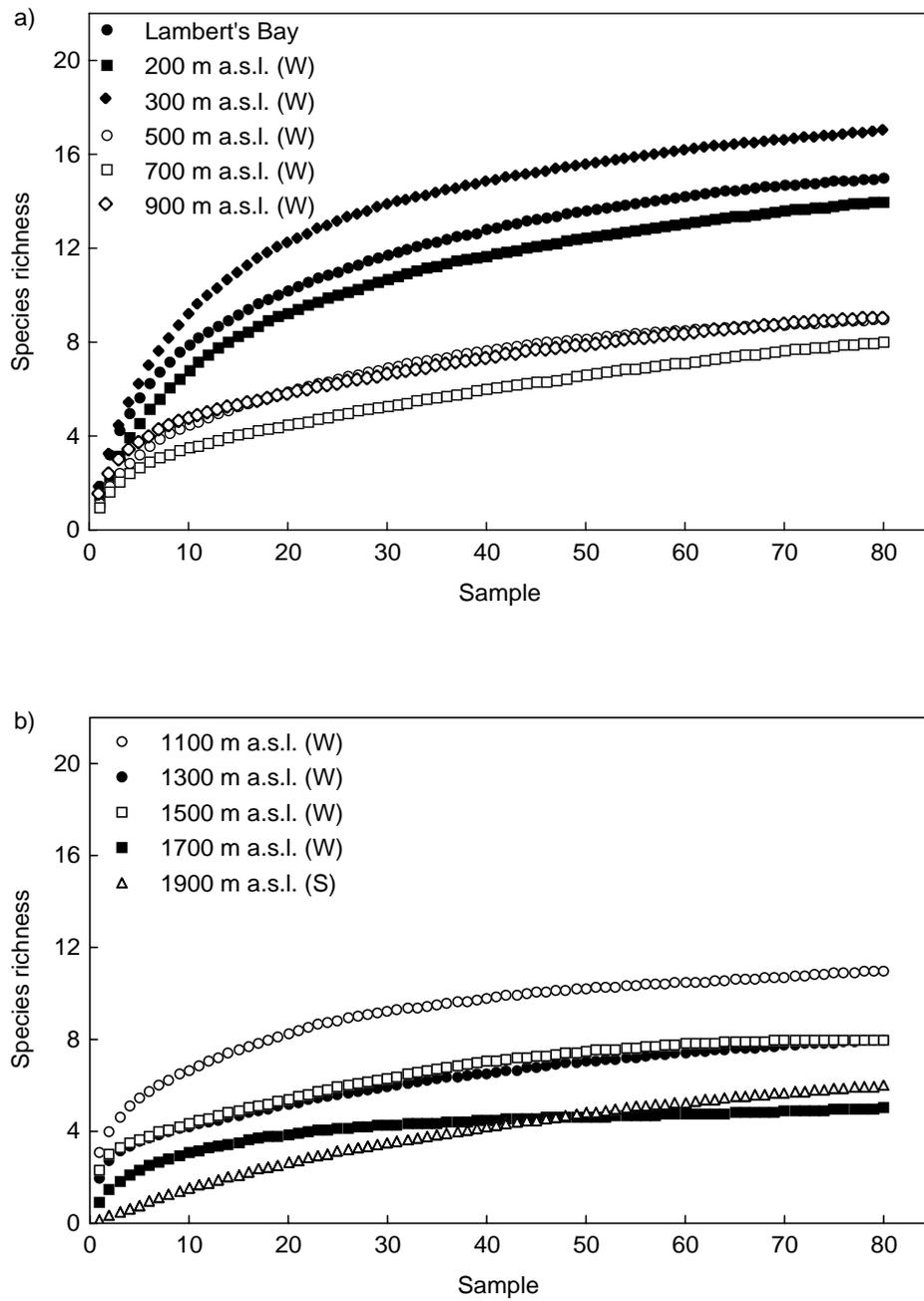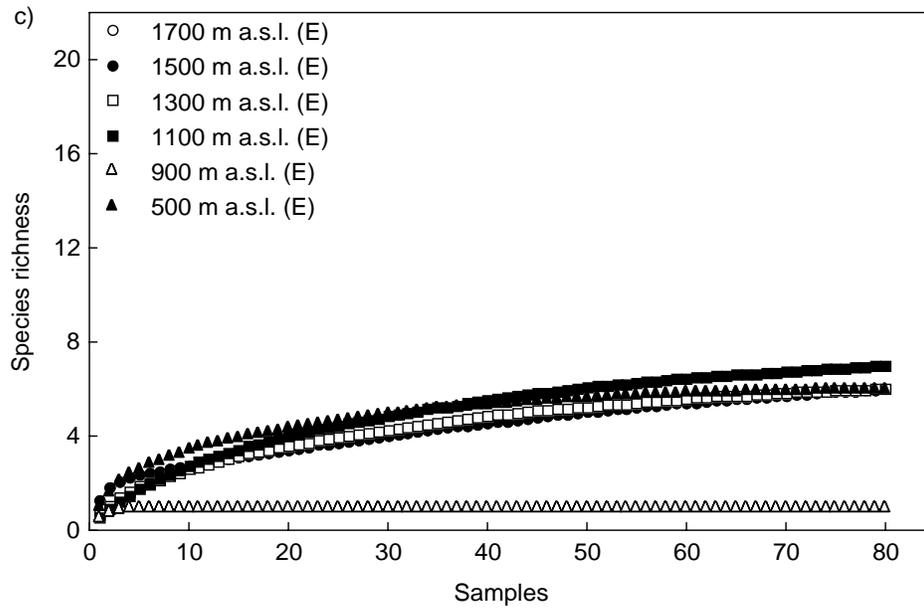
Figure 1 Sample-based species rarefaction curves of beetle assemblages at a) sea level to 900 m above sea level on the western slope (W), b) 1100 – 1900 m above sea level on the western slope and c) 1700 – 500 m above sea level on the eastern slope (E).

Table 2 The number of species observed in the pooled samples (Sobs), Incidence-based Coverage Estimator of species density (ICE) and the Michaelis-Menten richness estimator (MMMean) of the sample-based rarefaction curves.

Sites (m a.s.l.)	Sobs	ICE (± S.D.)	MMMean
Western slope			
0 m	15	16.27 ± 0.44	15.86
200 m	14	16.40 ± 0.59	15.61
300 m	17	18.75 ± 0.44	18.70
500 m	10	9.92 ± 0.24	9.52
700 m	8	14.09 ± 0.02	7.85
900 m	9	10.67 ± 0.00	8.72
1100 m	12	11.81 ± 0.32	10.62
1300 m	8	9.24 ± 0.01	7.34
1500 m	8	8.00 ± 0.19	7.57
1700 m	5	5.45 ± 0.18	5.11
1900 m	6	8.64 ± 0.00	10.50
Eastern slope			
1700 m	6	8.00 ± 0.97	5.33
1500 m	5	8.22 ± 0.02	4.45
1300 m	6	6.93 ± 0.01	6.42
1100 m	7	8.14 ± 0.01	8.21
900 m	1	1.00 ± 0.00	1.02
500 m	6	6.00 ± 0.00	6.23

with the lowest number of individuals was extrapolated to this point to allow for meaningful comparisons. The highest species richness was recorded at the three lowest altitudes on the western slopes (Fig. 2), whilst the lowest richness was recorded at 900 m on the eastern slope where only a single species was collected across both sampling periods (*Zophosis gracilicornis*) (Fig. 2).

Species richness and density across the entire transect were significantly related to available area (see Table 1 in Chapter 2 for areas) (Richness: $\chi^2 = 6.04$, P = 0.01, $R^2 = 35.54$, deviance = 10.95, df = 15, estimate = +0.0003 ± 0.0001; Density: $\chi^2 = 11.81$, P < 0.01, $R^2 = 37.92$, deviance = 19.34, df = 15, estimate = +0.0003 ± 8.55 x 10^{-5}). Within Mountain Fynbos species richness and density were also significantly related to area (Richness: $\chi^2 = 14.77$, P < 0.01, $R^2 = 48.59$; deviance = 15.62, df = 13, estimate = 0.0006 ± 0.0001; Density: $\chi^2 = 11.84$, P < 0.01, $R^2 = 45.55$, deviance = 14.16, df = 13, estimate = 0.0006 ± 0.0002).

Total species density and abundance of beetles across the whole transect, within Mountain Fynbos, and separately for carabids and tenebrionids were significantly related to several environmental variables, and in particular to mean temperature, mean monthly temperature range, and absolute minimum and maximum temperatures (Table 3). However, after controlling for space, few environmental variables remained significant in both the species density and the abundance models. This result is a consequence of substantial spatial structure in the environmental variables, as indicated by the relatively high proportion of variance explained by the spatially structured environmental component (Table 3), and the autocorrelation structure of the environmental variables (see Chapter 2).

The spatially structured environmental component contributed a large proportion of the explained variance (Table 3). In the final model species density of the Mountain Fynbos beetles was positively related to mean monthly temperature (Table 3), whilst the species density of beetles across the whole transect and within Mountain Fynbos were negatively related to absolute minimum monthly temperature (Table 3). The latter is unusual by comparison with other work (see Discussion). However, species density showed a weak unimodal relationship with absolute minimum monthly temperature, which may have influenced the model, especially owing to two outliers which had low absolute minimum monthly temperature values and high species density (300 m on the western slope and 1700 m on the eastern slope, see Fig. 1 and Fig. 2, and Fig. 4 in Chapter 2). This unimodal relationship likely explains the negative relationship between species density and absolute minimum monthly temperature, when the opposite might usually be expected. The species
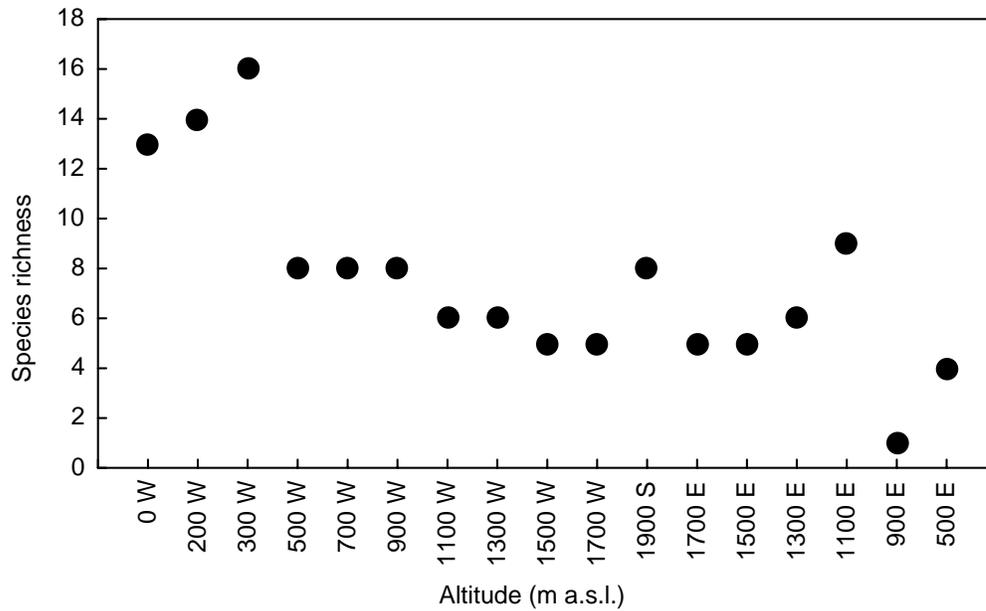
Figure 2 Species richness values derived from individual-based species accumulation curves of ground-dwelling beetle assemblages across the different altitudinal bands. W=western side and E = eastern side of transect, S = summit.

Table 3 Generalized linear model (Poisson error distribution, log link function, Type III model corrected for overdispersion) outcomes for the relationships between spatial terms and environmental variables on species density and abundance of beetle assemblages across the transect and within Mountain Fynbos, and on the abundance and species density of carabids (including cicindellids) and tenebrionids. Estimates are given in brackets. * P < 0.05, ** P < 0.01, *** P < 0.001. (a) Nonenvironmental spatial component, (b) spatially structured environmental component, (c) non-spatial environmental component. Mtemp = mean temperature, Amin/Amax = absolute minimum/maximum temperature, MMrange = mean monthly temperature range, BG = bare ground, vegcover = percentage vegetation cover, vegage = post-fire vegetation age, Vcompl = vertical complexity of vegetation.

Variable	df	Dev/Df	Environmental terms	Spatial terms	Percentage variance explained			
					(a)	(b)	(c)	Total
Species density:								
Whole transect	123	1.032	Mtemp (+0.028), MMrange (-0.017), Amax (+0.011), Amin (-0.063***), pH (+0.014)	x (-3.224), x^2 (-45.239***), y^2 (-200.193*), y^3 (-2833.830**), xy (+194.424**), x^2y (-610.502**), xy^2 (3125.470***)	5.56	56.45	5.04	67.05
Mountain Fynbos	109	1.020	Mtemp (+0.157*), MMrange (-0.086), Amax (+0.015), Amin (-0.109**), vegcover (+0.004), vegage (+0.008)	x (-0.414), x^3 (+30.064**), y^2 (-226.710*), xy (146.790**)	4.23	55.07	6.74	66.04

Table 3 (continued)

Variable	df	Dev/Df	Environmental terms	Spatial terms	Percentage variance explained			
					(a)	(b)	(c)	Total
Carabidae	125	0.913	Mtemp (-0.001), MMrange (-0.076), Amin (-0.082), clay (-0.057), BG (+0.020**), vegage (+0.017)	x^2 (-44.348*), x^3 (-122.769*), y^2 (+122.936**), x^2y (++314.735*)	5.63	20.38	7.17	33.18
Tenebrionidae	119	1.160	Mtemp (-0.046), MMrange (+0.159), Amax (-0.017), Amin (+0.007), pH (+0.323**), C (+0.394), clay (+0.124**), silt (-0.038), Vcompl (+0.001)	y (+20.461**), x (-10.059**), x^3 (+231.148***), y^2 (-712.308***), xy (+200.369***), x^2y (-2034.700***), xy^2 (+4902.985***)	8.88	43.09	12.42	64.39
Total abundance:								
Whole transect	127	0.982	Area (-0.001), Mtemp (+0.313*), MMrange (-0.174), Amax (+0.033), Amin (-0.261), pH (+0.263), C (+0.407***), Vcompl (-0.025)	x^2 (-65.492**), y^2 (-383.836*), y^3 (-4470.770*), xy (315.869*), x^2y (-1049.670*), xy^2 (+5156.156**)	3.93	54.64	10.89	69.46
Mountain Fynbos	103	0.955	area (-0.003*), Mtemp (+0.351), MMrange (+0.005), Amax	y (+66.232*), x^2 (-250.631*), x^3 (+57.537), y^2 (-2257.140**), y^3	4.17	62.41	9.09	75.67

Table 3 (continued)

Variable	df	Dev/Df	Environmental terms	Spatial terms	Percentage variance explained			
					(a)	(b)	(c)	Total
			(+0.109), Amin (-0.315), pH (+0.389), C (+0.277*), vegage (+0.022)	(-22233.500**), xy (+743.246*), x^2y (-7219.060**), xy^2 (+31615.830***)				
Carabidae	120	0.679	Mtemp (+0.763**), MMrange (-0.595**), Amax (+0.077), Amin (-0.282), pH (-1.070*), BG (+0.015), vegcover (+0.025), Vcompl (-0.065)	y (-37.761*), x (+28.201*), x^2 (-186.393**), x^3 (-590.026**), y^3 (-8783.680*), xy (+618.879**), xy^2 (+2584.459**)	7.96	49.47	12.66	70.09
Tenebrionidae	121	1.048	Area (-0.001), Mtemp (+0.121), MMrange (-0.034), Amax (-0.012), Amin (-0.167), pH (+0.256), C (+0.509)	y (+25.248*), x (-6.750), x^3 (+257.309**), y^2 (-802.885), xy (+210.012*), x^2y (-2453.240**), xy^2 (5963.202**)	7.25	48.89	9.60	65.74

density of carabids was also positively related to the proportion of bare ground, and the species density of the tenebrionids was positively related to soil pH and the percentage clay in the soil (Table 3). Furthermore, beetle abundance was positively related to organic carbon while the abundance of the beetles across the whole transect was positively related to mean monthly temperature (Table 3). The abundance of carabids was positively related to mean temperature and negatively to mean monthly temperature range and soil pH (Table 3). Neither the density nor the abundance of beetles in Mountain Fynbos was significantly related to post-fire vegetation age.

Beetle assemblage structure did not differ between sampling periods (Global $R = -0.011$, P = 0.978). The data were thus combined for the two sampling periods for all subsequent analyses. Five Alpine Fynbos sites were identified as outliers on the nMDS ordinations and were excluded. Beetle assemblages occurring in the three main vegetation types differed significantly from each other (Fig. 3a). Assemblage structure of beetles occurring in Strandveld was the most distinct (Pair-wise ANOSIM tests between Strandveld and Succulent Karoo: $R = 0.997$, P = 0.001; and between Strandveld and Mountain Fynbos: $R = 0.662$, P = 0.002). Assemblages occurring in Mountain Fynbos and Succulent Karoo were not significantly different from each other ($R = 0.052$, P = 0.307). Within Mountain Fynbos, beetle assemblages differed significantly between the four different structural types (Fig. 3b). Pair-wise ANOSIM tests showed that the most distinct assemblages occurred in Alpine Fynbos (Alpine vs. Ericaceous Fynbos: $R = 0.730$, P = 0.001; Alpine vs. Proteoid Fynbos: $R = 0.897$, P = 0.001; Alpine vs. Restioid Fynbos: $R = 0.915$, P = 0.001). Restioid and Ericaceous Fynbos beetle assemblages were the most similar (lowest R-value, $R = 0.228$, P = 0.002). Proteoid Fynbos assemblages were more similar to those in Restioid Fynbos (R = 0.325, P = 0.001) than to those in Ericaceous Fynbos ($R = 0.401$, P = 0.001). All significant P-values remained so after correction for multiple comparisons (García, 2004).

IndVal analyses revealed that four species were characteristic of Strandveld and one of Succulent Karoo (Table 4). No species could be regarded as characteristic of any or all of the four Mountain Fynbos vegetation types (Table 4). Furthermore, 16 species were identified as characteristic of certain altitudes (Table 4). Two of these were characteristic of a range of altitudes spanning more than one vegetation type (Table 4).

a)

Global *R* = 0.447; P = 0.001
Stress = 0.16

○ Mountain Fynbos
△ Strandveld
● Succulent Karoo

MDS axis 2

MDS axis 1

b)

Global *R* = 0.348; P = 0.001
Stress = 0.15

■ Alpine
○ Ericaceous
□ Proteoid
▲ Restioid

MDS axis 2

MDS axis 1
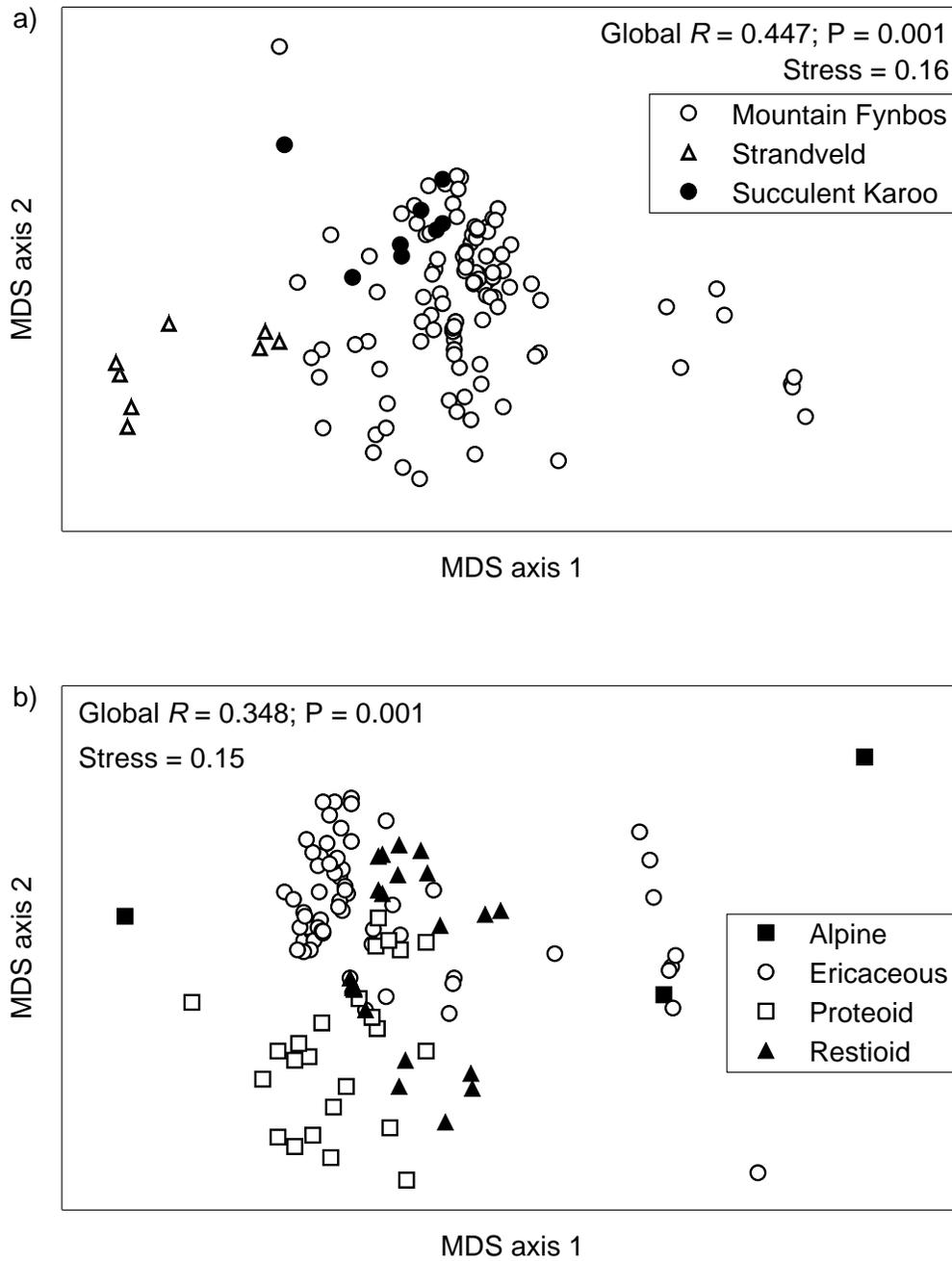
Figure 3 Non-metric MDS ordinations of beetle assemblage structure based on a) the three main vegetation types, and b) within Mountain Fynbos.

Table 4 Percentage indicator values (*IndVal* > 70 %) of beetle species for each vegetation type (hierarchical clustering) and altitudinal band (non-hierarchical clustering). * = Maximum *IndVal* values. W = western slope, E = eastern slope.

Vegetation type/altitude	Species	*% IndVal*
Vegetation type		
Strandveld	*Scarites* sp. 2	100.00*
	Cryptochile namaquana	100.00*
	Zophosis hirundu	81.74
	Platychila pallida	74.38
Succulent Karoo	*Cryptochile fallax fallax*	78.44
Altitude		
0 m (Lambert's Bay)	*Scarites* sp. 2	100.00*
	Cryptochile namaquana	100.00*
	Platychila pallida	74.46
	Zophosis hirundu	72.99
200 m W	*Horatoma parvula*	89.26
300 m W	*Broomium nadum*	82.94*
500 m W	*Broomium mutilla*	90.00
	Cryptochile minuta	88.75
300 – 700 m W	*Sacophorella cephlica*	83.33*
1900 m (Sneeukop)	*Cicindela quadriguttata*	100.00*
	Hystrichopus mnizechi	100.00*
1100 m E	Carab sp. 1	81.21
	Hypomelus peronatus	80.22
	Carab sp. 3	77.95
1100 – 1300 m E	*Cicindela lurida*	90.09
500 m E (Wupperthal)	*Cryptochile fallax fallax*	70.33*

DISCUSSION

The number of carabid (6 species) and tenebrionid (17 species) beetle species collected in Proteoid Fynbos here is comparable to that found by Donnelly and Giliomee (1988) in Proteoid Mountain Fynbos in the Jonkershoek Valley, some 250 km South of the transect in this study (South Africa). They collected eight carabid and 12 tenebrionid species in six different sites that differed in post-fire vegetation age. These areas were sampled once a month (June 1979 – July 1980) for 24 hours using pitfall traps. Donnelly and Giliomee's (1988) study is to our knowledge the only ecological one that has examined ground-dwelling beetle assemblages in the CFR: the others have been concerned with the taxonomy of the fauna (e.g. Endrödy-Younga, 1978, 1996; Penrith, 1981, 1988). This is surprising given the considerable attention that has been paid to the CFR in all other respects (for review see Cowling, 1992, and compare Giliomee, 2003 with Cowling *et al*., 1992, and Cowling & Lombard, 2002). However, it does reflect the general lack of information on regional-scale diversity patterns of insects in southern Africa (Samways, 1990; Scholtz & Chown, 1993; Koch *et al*., 2000), (by contrast with local scale studies – e.g. Chambers & Samways, 1998; van Rensburg *et al.*, 1999; Parr *et al.*, 2004) and the notable shortage of quantitative investigations of variation in animal diversity across the region (see Andrews & O'Brien, 2000; van Rensburg *et al*., 2002, 2004; Chown *et al*., 2003 for exceptions).

In keeping with theoretical expectations (reviewed in Rosenzweig, 1995) species density and species richness of ground-dwelling beetles were positively, though weakly related to available area of the altitudinal bands. However, area was not included in the best-fit generalized linear models, whilst temperature, edaphic and vegetation variables often remained significant even when space was included. Increases in species density with increasing temperature are typical of epigaeic beetle assemblages elsewhere (Chen & Wilson, 1996; Crist & Ahern, 1999; Hosoda, 1999; McIntyre, 2000; Nelson, 2001; de los Santos, 2002a), and suggest that the ambient energy or productivity hypotheses (Turner *et al.*, 1987; Currie, 1991; Willig *et al.*, 2003; Evans *et al*., 2005) might explain variation in species richness across the transect. The strong spatial signal both in the environmental variables (see also Chapter 2) and in species density, and the considerable variation between sites in species density that was explained by spatially structured environmental variation also support the idea that spatial variation in energy has a considerable influence on species density. Moreover, the positive relationship between abundance and mean temperature (and absolute maximum temperature) suggests that increasing energy availability, rather than a change in environmental stress, is driving increases in species density across the transect. However,

110

disentangling the mechanisms that might be responsible for the relationship is not straightforward and requires data which are not available in this instance (for discussion see Evans *et al.*, 2005).

Several other studies have shown that abundance of ground-dwelling beetles increases with warmer temperatures. For example, McIntyre (2000) showed that the abundance of *Eleodes* beetles in the shortgrass steppe in Colorado increases with warmer temperatures, and de los Santos (2002b) demonstrated that population sizes of tenebrionids on the Cañadas of Teide in Tenerife are positively correlated with temperature. Similarly, Hosoda (1999) showed that the abundance of carabids on Mt. Kurobi (Japan) strongly depend on soil temperature, with fewer individuals collected in colder areas. That edaphic variables had an influence on both species density and abundance of each of the major taxa was also not unexpected. For example, Crist and Ahern (1999) and Heliölä *et al.* (2001) demonstrated that open areas host more species of ground-dwelling carabids than densely vegetated areas. Imler (2003) and Hosoda (1999) showed that differences in the abundance of carabids between habitats can be attributed to their preferences for certain soil types, soil pH and soil water content. In addition, Ayal and Merkl (1994) found that species richness of tenebrionids is higher in compact soil habitats than in sandy habitats, while several studies have shown that tenebrionid species which are distributed among different soil textural classes tend to have the highest abundance on a specific soil type (Marcuzzi, 1964; Calkins & Kirk, 1975; Thomas, 1983; Ayal & Merkl, 1994; Krasnov & Shenbrot, 1996). Thus, the habitat specificity and fidelity of several of the species in this study, and the clear distinctions between the vegetation types across the transect are not surprising. Similar, clear distinctions between beetle assemblages occupying different habitats have commonly been found elsewhere (Luff *et al.*, 1989; Niemelä, 1990; Gardner, 1991; Holmes *et al.*, 1993; Ayal & Merkl, 1994; De los Santos *et al.*, 2002a).

The environmental correlates of abundance and species density in the ground-dwelling beetles were similar to those identified for ants across the transect (Chapter 2). Most significantly, species density and abundance of both taxa were positively related to several temperature variables. However, in the ants there was a marked difference in the proportion of variance in species density (36-38%) and in abundance (64-70%) explained by each of the full models (space and environmental variables). By contrast, in the beetles the proportion of variance explained by the full model was similar for both species density and abundance (66-67% and 69-75%, respectively). However, this was due largely to the tenebrionids, in which the full model explained 64% of the variance in species density. In the carabids, the variance

explained was much lower (33%), making them more similar to the ants. There are several likely explanations for these differences between the tenebrionids and the two other families of insects.

The most intuitively obvious might be that the tenebrionids simply respond to the environment (both the spatially and the non-spatially structured components thereof) more strongly than do the other two families. If the analyses are taken at face value this certainly seems to be the case. However, there is no intrinsic reason for expecting such differential responses, especially because both ants and ground beetles are known to respond significantly to variation in temperature and in several other environmental variables (Andersen, 1995; Chen & Wilson, 1996; Cerdá *et al*., 1998; Crist & Ahern, 1999; Hosoda, 1999; Bestelmeyer, 2000). An alternative explanation might be that the relationship between abundance and species density is non-linear in the ants and carabids, but not in the tenebrionids. Botes *et al.* (in press, Chapter 2) suggested that such non-linearity might well explain differences in the variance explained by the full models for ant species density and abundance. The typically unimodal relationship between ant abundance (and especially that of the dominant ants) and species richness (see Parr *et al*., 2005) means that species richness (or density) can be low at both low and high abundances. If the pattern is driven by a combination of environmental stress and competition, which is likely (Hölldobler & Wilson, 1990; Parr *et al*., 2005), then the environment will appear to have a larger linear influence on abundance than on richness, so resulting in a greater proportion of the variance being explained in linear models of the former, than of the latter. Carabid assemblages are also thought to be structured by interspecific competition (e.g. Lenski, 1982; Davies, 1987), and the same might apply to them. However, competition is certainly not unknown in darkling beetle assemblages (e.g. Ward & Seeley, 1996), making the argument perhaps less plausible, especially in the absence of information on horizontal interactions for these particular assemblages, and for the carabids in particular.

Both of the above explanations assume that richness variation is solely a function of the contemporary environment, although this is unlikely to be the case (Ricklefs, 2004). Rather, there might also be a considerable historical signal that is collinear with the contemporary environmental variables as has been found elsewhere (Latham & Ricklefs, 1993; Chown *et al.*, 1998). Here, it is noticeable that whilst species density of the tenebrionids declines with elevation (and with temperature: ordinary least squares regression of density on temperature $R^2 = 0.54$, $p < 0.006$) on the western slopes of the Cederberg, the same is not true
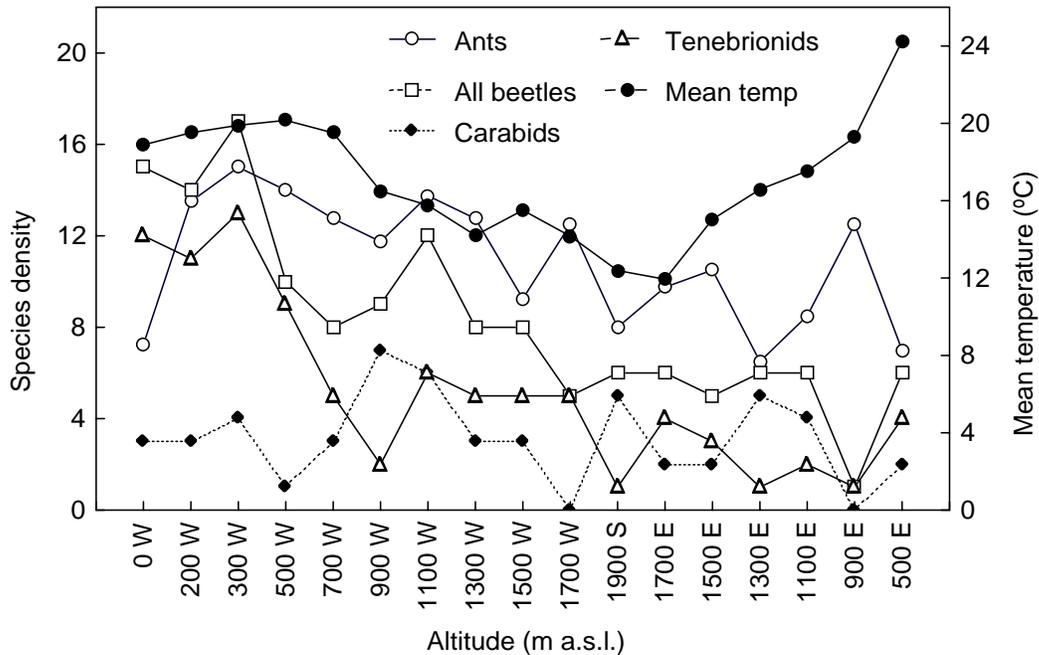
Figure 4 Species density of ants, carabids (including Cicindellidae), tenebrionids, all beetles combined and mean annual temperature across the different altitudinal bands. W = western side and E = eastern side of transect, S = summit.

of the eastern slope (OLS of density and temperature, $p > 0.96$) (Fig. 4). Thus, whilst temperature initially appears to be a strong correlate of species density, it is unlikely to be the causal factor because it does not operate similarly on both sides of the mountain range.

Although water availability might be an alternative causal mechanism influencing density, this seems improbable given similar arid conditions on the lower western and eastern reaches of the transect (Low & Rebelo, 1996). What seems more plausible is that the decline in richness towards the east reflects movement away from an area that constitutes the southern end of a south-west African centre of tenebrionid endemism and diversity (Scholtz & Holm, 1985; Penrith, 1986; Penrith & Endrödy-Younga, 1994). The comparatively high richness and endemism of the first three western sites along the transect (they include 23 species, of which 16 are restricted to them) certainly suggests that this is the case, as does their membership of the Tentyriinae, a subfamily best known for its arid zone diversity in southern Africa (Scholtz & Holm, 1985). By contrast, there is no such linear and rapid decline in diversity away from

113

the western sites in the carabids and ants (Fig. 4), and the area is not known as a centre of endemism or diversity for either of the groups (Scholtz & Holm, 1985; Marsh, 1990).

If the above explanation for the differences in explained variance in species density between the groups is correct, it suggests that caution should be exercised when interpreting environmental correlates of species density. In some cases, such as the present one, the correlates might well reflect collinear historical processes, rather than a causal relationship between contemporary environmental variables and species density (see Jetz *et al.*, 2004 for additional discussion). Whilst collinearity of historical and contemporary explanatory variables present obvious challenges for explaining current patterns in diversity (for discussion and solutions see Endler, 1982; Ricklefs, 1987; Chown *et al.*, 1998; Hawkins & Porter, 2003; Jetz *et al*., 2004), they also have profound implications for predicting the biological implications of regional climate change. Several studies have suggested that warming and drying will have profound effects on the diversity of the south western parts of southern Africa, resulting in total loss of the Succulent Karoo and substantial contraction of the Fynbos biome (Rutherford *et al.*, 1999; Midgley *et al.*, 2002, 2003; Hannah *et al.*, 2005). Substantial range contractions towards the east have also been predicted for a wide range of animal groups (Erasmus *et al.*, 2002). These studies are typically based on bioclimatic modelling, where correlates between current climate and species distributions are established, the climate altered, and distributions mapped back onto geographic space. The present results provide further evidence for considering such modelling exercises as a first and coarse approximation of what the outcome of climate change might be. If there is collinearity between historical and current environmental correlates of diversity patterns, but history is causal, then the modelling outcomes may not accurately reflect the outcome of climate change. Other concerns with bioclimatic modelling include the extent to which the models are predictive (i.e. can be extrapolated, see Samways *et al.*, 1999), the fact that they rarely incorporate the physiological flexibility and capacity for rapid evolution typical of many taxa (Chown & Nicolson, 2004; Helmuth *et al.*, 2005), and the difficulty of including complex interactions and feedback within them (Karnosky *et al.*, 2003; Chapter 2). Admittedly such models provide a rapid way of gaining insight into what the effects of climate change might be, and are therefore useful given the current conservation crisis (see Thomas *et al.*, 2004). However, they should be supplemented by additional investigations, which enable the full complexity of likely responses to change to be more thoroughly comprehended.

114

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115

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TESTING RAPOPORT'S ELEVATIONAL RULE:
EPIGAEIC ANTS AND BEETLES IN THE CEDERBERG

INTRODUCTION

The tendency for the range size of species to increase with an increase in latitude was termed 'Rapoport's rule' by Stevens (1989). Support for Rapoport's rule has been found in several taxa, including birds, mammals, plants, marine invertebrates, and freshwater and marine fish (Table 1). Rapoport's rule has also been extended to altitudinal gradients (Stevens, 1992, 1996). Nonetheless, in relation to the number of studies examining patterns in range size across latitudinal gradients, few studies have investigated the altitudinal equivalents of this latitudinal pattern (see Table 1). Stevens (1992) found that when Rapoport's rule was extended to altitudinal gradients, the altitudinal ranges of six different taxa (trees, mammals, birds, reptiles, insects and amphibians) increased with increasing elevation. He further tested whether Rapoport's rule can be extended to bathymetric gradients, and found that the bathymetric range of marine fish assemblages declined with depth (Stevens, 1996). Strong Rapoport effects have also been reported in montane butterfly communities (Fleishman *et al.*, 1998) and more recently for North American ants (Sanders, 2002).

Nonetheless, it has been argued that Rapoport's rule is mainly a regional phenomenon because it has been shown to apply only to certain taxa (mainly vertebrates) between 40-50°N (Rohde & Heap, 1996; Rohde, 1996; Gaston *et al.*, 1998, Gaston & Chown, 1999a) and sometimes between 20-30°N (Blackburn & Gaston, 1996; Gaston *et al.*, 1998). Moreover, no strong evidence for Rapoport's rule has been found in the southern hemisphere (Blackburn & Gaston, 1996; Mourelle & Ezcurra, 1997; Ruggiero & Lawton, 1998). Another criticism of this 'rule' is that it can arise due to sampling bias alone. Colwell and Hurtt (1994) showed that even if sampling effort is equal at all latitudes or altitudes, per-species sampling effort would decrease as species richness increases. In other words, the more species there are, the more likely it is that a species will be missed. If a species is not sampled at the edge of its range, the range size of that species will be underestimated, causing the appearance of a spurious Rapoport effect (Colwell & Hurtt, 1994).

Studies that investigate Rapoport's rule may also suffer from spatial non-independence (Rohde *et al.*, 1993; Letcher & Harvey, 1994), phylogenetic non-independence

Table 1 Examples of studies that tested Rapoport's rule across latitudinal, altitudinal and bathymetric gradients.

Reference	Taxon	Locality	Support
Latitude			
Arita *et al.* (2005)	Mammals	North America	Yes
Blackburn & Gaston (1996)	Birds	North and South America	Yes
Cowlishaw & Hacker (1997, 1998)	Primates	Africa	Variable
Folgariat *et al.* (2005)	Phorid flies	South America	Yes
France (1992)	Freshwater crayfish and amphipods	Northern hemisphere	Yes
Fortes & Absalão (2004)	Marine molluscs	North and South America	Yes
Gaston & Blackburn (1996a)	Wildfowl	World wide	No
Hecnar (1999)	Turtles	Northern hemisphere	Opposite
		Nearctic and Palearctic	Yes
Hernández *et al.* (2005)	Polychaetes	Southeastern Pacific Ocean	No
Huges *et al.* (1996)	Eucalypts	Australia	No
Johnson (1998)	Mammals	Australia	Yes
Koleff & Gaston (2001)	Parrots and woodpeckers	North and South America	Variable
Letcher & Harvey (1994)	Mammals	Palearctic	Yes
Lyons & Willig (1997)	Bats and marsupials	Australia	Variable
MacPherson & Duarte (1994)	Marine Fishes	East Atlantic Ocean	No
Mourelle & Ezcurra (1997)	Columnar cacti	Argentina and Mexico	Yes
Pagel *et al.* (1991)	Mammals	North America	Yes

125

Table 1 (continued)

Reference	Taxon	Locality	Support
Reed (2003)	Snakes	North and South America	No
Rohde (1999)	Marine parasites	World wide	Opposite
Rohde & Heap (1996)	Marine teleost fish	Atlantic and Indo-pacific oceans	No
Rohde *et al.* (1993)	Marine teleost fish	Atlantic and Indo-pacific oceans	No
	Freshwater fishes	Nearctic	Yes
		Northern Europe	Yes
		Australia	No
Roy *et al.* (1994)	Marine molluscs	Eastern Pacific	No
Ruggiero & Lawton (1998)	Birds	South America	No
Ruggiero (1994)	Mammals	South America	No
Sax (2001)	Exotic species	North and South America, Europe, Asia, Africa, oceanic islands	Yes
Smith *et al.* (1994)	Mammals	Australia	No
Stevens (1989)	Trees, marine molluscs, freshwater and coastal fishes, amphibians, reptiles, mammals	North America	Yes
	Birds	Soviet Union	Yes
Stevens (1996)	Marine fishes, amphibians and reptiles	Pacific Ocean	Yes
Taylor & Gotelli (1994)	*Cyprinella* minnows	North America	Yes

126

Table 1 (continued)

Reference	Taxon	Locality	Support
Altitude			
Chatzaki *et al*. (2005)	Ground spiders	Greece	Yes
Fleishman *et al.* (1998)	Butterflies	North America	Yes
Fortes & Absalão (2004)	Marine molluscs	North and South America	Yes
Fu *et al.* (2004)	Freshwater fishes	China	No
Gaston & Chown (1999b)	Dung beetles	South Africa	Yes
Patterson *et al*. (1996)	Bats	Peru	
Ruggiero & Lawton (1998)	Birds	South America	Variable
Sanders (2002)	Ants	North America	Yes
Stevens (1992)	Trees, mammals, amphibians, reptiles, Orthoptera, birds	North and South America	Yes
Bathymetric			
Stevens (1996)	Marine fishes	Pacific Ocean	Yes
Smith & Gaines (2003)	Marine fishes	Northeast Pacific	Yes
	Marine gastropods	Northwest Atlantic	Yes
Smith & Brown (2002)	Pelagic fishes	Northeast Pacific	Yes

127

(Pagel *et al.*, 1991; Letcher & Harvey, 1994; Taylor & Gotelli, 1994; Blackburn & Gaston, 1996; Gaston & Blackburn, 1996a) and boundedness (Colwell & Hurtt, 1994). Spatial non-independence arises because, within latitudinal bands, a higher proportion of the same species are shared between bands that are closer to each other than in bands that are further apart. This problem occurs when Stevens' (1989) method of determining average range sizes of species in an altitudinal band is used. The method uses the range sizes of all species occurring in an altitudinal band to calculate the average range size of a species occurring in that band. Latitudinal bands therefore share the same average geographic range sizes because they share the same species (Rohde *et al.*, 1993; Letcher & Harvey, 1994). Steven's method thus demonstrates the variation in average range size of all the species occurring at a particular latitude. By contrast, the mid-point method (Rohde *et al.*, 1993) uses only those species that have their range midpoints in a particular band to calculate the average range size of the species for that band. Using this method provides a means to overcome problems of spatial non-independence because it treats species as individual data points. The midpoint method therefore evaluates the relationship between the latitudinal variation in range size and the position of range midpoint. However, the midpoint method introduces the problem of phylogenetic non-independence, causing complications in the interpretation of the results of empirical studies because these species are not independent data points (Gaston *et al.*, 1998). Although the effects of phylogeny have not been widely examined, several studies have done so and found that significant relationships between range size and latitude (or altitude) were still found, even when phylogeny was taken into account (e.g. Pagel *et al.*, 1991; Letcher & Harvey, 1994; Blackburn & Gaston, 1996; Gaston & Blackburn, 1996a; Gaston & Chown, 1999b).

The third complication in testing Rapoport's rule is that of boundedness. That is the existence of impermeable (or hard) boundaries to the occurrence of species (Colwell & Hurtt, 1994), such as the edge of a continent for terrestrial animals. These hard boundaries place a limitation on the relationship between range size and range midpoint in such a way that species with their range midpoint near the boundary will necessarily have small ranges, while species with large ranges will have their range midpoints closer to the centre of the bounded area (see Colwell & Lees, 2000). The constraint that boundedness places on range size has been shown to apply to altitude (Graves, 1985), latitude (Rohde *et al.*, 1993) and depth gradients (Pineda, 1993). Even so, Colwell and Hurtt (1994) were the first to demonstrate that the Rapoport effect can be caused by geometric constraints alone. Several studies followed theirs, further developing geometric constraint models (e.g. Taylor & Gaines, 1999, see

128

Colwell & Lees, 2000 for review). These studies have demonstrated that when the latitudinal midpoint of the ranges of species are placed randomly within a bounded geographical area, and the latitudinal range of the species are drawn from all the permissible ranges given the constraint that the latitudinal range of the species may not cross the hard boundaries, then the mean latitudinal range of the species declines in relation to how close the midpoint lies to the boundaries (see also Lyons & Willig, 1997). Therefore, either a reversed Rapoport effect (range sizes should increase towards the middle of the domain) is predicted, or range size should not vary along an environmental gradient, especially if all range sizes are small (Colwell & Hurtt, 1994; Colwell & Lees, 2000).

In this Chapter, Rapoport's elevational rule (Stevens, 1992) is tested by determining whether the altitudinal range sizes of epigaeic ants and tenebrionid beetles are larger at high altitudes than at low altitudes across an altitudinal gradient in the Cederberg (South Africa). Specifically, I tested whether the range sizes of the epigaeic ants and beetles increase with increasing altitude, or whether a reversed Rapoport effect exists as a result of geometric constraints (Colwell & Lees, 2000). In addition, I tested whether the range sizes of the two taxa are related to temperature variability. This was done as an indirect test of whether the climatic variability hypothesis proposed by Stevens (1989, 1992, 1996, see also Addo-Bediako *et al.*, 2000) as the principal mechanism explaining Rapoport's rule across latitude, altitude and bathymetric gradients might be responsible for the observed range size patterns.

MATERIAL AND METHODS

Study site and sampling

This study took place in the Greater Cederberg Biodiversity Corridor, which is a mega-reserve spanning a west-east gradient from coastal lowlands, to Mountain Fynbos and Succulent Karoo. It includes the northernmost extremity of the Cape Floristic Region, with the Cederberg Wilderness Area forming the core (Anonymous, 2004). The study was conducted across an altitudinal transect covering the major vegetation types on both aspects of the Cederberg, encompassing the full range of vegetation. The transect ranged from sea level at Lambert's Bay, to Sneeukop (1926 m a.s.l.), and down the eastern slopes to Wupperthal (approximately 500 m a.s.l.) (see Chapter 2). The highest altitude sampled in this study lay approximately in the middle of the study area, whereas in previous studies that have examined altitudinal Rapoport effects or mid-domain models, the domain typically stretched from the lowest to the highest altitude sampled (e.g. Ruggiero & Lawton, 1998; Grytnes &

Vetaas, 2002). A total of seventeen altitudinal bands was sampled at 200 m altitudinal intervals across the transect (see Chapter 2) representing Strandveld Succulent Karoo (one site), Mountain Fynbos (15 sites) and Lowland Succulent Karoo (one site). Sites are described in detail elsewhere (Chapter 2).

Epigaeic ants were sampled during October 2002 and March 2003 (periods of peak ant activity), and tenebrionids during the Octobers of 2002 and 2003 (periods of peak beetle activity). A total of forty pitfall traps, divided into four groups of ten pitfalls each, was placed at each site during each sampling event. The four groups of pitfall traps were placed in such a way that they were at least 300 m apart. The disturbance caused by placing the pitfall traps was minimized and the vegetation around the traps was not cleared. The "digging-in" effect (Greenslade, 1973) was thus considered negligible and the traps were set immediately. The traps contained 50 ml of a 50 % propylene glycol solution as preservative and were left open for a period of five days per sampling event. The samples were washed and placed in 70 % ethanol in the laboratory. All tenebrionid beetles were pinned and a representative sample of the ants was mounted on cardboard triangles. All specimens were identified to species level where possible or assigned to morphospecies. Voucher specimens of each ant and beetle species collected are held at the University of Stellenbosch and will be placed in the Iziko Museums of Cape Town.

Predictor variables

The mean temperature and the coefficient of variation of mean temperature were calculated from soil temperature measured at each altitudinal band using Thermocron iButtons (Semiconductor Corporation, Dallas/Maxim, Model DS1920). These data loggers were buried 10 mm beneath the soil surface at each sampling site in an area where vegetation cover was low to ensure minimum shade cover. The iButtons were set to record temperature at one-hour intervals. Data collected from June 2002 to October 2003 were used to calculate mean temperature for each altitudinal band across the 16-month period. A mean temperature was calculated for each month and a mean monthly temperature was then calculated using these 16 mean temperatures. The coefficient of variation (CV) of the mean temperature for each altitudinal band was calculated using the mean monthly temperatures and was used as a measure of temperature variability.

Data analysis

Several potential boundaries to species dispersal exist across the altitudinal transect. In consequence, three different domains were identified: 1) 0 m a.s.l. on the western slope (boundary, i.e. the Atlantic Ocean) – 500 m a.s.l. on the eastern slope (boundary to Mountain Fynbos species, i.e. Succulent Karoo); 2) 0 m a.s.l. on the western slope – 1900 m a.s.l. (summit, boundary to altitudinal distribution); and 3) 200 m a.s.l. on the western slope (boundary to Mountain Fynbos species, i.e. Strandveld) – 500 m a.s.l. on the eastern slope (boundary to Mountain Fynbos species, i.e. Succulent Karoo). For the purpose of this study, domains 1 and 3 are considered complete, whereas domain 2 is a partial one (see Blackburn & Gaston, 1998).

The altitudinal range of each ant and beetle species within the domain stretching from sea level to the highest point was calculated as the difference between the minimum and maximum altitude at which the species was collected within the survey site range. A species collected in a single altitudinal band was assigned an altitudinal range of 200 m (the width of an altitudinal band, see Stevens, 1992). The average altitudinal range of species in each altitudinal band was then determined by calculating, for each band, the mean altitudinal range of all species with a range midpoint in the focal altitudinal band (midpoint method, Rohde *et al.*, 1993). This was done for ants and tenebrionids separately. In addition, the range size of each species across the transect (domain 1) and within Mountain Fynbos (domain 3) was calculated as the number of altitudinal bands between the lowest bands on the western and eastern slopes in which the species was collected, multiplied by 200 (the width of an altitudinal band). Again, a species collected in a single altitudinal band was assigned an altitudinal range of 200 m, and the midpoint method (Rohde *et al.*, 1993) was used to calculate the average range size of species in each altitudinal band. Two data sets were compiled for each of the domains. In the first, species ranges were interpolated if a species was present in several bands but missing from bands between them (i.e. interpolation between each end of the range). This was not done if the species range was disjunct on the eastern and western sides of the transect (i.e. if it did not occupy the highest altitudinal band). In the second, no interpolations were made.. These two data sets were used because it has been shown that interpolation of ranges may create artificial patterns when mid-domain models are used (Grytnes & Vetaas, 2002).

Even though the midpoint method introduces the problem of phylogenetic non-independence (Gaston *et al.*, 1998) the problem could not be accounted for in this study. Presently a working phylogeny for the tenebrionids does not exist and the phylogenetic tree

131

obtainable for the ants from the literature (e.g. Grimaldi & Agosti, 2000) extends only to the tribe level.

The range size frequency distributions, with range size logarithmically transformed, were determined for the whole transect, western slope and Mountain Fynbos, using interpolated and non-interpolated data sets. Ten size classes were used because of the small number of tenebrionid species collected (see Sokal & Rohlf, 1995) and to keep it consistent between the two taxa the same number of size classes was used for the frequency distributions of the ants. In addition, the number of altitudinal bands occupied by the individual species, and the midpoints of the range sizes of these species, were compared between the whole transect and the western slope, the whole transect and Mountain Fynbos, and between the western slope and Mountain Fynbos by inspection to determine whether the midpoints and number of altitudinal bands differ from the line of equality. This was done separately for ants and beetles to examine the effect that redefinition of the domain boundaries has on these variables.

Geometric constraints models

Two geometric constraint models (or mid-domain null models) were used to test how well the observed data fit predicted range distributions. These models were generated using Visual Basic 2000. Model A is equivalent to model 2 of Colwell and Hurtt (1994) and the binomial model of Willig and Lyons (1998). In model A an altitudinal range and -midpoint combination for each species was generated from all possible range size and midpoint combinations. Any combination of an altitudinal range and -midpoint was allowed as long as the whole range was included within the boundaries of the transect (sea level on the western slope and 500 m a.s.l. on the eastern slope). This model makes no assumptions about the real distribution of the ants and beetles except for the constraint of boundaries and is therefore a true null model (Koleff & Gaston, 2001; but see discussion in Colwell *et al.*, 2004, 2005; Zapata *et al.*, 2003, 2005).

Model B is equivalent to model D of Koleff and Gaston (2001) and the model of Lees *et al*. (1999). First, the altitudinal range for each species was selected at random without replacement from the observed range size frequency distribution, and then the altitudinal midpoint was chosen at random with replacement from all possible midpoints (see Colwell & Lees, 2000 Box 3). This model makes explicit assumptions about the maximum range of the species because it takes the empirical ranges into account.

The two models were iterated 1000 times each, separately for the ants and

tenebrionids, and for each of the three domains and the two data sets (interpolated and non-interpolated). After each iteration the predicted average range size of species occurring in a particular altitudinal band was calculated using the midpoint method (Rohde *et al.*, 1993). Mean range size (and standard error of the mean) was then calculated for each altitudinal band after the 1000 model iterations.

To determine whether altitude, the coefficient of variation of mean temperature, and the predicted range sizes by the two mid-domain models significantly explain the observed mean range sizes of the species in each altitudinal band, generalized linear models (Normal error distribution with an identity link function) (Dobson, 2002) were used. First, it was determined whether the predictor variables (i.e. altitude, temperature CV and the predicted range sizes by mid-domain models A and B) separately, significantly explained the observed mean range sizes per altitudinal band, and then best-fit models were selected by including all the predictor variables in a final model selection procedure (see below). Quadratic terms of altitude and temperature CV were included in the analyses to account for potential non-linear relationships between these variables and the observed range sizes. All analyses were done separately for the ants and tenebrionids across the three domains (whole transect, western slope and Mountain Fynbos) using the interpolated and non-interpolated data sets.

The models that best explained the variation in the observed mean range sizes per altitudinal band were selected using the Akaike Information Criterion (AIC). However, it is not sufficient to select only one model based on the smallest AIC value because other models might have AIC values close to that of the best model, which contributes to model uncertainty (Westphal *et al.*, 2003). Therefore, Akaike weights (w_i) were used as an indicator of the strength of evidence for a particular model (Burnham & Anderson, 2002; Johnson & Omland, 2004). The Akaike weight of a model is the probability that that particular model is the best in the set of models being considered (Burnham & Anderson, 2002). A set of plausible models were selected by including only models with $w_i \geq 0.1$ (Burnham & Anderson, 2002; Westphal *et al.*, 2003). However, if more than three models had $w_i > 0.1$, then only the three best models were reported. When no models had $w_i > 0.1$ the model with the highest Akaike weight was reported.

Spatial autocorrelation (the degree to which two neighbouring samples are more similar (positively autocorrelated) or more dissimilar (negatively autocorrelated) to each other than expected, Legendre 1993; Legendre & Legendre, 1998) violates the assumption of independence between samples of most statistical tests (Legendre 1993). Spatial non-independence could also affect the results and interpretation of the observed patterns (Lobo *et*

133

al., 2002; van Rensburg *et al.*, 2002). Therefore, the spatial component of the variation in range size was modelled using a third-order polynomial that extracts linear and more complex spatial features (e.g. patches and gaps) from the data: $f(x, y) = b_0 + b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$, where x and y are longitude and latitude respectively (Borcard *et al.*, 1992; Legendre, 1993). The best-fit spatial terms selected by the AIC and Akaike weights were then included in the final model selection procedure together with temperature CV and its quadratic term and the predicted range sizes by the mid-domain models. The range sizes predicted by mid-domain models A and B were used separately in the best-fit model selection procedure (i.e. the predicted range sizes by mid-domain models A and B were never included in the same analysis).

RESULTS

A total of 81 ant species and 33 tenebrionid species was collected during the two sampling periods. Twenty-eight ant species occurred only on the western slopes of the transect while four species occurred only on the eastern slopes. Fourteen ant species occurred in a single altitudinal band. Twenty-seven of the tenebrionids only occurred on the western slope of the transect and 12 species occurred in a single altitudinal band. No tenebrionid species were only collected on the eastern slope. The difference in the number of 'species' (if each separate range is considered a species in the non-interpolated data set) in the interpolated and non-interpolated data sets was substantial for ants (numbers of species are given in Fig. 1). However, the data sets for the tenebrionids were very similar (Fig. 1).

The range size frequency distributions (Fig. 1) indicated that, when interpolated ranges were used, even though many of the ant species had small range sizes, most species had range sizes in the larger size classes (Fig. 1a-c). However, when using non-interpolated ranges most species had small ranges (Fig. 1d-f). By contrast, the large majority of the tenebrionid species had small ranges whether interpolated (Fig. 1g-i) or non-interpolated (Fig. 1j-l) ranges were used. Only six tenebrionid species occurred in more than three altitudinal bands.

Redefining the domain boundaries had large effects on the number of altitudinal bands occupied by individual ant species (Fig. 2a-f) and on the position of the midpoints of their ranges (Fig. 3a-f). These effects were particularly apparent when comparing the western slope with the whole transect and Mountain Fynbos. For the tenebrionids, the effects were not as pronounced (Fig. 2g-l and Fig. 3g-l). Twenty-one of the tenebrionid species had the midpoints of their distributions within the four lowest altitudinal bands on the western slope and only six
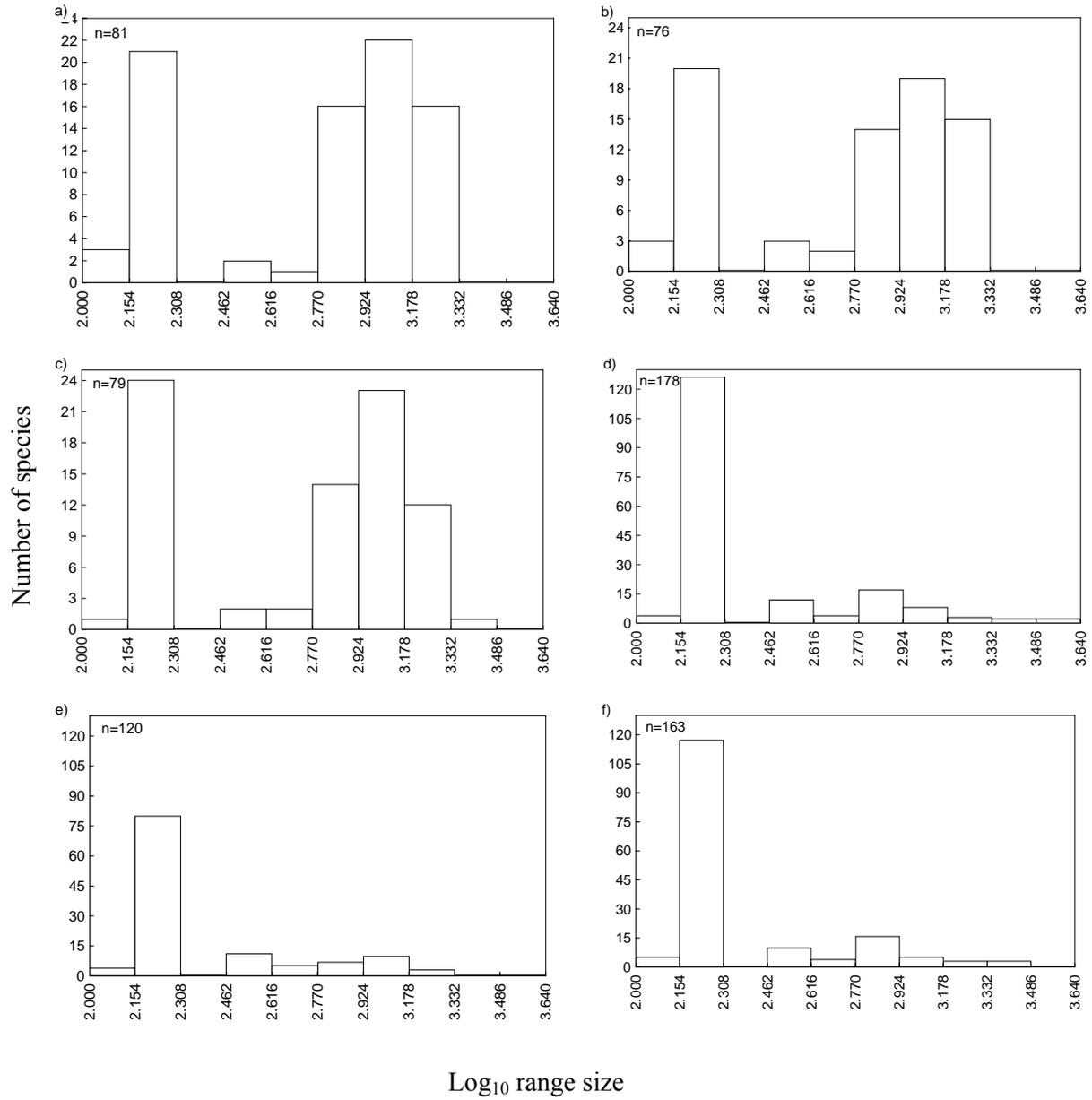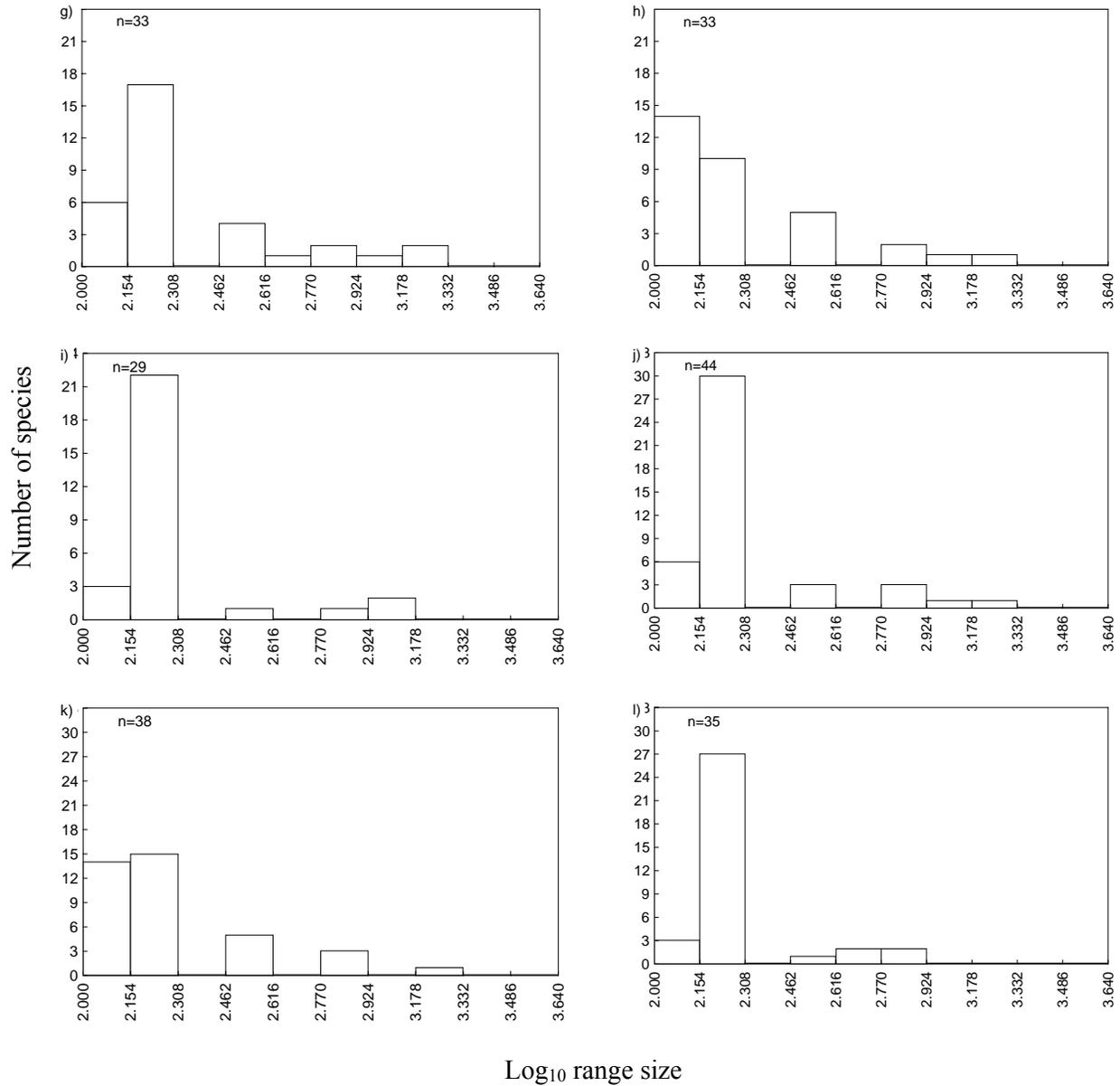
Figure 1 (a-f)

Figure 1 Range size frequency distributions of interpolated (a-c) and non-interpolated (d-f) ranges for the ants, and interpolated (g-i) and non-interpolated (j-l) ranges for the tenebrionids. 'n' denotes the number of species and ranges used in the case of non-interpolated data.

136

species' interpolated ranges extended over the altitudinal transect. Therefore, redefining the domain boundaries only affected these six species' range midpoints and the number of altitudinal bands they occupy.

The interpolated and non-interpolated mean range sizes of the ants showed a positive, linear relationship with altitude across the whole transect and within Mountain Fynbos (Table 2). The relationship between mean range size of ants and altitude was unimodal on the western slope when using either interpolated or non-interpolated range sizes (Table 2). Therefore, evidence for a Rapoport effect was found for interpolated and non-interpolated ranges of ants across the whole altitudinal gradient and within Mountain Fynbos. Nonetheless, less than half of the variation in range size was explained by altitude for the ants, except on the western slope using interpolated data (Table 2). No relationships between altitude and the interpolated mean range sizes of the tenebrionids were found (Table 2). However, the mean observed non-interpolated ranges of the tenebrionids showed a unimodal relationship with altitude across the western slope and within Mountain Fynbos (Table 2).

The mean interpolated observed altitudinal range of ants and tenebrionids showed a positive exponential relationship with the coefficient of variation of mean temperature across the whole transect (Table 3). The relationship between the mean interpolated observed range sizes of ants within Mountain Fynbos and the coefficient of variation of mean temperature was positive (Table 3). No relationship existed between the mean interpolated observed range sizes on the western slope and the coefficient of variance of mean temperature, or between the mean non-interpolated range sizes across the whole transect and within Mountain Fynbos, and the coefficient of variance of mean temperature (Table 3). There was a unimodal relationship between the mean observed non-interpolated ranges of the tenebrionids and the coefficient of variance of mean temperature (Table 3).

The mean range size per altitudinal band of the ant species was largest towards the middle of the domains (Fig. 4). In addition, both of the mid-domain models predicted a peaked relationship between the range sizes of the ant species and the midpoints of these ranges, with the peak in the middle of the domain whether interpolated or non-interpolated data were used (Fig. 4). By contrast with the ants, no clear pattern existed in observed interpolated and non-interpolated observed range sizes of the tenebrionids across the three domains (Fig. 5). Furthermore, only Mid-domain model A predicted a peaked relationship between range size and range midpoint for tenebrionids with the peak in the middle of the domain and Mid-domain model B (using interpolated and non-interpolated data) predicted

137
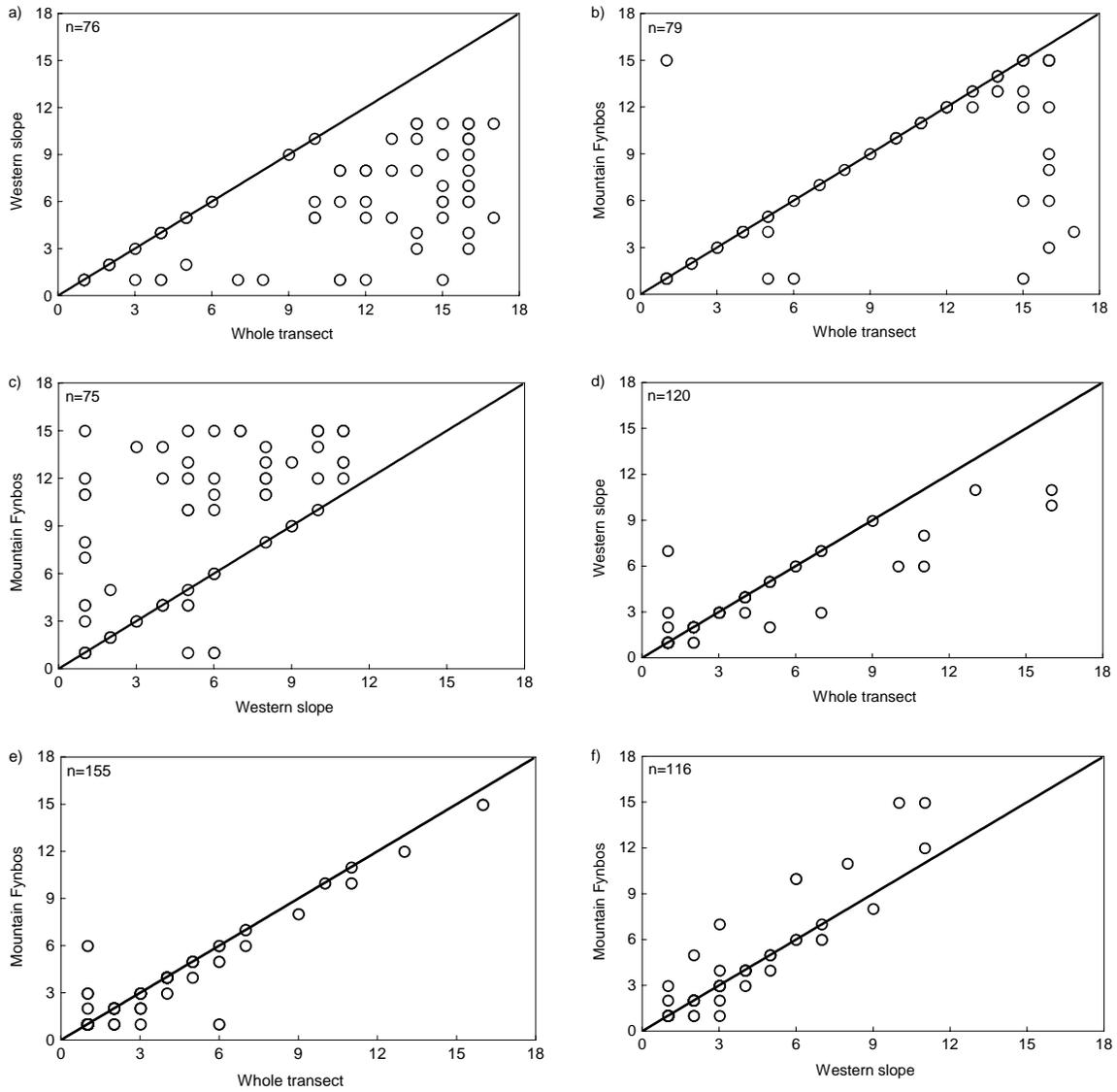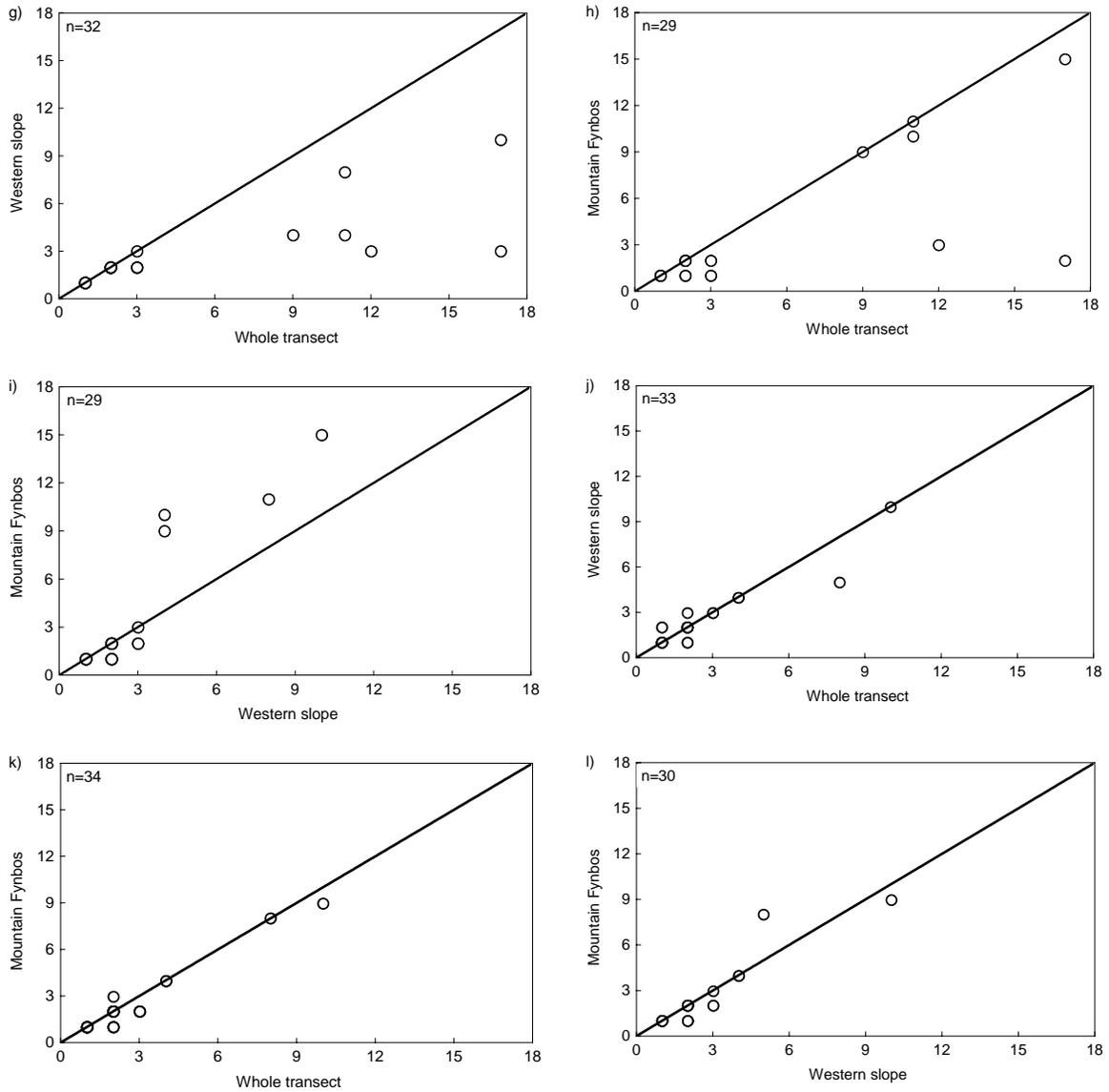
Figure 2 (a-f)

Figure 2 Comparisons between the number of altitudinal bands occupied using interpolated (a-c) and non-interpolated (d-f) ranges for each species of the ants, and interpolated (g-i) and non-interpolated (j-l) ranges for each species of the tenebrionids. 'n' denotes the number of species and ranges used in the case of non-interpolated data. Where the number of data points in the figures does not equal the indicated number of species, data points are overlaid. The line denotes equality.

139

Figure 3 (a-f)

140

Figure 3 Comparisons between midpoints of the interpolated (a-c) and non-interpolated (d-f) ranges for each species of the ants, and interpolated (g-i) and non-interpolated (j-l) ranges for each species of the tenebrionids. 'n' denotes the number of species and midpoints used in the case of non-interpolated data. Where the number of data points in the figures does not equal the indicated number of species, data points are overlaid. The line denotes equality.

141

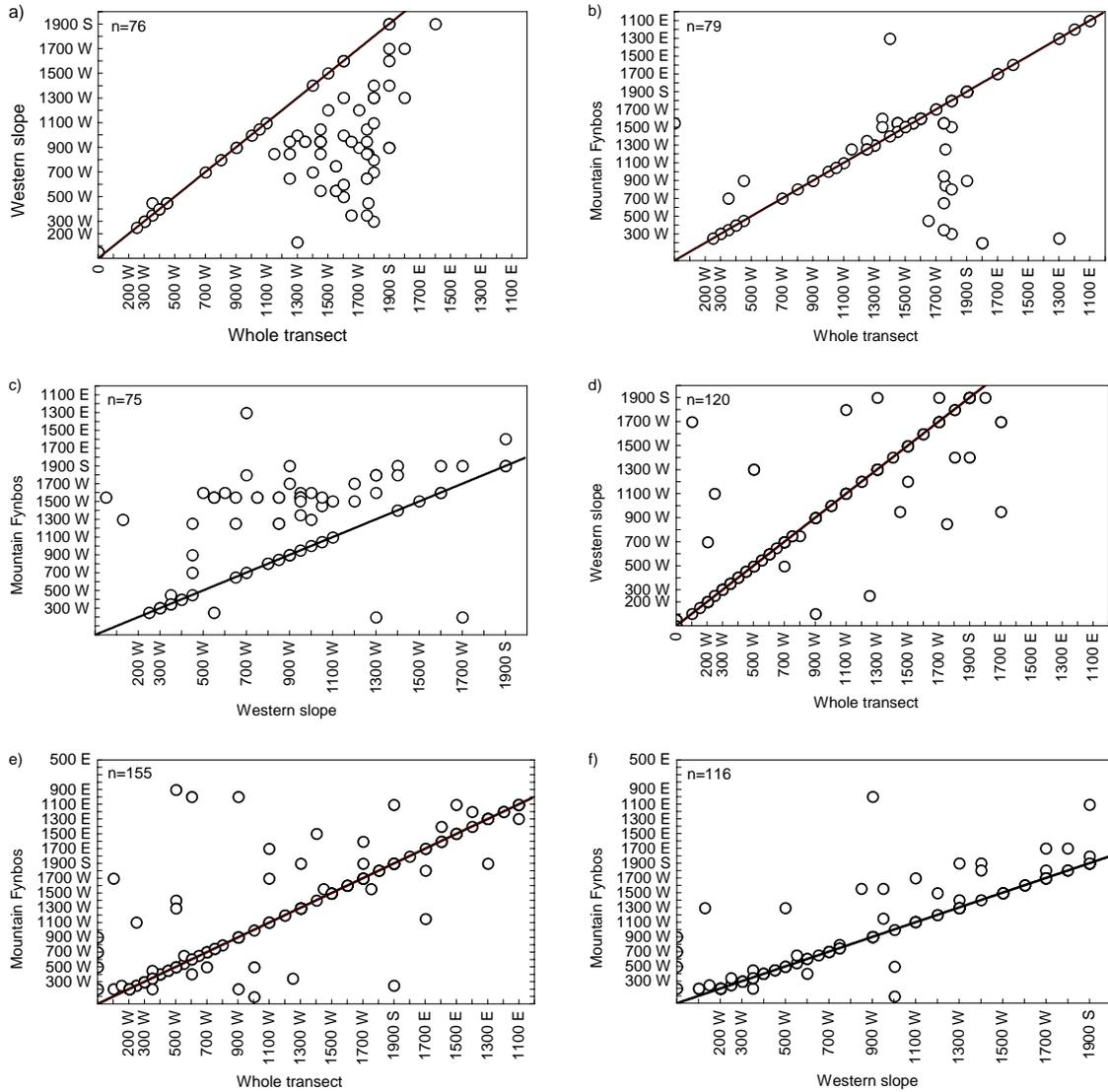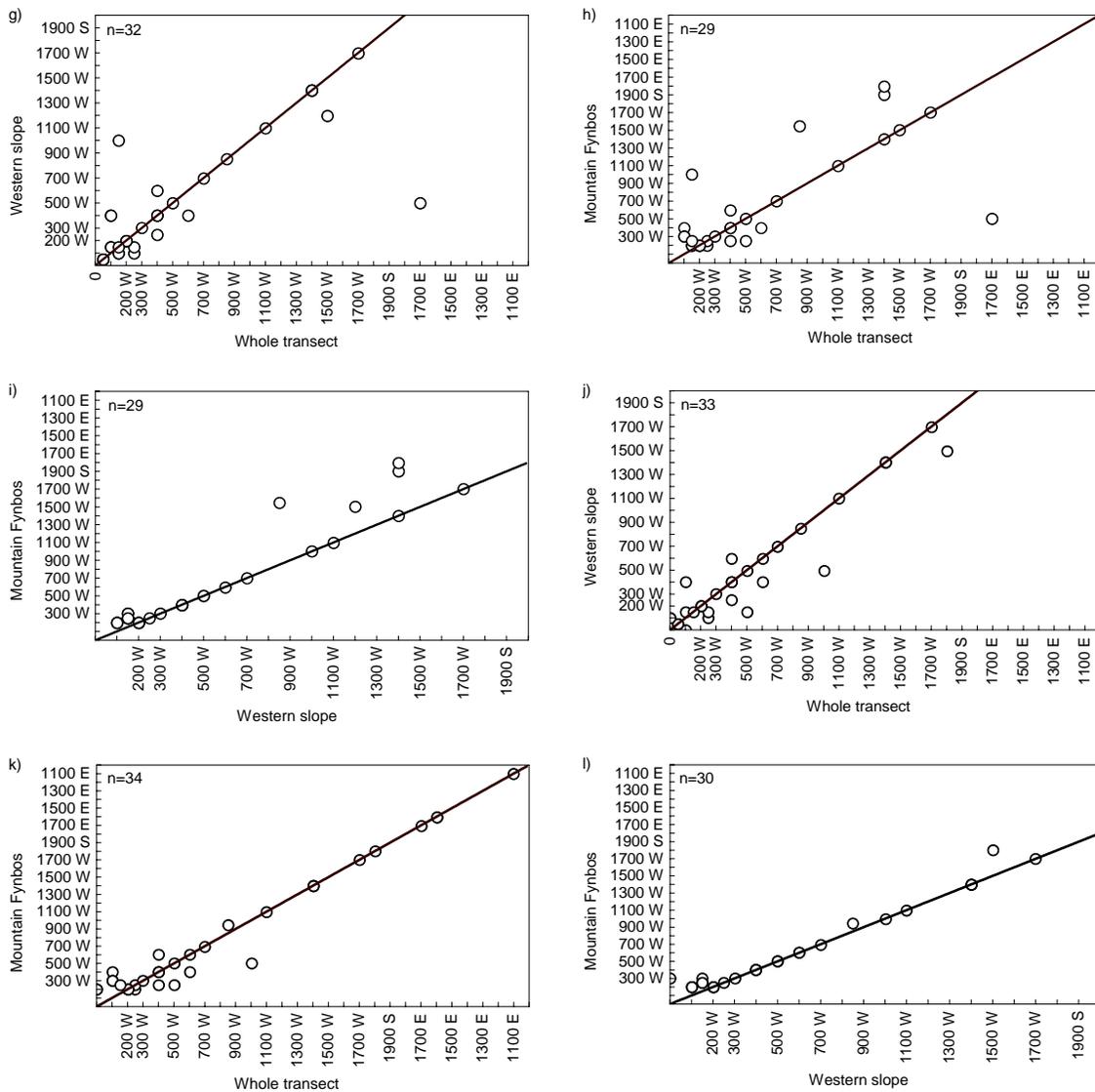**Table 2** Generalized linear model (Normal error distribution, identity link function) outcomes for the relationships between altitude and its quadratic term, and observed range sizes of ants and tenebrionids across the altitudinal transect. Estimates are given in brackets. * P < 0.05, ** P < 0.01, *** P < 0.01. Dev = Scaled deviance, %Expl = Percentage deviance explained.

Model type	Df	Dev/Df	Predictors	AIC	w_i	%Expl
Ants:						
Interpolated ranges						
Whole transect	14	1.21	altitude (+0.599**)	261.15	0.48	32.70
	15	1.13	altitude^2 (+0.000*)	261.79	0.35	28.79
	14	1.21	altitude (+0.678), altitude^2 (+0.000)	263.14	0.18	32.73
Western slope	15	1.13	altitude (+2.539***), altitude^2 (-0.001***)	161.68	0.97	63.41
Mountain Fynbos	15	1.13	altitude (+0.588**)	226.43	0.48	33.78
	13	1.15	altitude^2 (0.000*)	227.18	0.33	26.86
	12	1.25	altitude (+0.990), altitude^2 (+0.000)	228.27	0.19	34.49
Non-interpolated ranges						
Whole transect	15	1.13	altitude (+0.001**)	221.26	0.47	40.00
	14	1.21	altitude^2 (+0.000**)	221.34	0.46	39.00
	15	1.13	altitude (+0.003), altitude^2 (+0.000)	223.17	0.18	40.00
Western slope	15	1.13	altitude (+0.003***), altitude^2 (-0.000***)	125.16	1.00	86.55
	9	1.22	altitude (+0.0002)	144.29	0.00	8.18
	15	1.13	altitude^2 (+0.000**)	145.12	0.00	1.01

Table 2 (continued)

Model type	Df	Dev/Df	Predictors	AIC	w_i	%Expl
Mountain Fynbos	15	1.13	altitude (+0.001*)	190.13	0.44	29.55
	13	1.15	altitude^2 (+0.000*)	190.34	0.40	28.54
	12	1.25	altitude (+0.0004), altitude^2 (+0.001)	192.12	0.16	29.56

Tenebrionids:

Interpolated ranges

Whole transect			no significant models			
Western slope			no significant models			
Mountain Fynbos			no significant models			

Non-interpolated ranges

Whole transect			no significant models			
Western slope	12	1.25	altitude (+0.066**), altitude^2 (+0.000**)	153.96	1.00	80.86
Mountain Fynbos	13	1.15	altitude (-0.006**), altitude^2 (+0.000**)	206.65	0.60	66.89
	13	1.15	altitude^2 (+0.000***)	208.50	0.24	57.22
			altitude (+0.007***)	209.23	0.17	55.07

Table 3 Generalized linear model (Normal error distribution, identity link function) outcomes for the relationships between the coefficient of variance of mean temperature and its quadratic term, and observed range sizes of ants and tenebrionids across the altitudinal transect. Estimates are given in brackets. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.01$. Dev = Scaled deviance, %Expl = Percentage deviance explained.

Model type	Df	Dev/Df	Predictors	AIC	w_i	%Expl
Ants:						
Interpolated ranges						
Whole transect	15	1.13	temperature CV^2 (+0.301**)	260.56	0.46	36.03
	15	1.13	temperature CV (+0.040**)	261.01	0.36	36.25
	14	1.21	temperature CV (-31.381), temperature CV^2 (+0.619)	262.39	0.18	35.67
Western slope			no significant models			
Mountain Fynbos	13	1.15	temperature CV (+27.620**)	227.00	0.44	31.21
	13	1.15	temperature CV^2 (+0.030*)	227.19	0.40	28.19
	12	1.25	temperature CV (+44.470), temperature CV^2 (-0.160)	228.97	0.16	31.36
Non-interpolated ranges						
Whole transect			no significant models			
Western slope	8	1.38	temperature CV (+44.470), temperature CV^2 (-0.160)	139.64	1.00	49.83
Mountain Fynbos			no significant models			

Table 3 (continued)

Model type	Df	Dev/Df	Predictors	AIC	w_i	%Expl
Tenebrionids:						
Interpolated ranges						
Whole transect			no significant models			
Western slope			no significant models			
Mountain Fynbos			no significant models			
Non-interpolated ranges						
Whole transect	14	1.21	temperature CV^2 (+0.001**)	254.63	0.43	30.62
	15	1.33	temperature CV (+0.074**)	255.18	0.32	28.32
	15	1.33	temperature CV (-0.167), temperature CV^2 (+0.002)	255.71	0.25	34.25
Western slope			no significant models			
Mountain Fynbos	12	1.25	temperature CV (-0.297**), temperature CV^2 (+0.003**)	199.67	0.61	79.22
	13	1.15	temperature CV^2 (+0.001***)	201.44	0.25	73.28
	13	1.15	temperature CV (+0.113***)	202.67	0.14	70.99

flat relationships between tenebrionid range sizes and the midpoints of the range sizes across the whole transect and within Mountain Fynbos (Fig. 5a, c). These patterns were not surprising given that approximately 82% of the tenebrionids only occurred on the western slopes and 36% of the species occurred only in one altitudinal band. Twenty-one of these tenebrionid species had the midpoints of their distributions within the four lowest altitudinal bands on the western slope. In addition, only six species occurred in more than three altitudinal bands. Therefore, most of the observed range sizes of the tenebrionids were small. Therefore it is not surprising that the range size distributions predicted by Mid-domain model B are flat. The range sizes predicted by the two mid-domain models explained a significant and substantial proportion of the variation in the observed mean range sizes of the ants (Table 4). Mid-domain model A best predicted the mean interpolated observed range sizes of the ants in all three domains. This is unexpected because random ranges and midpoints were used in this model, whereas the observed range size frequency distribution was used in mid-domain model B (see Koleff & Gaston, 2001). Mid-domain model B best explained the mean observed non-interpolated ranges across the western slope and within Mountain Fynbos (Table 4). When the range sizes predicted by the two mid-domain models were both included in the best-fit models for the ants, none of the terms were significant (Table 4). Nonetheless, in most cases mid-domain model B explained a larger proportion of the variance in the mean observed interpolated and non-interpolated range sizes of the ants (Table 4). The largest proportions of the variance in mean observed interpolated and non-interpolated ranges were explained across the western slope for the ants (Table 4). By contrast, the mid-domain models were not good predictors of the mean observed interpolated and non-interpolated ranges of the tenebrionids across the whole transect and within Mountain Fynbos (Table 4). Across the western slope both mid-domain models were included in the best-fit models for mean observed interpolated and non-interpolated tenebrionid ranges (Table 4).

Only a small amount of explained variation in mean observed interpolated and non-interpolated range size was added by including temperature CV and/or its quadratic term into the best-fit models (Table 5). Therefore, the range sizes predicted by the mid-domain models best explained the observed range sizes for ants. Furthermore, the mean observed interpolated and non-interpolated range sizes had negative relationships with the coefficient of variation of the mean temperature in the best-fit models (Table 5) even though there were significant positive relationships between these variables in single term analyses (Table 3). However, this predictor was either not significant, or in a few cases only weakly significant in the best-fit

146
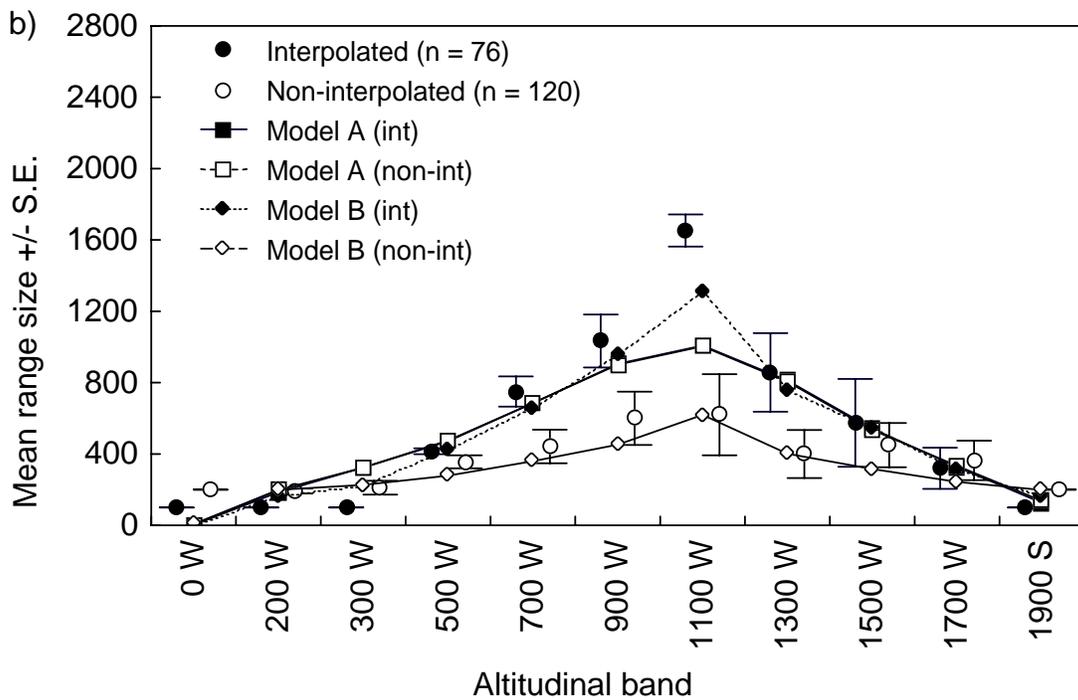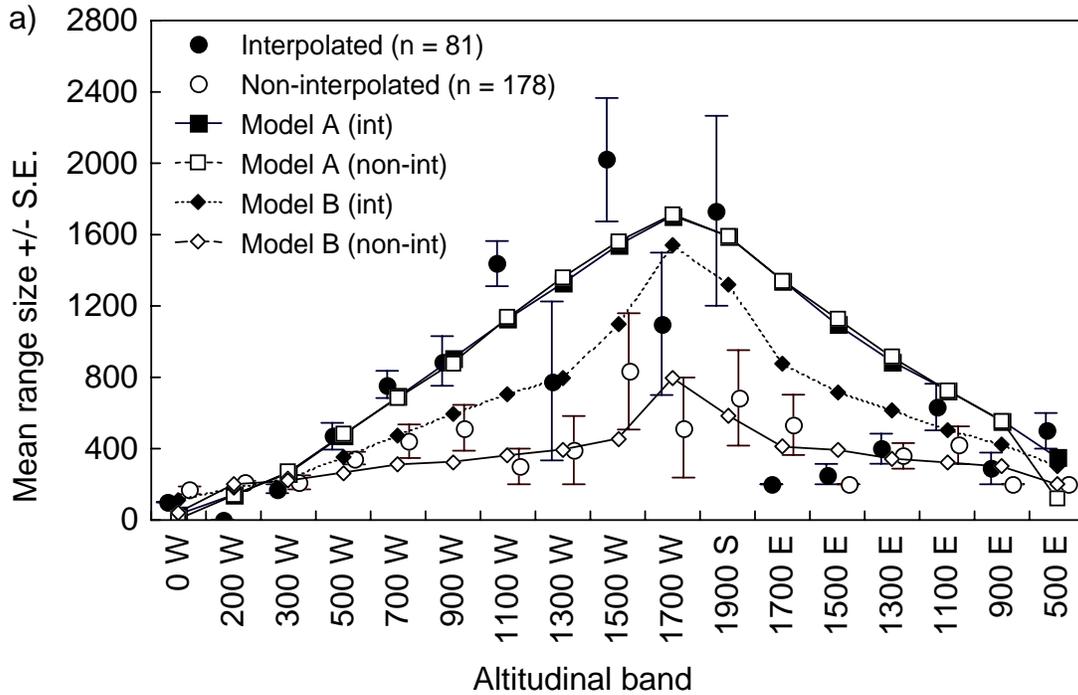
Figure 4 Observed and predicted mean range sizes of ants in each altitudinal band across a) the whole transect, b) the western slope of the transect, and c) in Mountain Fynbos. Standard errors of the predicted values are not shown because they are indistinguishable. 'n' denotes the number of species and ranges used in the case of non-interpolated data.
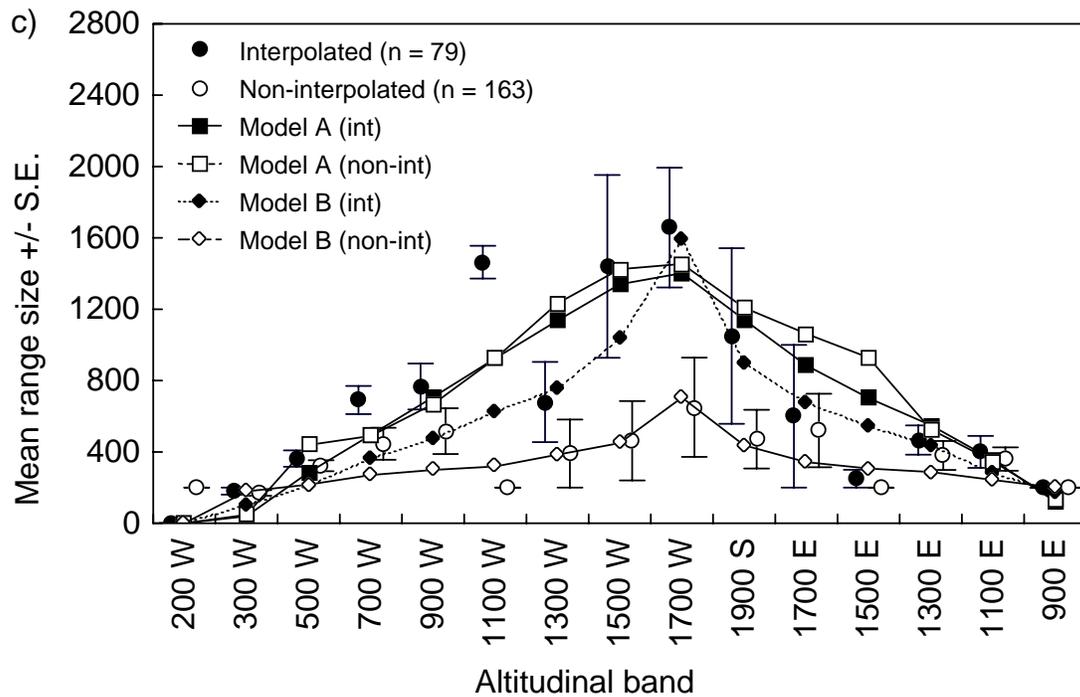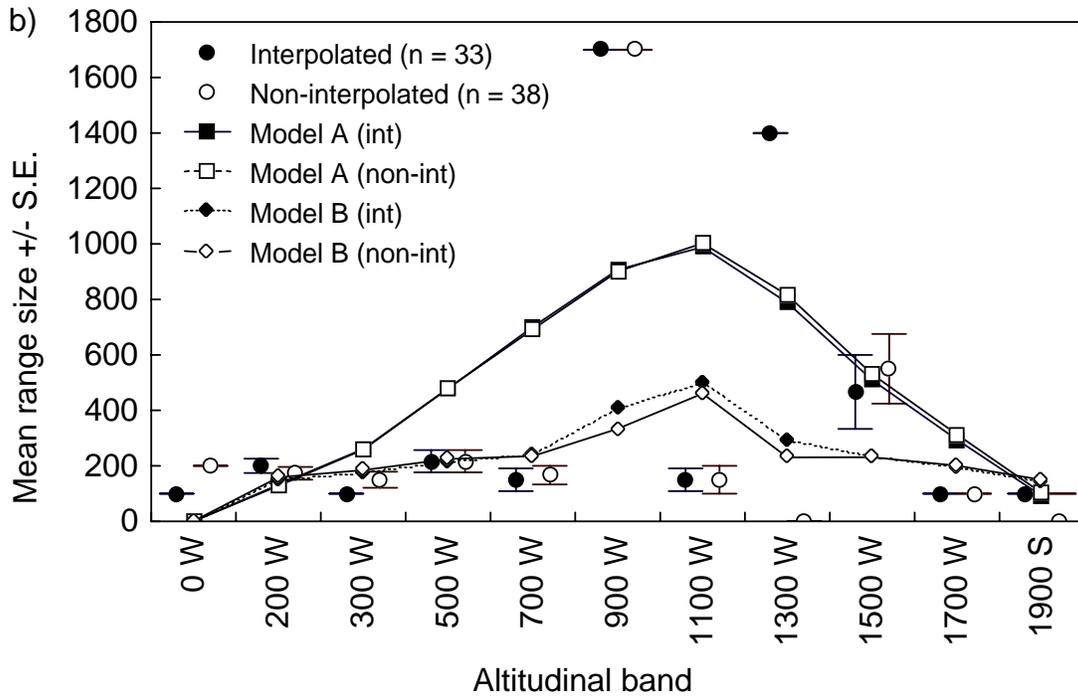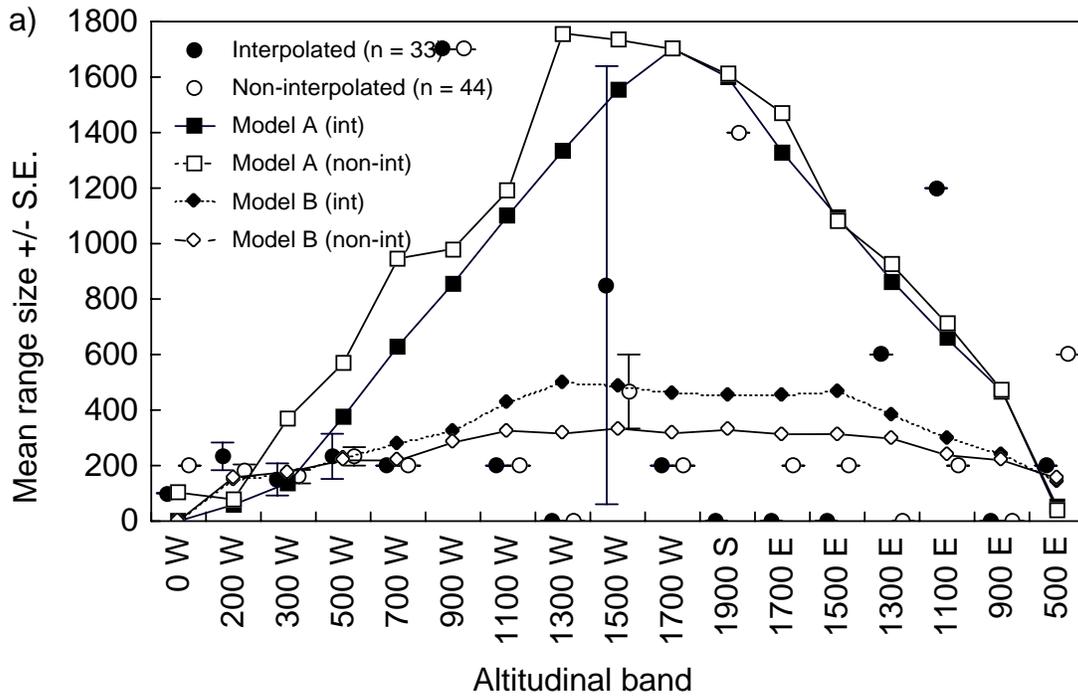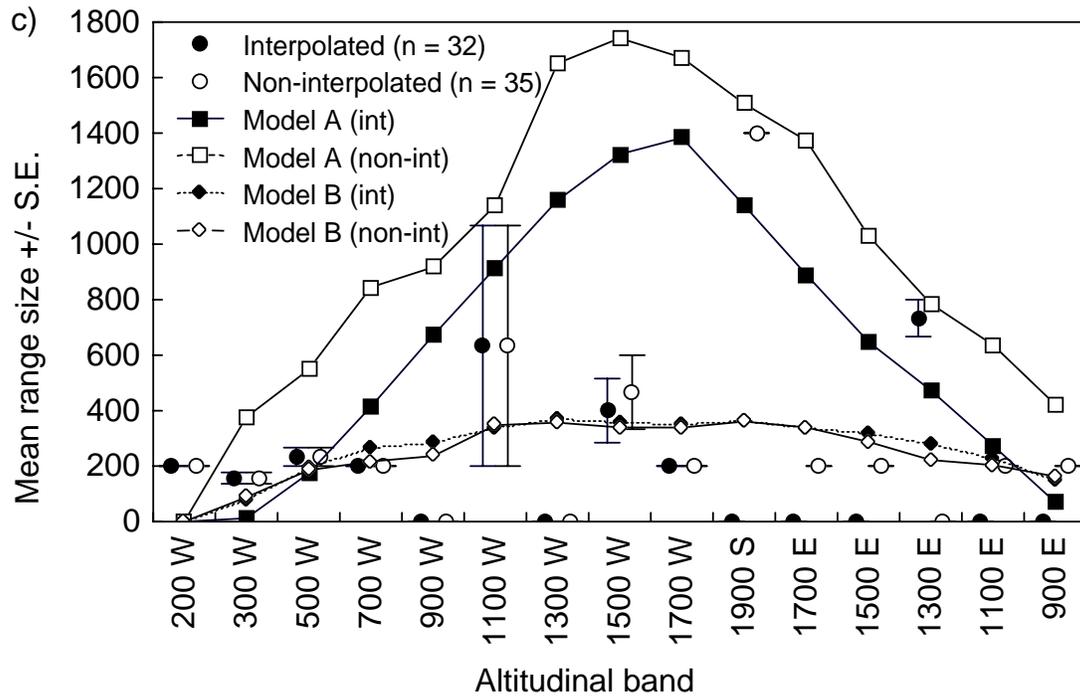
Figure 5 Observed and predicted mean range sizes of tenebrionids in each altitudinal band across a) the whole transect, b) the western slope of the transect, and c) in Mountain Fynbos. Standard errors of the predicted values are not shown because they are indistinguishable. 'n' denotes the number of species and ranges used in the case of non-interpolated data.

Table 4 Generalized linear model (Normal error distribution, identity link function) outcomes for the relationships between the predicted range sizes by the two mid-domain models, and observed range sizes of ants and tenebrionids across the altitudinal transect. Estimates are given in brackets. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.01$. Dev = Scaled deviance, %Expl = Percentage deviance explained.

Model type	Df	Dev/Df	Predictors	AIC	w_i	%Expl
Ants:						
Interpolated ranges						
Whole transect	15	1.13	Mid-domain model A (+0.798***)	255.45	0.61	51.12
	14	1.21	Mid-domain model A (+0.002), Mid-domain model B (-0.0003)	257.29	0.24	52.32
	15	1.13	Mid-domain model B (+1.049***)	258.28	0.15	50.66
Western slope	8	1.38	Mid-domain model A (+0.002), Mid-domain model B (+0.0005)	134.87	0.53	96.80
	9	1.22	Mid-domain model A (+1.402***)	135.18	0.45	87.90
	9	1.22	Mid-domain model B (+1.243***)	141.43	0.02	97.60
Mountain Fynbos	13	1.15	Mid-domain model A (+0.953***)	211.54	0.69	74.17
	12	1.25	Mid-domain model A (+0.001), Mid-domain model B (+0.0001)	213.37	0.27	75.73
	13	1.15	Mid-domain model B (+1.065***)	217.13	0.04	74.41

Table 4 (continued)

Model type	Df	Dev/Df	Predictors	AIC	w_i	%Expl
Non-interpolated ranges						
Whole transect	16	1.13	Mid-domain model A (+0.001***)	229.63	0.64	49.98
	15	1.20	Mid-domain model A (+0.001**), Mid-domain model B (-0.001)	230.95	0.33	51.84
	16	1.13	Mid-domain model B (+0.001**)	235.57	0.03	30.44
Western slope	9	1.22	Mid-domain model A (+0.001***)	123.68	0.70	85.91
	8	1.38	Mid-domain model A (+0.001*), Mid-domain model B (-0.001)	125.67	0.26	85.91
	9	1.22	Mid-domain model B (+0.002***)	128.99	0.05	77.16
Mountain Fynbos	13	1.15	Mid-domain model B (+0.001***)	183.68	0.64	54.16
	12	1.25	Mid-domain model A (+0.001), Mid-domain model B (+0.001*)	185.60	0.25	54.40
	13	1.15	Mid-domain model A (+0.001**)	187.20	0.11	42.02

152

Table 4 (continued)

Model type	Df	Dev/Df	Predictors	AIC	w_i	%Expl
Tenebrionids:						
Interpolated ranges						
Whole transect			no significant models			
Western slope	8	1.38	Mid-domain model A (+0.180*), Mid-domain model B (-0.190*)	154.56	1.00	85.07
	9	1.22	Mid-domain model A (+1.025**)	168.71	0.00	38.93
Mountain Fynbos			no significant models			
Non-interpolated ranges						
Whole transect			no significant models			
Western slope			no significant models			
Mountain Fynbos			no significant models			

models (Table 5). In addition, the coefficient of variation of the mean temperature had a unimodal distribution across the transect (Fig. 6), a pattern similar to the range sizes predicted by the two mid-domain models (see Fig. 4 and 5). Therefore, when both these variables are added in the best-fit models, the best predictor (i.e. the predicted range size distributions by the mid-domain model) will explain the main proportion of the variance in the observed ranges (see above) and the coefficient of variance of mean temperature will explain the remaining variation, which in this case is a weak negative trend. The largest percentage of the variation in mean observed range sizes of the ants was explained across the western slope and less variation was explained for non-interpolated ranges compared to that of interpolated ranges (Table 5). The only exception to both these patterns occurred when using mid-domain model B in selecting best-fit models for the non-interpolated ranges of the ants within Mountain Fynbos (Table 5). For both ants and tenebrionids, several spatial variables were highly significant and retained in the best-fit models, indicating significant spatial structuring in the range sizes.

No significant models were selected for mean observed interpolated tenebrionid range sizes across the whole transect and within Mountain Fynbos when adding the predicted range distributions from Mid-domain model A (Table 5). However, best-fit models including the predicted ranges by Mid-domain model A, the coefficient of variation in temperature and several spatial terms significantly explained the variation in mean observed non-interpolated tenebrionid ranges (Table 5). These models explained a large proportion of the variation in mean observed non-interpolated ranges even though the Akaike weights of the models were sometimes low (Table 5). Across the western slope the predicted range sizes by Mid-domain model A best explained variation in interpolated tenebrionid ranges, but no significant models were selected to explain mean observed non-interpolated ranges in this domain (Table 5). Furthermore, no significant models were selected for either mean observed interpolated tenebrionid ranges within Mountain Fynbos or for mean observed interpolated and non-interpolated ranges across the western slope when the results from Mid-domain model B was added (Table 5). Best-fit models for mean observed non-interpolated tenebrionid ranges across the whole transect and within Mountain Fynbos did not include the predicted ranges Mid-domain model B (Table 5). The best-fit models for mean observed interpolated ranges across the whole transect when adding the results from Mid-domain model B only explained a small amount of the variation (Table 5). However, the selected terms were not significant in the best-fit models (Table 5), which could explain the latter result.

154

Table 5 Generalized linear model (Normal error distribution, identity link function) outcomes for the relationships between the coefficient of variation (CV) of temperature, the predicted range sizes by two geometric constraint models (see text for detail) and spatial terms, and range sizes of ant and tenebrionids across the altitudinal transect. * P < 0.05, ** P < 0.01, *** P < 0.01. Dev = Scaled deviance, w_i = Akaike weight, %Expl = Percentage deviance explained.

Model type		Df	Dev/Df	Predictor	AIC	w_i	%Expl
Ants:							
Interpolated data, including Model A							
Whole transect:	best-fit model 1	16	1.13	Mid-domain model A (+0.001***)	202.96	0.07	49.98
Western slope:	best-fit model 1	5	1.23	temperature CV^2 (+0.500), Mid-domain model A (+0.700*), x^3 (+3669.500*), y^2 (+131162.500**), xy (-45261.700**)	141.59	0.19	97.05
	best-fit model 2	5	1.23	temperature CV (+38.200), temperature CV^2 (-0.400), x^2 (+5505.400***), y^2 (+213180.300***), xy (-73584.600***)	142.11	0.15	96.42
	best-fit model 3	6	1.83	temperature CV^2 (+0.010), x^2 (+5634.60***), y^2 (+223131.700***), xy (-77627.600***)	142.18	0.14	95.68

Table 5 (continued)

Model type		Df	Dev/Df	Predictor	AIC	w_i	%Expl
Mountain Fynbos:	best-fit model 1	13	1.15	Mid-domain model A (+0.95***)	212.31	0.25	74.17
	best-fit model 2	12	1.25	Mid-domain model A (+0.837***), y (+1905.885)	213.00	0.18	76.36
	best-fit model 3	12	1.25	Temperature CV (-8.683), Mid-domain model A (+1.097***)	213.47	0.14	75.56
Non-interpolated data, including Model A							
Whole transect:	best-fit model 1	16	1.13	Mid-domain model A (+0.001***)	202.96	0.07	49.98
Western slope:	best-fit model 1	9	1.22	Mid-domain model A (+0.001***)	123.68	0.36	85.91
		8	1.38	Mid-domain model A (+0.001***), temperature CV (+0.001)	125.64	0.13	85.96
		8	1.38	Mid-domain model A (+0.001***), temperature CV^2 (+0.000)	125.67	0.13	85.92

Table 5 (continued)

Model type		Df	Dev/Df	Predictor	AIC	w_i	%Expl
Mountain Fynbos:	best-fit model 1	11	1.36	Mid-domain model A (+0.001*), y (+6.210), y^2 (-88.753)	186.86	0.12	56.60
	best-fit model 2	12	1.25	Mid-domain model A (+0.001***), y (-30.233),	186.89	0.12	50.31
	best-fit model 3	13	1.15	Mid-domain model A (+0.001**)	187.20	0.10	42.02
Interpolated data, including Model B							
Whole transect:	best-fit model 1	11	1.45	temperature CV (-148.420*), temperature CV^2 (+1.349*), Mid-domain model B (+1.022**), y (+5412.416**)	240.19	0.27	69.78
	best-fit model 2	13	1.23	Mid-domain model B (+0.850**), y (+3036.303)	240.65	0.22	60.05
	best-fit model 3	15	1.13	Mid-domain model B (+1.049***)	2.41.85	0.12	50.66
Western slope:	best-fit model 1	8	1.38	Mid-domain model B (+1.248***), y^2 (+7475.205***)	118.29	0.16	99.29

Table 5 (continued)

Model type		Df	Dev/Df	Predictor	AIC	w_i	%Expl
Mountain Fynbos:	best-fit model 1	12	1.25	Mid-domain model B (+0.905***), y (+3545.188**)	207.01	0.40	84.12
	best-fit model 2	11	1.36	Temperature CV (-5.821), Mid-domain model B (+0.991***), y (+3774.514**)	208.29	0.21	84.86
	best-fit model 3	11	1.36	temperature CV^2 (-0.087), Mid-domain model B (+0.346), y (+1340.381)	208.55	0.19	81.31
Non-interpolated data, including Model B							
Whole transect:	best-fit model 1	11	1.45	temperature CV^2 (+0.000), y (+20.467***), y^2 (-347.701***), xy (+70.420***)	205.67	0.10	67.24
Western slope:	best-fit model 1	9	1.22	Mid-domain model B (+0.002***)	128.99	0.19	77.16
	best-fit model 2	7	1.57	temperature CV (+0.097), temperature CV^2 (-0.001), Mid-domain model B (+0.002***)	129.70	0.13	83.05
	best-fit model 3	8	1.38	Mid-domain model B (+0.001), y (+2.222)	130.03	0.11	79.09

Table 5 (continued)

Model type		Df	Dev/Df	Predictor	AIC	w_i	%Expl
Mountain Fynbos:	best-fit model 1	14	1.36	Mid-domain model B (+0.002***), y (+0.196), x^2 (-0.050)	183.23	0.20	54.95
	best-fit model 2	13	1.15	Mid-domain model B (+0.001***)	183.68	0.16	54.16
Tenebrionids:							
Interpolated data, including Model A							
Whole transect:				no significant models			
Western slope:	best-fit model 1	9	1.22	Mid-domain model A (+1.025**)	168.05	0.46	38.93
Mountain Fynbos:				no significant models			
Non-interpolated data, including Model A							
Whole transect:	best-fit model 1	12	1.33	temperature CV (+0.015), y (+0.672), x^2 (-1.474)	205.36	0.29	89.69

159

Table 5 (continued)

Model type		Df	Dev/Df	Predictor	AIC	w_i	%Expl
	best-fit model 2	11	1.45	temperature CV (-0.017), Mid-domain model A (+0.001***), y (+0.379), x^2 (-0.754)	205.56	0.26	94.35
	best-fit model 3	12	1.33	temperature CV^2 (+0.001), y (+0.708), x^2 (-1.548)	207.08	0.12	89.85
Western slope:				no significant models			
Mountain Fynbos:	best-fit model 1	11	1.36	temperature CV (-0.343**), temperature CV^2 (+0.004**), y^2 (+3.340)	199.66	0.10	80.04
	best-fit model 2	12	1.25	temperature CV (-0.297**), temperature CV^2 (+0.003**)	199.67	0.10	79.22
Interpolated data, including Model B							
Whole transect:	best-fit model 1	13	1.31	temperature CV (+146.960), temperature CV^2 (-1.390), Mid-domain model B (-1.050)	227.25	0.44	13.76

Table 5 (continued)

Model type		Df	Dev/Df	Predictor	AIC	w_i	%Expl
	best-fit model 2	14	1.21	temperature CV^2 (-0.070), Mid-domain model B (+0.570)	228.42	0.25	1.09
Western slope:				no significant models			
Mountain Fynbos:				no significant models			
Non-interpolated data, including Model B							
Whole transect:	best-fit model 1	12	1.33	temperature CV (+0.015), y (+0.672), x^2 (-1.474)	205.36	0.54	89.69
	best-fit model 2	12	1.33	temperature CV^2 (+0.001), y (+0.708), x^2 (-1.548)	207.08	0.23	89.85
	best-fit model 3	11	1.45	temperature CV (+0.126), temperature CV^2 (+0.000), y (+33.612***), x^2 (-207.944***)	207.33	0.20	94.13
Western slope:				no significant models			
Mountain Fynbos:	best-fit model 1	11	1.36	temperature CV (-0.343**), temperature CV^2 (+0.004**), y^2 (+3.340)	199.66	0.09	80.04
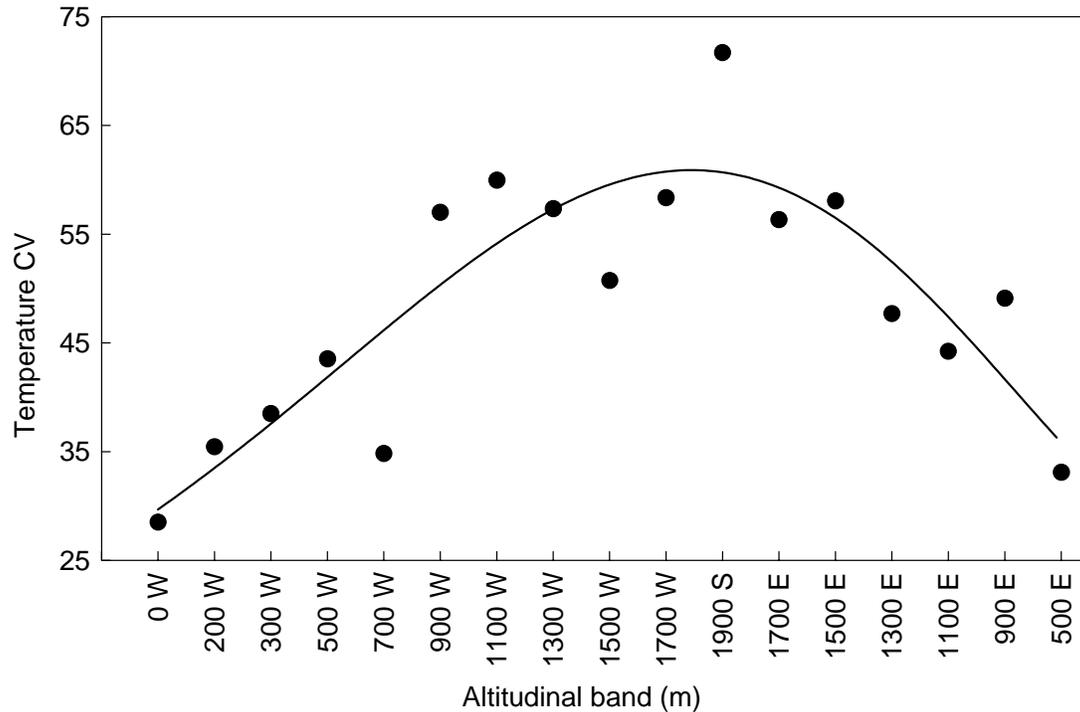
Figure 6 The coefficient of variation of mean temperature across the altitudinal transect. The fitted line indicates the unimodal nature of temperature CV, but because of the likely effects of spatial autocorrelation no equation for the line is provided.

DISCUSSION

To date, this is only the third study that has explicitly tested, and found evidence for Rapoport's rule along an altitudinal gradient in insects, and the first to do so in the southern hemisphere. Fleishman *et al.* (1998) were the first to show that a Rapoport effect exists in montane butterflies along an 1300 m altitudinal gradient in the Toiyabe Range, Nevada. They argued that the pattern did not result from sampling bias as predicted by Colwell and Hurt (1994) as the sampling effort was proportional to the altitudinal band area and sampling was done during times that were most favourable to flight (Fleishman *et al.* 1998). In a second study, Sanders (2002) showed that Rapoport's rule holds for ants along altitudinal transects in three states in North America (Colorado, Nevada and Utah). He argued that the distribution of the ants might also be a consequence of geometric constraints, although he provided little

analysis to substantiate this assertion. To date, few studies have investigated variation in range size along environmental gradients in the context of geometric constraint models. This is particularly unusual as mid-domain models are based fundamentally on the placement of ranges within bounded areas. Studies that have considered geometric constraints when investigating range size variation have demonstrated that the observed patterns can be significantly influenced by such constraints. Pineda (1993) showed that depth ranges of benthic marine organisms declined towards the edges of the bathymetric gradient, while Roy *et al.* (1994) found the latitudinal ranges of Pacific marine molluscan species to be strongly influenced by the major oceanographic barriers. Ruggiero and Lawton (1998) observed that the altitudinal Rapoport effect in Andean passerine birds disappeared when geometric constraints were controlled for by omitting the species of which the ranges abutted the boundaries. By contrast, studies conducted on New World birds (Koleff & Gaston, 2001) and mammals (Lyons & Willig, 1997; Arita *et al.*, 2005) have found that geometric constraints did not generate the observed patterns in range distribution. Thus, Lyons and Willig (1997) found that factors other than geometry and chance are responsible for range size patterns in bats and marsupials. Likewise, Koleff and Gaston (2001) showed that, for woodpeckers and parrots, the fit between the empirical latitudinal range distributions and predicted patterns by five mid-domain models were weak. They argued that mid-domain models are either too simplistic or do not adequately explain geographical variation in diversity of the two taxa (Koleff & Gaston, 2001). More recently, Arita *et al.* (2005) demonstrated that the observed patterns in species richness and range size distributions of bats and non-volant mammals deviate sharply from those predicted by a fully stochastic mid-domain model. They argued that this inconsistency between observed and predicted patterns of richness and range distributions provide proof that assemblages are highly structured and not purely a result of stochastic processes.

In the present study, I tested the hypothesis that geometric constraints are responsible for the observed patterns in range size distributions of the two taxa along an altitudinal gradient that was laid out from sea level to the top of a mountain and down the other side thereof, with the highest sites approximately in the middle of the domain. No other study has investigated patterns in range size or the applicability of mid-domain models to range distributions across such an altitudinal gradient. Mid-domain models predict a peak in range sizes in the middle of a bounded domain and at mid-altitudes (i.e. a reversed Rapoport effect) (Colwell & Hurt, 1994). Consistent with this prediction, the ants in this study showed peaks in range sizes in the middle of all three domains. However, the altitude at which the peak in

range sizes occurs differed between the three domains, which is a consequence of the definition of the domain boundaries. The range sizes of species (and ultimately the position of the midpoints of these ranges) were altered as the domain boundaries were redefined, and especially so when only the western slope was considered. This is particularly true for interpolated ranges. For example, a species that occurred at 200 – 1100 m a.s.l. on the western slope and at 500 – 900 m a.s.l. on the eastern slope would have an interpolated altitudinal range of 3100 m and a midpoint at 1750 m a.s.l. on the western slope when the whole transect is considered as the domain. However, if the western slope is defined as the domain, this species will have a range size of 400 m and a midpoint at 700 m a.s.l. on the western slope. Zapata *et al.* (2003, 2005) criticized the arbitrary way in which domain limits are specified. They argued that specified boundaries might limit the dispersal of certain species, whereas this might not be the case for others (Zapata *et al.*, 2003, 2005). In this study several of the ant species occurred across the whole transect, including the highest altitude sampled. The distributions of these species were thus not restricted by altitude. Moreover, some of the species had distributions that covered most of Africa (e.g. *Anoplolepis* c.f. *custodiens*, Prins, 1963; Breytenbach, 1988). Therefore, the way in which the boundaries of the three domains were selected might also have constrained the ranges of the species to show peaks in the middle of the three different domains, and in consequence there was a good fit between observed and predicted range distributions in all three domains.

Thus, this study has shown that simply by defining range boundaries in a particular way, investigations are likely to bias the outcomes of studies. Here, the complete analysis (see Gaston & Blackburn, 1996b, Blackburn & Gaston, 1998) showed that range sizes increase towards higher elevations, and that the increase can be explained by geometric constraints models. However, temperature CV and the mid-domain model predictions were wholly collinear. When the domain is defined as the Western slope (i.e. the analysis is a partial one), this collinearity is weakened and the geometric constraints models are no longer as important for explaining variation in range size as they are in the complete analysis. Although concerns about the definition of domain boundaries have been raised previously (Koleff & Gaston 2001; Zapata *et al*. 2003, 2005), this particular issue has not enjoyed attention. Moreover, it draws attention to the fact that the geometric constraints models do not always predict a reverse Rapoport effect (see Introduction), but rather this depends on the domain that is being considered. In those cases where the models predict a Rapoport effect and one is found, it will be difficult to determine which of the two underlying mechanisms (random range placement or climatic variability) are operational. Only physiological data will enable the mechanisms to

be distinguished because the climatic variability mechanism also predicts broader tolerances in the species with the largest ranges (Stevens, 1989; Addo-Bediako et al., 2000). To date, only one study has investigated such trends in insects in montane areas in South Africa (Gaston & Chown, 1999b). They found that dung beetles have greater thermal tolerance at higher than at lower altitudes and that the altitudinal range of dung beetles increases with increasing altitude (Gaston & Chown, 1999b). Indirect tests of the climatic variability mechanism have also been conducted across latitudinal (Letcher & Harvey, 1994; Ruggiero & Lawton, 1998) and bathymetric gradients (Smith & Brown, 2002). Letcher and Harvey (1994) found that annual temperature range is a good predictor of the range sizes of mammals in the Palearctic. By contrast, Ruggiero and Lawton (1998) argued that the climatic variability mechanism does not account for range variation in Andean passerine birds because annual variation in temperature is not a strong enough selective force in the southern Andes to have substantial effects on ranges. Smith and Brown (2002) found pelagic marine fish species with the narrowest ranges to occur in the most variable environment, and therefore the climatic variability hypothesis cannot account for the Rapoport effect they found for this group. Tests of the climatic variability hypothesis incorporating physiological assessments of tolerance are the only way in which this hypothesis can be distinguished from a mid-domain model. However, such work remains to be done in this particular system.

Grytnes and Vetaas (2002) have shown that interpolation of ranges creates artificial patterns in species richness along environmental gradients because species richness will be overestimated in areas where species ranges are interpolated. Similarly, Zapata et al. (2003) have argued, using results obtained by Jetz and Rahbek (2001), that fragmented ranges do not produce a mid-domain effect in species richness, and that a mid-domain effect would become more apparent as ranges become less fragmented (see also Hawkins & Diniz-Filho, 2002). However, the effect of range interpolation when testing for a Rapoport effect has not yet been investigated. Interpolation is generally used to account for sampling inadequacies such as uneven sampling effort and incomplete sampling (e.g. Lees et al., 1999), although it might result in a species having a larger range than it actually has. For example, a species might not be present in all the altitudinal bands between its two extremes along an altitudinal gradient because of a lack of suitable habitat or factors such as competitive exclusion (Grytnes & Vetaas, 2002). Therefore, this study repeated the analyses using all species and then only the species of which the altitudinal ranges were not interpolated. Generally, similar patterns were observed between the two data sets for ants even though the number of species with non-interpolated ranges was considerably smaller than the full data set. However, tenebrionids

165

displayed very different results between the interpolated and non-interpolated data sets in Table 3. This is unusual as most of the species were retained after those with interpolated ranges were removed from analyses. This suggests that the pattern observed for the full data set is predominantly a result of the few wide ranging species with interpolated ranges. This was indeed the case because the only six species that occurred in more than four altitudinal bands had interpolated ranges.

The tenebrionids in this study show considerably different patterns than the ants in all respects. No evidence of a Rapoport effect was found and in only a few cases did geometric constraint or the coefficient of variance of mean temperature sufficiently explain the observed patterns in range distributions. Botes *et al*. (submitted/Chapter 3) argued that historical processes play important roles in shaping tenebrionid assemblages across this altitudinal transect because of the high species richness and specificity of the first three sites on the western slopes and the fact that the majority of the species belong to a subfamily with high diversity in arid areas. Furthermore, they showed that species density declined towards the eastern slopes, away from an area that comprises the southern end of a south-west African centre of tenebrionid endemism and diversity (Scholtz & Holm, 1985; Penrith, 1986; Penrith & Endrödy-Younga, 1994). The present analyses lend support to these conclusions by demonstrating that not only do the lower altitudinal sites on the western slope of the transect have high richness (Chapter 3), but the vast majority (81%) of the species that occur here have extremely small ranges.

In conclusion, this study provides a novel and significant investigation of the existence of a Rapoport effect for two insect taxa across an altitudinal gradient. Ashton (2001) argued that there is insufficient evidence to dismiss Rapoport's rule (e.g. to date only five studies have investigated Rapoport's rule in the southern hemisphere, see Table 1), and that the mechanisms underlying the pattern require further investigation. By comparing two major taxa across three domains using both interpolated and non-interpolated data the present work has shown that there is some way to go before mechanisms underlying an altitudinal Rapoport effect can be fully resolved. The collection of physiological data (see Gaston & Chown, 1999b) and an assessment of beta-diversity (Koleff & Gaston, 2001) would go some way towards addressing these issue for this assemblage of ants and tenebrionids.

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SPECIES DIVERSITY PATTERNS ACROSS AN ALTITUDINAL GRADIENT: TESTING THE SPECIES-ENERGY RELATIONSHIP

INTRODUCTION

Many hypotheses have been proposed to explain large-scale species richness variation (Pianka, 1966; Brown, 1988; Rohde, 1992, 1999; Gaston, 1996; Gaston & Blackburn, 2000; Whittaker *et al.*, 2001). Of these, six have come to enjoy primacy. These are the geographic area mechanism, Rapoport-rescue hypothesis, geometric constraints model, evolutionary speed hypothesis, and the productivity and ambient energy hypotheses (Willig *et al.*, 2003). Currently, considerable evidence exists for the productivity hypothesis for a variety of groups, especially vertebrates and plants over broad latitudinal gradients (for reviews see Waide *et al.*, 1999; Gaston, 2000; Mittelbach *et al.*, 2001, Hawkins *et al.*, 2003; Bonn *et al.*, 2004; Rodríguez *et al.*, 2005). The form of this richness-productivity relationship varies substantially among studies (Waide *et al.*, 1999; Mittelbach *et al.*, 2001; Whittaker & Heegaard, 2003). It is predominantly unimodal in vascular plants, whilst positive, negative and unimodal relationships have been reported for animals (Waide *et al.*, 1999; Mittelbach *et al.*, 2001; Bonn *et al.*, 2004). Nonetheless, there is growing evidence for the effect of spatial scale on the form of the relationship (Waide *et al.*, 1999; Mittelbach *et al.*, 2001; Whittaker *et al.*, 2001; Chase & Leibold, 2002; van Rensburg *et al.*, 2002; Storch *et al.*, 2005). At small spatial scales, it is often unimodal (Abramsky & Rosenzweig, 1984; Rosenzweig, 1995; Ritchie & Olff, 1999; Waide *et al.*, 1999; Dodson *et al.*, 2000; Mittelbach *et al.*, 2001; Chase & Leibold, 2002) while at larger (regional) scales richness typically increases monotonically with increasing productivity (Currie & Paquin, 1987; Currie, 1991; Rosenzweig, 1995; Waide *et al.*, 1999; Mittelbach *et al.*, 2001; Chase & Leibold, 2002, but see Kerr & Packer, 1997; Chown & Gaston, 1999).

The pattern across altitude is less clear. Initially it was thought that species richness declines monotonically with elevation. However, few early studies standardized for sampling effort and area. Once this was done it was found that the relationship between altitude and species richness is more typically unimodal (Whittaker & Niering, 1975; Lawton *et al.*, 1987; Rahbek, 1997; Sanders, 2002). Early studies also assumed that productivity declines with increasing altitude (MacArthur, 1969; Orians, 1969; Terborgh, 1971; 1977; Terborgh & Weske, 1975). Therefore, the negative monotonic relationship between species richness and

altitude was used as evidence for a positive richness-productivity relationship (Orians, 1969; MacArthur, 1972; Terborgh, 1977). However, Rahbek (1997) pointed out that this extrapolation cannot be accepted without accounting for the effect of available area on species richness patterns. Later, he argued that the relationship between richness and productivity might take one of three forms depending on the elevation-productivity relationship and the elevation-richness relationship (Rahbek, 2005). In consequence, remarkably few robust generalizations can be made about the relationship between richness and productivity across altitudinal gradients. Nonetheless, variation in richness has been attributed to a variety of energy-related variables, such as temperature (Rahbek, 1997; Buse *et al.*, 2001; Kessler, 2001; Brehm *et al.*, 2003; Moser *et al.*, 2005), potential evapotranspiration (Bhattarai *et al.*, 2004; Moser *et al.*, 2005), and water availability (Fleishman *et al.*, 2000; Blanche & Ludwig, 2001; Bhattarai *et al.*, 2004), as well as to variation in area (MacArthur, 1972; Rahbek, 1995, 1997; Odland & Birks, 1999; Kaspari *et al.*, 2003) and in soil nutrients (Austrheim, 2001), and to geometric constraints (Rahbek, 1997; Kaspari *et al.*, 2003; Carpenter, 2005).

Despite the importance of energy as a correlate of species richness, the mechanistic basis of this relationship has not been extensively explored (Gaston, 2000). Evans *et al.* (2005a) identified nine mechanisms that might underlie positive relationships between species richness and energy availability (either ambient energy or productive energy). Of these, the more individuals hypothesis (also known as the "abundance-extinction" mechanism - Kaspari *et al.*, 2003, or "increased population size" mechanism - Evans *et al.*, 2005a) is most widely thought to explain the increase in richness with increasing energy availability. If productivity is a limiting factor, then more productive sites can support higher total abundances and because species richness increases with increasing abundance (the probability of extinction is higher for species with low abundances, see Leigh, 1981; Pimm *et al.*, 1988), species richness will be higher in more productive areas (Wright, 1983; Rosenzweig & Abramsky, 1993). Hurlbert (2004) found support for the more individuals hypothesis in bird communities in North America. However, he argued that this mechanism did not operate alone in determining the richness patterns. The relative abundance distributions of communities in more productive sites were more even than those in less productive sites. In consequence, a given abundance yielded more species in more productive sites (Hurlbert, 2004). In addition, structurally more complex habitats were more species rich than less structurally complex habitats after controlling for energy (Hurlbert, 2004). Hurlbert (2004) argued that habitat complexity thus also plays an important role in structuring bird communities. In one of the few studies using insects, Kaspari *et al.* (2003) tested six mechanisms proposed to account for diversity patterns

174

using ant communities at three spatial grains across altitudinal and latitudinal gradients in the New World. These were the abundance-extinction hypothesis (i.e. more individuals hypothesis), the sampling hypothesis (higher productivity translates into higher abundance and, if assemblages comprise individuals randomly selected from a regional species pool, then more species will be added to the assemblage as abundance increase; see Evans *et al.*, 2005a for discussion), the energy-speciation hypothesis (evolutionary rates are limited by solar energy and species richness will thus increase with environmental temperature, see Currie, 1991; Rohde, 1992), the mass-effect hypothesis (populations can reproduce in a limited number of habitats; the species richness of adjacent habitats will be increased when offspring are dispersed to these areas where they can survive but fail to reproduce, Schmida & Whittaker, 1981; Stevens, 1992; Rahbek, 1997), area (Rosenzweig, 1995) and the mid-domain hypothesis (Colwell & Hurtt, 1994; Colwell & Lees, 2000). Their results supported the sampling and abundance-extinction hypotheses at small spatial scales (Kaspari *et al.*, 2003) and at the largest spatial scale the area and energy-speciation hypotheses were strongly supported (Kaspari *et al.*, 2003). By contrast, Srivastava & Lawton (1998) found no support for the more individuals hypothesis in the tree hole communities they investigated. More productive tree holes supported more species, but not more individuals. They concluded that this mechanism is an inadequate explanation for the richness-productivity relationship because it does not account for processes that cause local extinctions and colonization and does not allow for a correlation between body size and extinction risk.

Nonetheless, the number of studies that have investigated the species richness-productivity relationship and its underlying mechanisms in invertebrates is small, and the majority of these concern aquatic invertebrates (see Mittelbach *et al.*, 2001) such as chydorids (e.g. Whiteside & Harmsworth, 1967), benthic invertebrate communities (Death & Winterbourn, 1995), zooplankton (Leibold, 1999; Dodson *et al.*, 2000) and corals (Porter, 1972; Huston, 1985; Fraser & Currie, 1996). Moreover, investigations of energy-richness relationships across altitudinal gradients are even rarer. Investigations of variation in insect richness with elevation have been undertaken at a wide range of sites and over several scales (McCoy, 1990). These have included studies on single groups (such as drosophilid flies, Ichijo *et al.*, 1982) and restricted habitats (e.g. cole crops, Sachen & Gangwere, 1980), and others that have dealt with a wide range of taxa and several habitats (Wolda, 1987). Typically the studies have found that richness declines monotonically with elevation, although when corrections are made for area species richness either does not decline with elevation (Lawton *et al.*, 1987) or it shows a hump-shaped relationship with a peak at mid-altitudes (Lees *et al.*,

1999; Sanders, 2002). In addition, several studies have found distinctly non-linear patterns (Janzen, 1973; Janzen *et al.*, 1976; McCoy, 1990; Olson, 1994; Fisher, 1998, 1999; Fleishman *et al.*, 1998, 2000; Lees *et al.*, 1999; Blanche & Ludwig, 2001; Pyrcz & Wojtussiak, 2002; Sanders, 2002; Escobar *et al.*, 2005) whilst others have documented increases in richness with elevation (Turner & Broadhead, 1974; Holloway, 1987; Horstmann *et al.*, 1999; Brehm *et al.*, 2003). Unfortunately, many of these studies either do not encompass the full altitudinal gradient or do not provide explicit investigations either of the range of energy variables or the mechanisms underlying associations found with available energy (but see Lawton *et al.*, 1987; Fernandes & Price, 1988; Fleishman *et al.*, 1998, 2000; Lees *et al.*, 1999; Blanche & Ludwig, 2001; Buse *et al.*, 2001; Sanders, 2002; Brehm *et al.*, 2003).

In this Chapter I therefore investigate variation in ant and tenebrionid beetle species richness across a full altitudinal gradient in the Cederberg of South Africa. Following documentation of the patterns, I test whether ambient energy, productivity, area, the vertical complexity of vegetation or geometric constraints explains species richness variation across the gradient. In addition, I explicitly test predictions of the five mechanisms that might underlie the observed relationships, and discuss the likelihood of the other four given the available information.

MATERIAL AND METHODS

Study site and sampling

This study took place in the Greater Cederberg Biodiversity Corridor, which is a mega-reserve spanning a west-east gradient from coastal lowlands, to Mountain Fynbos and Succulent Karoo. It includes the northernmost extremity of the Cape Floristic Region, with the Cederberg Wilderness Area forming the core (Anonymous, 2004). The study was conducted across an altitudinal transect covering the major vegetation types on both aspects of the Cederberg, encompassing the full range of vegetation. The transect ranged from sea level at Lambert's Bay, to Sneeukop (1926 m a.s.l.), and down the eastern slopes to Wupperthal (approximately 500 m a.s.l.) (see Chapter 2). A total of seventeen altitudinal bands was sampled at 200 m altitudinal intervals across the transect (see Chapter 2) representing Strandveld Succulent Karoo (one site), Mountain Fynbos (15 sites) and Lowland Succulent Karoo (one site).

Epigaeic ants were sampled during October 2002 and March 2003 (periods of peak insect activity), and tenebrionids during October 2002 and October 2003 (periods of peak

176

beetle activity). A total of forty pitfall traps, divided into four groups of ten pitfalls each, was placed at each site during each sampling event. The four groups of pitfall traps were placed in such a way that they were at least 300 m apart. The disturbance caused by placing the pitfall traps was minimized and the vegetation around the traps was not cleared. The "digging-in" effect (Greenslade, 1973) was thus considered negligible and the traps were set immediately. The traps contained 50 ml of a 50 % propylene glycol solution as preservative and were left open for a period of five days per sampling event. The samples were washed and placed in 70 % ethanol in the laboratory. All tenebrionid beetles were pinned and a representative sample of the ants was mounted on cardboard triangles. All specimens were identified to species level where possible or assigned to morphospecies. Voucher specimens of each ant and beetle species collected are held at the University of Stellenbosch and will be placed in the Iziko Museums of Cape Town.

Predictor variables

Two Thermocron iButtons (Semiconductor Corporation, Dallas/Maxim, Model DS 1920) were buried 10 mm beneath the soil surface at each sampling site in an area where vegetation cover was low to ensure minimum shade cover to measure soil temperature. The iButtons were set to record temperature at one-hour intervals. Data collected from June 2002 to October 2003 were used to calculate mean temperature for each altitudinal band across the 16-month period. A mean temperature was calculated for each month and a mean annual temperature was then calculated using these 16 mean monthly temperatures. The coefficient of variation (CV) of the mean temperature for each altitudinal band was calculated using the mean monthly temperatures.

The normalized difference vegetation index (NDVI) of each sampling grid (30 x 30 m resolution) was obtained from the Satellite Application Centre of the CSIR (Council for Scientific and Industrial Research) in Pretoria (South Africa). NDVI is a measure of greenness and is calculated from the reflected red and near infrared portions of the electromagnetic spectrum. NDVI is correlated with net primary productivity (Paruelo *et al.*, 1997) and precipitation (Nicholson *et al.*, 1990; Paruelo *et al.*, 1993; Potdar *et al.*, 1993; Paruelo & Lauenroth, 1995; Kerr & Ostrovsky, 2003). Monthly NDVI values were obtained for a five-year period (January 2000 – December 2004). For each sampling grid the mean NDVI was calculated for each month across the five years and then a mean NDVI was calculated across the twelve monthly values for each of the grids. The coefficient of variation

(CV) of the mean NDVI was also calculated for each grid across the twelve monthly NDVI values and used as a measure of the variability of NDVI.

Because of the influence that available area (Rosenzweig, 1995) and habitat complexity (MacArthur, 1972) has on species richness patterns these two variables were included in the model building procedures (see Data analysis). The vertical complexity of the vegetation was used as a measure of overall habitat complexity. Details on data collection for these two variables are provided in Chapter 2.

Data analysis

Sample-based rarefaction curves for the tenebrionids and ants (reported in Chapter 2) were compiled for each of the sites to determine the degree of sampling representivity (EstimateS V5, R.K. Colwell, 1997, http://viceroy.eeb.uconn.edu/estimates, see also Gotelli & Colwell, 2001). The non-parametric incidence-based second order jacknife richness estimator provided by EstimateS was used as an estimate of species richness (Colwell & Coddington, 1994). This estimate has been shown to be a reliable estimator of richness (Colwell & Coddington, 1994; Brose *et al.*, 2003; Brose & Martinez, 2004) and it removes the influence of the sampling effect by taking the number of species that are collected in a single and in two samples into account (Colwell & Coddington, 1994).

Geometric constraints models

Two geometric constraint models (or mid-domain null models) were used to test how well the observed data (jacknife 2 estimate) fit predicted distributions. These models were generated using Visual Basic 2000. Model A is equivalent to model 2 of Colwell and Hurtt (1994) and the binomial model of Willig and Lyons (1998). The model randomly generates an altitudinal range and -midpoint combination for each species from all of the possible ranges and midpoints within the domain. Any combination of an altitudinal range and –midpoint was allowed as long as the whole range was included within the boundaries of the transect (sea level on the western slope and 500 m a.s.l. on the eastern slope). This model makes no assumptions about the real range sizes of the ants and beetles except for the constraint of boundaries and is therefore a true null model (Koleff & Gaston, 2001; but see also discussion in Colwell *et al.*, 2004, 2005; Zapata *et al.*, 2003, 2005).

Model B used the altitudinal range of each species (determined for the test of Rapoport's rule in Chapter 4) and the midpoint of that range to calculate predicted values of species richness within the hard boundaries. Model B is equivalent to model D of Koleff and

Gaston (2001) and the model of Lees *et al.* (1999). First, the altitudinal range for each species was selected at random without replacement from the observed range size frequency distribution, and then the altitudinal midpoint was chosen at random with replacement from all possible midpoints for that range size (see Colwell & Lees, 2000 Box 3). This model makes explicit assumptions about the maximum range of the species because it takes the empirical ranges into account. The two models were iterated 1000 times each, separately for the ants and tenebrionids. After each iteration the predicted species richness at each altitudinal band was calculated as the number of predicted altitudinal ranges overlapping in the altitudinal band. Mean species richness (and standard error of the mean) was then calculated for each altitudinal band after the 1000 model iterations.

Generalized linear models assuming a Poisson error distribution with a log link function (Type III model corrected for over-dispersion) (Dobson, 2002) were used to determine the relationship between the second order jacknife estimates (hereafter species richness) of ants and tenebrionids and the predicted species richness from the two mid-domain models. The species richness per altitudinal band was used for the analyses because the mid-domain models can only predict species richness for each altitudinal band and not for each grid in a band.

Species richness predictors

To determine whether ambient energy (mean and CV of temperature), productivity (mean and CV of NDVI), area or habitat heterogeneity best predicted the species richness per sampling grid of ants and tenebrionids across the altitudinal gradient, generalized linear models (Poisson error distribution with a log link function, Type III model corrected for over-dispersion) (Dobson, 2002) were used. Spatial autocorrelation (the degree to which two neighbouring samples are more similar (positively autocorrelated) or more dissimilar (negatively autocorrelated) to each other than expected, Legendre 1993; Legendre & Legendre, 1998) violates the assumption of independence between samples of most statistical tests (Legendre, 1993). Spatial non-independence also affects the results and interpretation of the observed patterns (Lobo *et al.*, 2002; van Rensburg *et al.*, 2002). Therefore, the spatial component of the variation in species richness and abundance was modelled using a third-order polynomial that extracts linear and more complex spatial features (e.g. patches and gaps) from the data: $f(x, y) = b_0 + b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$, where x and y are longitude and latitude respectively (Borcard *et al.*, 1992; Legendre, 1993). The spatial models that best explained the variation in species richness were selected

179

using the Akaike Information Criterion (AIC). However, it is not sufficient to select only one model based on the smallest AIC value because other models might have AIC values close to that of the best model, which contributes to model uncertainty (Westphal *et al.*, 2003). Therefore, Akaike weights (w_i) were used as an indicator of the strength of evidence for a particular model (Burnham & Anderson, 2002; Johnson & Omland, 2004). The Akaike weight of a model is the probability that that particular model is the best in the set of models being considered (Burnham & Anderson, 2002). A set of plausible models should be selected by including only models with $w_i \geq 0.1$ (Burnham & Anderson, 2002; Westphal *et al.*, 2003). The best-fit spatial terms selected by the AIC and Akaike weights were then included with the environmental terms in the final model. Quadratic terms for mean temperature, temperature CV, mean yearly NDVI and NDVI CV were included in the model selection to account for non-linear relationships between these predictors and species richness. In all cases the independent variables were checked for normality. No transformations to normalize the data were required.

Tests of the mechanisms

Because energy variables were typically identified as predictors of species richness, five of the nine mechanisms reviewed by Evans *et al.* (2005a) were tested explicitly. These are the sampling, increased population size (or more individuals hypothesis), niche position, niche breadth and more trophic levels mechanisms. The sampling and increased population size mechanisms make the predictions that abundance is positively related to productivity and that species richness has a positive decelerating relationship with abundance and with energy (power function with an exponent smaller than 1, or a significant quadratic term in the relationship) (Kaspari *et al.*, 2003; Evans *et al.*, 2005a). However, the increased population size mechanism can be distinguished from the sampling mechanism by the fact that in the former case these relationships should hold after the effects of sampling have been removed (e.g. by using the jacknife 2 estimator) (Kaspari *et al.*, 2003; Evans *et al.*, 2005a). To test these predictions, the relationships between species richness (jacknife 2) and abundance, and between abundance and the predictor variables (mean temperature, temperature CV, NDVI, NDVI CV, and their quadratic terms, and area and vegetation complexity) were investigated using Generalized linear models (assuming a Poisson error distribution with a log link function, Type III model corrected for over-dispersion). Abundance was $\log_{10}$-transformed before determining its relationship with the jacknife 2 estimate. This was done to create a power function between species richness and abundance and therefore to test the prediction

that the slope should be smaller than 1 (Kaspari *et al.*, 2003). The AIC and Akaike weights were used to determine the best-fit models of the predictor variables (Burnham & Anderson, 2002; Westphal *et al.*, 2003).

The niche position mechanism makes the same predictions as the increased population size mechanism (i.e. a positive, decelerating relationship between richness and abundance and positive relationship between abundance and productivity, see Kaspari *et al.*, 2003; Evans *et al.*, 2005a), but argues that the responses will be much stronger in niche position specialists (Evans *et al.*, 2005a, b). By contrast, the increased population size mechanism states that rare species will show the strongest species-energy relationships (Evans *et al.*, 2005a). To test the niche position mechanism the same procedure was followed as that used to test the increased population size mechanism, but now using the species richness and abundance per sampling grid of the 25% most abundant and 25% least abundant species across the transect. If the 25% least abundant species show the strongest species-energy relationships, then the predictions of the increased population size mechanism would be satisfied (Evans *et al.*, 2005a). In addition, the inclusion of habitat heterogeneity as a potential predictor of species richness provided an additional way of examining this mechanism. If increases in resource diversity promote viability of niche position specialists and lead to increasing habitat heterogeneity, then a positive relationship between habitat heterogeneity and richness could be taken as circumstantial evidence in favour of this mechanism (Evans *et al.*, 2005a).

The more trophic levels hypothesis predicts a positive relationship between the number of trophic levels and the available productive energy in an area. Whilst the only diagnostic test of the mechanism is an assessment of the relationship between number of trophic levels and energy availability, it does also make the prediction that nested species distribution patterns will be found. To test the latter prediction the nestedness of the ant and beetle assemblages across the altitudinal gradient was determined (separately) by using a new metric proposed by Greve *et al.* (2005). This metric, *d1*, is a modification of Brualdi and Sanderson's (1999) discrepancy metric (see Greve *et al.*, 2005 for discussion) and has a value of between zero (perfectly nested) and one (no nestedness) (Greve *et al.*, 2005). The value found for each of the matrices was tested for its significance using a resampling protocol.

The niche breadth mechanism predicts narrower niche breadths in high energy areas, and a reduction in interspecific competition in these areas, so promoting the coexistence of more species than in low energy areas. The underlying assumptions of the mechanism are problematic in several ways (see Evans *et al.*, 2005a). However, assuming that the problems are not insurmountable, the prediction can be made that in ants, for which interspecific

competition is a hallmark (Hölldobler & Wilson, 1990) typically resulting in a unimodal dominance-richness relationship (Parr *et al.*, 2005), increasing energy availability should lead to a shallower descending part of the dominance-richness curve. It is the declining portion of the dominance-richness curve that is thought to be the consequence of interspecific competition (Parr *et al.*, 2005). The same prediction can be made for the consumer pressure mechanism, which is also based on changes in the extent of interspecific competition. To test this prediction, quantile regression (Scharf *et al.*, 1998; Parr *et al.*, 2005) was used to determine the relationship between species richness and the abundance of the 25% most abundant ants (see Parr *et al.*, 2005 for justification), in each sampling grid using the data collected per pitfall trap. The effect of energy availability (mean NDVI and mean temperature, respectively) on the coefficient of the quadratic term of the relationship was then examined using generalized linear models (assuming a Normal error distribution with a identity link function), with the expectation that the relationship should be negative if either of these mechanisms is operational. These analyses were not applied to the tenebrionid data because no relationship between the abundance of the dominant species and species richness has been found in this group.

RESULTS

A total of 81 ant species and 33 tenebrionid species was collected during the sampling periods (Appendix A and D). Sample-based species rarefaction curves approximated asymptotes for the two sampling periods indicating that most of the ant and tenebrionid species at the different sites were collected (see Fig. 3 in Chapter 2 and Fig. 1).

Both mid-domain models (Model A and Model B) predicted a smooth parabolic curve and a peak in species richness at the highest altitudes sampled. Ant richness showed no clear altitudinal trend (Fig. 2a) and richness (i.e. the jacknife 2 estimate thereof) was not related to predicted species richness (Jacknife 2 vs. Mid-domain model A: $\chi^2_{(15)} = 0.857$, P = 0.355; Jacknife 2 vs. Mid-domain model B: $\chi^2_{(15)} = 0.944$, P = 0.331). By contrast, tenebrionids had high species richness on the western slopes compared to the eastern slopes and showed a decrease in species richness with altitude on the western slopes (Fig. 2b). The jacknife 2 estimate of species richness for the tenebrionids was not related to richness predicted by Mid-domain model A ($\chi^2_{(15)} = 0.217$, P = 0.641) nor to richness predicted by Mid-domain model B ($\chi^2_{(15)} = 0.376$, P = 0.540).

None of the best-fit models for species richness had Akaike weights of 0.1 or higher. Therefore, the best-fit model with the highest Akaike weight for species richness of the ants

Figure 1 (a, b)

183

c)
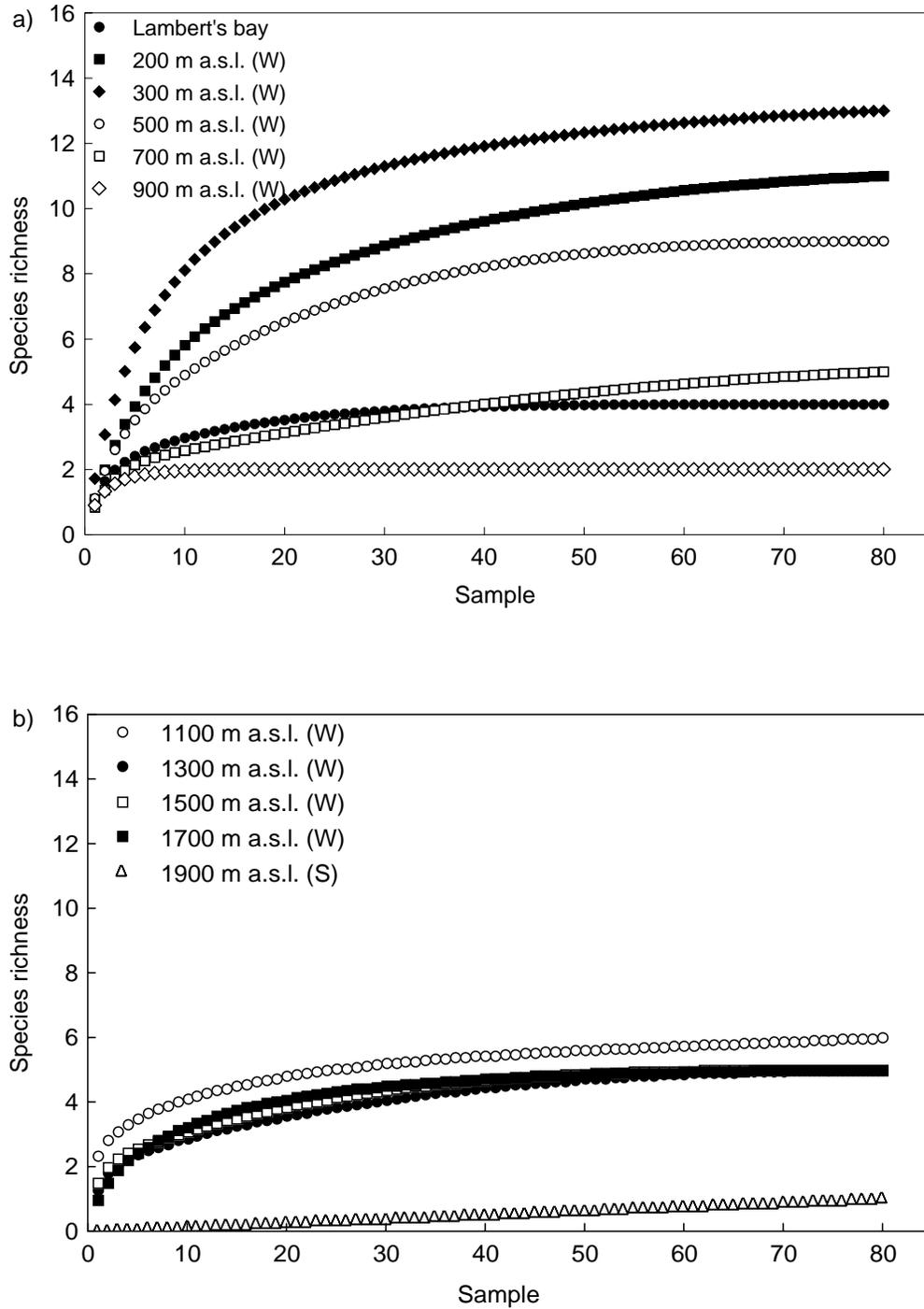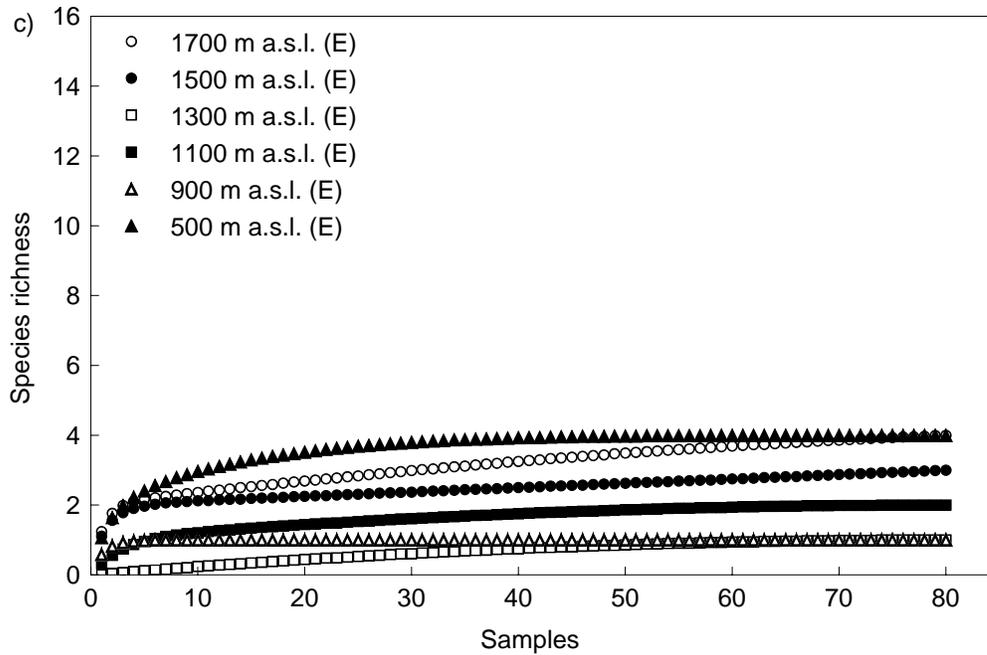
Figure 1 Sample-based species rarefaction curves of tenebrionid assemblages of a) sea level to 900 m above sea level on the western slope, b) 1100 – 1900 m above sea level on the western slope (W) and c) 1700 – 500 m above sea level on the eastern slope (E).
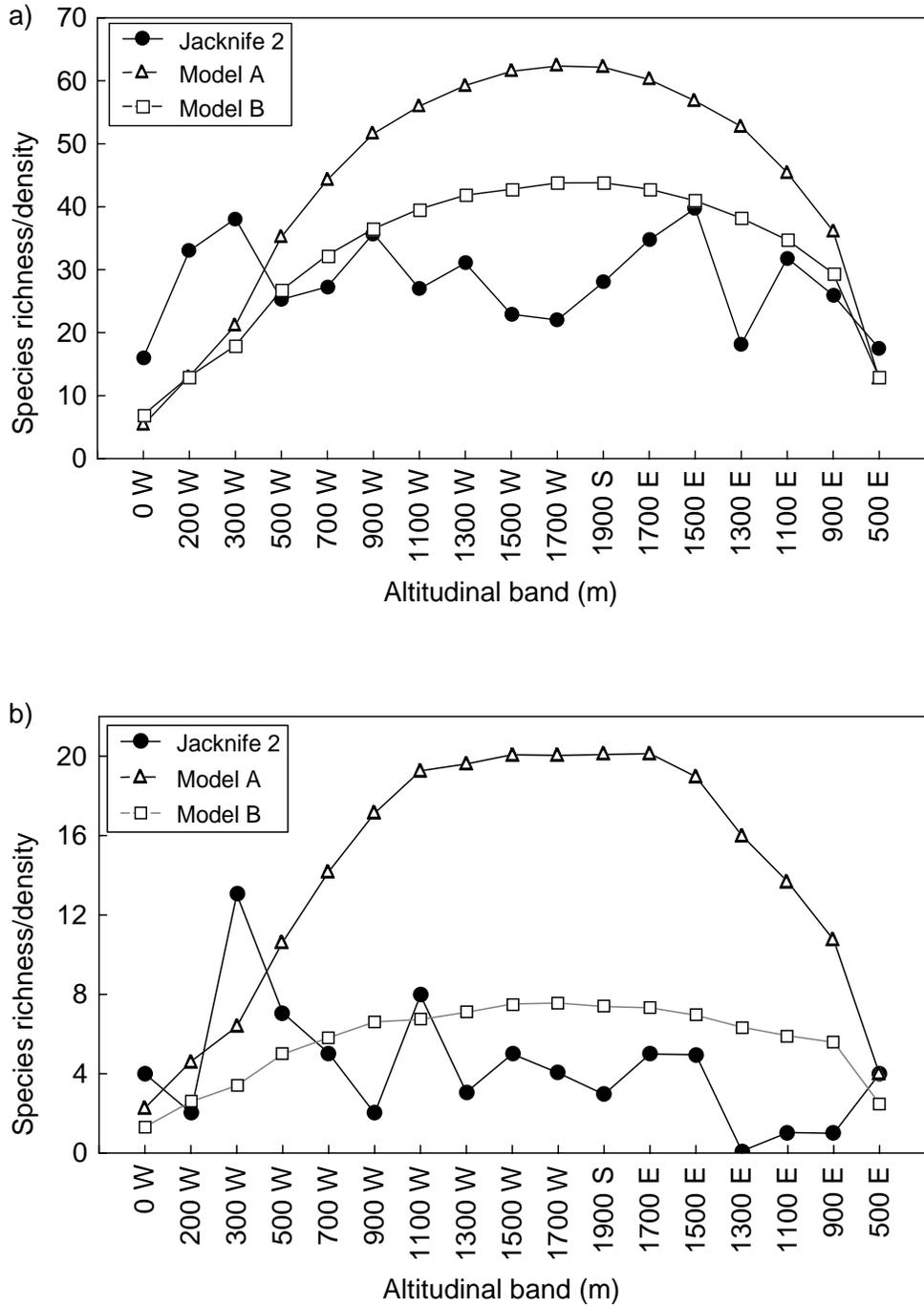
Figure 2 Observed and predicted mean species richness in each altitudinal band of a) ants and b) tenebrionids. Standard errors of the predicted values are not shown because they are close to the mean values. Jacknife 2 = non-parametric incidence-based second order jacknife richness estimator provided by EstimateS (Colwell, 1997). W = western slope, E = eastern slope, S = summit.

and tenebrionids is reported in Table 1. NDVI and its quadratic term were significant predictors of ant species richness indicating a unimodal relationship between energy availability and richness (Table 1). The coefficient of variation of NDVI and vegetation complexity also entered the best-fit model for ant species richness, but were not significant (Table 1). The species richness of tenebrionids was significantly related to available area in the altitudinal bands (Table 1). The coefficient of variation of mean temperature and its quadratic term entered the best-fit model, but were not significant (Table 1). For both groups, several spatial variables were highly significant and retained in the best fit model, indicating significant spatial structuring. The positive relationships between tenebrionid richness, and area and several longitudinal terms (y in this case), and the lack of significance of the energy variables is noteworthy. For both taxa, approximately half of the variation in richness was explained by the selected terms in the best-fit models (Table 1).

Ant species richness showed a significant positive, decelerating relationship with abundance ($\chi^2 = 5.838$, P = 0.016, $R^2 = 8.13$, scaled deviance = 66.20, df = 66, estimate = +0.202 ± 0.084). In addition, the relationship between ant abundance and productivity (NDVI and $NDVI^2$) was unimodal, and ant abundance was also positively related to vegetation complexity (Table 1). No relationship was found between ant species richness and abundance of the 25% most abundant species ($\chi^2_{(66)} = 0.477$, P = 0.490) or between ant species richness and abundance of the 25% least abundant ant species ($\chi^2_{(66)} = 0.006$, P = 0.936). The species richness per sampling grid of the 25% most abundant species had a positive relationship with vegetation complexity, while the species richness of the 25% least abundant species had a unimodal relationship with the coefficient of variation of temperature (Table 1) The abundance of the 25% most abundant ant species had a positive, hump shaped relationship with productivity (NDVI and $NDVI^2$) and a positive relationship with vegetation complexity (Table 1), but no significant models were selected that explained the variability in the abundance of the 25% least abundant ant species (Table 1). Ant assemblages did not have a nested distribution (*d1* = 0.388, P = 0.324). In addition, the quadratic term of the dominance-richness relationships had unimodal relationships with both temperature (temperature: $\chi^2 = 6.577$, P = 0.010, estimate = +0.018 ± 0.007; $temperature^2$: $\chi^2 = 4.876$, P = 0.027, estimate = -0.0004 ± 0.0002, $R^2 = 20.48$, = 68, df = 65,) and productivity (NDVI: $\chi^2 = 7.155$, P = 0.007, estimate = +0.660 ± 0.240; $NDVI^2$: $\chi^2 = 5.862$, P = 0.015, estimate = -0.879 ± 0.355, $R^2 = 13.25$, scaled deviance = 68, df = 65). Therefore, the niche breadth and consumer pressure

Table 1 Generalized linear model (Poisson error distribution, log link function) outcomes for the relationships between environmental predictors and spatial terms on species richness (incidence-based second order jacknife estimate) and abundance of ant and tenebrionid assemblages across the altitudinal transect. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.01$. %Expl = Percentage deviance explained, w_i = Akaike weight.

Model type	Df	Dev/Df	Predictor	Estimate ± S.E.	AIC	w_i	%Expl
Ants:							
Species richness (jacknife 2 estimate)	60	1.07	NDVI	+12.16 ± 3.89**	201.09	0.025	45.08
			NDVI^2	-16.5 ± 5.62**			
			NDVI CV	+1.36 ± 0.83			
			Vegetation complexity	-0.02 ± 0.01			
			x	-2.28 ± 0.47***			
			x^3	+13.03 ± 2.33***			
			xy	+26.79 ± 5.36***			
Richness: 25% most abundant species	66	1.07	Vegetation complexity	+0.075 ± 0.034*	134.110	0.027	5.89
Richness: 25% least abundant species	62	1.00	Temperature CV	+0.112 ± 0.025***	202.50	0.013	62.00
			Temperature CV^2	-0.001 ± 0.0002***			
			x	-2.719 ± 0.376***			
			x^3	+9.411 ± 1.266***			
			y^2	49.760 ± 8.576***			

Table 1 (continued)

Model type	Df	Dev/Df	Predictor	Estimate ± S.E.	AIC	w_i	%Expl
Total abundance	61	0.80	NDVI	+27.80 ± 0.49*	35534.00	0.924	48.64
			$NDVI^2$	-40.63 ± 0.73*			
			Vegetation complexity	+11.53 ± 0.001***			
			y	-4.11 ± 0.13			
			x^3	-1.37 ± 0.13			
			y^2	-4.09 ± 1.50			
Abundance: 25% most abundant species	61	0.79	NDVI	+20.90 ± 0.54*	33035.00	1.00	51.22
			$NDVI^2$	-30.73 ± 0.79*			
			Vegetation complexity	+0.084 ± 0.001***			
			x	-3.23 ± 0.06*			
			x^3	+7.72 ± 0.22			
			y^2	+53.16 ± 1.66			
Abundance: 25% least abundant species			No significant models				

Table 1 (continued)

Model type	Df	Dev/Df	Predictor	Estimate ± S.E.	AIC	w_i	%Expl
Tenebrionids							
Species richness (jacknife 2 estimate)	58	1.07	Area	+0.001 ± 0.000***	227.15	0.082	51.00
			Temperature CV	+0.16 ± 0.12			
			Temperature CV^2	+0.001 ± 0.001			
			y	+33.53 ± 11.02***			
			x^3	+228.76 ± 60.08***			
			y^2	-1124.30 ± 284.97***			
			xy	+251.19 ± 75.80***			
			x^{2}y	-2380.29 ± 633.88***			
			xy^2	5892.90 ± 1556.5***			
Richness: 25% most abundant species	60	1.00	Temperature CV	+0.239 ± 0.078**	198.585	0.033	56.53
			Temperature CV^2	-0.002 ± 0.0008**			
			y	+11.465 ± 1.937***			
			x	-11.981 ± 1.900***			
			x^2	+73.263 ± 10.880***			
			x^3	+254.796 ± 37.927***			
			x^{2}y	-632.098 ± 95.276***			
Richness: 25% least abundant species	66	1.00	x	-3.236 ± 0.501***	54.767	0.019	36.60

Table 1 (continued)

Model type	Df	Dev/Df	Predictor	Estimate ± S.E.	AIC	w_i	%Expl
Total abundance	60	1.06	Area	$+2.53 \times 10^{-4} \pm 6.52 \times 10^{-5}$***	2326.20	0.998	63.35
			Temperature CV	$+0.29 \pm 0.03$*			
			Temperature CV^2	$-3.00 \times 10^{-3} \pm 2.54 \times 10^{-4}$*			
			x^3	$+41.33 \pm 1.92$***			
			xy	$+81.69 \pm 2.76$***			
			x^2y	-213.40 ± 15.69*			
			xy^2	$+591.30 \pm 42.35$*			
Abundance: 25% most abundant species	61	1.08	Temperature CV	$+0.29 \pm 0.03$*	2302.30	1.000	64.44
			Temperature CV^2	$-0.003 \pm 2.56 \times 10^{-4}$*			
			x^3	$+47.17 \pm 2.25$***			
			xy	$+81.75 \pm 2.87$***			
			x^2y	-266.70 ± 15.93**			
			xy^2	698.50 ± 41.80**			
Abundance: 25% least abundant species	65	0.45	Area	$+0.001 \pm 0.0003$***	56.85	0.849	43.12
			Vegetation complexity	$+0.16 \pm 0.07$*			

 mechanisms were not operational because the relationship between the coefficient of the quadratic term of the dominance-richness relationship and energy availability was not negative.

Because tenebrionid species richness was not significantly related to any of the energy variables, no further tests of potential mechanisms were undertaken. Nonetheless, weak relationships between area and coefficient of variation of temperature and abundance were found (Table 1). Moreover, the tenebrionid assemblages were significantly nested ($d1 = 0.427, P = 0.038$).

DISCUSSION

Ant species richness did not vary consistently across this 1926 m altitudinal gradient, and tenebrionid species richness peaked at a low western elevation (300 m) and then declined up the western side of the gradient and continued to decline down the eastern side. In consequence, the present findings differ from the conventional monotonically declining (e.g. Ichijo *et al.*, 1982; Wolda, 1987) or unimodal (e.g. Lees *et al.*, 1999; McCoy, 1990; Rahbek, 1995) richness patterns obtained for a variety of insect taxa. In addition, the results found here for ants are in stark contrast to what has been documented for ants elsewhere. For example, a peak in species richness at mid-altitudes was found for ants in Panama (Olson, 1994), Madagascar (Fisher, 1998, 1999), the Philippines (Samson *et al.*, 1997) and in North America (Sanders, 2002), whilst ant species richness in Malaysia decreased exponentially with altitude (Brühl *et al.*, 1999; see also Fisher, 1996; Robertson, 2002). The difference between the present findings for ants and the results of previous studies are likely a consequence of the specific nature of this altitudinal gradient. Change in vegetation type across the gradient is not dramatic (Campbel, 1985), and there is a west-east gradient in productivity that shows complex spatial structure. Nonetheless, as I show below, ant richness is strongly related to energy availability.

The decline in richness of tenebrionids with altitude seems to be similar to several other studies that have demonstrated declines in insect species richness with altitude (e.g. Wolda, 1987; McCoy, 1990; Rahbek, 1995; Lees *et al.*, 1999). However, the decline in tenebrionid richness here persisted down the eastern side of the gradient, suggesting that the mechanisms underlying richness variation might be quite different to those proposed in other studies. The strong influence of the longitudinal spatial variables, and the significantly nested assemblages indicate that there is simply a decline in richness away from the western side of the transect, which is not associated with energy availability and only weakly so with area.

Indeed, what appears to be the case is that the sampling simply detected the increase in distance towards the east of a centre of tenebrionid richness and endemism in the south-west. This finding is in keeping with what is known of the group (see Chapter 3). Of course, it might reasonably be expected that some present mechanism is allowing retention of high richness to the west, and it may well be the long-term presence of predictable fog (Nicolson, 1990). This would enable western tenebrionids to take advantage of accumulated detritus in the area, but would not have been detected in this study because no data on fog are available.

In terms of the mechanisms underlying variation in richness across the gradient, it is clear that mid-domain models were unimportant in both groups. Several recent studies have argued that geometric constraints models are the most appropriate null models for species richness gradients (Colwell & Lees, 2000; Jetz & Rahbek, 2001) and that they are a contributing cause of these gradients (Willig & Lyons, 1998; Colwell & Lees, 2000). It has therefore been suggested that they should form the first step in any analysis of species richness variation across space, and their output should be included as covariates in any model seeking to explain variation in species richness on the grounds of other variables (Colwell *et al*., 2004, 2005; Jetz *et al*., 2004). However, several other authors have argued that mid-domain models make inappropriate assumptions and are typically weakly supported (e.g. Hawkins & Diniz-Filho, 2002; Zapata *et al*., 2003). Controversy over the importance of these models and the need to include them in analyses has subsequently been vigorous (Colwell *et al*., 2004, 2005; Pimm & Brown, 2004; Hawkins *et al*., 2005; Zapata *et al*., 2005). In this study, mid-domain models were tested and neither the most liberal nor the most conservative of the models explained any of the species richness variation in either of the groups. In consequence, the models were not considered any further. In the case of the ants, this finding is different to what Sanders (2002) found for altitudinal species richness variation of ants in three western US states (Colorado, Nevada and Utah). In two of the states (Colorado and Utah) available area explained a greater proportion of variation in ant species richness than geometric constraints. However, the two variables together explained a large proportion of the variation in two of the states (90 % in Colorado and 99 % in Nevada), and more than half of the variability in the other (57 % in Utah).

Ant species diversity (richness and abundance) had a unimodal relationship with productivity. This is in keeping with the species-energy theory (Wylie & Currie, 1993; Rosenzweig, 1995; Hawkins *et al*., 2003; Evans *et al*., 2005a). The shape of the relationship is not surprising given that richness-productivity relationships are often unimodal at relatively small spatial scales (Abramsky & Rosenzweig, 1984; Rosenzweig, 1995; Ritchie & Olff,

192

1999; Waide *et al.*, 1999; Dodson *et al.*, 2000; Mittelbach *et al.*, 2001; Chase & Leibold, 2002). Similarly, Kaspari *et al.* (2000) demonstrated a positive, decelerating relationship between ant richness and net aboveground productivity along a productivity gradient ranging from desert to rain forest (see also Kaspari *et al.*, 2004). Botes *et al.* (in press/Chapter 2) argued that variation in precipitation might also have a substantial influence on variation in ant species richness. The measure for productivity used in the present study, NDVI, is strongly related to precipitation (see Nicholson *et al.*, 1990; Paruelo *et al.*, 1993; Potdar *et al.*, 1993; Paruelo & Lauenroth, 1995; van Rensburg et al. 2002). Therefore, the present results support Botes *et al.*'s (in press/Chapter 2) contention that water availability influences ant diversity patterns across the altitudinal transect. Hawkins *et al.* (2003) argued that water-energy relationships strongly influences animal and plant distributions and that water availability is much more likely to be a strong correlate of richness than is absolute energy availability in water-limited systems (see also Linder, 1991; O'Brien *et al.*, 2000; Hawkins *et al.*, 2003), such as those of the south-western Cape (Deacon *et al.*, 1992). That NDVI includes a measure of the effects of both ambient energy and water availability on productivity might explain why in this analysis a relationship was found between ant richness and NDVI and not between richness and temperature in this study, even though it has previously been shown that there is a strong relationship between ant richness and temperature across this transect (Chapter 2).

Because tenebrionid richness was not related to energy availability, at least not the measures used here, they are excluded from further discussion, which therefore solely concerns the ants. Of the nine mechanisms that are thought to underlie the relationship between richness and productivity (Evans *et al.*, 2005a), five were tested directly, and information from the study made it possible to comment on another three of them. The final mechanism, diversification rate, seems unlikely to be of great importance at this spatial scale, and was not directly tested. The absence of a significant temperature effect on richness suggests that it is not a significant mechanism (see Allen *et al.*, 2002; Kaspari *et al.*, 2003), and it is typically also not thought to be important in accounting for high richness of the Cape flora (Linder, 2001, 2003).

Because the positive relationships between productivity and richness, and between abundance and richness, remained despite the use of the jacknife 2 estimator, the sampling mechanism can be discounted (Kaspari *et al.*, 2003). The ant assemblages were not nested either, and therefore the range limitation mechanism can be rejected, although data on the environmental tolerances of each of the species would have made a test of this hypothesis

more straightforward. It was not possible to test the dynamic equilibrium and more trophic levels directly, because their unique predictions (see Evans *et al.*, 2005a – Table 3) could not be evaluated. However, both mechanisms predict that assemblages should be nested under some circumstances. The absence of nestedness provides circumstantial evidence that the mechanisms might not be of significance. Moreover, the more trophic levels mechanism does not predict positive decelerating relationships between abundance and productivity for the most abundant species only, as was the case here. A further, important prediction of the dynamic equilibrium mechanism is that disturbance should have differential relationships on abundances in high and low energy areas. In Fynbos, one of the most significant disturbances is fire (see Cowling, 1992 for a discussion of fire in Fynbos systems). However, fire never explained variation in diversity in the ant assemblages investigated here (see Chapter 2). Indeed, it seems likely that ants are highly resilient to fire in many southern African systems (Parr *et al.*, 2004). In addition, Donnelly and Giliomee (1985) showed that, even though ant diversity (species number and evenness) of ants was higher in a newly burnt plot in Fynbos compared to that of 39-year-old vegetation, ant species composition was not markedly affected by fire.

The niche breadth and consumer pressure mechanisms both predict that in high energy areas interspecific competition should be less significant than in low energy areas, but for different reasons (Evans *et al.*, 2005a). Interspecific competition is thought to be extremely important as a mechanism structuring ant assemblages (Savolainen & Vepsäläinen, 1988; Hölldobler & Wilson, 1990; Andersen & Patel, 1994; Majer *et al.*, 1994; Sanders *et al.*, 2003). Moreover, although other factors can be important, it is thought that this competition is a major cause of the declining part of the unimodal relationship between abundance of the dominant ants in an assemblage and species richness (Andersen, 1992; Parr *et al.*, 2005). Therefore, it might be expected that if the niche breadth and consumer mechanisms were important for generating the relationship between productivity and richness in the current study, a negative relationship between energy and the strength of the quadratic term in the upper quantile of the relationship between abundance of the dominant ants and richness would be found. No such relationship was documented, and therefore both mechanisms were rejected.

Of the nine mechanisms likely accounting for the relationship between richness and energy availability, only two therefore remain. Both the increased population size (more individuals) and niche position mechanisms predict positive decelerating relationships between productivity and richness and between abundance and richness, and a positive

194

relationship between productivity and abundance. However, the former predicts that the relationship should be strongest in rare species, whilst the latter also posits a relationship between richness and habitat heterogeneity (Evans *et al.*, 2005a). Here, it was not possible to fully reject either mechanism. Rare species did not show a stronger relationship between abundance and richness, productivity and richness, and productivity and abundance, than the 25% most abundant species. Rather, the converse was true. However, species richness was not related to habitat heterogeneity, suggesting that patterns could not be fully accounted for by the niche position hypothesis. In addition, it cannot simply be assumed that the most abundant species are high niche position species (see Gregory & Gaston, 2000; Gaston, 2003; Evans *et al.*, 2005b for a discussion of niche position) because some circularity is necessarily introduced into the argument. Therefore, at this point it seems safest to assume, in the absence of other data, that both the increased population size and niche position mechanisms are responsible for the relationships between productive energy and species richness found here.

The increased population size mechanism is also thought to be responsible for productivity-richness relationships in ants (Kaspari *et al*., 2003) and birds (Hurlbert, 2004; Pautasso & Gaston, 2005). In both cases other mechanisms are also likely to be responsible for the positive relationships between energy availability and richness (e.g. habitat heterogeneity in birds and diversification rates in ants) (Hurlbert & Haskell, 2003; Kaspari *et al.*, 2003; Hurlbert, 2004; Kaspari, 2005). Moreover, the increased population size mechanism is not universally supported for birds (see e.g. Currie *et al.*, 2004; Evans *et al*., 2005b), and is certainly not thought to be important in treehole communities at fine spatial scales (Srivastava & Lawton, 1998).

In conclusion, this study has demonstrated that different processes structure ant and tenebrionid assemblages across the same altitudinal transect. Historical factors appear to be more important for the tenebrionid beetles than the ants, whereas the converse is true for contemporary energy variables. Thus, this study provides further support for the idea that both historical and current factors are likely to influence species richness gradients (see also Ricklefs, 2004), and that deconstructing species richness patterns by taxon can provide considerable insight into the mechanisms underlying them (see Marquet *et al*., 2004).

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196

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"Life is about diversity, heterogeneity, and novelty. The understanding of how these properties interact, emerge, are maintained, and eventually destroyed is at the core of the research programs of biogeography, ecology, and evolution."   - Marquet *et al.* (2004)

I have now examined the patterns in species diversity and range sizes of two ecologically important taxa across a full altitudinal transect and the patterns found were unusual. Epigaeic ants and tenebrionids in the Cederberg did not show the predicted monotonic decline or unimodal richness patterns across altitude typically found in a variety of insect taxa (e.g. Wolda, 1987; Lees *et al.*, 1999; McCoy, 1990; Rahbek, 1995). Patterns in ant diversity here also differed from those found for ants elsewhere (e.g. Olson, 1994; Fisher, 1996, 1998, 1999; Brühl *et al.*, 1999; Sanders, 2002). This study further demonstrated that different processes structure ant and tenebrionid assemblages across the same altitudinal transect. Empirical evidence supported the idea that productivity is an important correlate of ant species richness, so providing further support for species energy theory (see Evans *et al.*, 2005a for review). Moreover, this study also showed that the more individuals hypothesis (increased population size mechanism - Evans *et al.*, 2005a) at least partly underlies the richness-productivity relationship in ants (Kaspari *et al.*, 2003), so providing another study in support of this mechanism (see also Hurlbert, 2004; Pautasso & Gaston, 2005). However, it also seems likely that the niche position mechanism is significant too. Previous studies have failed to find evidence for this mechanism (Evans *et al*. 2005b), although it is theoretically attractive (see also Gaston & Blackburn, 2000). In short, these findings further our knowledge of species-energy relationships in invertebrates across a full altitudinal gradient and provide an explicit investigation of the mechanisms underlying the association found with available energy, while taking confounding variables such as available area and spatial autocorrelation into account.

By contrast, historical factors, and not contemporary energy variables, appear to play a more important role in structuring tenebrionid beetle assemblages. This hypothesis was not tested explicitly because historical influences are difficult to quantify (Fraser & Currie, 1996). Nonetheless, circumstantial evidence was found that such influences might have structured these beetle assemblages. Initially, temperature appeared to be a strong correlate of

207

tenebrionid species density (Chapter 3). However, species density of the tenebrionids declined with elevation and temperature on the western slope of the Cederberg, but not on the eastern slope, suggesting that temperature is not the causal factor because it does not operate similarly on both sides of the mountain range. I therefore argued that there might be collinearity between historical signal and the environmental variables (see also Latham & Ricklefs, 1993; Chown *et al.*, 1998) that structured these assemblages. Indeed, the decline in species density towards the east reflects movement away from an area that constitutes the southern end of a south-west African centre of tenebrionid endemism and diversity (Scholtz & Holm, 1985; Penrith, 1986; Penrith & Endrödy-Younga, 1994). In chapter 5 I showed that the decline in richness towards the east is not associated with energy availability and only weakly with area. In addition, the first three western sites had comparatively high richness and endemism and most of the species belonged to the subfamily Tentyriinae (which is best known for its arid zone diversity in southern Africa, Scholtz & Holm, 1985) (Chapter 3) and twenty-one of the thirty-three species had the midpoints of their distributions within the four lowest altitudinal bands on the western slope (Chapter 4). Furthermore, the vast majority of the species only occurred on the western slope whereas no species were only collected on the eastern slope (Chapter 4).

These results further support the idea that both historical and current factors are likely to influence species richness gradients. Recently, debate about whether regional or local processes are more important in structuring species assemblages has been vigorous (e.g. Currie & Francis, 2004; Qian & Ricklefs, 2004). It is thus crucial to understand how these processes interact (Ricklefs, 1987, 2004; Lawton, 1999; Currie & Francis, 2004). For example, regional processes (e.g. energy/productivity/historical factors) might determine local assemblage structure (e.g. Ricklefs, 1987, 2004; Lawton, 1999) while local factors (e.g. competition, environmental patchiness) may alter assemblages further. One way of approaching this challenge might be to adopt the idea of deconstruction of richness patterns (Marquet *et al.*, 2004). For example, deconstructing species richness patterns by taxon can provide considerable insight into the mechanisms underlying species richness gradients (see Marquet *et al.*, 2004). The principal idea behind such deconstruction is to split species into internally homogenous groups in terms of sharing the same trait (Marquet *et al.*, 2004). Species can be deconstructed in terms of their physiology (e.g. endotherms vs. ectotherms), taxonomy (e.g. vertebrates vs. invertebrates) and ecology (e.g. food web position) (Marquet *et al.*, 2004). Such an approach seems likely to provide substantial insight into why different groups react differently to certain environmental variables when investigating patterns across

208

the same environmental gradients. The more different types of organisms are included in a species group, the more mechanisms are likely to structure the observed patterns (Huston, 1994). In this study, the taxa were considered separately in all analyses and the results indicated that they show different patterns in terms of richness and range sizes across the same altitudinal gradient. Thus, in a way, this study is the first to deconstruct species richness relationships across altitudinal gradients (though see Fleishman *et al.*, 2005 for a novel approach to bioindication applying a similar rationale).

In addition to the differences in species richness and range size patterns between the taxa, differences were also found in the ability of mid-domain models to predict these two variables. The two mid-domain models that were tested in this study explained large proportions of the variance in range sizes (Chapter 4) but were not important in explaining species richness patterns (Chapter 5), particularly for the ants. The opposite result has been found by Koleff and Gaston (2001) who showed that species richness patterns of woodpeckers and parrots in the New World were explained reasonably well by one of the mid-domain models they tested, but the fit between the latitudinal range distributions and predicted patterns by five mid-domain models were particularly poor. Their explanation for these contrasting results were that mid-domain models are either too simplistic or do not adequately explain geographical variation in diversity of the two taxa (Koleff & Gaston, 2001). This study, which included both complete and partial assessments (see Blackburn & Gaston, 1998), indicated that the way in which the boundaries of the three domains were selected might have constrained the ranges of the species to show peaks in the middle of the three different domains (Chapter 4). In consequence there was a good fit between observed and predicted range distributions in all three domains. However, the 'real' range sizes and midpoints of the species did not change, indicating that definition of the domain might constrain the data to fit the model, so making questionable its validity as a 'null model' approach. Moreover, the fact that mid-domain models predicted range size but not species richness across the domain suggests that they cannot explain diversity across the gradient. Therefore, it might be expected that beta-diversity will also be poorly accounted for by the models (Zapata *et al.* 2003, 2005), a next step in the testing and analysis process (see below)

Implications for climate change

A major outcome of this study is its implications for the predicted climate change in the area (Tyson, 1999; Giorgi *et al*., 2001; Midgley *et al*., 2002, 2003). The prediction is that the Western Cape Province (South Africa) will experience a 1.5ºC increase in temperature on the

coast and that low-lying areas will become dryer while mountains will experience slightly higher precipitation (Midgley *et al.*, 2005). More specifically, rainfall will increase during the summer months, while the coastal areas will become dryer and the mountainous inland wetter during June, July and August (Midgley *et al.*, 2005). As stated in the General Introduction of this thesis (Chapter 1), many predictions have been made of how the Cape Floristic Region (CFR) is going to change under future climatic conditions, but few attempts have been made to monitor what is happening. Moreover, these predictions are mainly based on the flora of the region (Midgley *et al.*, 2002, 2003; Thomas *et al.*, 2004; Hannah *et al.*, 2005) and very little work has been conducted on what the possible effects of the predicted changes are going to be on the fauna (Simmons, 1994). One such study has been conducted on the birds in southern Africa and showed that species that are restricted to the CFR (Fynbos and Succulent Karoo) are highly at risk (Simmons, 1994). This was particularly true for three endemic species, namely the Cape Sugarbird, the Orange breasted Sunbird and the Cape Bulbul, which are predicted to lose large portions (20 – 40%) of their distributions by 2050, especially in the northern Cederberg and Namaqualand region (Simmons *et al.*, 2004).

This study forms the basis of a long-term monitoring programme to establish baseline data for two ecologically important taxa (epigaeic ants and tenebrionid beetles) and to monitor the nature and pace of the change in these assemblages as it unfolds. The solid baseline data set that was collected for epigaeic ants and tenebrionids are invaluable as such data sets are often not available (McGeoch, 2002), which means that the effects of climate change on assemblages are difficult to determine. In Chapter 2, I demonstrated that there are likely to be substantial and complex changes to ant assemblages as climates change in the northern CFR. Differences in temperature and vegetation variables across the altitudinal gradient are responsible for the differences between ant assemblages within the main vegetation types and biomes across the altitudinal gradient (Chapter 2), while the ant species richness pattern across the whole gradient is structured by productivity (Chapter 5). Therefore, if the Western Cape is going to warm due to climate change as predicted, the observed patterns in the ant assemblages are likely to change. In Chapter two I showed that it is highly probable that higher altitude assemblages such as those typical of Alpine and Ericaceous Fynbos will give way to those more characteristics of Proteoid and Restioid Fynbos, and ultimately Succulent Karoo. Thus, the species that are most at risk are those that are restricted to specific habitat types or altitudes, especially those at high altitude (see also Haslett, 1997; Fleishman *et al.*, 1998, 2000; Hill *et al.*, 2002). Moreover, the importance of ants for ecosystem functioning in both Fynbos and Succulent Karoo systems (e.g. Johnson,

1992; Le Maitre & Midgley, 1992; Milton *et al*., 1992) suggests that there will be severe ramifications of changes in ant assemblages because the latter might also precipitate vegetation changes. The changes that are predicted to take place in the next 50 years in the CFR could be substantially exacerbated by such synergistic effects, which have major implications for long-term conservation plans.

However, the results of Chapter 3 suggest that caution should be exercised when interpreting environmental correlates of species richness because they might reflect collinear historical processes, rather than a causal relationship between contemporary environmental variables and species density (see also Jetz *et al.*, 2004). If history is causal, which might be the case in the tenebrionids, then the results of climatic modelling may not accurately reflect the outcome of climate change. Therefore, I am cautious of making any explicit predictions of the effect that predicted climatic changes might have on the tenebrionid assemblages.

Future research

The relationship between tourist and resident species was not investigated in this study. According to Gaston *et al.* (1993) tourists may increase the number of rare species sampled in a given area. However, little attention has been given to tourist species in investigations of species diversity patterns. It has been shown that tourist species do not significantly influence abundance-body size relationships (Gaston *et al.*, 1993; Blackburn & Gaston, 1997, but see Chown & Steenkamp, 1996) because these species are a minor component of species assemblages (Blackburn & Gaston, 1997). Nonetheless, a large number of the ant and tenebrionid beetle species were collected in low abundances (see Appendix A and D) and because most of the ant species were only identified to morphospecies the possibility exists that leaf litter specialists might have been included in the study. It is thus important that this possibility must be investigated further.

Furthermore, the data collected in this study are suited to the investigation of other macroecological patterns such as Bergmann's rule (the generally positive relationship between body size and increasing latitude in endothermic vertebrates, Rensch 1938; Mayr 1956, 1963). Even though this rule has been dismissed as primarily of historical interest because its generality is questionable (for discussion see Geist 1987; Blackburn *et al.* 1999), few studies have investigated its applicability to altitudinal gradients or to ectotherms such as insects. The relationships found between body size and latitude is rather inconsistent in insect taxa (Loder, 1997). Northern European worker ants follow Bergmann's rule (Cushmann *et al.*, 1993) while Australian and Afrotropical butterflies (Barlow, 1994) and North American

211

honey ants (Diniz-Filho & Fowler, 1998) follow the opposite trend. Lepidoptera have patterns that vary among biogeographical regions (Miller, 1991; Hawkins & Lawton, 1995) and eastern North American bees show no relation between body size and latitude (Hawkins & Lawton, 1995). Kaspari and Vargo (1995) argued that an ant colony can be seen as a superorganism and showed that tropical ants have smaller colony sizes than their temperate counterparts, in other words, that colony size increases with latitude. By contrast, Porter and Hawkins (2001) did not find a similar trend in termites and argued that the pattern found for ants can thus not be generalized to social insects. It would thus be interesting to determine whether the ants and beetles collected in my study show Bergman's rule. Both inter- and intraspecific (populations within species, termed 'James' rule', Blackburn *et al*, 1999) patterns in body size across the altitudinal gradient can be tested using the data collected in this study because several ant and beetle (both carabids and tenebrionids, see Chapter 2) species occur across the whole transect or large parts thereof.

In addition, the patterns in beta diversity (species turnover) across the altitudinal gradient must be investigated because they not only underlie the observed species richness and range size patterns (Lennon *et al.*, 2001; Willig *et al.*, 2003; Rodríguez & Arita, 2004), but also can be used to assess the applicability of the mid-domain model (Zapata *et al*., 2003, 2005). Rodríguez and Arita (2004) predicted that the latitudinal gradient in beta diversity should mirror that of species richness, but will be opposite to that of regional range size. The latter relationship will exist because beta diversity is higher where range sizes are small (i.e. at low latitudes) (Rodríguez & Arita, 2004). This idea could be tested across an altitudinal gradient using the data collected in this study.

Moreover, because this study initiated a long-term monitoring program it can be determined whether temporal variations in ant and tenebrionid assemblages are larger than spatial variation in the Greater Cederberg Biodiversity Corridor (GCBC). The effects of land use patterns on ant diversity could also be examined by comparing information collected from this study with that from remnants of natural vegetation at Piketberg, as well as from other disturbed and undisturbed sites (e.g. Kogelberg Nature Reserve, Elandsberg Nature Reserve, Riverlands). This will establish baseline information on spatial and temporal variability to form a platform for understanding the interactions of land use and climate change on ant diversity in the region. Understanding the determinants of diversity is not only a major goal of ecology, but also important for ensuring its conservation. The promulgation of the South African National Environmental Management: Biodiversity Act has placed a responsibility on

government to monitor and conserve biodiversity. Work such as this can go some way to help achieving these goals.

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Appendix A Ant subfamilies, tribes and species collected during October 2002 and March 2003 in the different vegetation types and biomes. The abundance of the species collected during each sampling period is given. SV = Strandveld Succulent Karoo, SK = Succulent Karoo, RF = Restioid Fynbos, PF = Proteoid Fynbos, EF = Ericaceous Fynbos, AF = Alpine Fynbos. * denote myrmecochores.

Subfamily and species	Oct 2002	Mar 2003	Vegetation type
Aenictinae			
Aenictini			
Aenictus rotundatus Mayr	3	2	RF; PF
Cerapachyinae			
Cerapachyini			
Cerapachys wroughtoni Forel	1	0	PF
Cerapachys sp. 2	1	0	EF
Dolichoderinae			
Dolichoderini			
Tapinoma sp. 1	40	20	RF; EF
Technomyrmex sp. 1	40	78	SV; PF; EF; AF
Dorylinae			
Dorylini			
Dorylus helvolus (Linneaus)	2	0	PF
Formicinae			
Camponotini			
Camponotus angusticeps Emery	51	117	RF; PF; EF
Camponotus baynei Arnold	1	0	EF
Camponotus fulvopilosus (De Geer)	104	59	RF; PF; EF; SK
Camponotus irredux Forel	2	2	EF
Camponotus mystaceus Emery	166	149	SV; RF; PF; EF
Camponotus niveosetosus Mayr	26	9	PF; EF; AF
Camponotus vestitus (F. Smit)	14	19	PF; EF
Camponotus sp. 1	19	11	EF; AF
Camponotus sp. 2 (near simulans Forel)	18	18	RF; EF; AF

Appendix A (continued)

Subfamily and species	Oct 2002	Mar 2003	Vegetation type
Camponotus sp. 3	2	0	EF; AF
Camponotus sp. 4 (*emarginatus*-group)	0	9	EF; AF
Camponotus sp. 5 (*emarginatus*-group)	15	17	RF; PF; EF
Camponotus sp. 6 (*foraminosus*-group)	22	25	SV; RF; PF; EF; AF
Camponotus sp. 7 (near *namacolus* Prins)	8	1	PF; EF
Camponotus sp. 8 (*mystaceous*-group)	0	1	RF
Camponotus sp. 9 (*mystaceous*-group)	1	0	AF
Camponotus sp. 10 (*emarginatus*-group)	3	5	EF; RF
Camponotus sp. 11 (*maculatus*-group)	27	68	SV; RF; PF; EF; AF
Camponotus sp. 12 (*maculatus*-group)	0	17	SV
Plagiolepidini			
Anoplolepis sp. 1	50	143	RF; PF; EF; SK
Anoplolepis sp. (c.f. *custodiens*)* (F. Smith)	1736	2027	RF; EF; AF
Anoplolepis sp. (c.f. *steinergroeveri*)* (F. Smith)	1576	2921	RF; PF
Lepisiota sp. 1	281	845	SV; RF; PF; EF; AF
Lepisiota sp. 2	90	0	RF
Lepisiota sp. 3	35	1	PF; EF
Lepisiota sp. 4	1	85	EF
Plagiolepis sp. 2	369	127	RF; PF; AF
Myrmicinae			
Crematogastrini			
Crematogaster melanogaster (Emery)	48	20	PF
Crematogaster sp. 1	402	21	SV; RF; PF; EF; AF
Crematogaster sp. 2	10	54	SV; RF
Crematogaster sp. 3	26	1	SV; RF; EF
Crematogaster sp. 5	1	0	EF
Crematogaster sp. 6	0	3	RF; PF
Dacetonini			
Strumigenys sp. 1	1	0	EF

Appendix A (continued)

Subfamily and species	Oct 2002	Mar 2003	Vegetation type
Formicoxenini			
Cardiocondyla shuckardi Forel	88	80	RF; PF; EF
Leptothorax sp. 1	19	0	SV; RF; PF, SK
Leptothorax sp. 2	10	15	PF
Leptothorax sp. 3	5	1	PF
Leptothorax sp. 4	21	39	EF
Leptothorax sp. 6	4	0	RF; PF
Meranoplini			
Meranoplus sp. 1	3	0	EF; AF
Myrmicariini			
Myrmicaria nigra (Mayr)	49	65	SV
Pheidolini			
Messor sp. 1	12	4	PF; EF; SK
Messor capensis (Mayr)	2	3	RF; EF; SK
Ocymyrmex barbiger Emery	909	2284	SV; RF; PF; EF; A; SK
Pheidole sp. 1	1040	648	RF; PF; SK
Pheidole sp. 2	1104	1708	RF; PF; EF
Pheidole sp. 3	32	11	PF; EF; AF
Pheidole sp. 4	78	121	RF; EF
Solenopsidini			
Monomorium fridae Forel	19987	26012	SV; RF; PF; EF; AF
Monomorium havilandi Forel	225	94	PF; EF
Monomorium macrops Arnold	95	24	SV; RF; PF; SK
Monomorium speculiceps Santchi	164	229	RF; EF; AF
Monomorium xanthognathum Arnold	233	15	RF; PF; EF
Monomorium sp. 2 (*salomonis*-group)	390	902	RF; PF; EF; AF; SK
Monomorium sp. 5 (*monomorium*-group)	13	1	PF; EF; AS; SK
Monomorium sp. 7 (*monomorium*-group)	307	693	RF; PF; EF; AF; SK
Monomorium sp. 8 (*monomorium*-group)	1	6	RF; AF
Monomorium sp. 9 (*monomorium*-group)	7	0	EF
Solenopsis puncticeps Mayr	73	15	SV; RF; PF; EF; AF

Appendix A (continued)

Subfamily and species	Oct 2002	Mar 2003	Vegetation type
Tetramoriini			
Tetramorium dichroum Santchi	26	5	RF; EF
Tetramorium erectum Emery	4	3	RF; EF
Tetramorium frigidum Arnold	50	81	RF; PF; EF; AF
Tetramorium jordani Santchi	227	8	PF; EF
Tetramorium quadrispinosum* Emery	739	815	RF; PF; EF; SK
Tetramorium solidum Emery	49	22	RF; EF; SK
Tetramorium sp. 2 (*simillimum*-group)	10	84	RF; PF
Tetramorium sp. 3 (*simillimum*-group)	196	108	RF; PF; EF; AF
Tetramorium sp. 4 (*simillimum*-group)	6	0	EF
Tetramorium sp. 7 (*simillimum*-group)	42	54	RF; PF; EF
Tetramorium sp. 12	33	2	EF
Ponerinae			
Ponerini			
Anochetus leviallanti Emery	0	2	PF; SK
Hypoponera sp. 1	0	1	EF
Pachycondyla cavernosa (Roger)	14	13	RF; PF
Pachycondyla pumicosa Forel	15	10	EF

Appendix B Pearson's product-moment correlations of the abiotic and biotic variables. Significant values are indicated in bold. Alt = Altitude, MMT = mean monthly temperature, Max = mean maximum monthly temperature, Min = mean minimum monthly temperature, Range = mean monthly temperature range, Amax = absolute maximum monthly temperature, Amin = absolute minimum monthly temperature, Cond = conductivity, BG = proportion of bare ground, ER = proportion of exposed rock, Veg = proportion of vegetation cover, TOTHITS = vertical complexity of the vegetation, Height = vegetation height.

	Alt	Area	MMT	Max	Min	Range	AMax	AMin
Alt								
Area	**-0.87**							
MMT	**-0.84**	**0.62**						
Max	**-0.68**	**0.45**	**0.90**					
Min	**-0.82**	**0.63**	**0.97**	**0.79**				
Range	-0.11	-0.03	**0.28**	**0.66**	0.06			
AMax	0.06	**-0.20**	0.02	**0.26**	-0.08	**0.52**		
AMin	**-0.44**	**0.38**	**0.59**	**0.29**	**0.71**	**-0.39**	**-0.29**	
PH	**-0.65**	**0.84**	**0.35**	0.12	**0.41**	**-0.31**	**-0.47**	**0.36**
H	**0.66**	**-0.70**	**-0.46**	**-0.28**	**-0.49**	0.14	0.05	**-0.33**
Cond	0.05	-0.11	-0.06	**0.21**	**-0.18**	**0.57**	0.16	**-0.43**
Rock	0.13	**0.27**	0.10	0.13	**0.17**	0.01	-0.04	0.07
P	0.08	-0.14	0.09	0.06	0.14	-0.08	-0.12	0.16
K	0.17	**-0.17**	0.09	0.04	**0.21**	**-0.19**	-0.16	**0.20**
C	**0.58**	**-0.59**	**-0.40**	**-0.34**	**-0.34**	-0.13	-0.13	**-0.22**
NO$_3$	**0.40**	**-0.34**	**-0.35**	**-0.47**	**-0.27**	**-0.44**	-0.11	0.03
Na	**-0.20**	**0.36**	0.16	-0.04	**0.26**	**-0.38**	**-0.51**	**0.35**
Ca	**-0.46**	**0.73**	**0.17**	-0.05	**0.22**	**-0.35**	**-0.58**	**0.31**
Mg	0.07	-0.04	-0.03	**-0.19**	0.10	**-0.44**	**-0.38**	0.15
Clay	**0.19**	**-0.27**	0.16	**0.24**	0.16	**0.20**	-0.11	0.07
Silt	**0.56**	**-0.57**	**-0.31**	**-0.30**	**-0.25**	-0.18	**-0.22**	-0.07
Sand	**-0.49**	**0.51**	**0.19**	**0.18**	0.13	0.13	**0.25**	0.01
BG	**-0.31**	**0.34**	**0.17**	0.09	0.09	0.04	0.09	0.05
Litter	**-0.44**	**0.35**	**0.43**	**0.34**	**0.46**	0.00	0.08	**0.39**
ER	**0.40**	**-0.37**	**-0.21**	-0.02	**-0.17**	**0.18**	0.06	**-0.18**
Veg	**0.18**	**-0.20**	**-0.22**	**-0.29**	**-0.17**	**-0.27**	**-0.23**	-0.08
TOTHITS	**-0.27**	0.01	**0.19**	0.16	**0.21**	0.00	0.03	0.07
Height	**-0.55**	**0.25**	**0.49**	**0.46**	**0.50**	0.14	**0.28**	**0.19**

Appendix B (continued)

	PH	H	Cond	Rock	P	K	C	NO$_3$	Na	Ca	Mg
H	**-0.70**										
Cond	-0.16	0.04									
Rock	-0.05	-0.02	0.11								
P	-0.01	0.11	-0.10	**0.38**							
K	0.04	0.03	-0.14	**0.70**	**0.40**						
C	**-0.47**	**0.80**	-0.02	**0.22**	**0.24**	**0.35**					
NO$_3$	**-0.28**	**0.33**	**-0.67**	**-0.19**	0.00	-0.01	**0.29**				
Na	**0.51**	**-0.18**	**-0.33**	**0.19**	**0.22**	**0.36**	0.03	-0.13			
Ca	**0.92**	**-0.48**	-0.14	-0.06	-0.01	0.02	**-0.25**	**-0.20**	**0.53**		
Mg	**0.24**	-0.08	**-0.28**	**0.36**	**0.21**	**0.75**	**0.26**	0.17	**0.56**	**0.26**	
Clay	**-0.32**	**0.25**	0.04	**0.30**	0.12	**0.43**	**0.20**	0.07	**0.17**	**-0.34**	**0.33**
Silt	**-0.35**	**0.51**	-0.13	**0.37**	**0.36**	**0.62**	**0.60**	**0.19**	**0.25**	**-0.23**	**0.47**
Sand	**0.35**	**-0.32**	0.14	**-0.41**	**-0.25**	**-0.59**	**-0.46**	**-0.26**	**-0.19**	**0.27**	**-0.50**
BG	**0.22**	**-0.39**	-0.02	**-0.38**	**-0.37**	**-0.41**	**-0.55**	-0.03	-0.07	0.15	**-0.23**
Litter	**0.23**	**-0.32**	-0.11	0.03	0.07	0.06	**-0.28**	-0.13	0.02	0.08	-0.04
ER	**-0.25**	**0.29**	**0.29**	**0.52**	**0.31**	**0.49**	**0.42**	**-0.17**	-0.02	**-0.18**	**0.21**
Veg	0.00	**0.28**	**-0.24**	-0.04	0.10	0.02	**0.34**	**0.29**	0.00	0.03	0.10
TOTHITS	-0.07	0.13	-0.09	-0.16	0.13	-0.15	0.13	0.01	-0.14	-0.16	-0.09
Height	0.02	**-0.18**	-0.04	-0.14	0.06	-0.13	**-0.17**	**-0.18**	-0.15	**-0.17**	-0.12

Appendix B (continued)

	Clay	Silt	Sand	BG	Litter	ER	Veg	TOTHITS
Silt	**0.45**							
Sand	**-0.57**	**-0.76**						
BG	**-0.18**	**-0.38**	**0.29**					
Litter	-0.11	**-0.24**	**0.23**	0.03				
ER	**0.25**	**0.40**	**-0.34**	**-0.61**	**-0.19**			
Veg	-0.07	**0.21**	-0.11	**-0.42**	-0.11	-0.17		
TOTHITS	-0.14	-0.06	0.15	**-0.33**	**0.24**	-0.10	**0.40**	
Height	-0.12	**-0.30**	**0.30**	-0.09	**0.38**	-0.13	0.06	**0.77**

225

Appendix C Soil characteristics and ground cover of the sampling sites. Soil characteristics were determined once in October 2002, and ground cover was measured during both sampling periods.

Site	Soil composition (%)				Soil variables					Ground cover (%)							
	Rock	Clay	Sand	Silt	P	NO$_3$	C	pH	Cond.	BG	Lit	ER	Veg	BG	Lit	ER	Veg
					(mg/kg)	(mg/kg)	(%)				October 2002				March 2003		
0 W	0.00	0.25	98.65	1.10	4.75	2.83	0.24	7.98	2052.50	56.13	13.13	0.00	30.75	59.63	1.75	0.00	38.88
200 W	0.00	1.10	97.88	1.03	3.50	16.36	0.60	4.10	1595.00	50.63	24.23	0.00	25.75	65.13	8.88	1.25	25.00
300 W	5.00	2.35	95.38	2.28	2.75	6.46	0.73	4.28	3165.00	44.13	1.38	8.88	45.63	60.63	5.50	5.25	28.63
500 W	4.00	2.05	95.63	2.33	3.25	9.20	0.90	4.13	2940.00	33.88	7.25	12.00	46.88	43.38	15.00	7.13	34.50
700 W	6.25	2.20	92.00	5.80	20.00	7.58	1.66	3.73	3165.00	25.38	2.25	29.63	42.75	17.00	16.25	24.13	42.63
900 W	5.00	1.93	93.33	4.75	9.75	8.20	1.44	3.68	3170.00	40.75	0.75	20.88	37.63	45.88	1.63	18.75	33.25
1100 W	14.50	1.70	92.40	5.90	24.75	13.91	1.51	4.50	1847.50	40.25	0.50	20.75	38.50	33.63	3.63	16.88	45.88
1300 W	6.50	4.05	85.28	7.95	4.50	17.48	1.29	4.28	1600.00	47.50	4.00	16.88	31.63	39.25	1.38	16.38	43.00
1500 W	10.50	3.50	86.90	7.68	13.50	31.21	2.92	3.53	1602.50	28.88	0.25	25.00	45.88	20.25	0.25	12.88	66.63
1700 W	5.25	3.25	90.13	5.20	8.00	22.10	2.11	3.35	1530.00	26.38	0.00	32.00	41.63	17.50	1.13	41.75	39.63
1900 S	1.25	1.80	93.38	4.73	7.50	26.47	1.13	2.95	1190.00	52.25	0.00	16.63	31.13	54.75	3.50	12.00	29.75
1700 E	14.25	2.58	93.08	5.28	10.25	0.23	1.56	3.30	6847.50	22.25	0.75	48.25	28.75	15.25	2.63	51.63	30.50
1500 E	5.25	1.83	91.20	5.83	9.00	9.89	1.94	3.18	3270.00	42.00	0.00	25.25	32.75	29.25	0.88	27.50	42.38
1300 E	4.25	2.53	91.68	6.23	6.50	18.40	1.47	3.03	1732.50	48.63	0.00	13.13	38.25	45.63	0.25	8.88	45.25
1100 E	0.75	3.33	92.13	4.08	5.25	13.37	0.91	3.13	3707.50	66.75	1.00	0.00	32.25	52.63	9.13	0.00	38.25
900 E	3.25	4.55	91.45	4.00	8.50	5.58	1.54	3.35	5660.00	55.00	0.00	25.13	19.88	49.88	1.00	25.25	23.88
500 E	21.50	5.43	88.25	6.33	21.25	1.68	0.83	4.50	1860.00	39.25	0.75	49.63	10.38	39.88	9.13	44.13	6.875

Appendix D Beetle families, subfamilies and species collected during October 2002 and 2003 in the different vegetation types and biomes. The abundance of the species collected during each sampling period is given. SV = Strandveld Succulent Karoo, SK = Succulent Karoo, RF = Restioid Fynbos, PF = Proteoid Fynbos, EF = Ericaceous Fynbos, AF = Alpine Fynbos.

Subfamily and species	2002	2003	Vegetation type
Carabidae			
Harpalinae			
Harpalus capicola Dejean	8	0	RF; EF; AF
Harpalus sp. 2	2	0	EF
Harpalus sp. 4	14	24	RF; EF; AF
Cratognathus grandiceps Boheman	3	3	EF; SK
Cratognathus mandibularus Dejean	6	9	SV; RF; EF; SK
Anthiinae			
Thermophilum decemguttatum (Linneaus)	225	271	RF; PF; EF
Microlestia obtusa Chand.	20	8	RF; EF
Cicindelinae			
Cicindelini			
Cicindela concolor Dejean	2	1	RF; EF
Cicindela lurida Fabricius	42	85	RF; EF; AF
Cicindela quadriguttata Wiedeman	1	2	EF; AF
Megacephalini			
Platychila pallida Fabricius	10	6	SV
Graphipterinae			
Graphipterus limbatus Castelnau	4	5	PF; EF
Labiinae			
Hystrichopus mnizechi Péringuey	7	6	AF
Scaritinae			
Scarites sp. 1	5	7	RF
Scarites sp. 2	16	25	SV

Appendix D (continued)

Subfamily and species	2002	2003	Vegetation type
Tenebrionidae			
Tentyriinae			
Adesmiini			
Adesmia porcata Solier	14	0	SV; RF
Amiantus sp. 1	3	4	PF
Stenocara dentata (Fabricius)	203	217	EF; SK
Stenocara longipes Olivier	11	4	SV; PF
Chryptochilini			
Cryptochile assimilis Solier	5	10	RF
Cryptochile fallax fallax Solier	236	598	RF; EF; SK
Cryptochile minuta Olivier	29	93	PF
Cryptochile namaquana Penrith	15	39	SV
Horatoma parvula Solier	18	24	RF; PF
Sacophorella cephlica Koch	26	133	PF
Epitragini			
Broomium mutilla Koch	3	9	PF
Broomium nadum Koch	4	16	PF
Molutini			
Hypomelus peronatus Germar	9	10	PF; EF
Hypomelus sp. 1	8	3	SV; RF
Hypomelus sp. 3	3	2	PF; EF
Hypomelus sp. 4	1	0	PF
Molorus globulicollis Solier	11	11	PF; EF; AF
Physadesmia aculeata Péringuey	9	9	SV
Psammodes grandis Solier	1	1	SV
Psammodes ovatus Solier	3	3	SV; PF
Psammodes sp. 4	2	0	SV; RF
Psammodes sp. 5	2	0	SV
Psammodes striatus Fabricius	1	2	PF
Somaticus gracilipes Haag-Rutenberg	3	8	SV; RF; PF

Appendix D (continued)

Subfamily and species	2002	2003	Vegetation type
Somaticus sp. 1	24	4	SV; RF
Zophosini			
Zophosis gracilicornis (Deirolle)	1084	1674	SV; RF; PF; EF; SK
Zophosis hirundu (Penrith)	80	74	SV; RF; PF; SK
Opatrinae			
Platynotini			
Gonopus tibialis Fabricius	2	0	RF; PF
Strongyliini			
Phaeostolus sp. 1	1	0	PF
Teneb sp. 7	1	0	RF
Teneb sp. 11	1	3	PF
Teneb sp. 12	1	13	EF
Teneb sp. 14	1	0	EF

229